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Morphology and metabolic traits related to swimming performance in Australasian snapper (*Chrysophrys auratus*) selected for fast growth

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Abstract

Changes in body shape are linked to swimming performance and become relevant for selective breeding programmes in cultured finfish. We studied how the selection for fast growth could affect phenotypes by investigating the relationship between swimming performance and body shape. We also investigated how swimming might affect plasma metabolite concentrations. Critical swimming speed (U_{Crit}), body traits (e.g., BW, body weight; BL, body length; K, condition factor), and plasma lactate and glucose concentrations were evaluated in two cohorts of Australasian snapper (*Chrysophrys auratus*): one derived from wild broodstock (F_1), and the other selected for fast growth (F_4). U_{Crit} tests ($n = 8$) were applied in groups of 10 snapper of similar BW (71.7 g) and BL (14.6 cm). The absolute or relative U_{Crit} values of both cohorts were similar (0.702 $m{\cdot}s^{-1}$ and 4.795 $BL{\cdot}s^{-1}$, respectively), despite the F_4 cohort displaying a higher K. A positive correlation between K and absolute U_{Crit} (Pearson's $r = 0.414$) was detected in the F_4 cohort, but not in the F_1 cohort, which may be linked to differences in body shape. A negative correlation between relative U_{Crit} and body size (Pearson's r between −0.682 and −0.501), but no correlation between absolute U_{Crit} and body size, was displayed in both cohorts. Plasma lactate and glucose concentrations were higher in the F_4 cohort at U_{Crit}. Whether a longer selective breeding programme could result in more changes in body shape, potentially affecting swimming performance, should be explored, along with the potential outcomes of the differences in metabolic traits detected.

KEYWORDS
aquaculture, critical swimming speed, fish phenotype, morphometrics, plasma lactate, selective breeding

1 | INTRODUCTION

Selective breeding is key to enhancing global fish aquaculture production by making existing species more suitable for farming (Gjedrem et al., 2012). Targets of breeding programmes include the improvement of traits related to fish performance, such as growth rate, fillet yield, and feeding efficiency (Besson et al., 2020; de Verdal et al., 2017; Vandeputte et al., 2019). However, identifying the individuals displaying improved phenotypes in fish aquaculture is challenging because of the interactions between genetic and environmental factors (Gjedrem & Rye, 2018). In this regard, phenotypic differences in the external morphology have been found between farmed and wild fish, including salmonids (Fleming et al., 1994; Pulcini et al., 2013; Solem et al., 2006; Stringwell et al., 2014; Tiffan & Connor, 2011), gilthead seabream (Arechavala-Lopez et al., 2012; Fragkoulis et al., 2021; Talijančić et al., 2021), European seabass (Arechavala-Lopez et al., 2012), and Atlantic cod (Wringe et al., 2015).

Swimming plays a critical role in the migration and habitat selection of fish species, along with predator–prey interactions, foraging, reproduction, and migration. Therefore, swimming performance may be considered a fundamental trait involving physiological and behavioral components that contribute to fitness and survival. However, considerable inter- and intraspecific variation in swimming performance is present in many fish species, which appears to be key to their ability to adapt to different environments (Oufiero & Whitlow, 2016). Indeed, swimming shows remarkable plasticity, which is often linked to different external morphological phenotypes (Binning et al., 2015). Both genetic divergence and phenotypic plasticity play important roles in the phenotypic differentiation of fish across contrasting water flow regimes (Langerhans, 2008). Swimming phenotype and water flow encompass a functional relationship, displaying phenotypic divergence within species in different environments (Binning et al., 2014). Streamlined shapes reduce drag and energy costs caused by water currents, affecting the swimming performance of fish (Grünbaum et al., 2007; Haas et al., 2010). Therefore, it is of significant importance to establish any correlation between swimming performance and differences in external morphological traits for a given species (Lu et al., 2020). More importantly, this may be useful for implementing selective breeding programmes, for example, by selecting individuals with enhanced phenotypes in different environments or production scenarios.

The tāmure/Australasian snapper (*Chrysophrys auratus*, hereafter referred to as snapper) is a marine species with the potential to diversify the New Zealand aquaculture sector (Wellenreuther et al., 2019). Snapper supports significant commercial, recreational, and customary fisheries (Parsons et al., 2014), and is widely distributed around northern and central Aotearoa/New Zealand, and southern Australia (Chiba et al., 2009). A selective breeding programme for snapper was implemented to improve growth (Ashton et al., 2019) and has resulted in fourth-generation elite snapper (F_4) with an improved feed conversion ratio, showing a 30%–50% body weight increase compared with wild snapper (Moran et al., 2023).

Fish swimming performance can be evaluated by implementing several types of tests. One of the most commonly used is critical swimming speed (U_{Crit}), a value calculated in a test using increasing speeds at established intervals until fish reach exhaustion (Beamish, 1978; Brett, 1967). In this U_{Crit} measurement, maximal aerobic capacity is reached by the end of the graded swimming protocol, which involves burst-and-glide swimming with increased involvement of glycolysis and lactate build-up at the onset of fatigue (Kieffer, 2010; Milligan & Mcdonald, 1988; Peake & Farrell, 2004; van Ginneken et al., 2004). Therefore, plasma lactate concentration is a relevant metabolic trait linked to swimming performance.

Selection for a high growth rate in farmed Nile tilapia (*Oreochromis niloticus*) over five generations has been linked to an increased height to length ratio of the body along with a more rounded midsagittal shape (de Oliveira et al., 2016). Another study on this species has shown that growth and swimming performances are negatively correlated after 18 generations of selective breeding (Mengistu et al., 2021). Wild gilthead seabream (*Sparus aurata*) have significantly higher swimming performance (absolute $U_{Crit} \sim 7\%$, relative $U_{Crit} \sim 8\%$) than their farmed counterparts (Basaran et al., 2007). Similarly, the U_{Crit} is higher in the offspring of wild individuals of European seabass (*Dicentrarchus labrax*) than in two selected lines (Vandeputte et al., 2016). Wild Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) performed better during repeated U_{Crit} tests than those fish groups reared in hatchery conditions (F_1), displaying 25%–30% higher values (Pedersen et al., 2008).

Interestingly, swimming performance could be linked to feeding efficiency and employed to infer bioenergetics models (de Verdal et al., 2017), to be used along with genetic markers to improve selective breeding. Thus, swimming performance, along with other related metabolic traits, may be of important consideration in selective breeding programmes. However, our present knowledge on how selective breeding targeted to maximize growth can modify body shape and its ensuing relationship with swimming performance remains to be established. This is highly relevant as cultured fish may have different genotypes when experiencing more uniform environmental conditions than their wild counterparts in nature.

This study aimed to test if the offspring of snapper individuals, which have undergone selective breeding for a higher growth rate (F_4 cohort), show changes in body shape and U_{Crit} compared with offspring derived from wild individuals reared in captivity (F_1 cohort). This was examined by investigating the relationship between morphology and swimming performance. In addition, this study investigated the changes occurring in plasma lactate and glucose concentrations involved in U_{Crit} tests, along with their relationship to swimming performance and morphology in both cohorts.

Based on previous findings in aquaculture species we hypothesized that F_4 cohort snapper would likely display lower swimming performance (U_{Crit}) than F_1 individuals, which could be related to changes in body shape occurring in selective breeding. We also hypothesized that snapper reaching fatigue in the F_4 cohort would likely display higher plasma lactate and glucose levels than F_1 individuals, which could be related to lower swimming performance.

2 | MATERIALS AND METHODS

2.1 | Experimental settings and animal use

This study took place between August and September 2022 at the Plant & Food Research Maitai Finfish Facility (PFR-FFF) located in Nelson, Aotearoa/New Zealand. The land-based facility is supplied with single-pass seawater from Nelson Haven that is pumped ashore. Fish used in this study were part of two large cohorts hatched on-site in the same period and maintained under the same conditions before the implementation of the trial. An F_4 cohort had undergone four rounds of domestication selection, with the last two rounds also involving genomics-informed selective breeding for a higher growth rate. In addition, an F_1 cohort was used, the offspring from wild-caught, captivity-acclimated broodstock. Owing to the scaling effects of fish body size on swimming performance (Beamish, 1978), snapper from both cohorts used to implement the U_{Crit} test in this study were selected to have similar body weights (BW) and body lengths (BL), despite the F_4 cohort having a small, although statistically significant higher mean condition factor K value ($p = 0.028$, Figure S1, Supporting Information).

A total of 120 fish from each cohort were assigned to 800-L tanks in triplicate, housing 40 fish per tank. In this experimental design, a group of fish housed in a particular tank was transferred to the swim flume 7 days apart, followed by terminal sampling. Tanks were provided with flow-through seawater (~40 L min^{-1}) with 35 ppt salinity. Seawater supplied to the tanks and swim flume was pre-conditioned in silos before being distributed to the tanks and the swim flume, being filtered and UV-treated, resulting in stable pH (~8.2) and temperature (17 ± 1°C). Water reached >90% air saturation by using continuous aeration with mixing. During this time, fish were maintained under natural light conditions and fed a commercial extruded diet (Otohime EP4, Marubeni Nisshin Feed Co., Ltd., Tokyo, Japan) twice a day (9:00 and 16:00 h) at a ration equivalent to 2% of their BW per day.

2.2 | Swimming test and sampling

U_{Crit} tests were implemented by transferring a group of 10 fish from the housing tanks to the swim flume and applying an incremental swimming speed protocol. The swimming tests were implemented in a Brett-type swim flume (Brett, 1964) with a volume of approximately 97 L and an effective swimming area of 46 × 42 × 50 cm (length, width, and depth, respectively) resulting in a fish density of 7.4 kg m^{-3}. This approach allowed the testing of 80 fish per cohort using one swim flume within 4 weeks of experimentation, thus minimizing large differences in body size between individuals, as these are known to affect U_{Crit} (Brett, 1964).

A group of 10 fish not subjected to previous tests were transferred from a housing tank to the swim flume 17 h before the test was implemented (at 16:00 h before feeding). Environmental parameters (17 ± 1°C, dissolved oxygen value >90%, 35 ppt salinity) were maintained at similar levels between the housing tanks and the swimming flume. The group was allowed to acclimatize in the swim flume, without feeding, with aeration and a low water current (~0.01 m·s^{-1}) before the tests were implemented, which started the following morning at 9:00 h.

In the U_{Crit} test, snapper were induced to swim in the flume by increasing the water flow every 45 min at increments of 0.15 m·s^{-1}. The water flow was produced by a water pump regulated with an electronic controller, which was previously calibrated with a vane wheel flow sensor (Höntzsch GmbH & Co., Waiblingen, Germany), and used to calculate swimming speed. The U_{Crit} was defined as the swimming speed for each snapper within the flume to reach fatigue, which was evident when the fish remained at the back grid of the swim flume for at least 10 s and did not continue to swim. At that point, fatigued fish was removed from the back grid of the swim flume by using two nets (~5 s). The time and water speed for each snapper reaching fatigue were recorded and used to calculate U_{Crit} (see "Calculations" section below). The maximal water speed achieved in this swim flume was 0.663 m·s^{-1}, reflecting a maximal absolute U_{Crit} of 0.813 m·s^{-1} that could be achieved by any fish tested. Some individuals did not fatigue at the maximum achievable speed in the flume and were therefore recorded as not reaching U_{Crit} (U_{Crit} above 0.813 m·s^{-1}). After fatiguing (U_{Crit} group) or 45 min at 0.663 m·s^{-1} (No U_{Crit} group), each fish was identified when removed from the flume and anesthetized in 75 mg L^{-1} tricaine methane sulfonate (MS222, Sigma) buffered with 150 mg L^{-1} $NaHCO_3$. Upon sedation, fish were weighed using an electronic balance to the nearest gram. Digital images were captured as described by Tuckey et al. (2022) by using a custom-built light box and a camera (16-megapixel Panasonic Lumix DMC-GH4, Panasonic Corporation, Osaka, Japan). Each image included a scale bar (150 mm) to define landmarks (Figure 1) and calculate several morph-morphometric meters with TPSDIG2 2.31

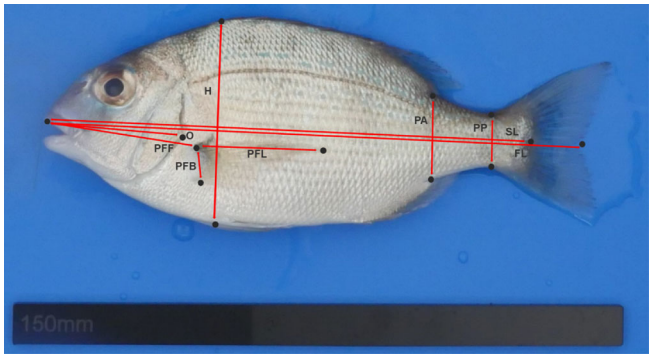

FIGURE 1 A digital image showing 13 landmarks in snapper that defined the nine linear dimensions used to quantify morphological traits in all the individuals of the F_4 and F_1 cohorts used in the swimming tests. Dimensions were FL, fork length (= to body length or BL in this study); H, height; O, operculum; PP, peduncle posterior; PA, peduncle anterior; PFF, pectoral-fin front; PFB, pectoral-fin base; PFL, pectoral-fin length; SL, standard length. Landmarks were identified, and dimensions were calculated using a scale bar (150 mm) and the software TPSDIG2 2.31 (Rohlf, 2017).

software (Rohlf, 2017). The blood was immediately sampled from the caudal vein using heparinized 1-mL syringes and 21 G × 1″ needles (Terumo Europe N.V., Belgium) and centrifuged at 2000*g* for 10 min at 4°C to obtain plasma, which was stored at −80°C for later analysis. After blood sampling, fish were euthanized by pithing.

2.3 | Quantification of plasma metabolite concentrations

Plasma lactate and glucose concentrations were quantified with commercial kits (L-Lactic acid kit, K-late 08/16, and D-glucose assay GOPOD-format, K-Gluc 10/15, Megazyme, Ireland) according to the manufacturer's instructions, using a microplate reader (Clario Star, BMG Labtech, Germany).

2.4 | Calculations

The critical swimming speed (U_{Crit}) for each fish was calculated as follows:

$$U_{Crit} = U_p + (T_f/T_i) \times U_i.$$

where U_p is the penultimate velocity at which the fish swam before exhaustion, T_f is the time elapsed between velocity increase and exhaustion, T_i is the time interval between increases in velocity, and U_i is the velocity increment applied. The U_{Crit} was expressed in absolute value ($m{\cdot}s^{-1}$), as well as a relative value ($BL{\cdot}s^{-1}$) by dividing the absolute U_{Crit} by the BL of each fish.

The Fulton condition factor (K) was calculated as follows:

$$K = 100 \times BW/BL^3.$$

where BW is the body weight in grams, and BL is the body length measured as fork length in centimeters.

2.5 | Statistical analysis

Differences between the U_{Crit} value in both cohorts were analysed by applying a two-sample *Student t-test*. Differences in the proportion of fish reaching U_{Crit} between cohorts were analysed by applying a logistic regression analysis (Logit) for binomial proportions and tested using approximate χ^2 probability. Differences between morphometric parameters and plasma metabolite concentrations for fish reaching U_{Crit} (or not) in each cohort were analysed by applying a one-way ANOVA analysis followed by Tukey's post hoc test to compare the mean values. The homogeneity of variance was verified by the Levene's test. A principal component analysis (PCA) was applied to all the morphometric parameters obtained to investigate their variability between groups. The relationship between U_{Crit} and morphometric parameters, U_{Crit} and plasma metabolite concentrations, as well as plasma metabolite concentrations and morphometric parameters, was fitted into unweighted linear models ($\mathbf{y} = \boldsymbol{a} + \boldsymbol{b} * \boldsymbol{x}$), where $\boldsymbol{a}$ is the intercept and $\boldsymbol{b}$ is the slope, followed by an ANOVA to test if the slope was different from zero. Differences in the slopes of the linear regressions obtained for each cohort were tested by applying an F-test. Results were expressed as means ± standard errors (SE). The level of significance used for the statistical tests was $p < 0.05$. The linear logistic regression model used to analyse possible differences between proportions was fitted using the statistical software Genstat, 22nd edition, version 22.1.0.532 (VSN International Ltd., UK). The rest of the analyses and all the graphical representations were implemented with Origin Pro software, version 2022b (OriginLab Corporation, Northampton, MA, USA).

3 | RESULTS

3.1 | Biometrics of the two cohorts of snapper

Figure 2 shows the distribution of selected biometric parameters measured in the F_4 and F_1 cohorts of snapper used in the U_{Crit} tests, including individuals reaching critical swimming speed (or not). No statistically significant differences were detected for BW, fork length (=BL), condition factor K, height, and peduncle anterior distances in the F_1 and F_4 cohorts reaching U_{Crit} or not (one-way ANOVA, p >0.05). In contrast, a significantly shorter distance (0.6 mm) was measured for the peduncle posterior in fish reaching U_{Crit} of the F_1 than for the equivalent group in the F_4 cohort (Figure 2f, Tukey's post hoc test, $p = 0.047$). Additional biometric parameters measured in both cohorts are presented in Figure S2 (Supporting Information), showing a lack of statistically significant differences in operculum, pectoral-fin front, pectoral-fin base, pectoral-fin length, and standard length distances in the F_1 and F_4 cohorts reaching U_{Crit} or not (one-way ANOVA, p >0.05).

Figure 3 shows the results of the PCA applied to 11 biometric characteristics measured in fish reaching U_{Crit} or not in both cohorts, to evaluate how these parameters varied between each group. Most of the variance (75.7%) was explained by PC1, with an eigenvalue of 8.33 given mainly by the combination of PA, BW, PP, H, PFB, SL, FL, O, and PFF parameters, which displayed similar loads. On the contrary, 10.8% of the variance was explained by PC2, which was due mainly to K, having an eigenvalue of 1.17. The 95% confidence ellipsoid showing the variability of these components of fish reaching U_{Crit} in the F_4 cohort had a wider distribution for PC2 than for PC1, whereas that associated with fish reaching U_{Crit} in the F_1 cohort had a more even distribution between both components. A similar pattern was observed for the 95% confidence ellipsoid in fish not reaching U_{Crit} in F_4 compared with the F_1 cohort.

3.2 | Swimming performance and its relationship with morphological traits

The absolute and relative critical swimming speed values (U_{Crit}) measured in F_1 and F_4 cohorts are presented in Figure 4a,b, respectively.

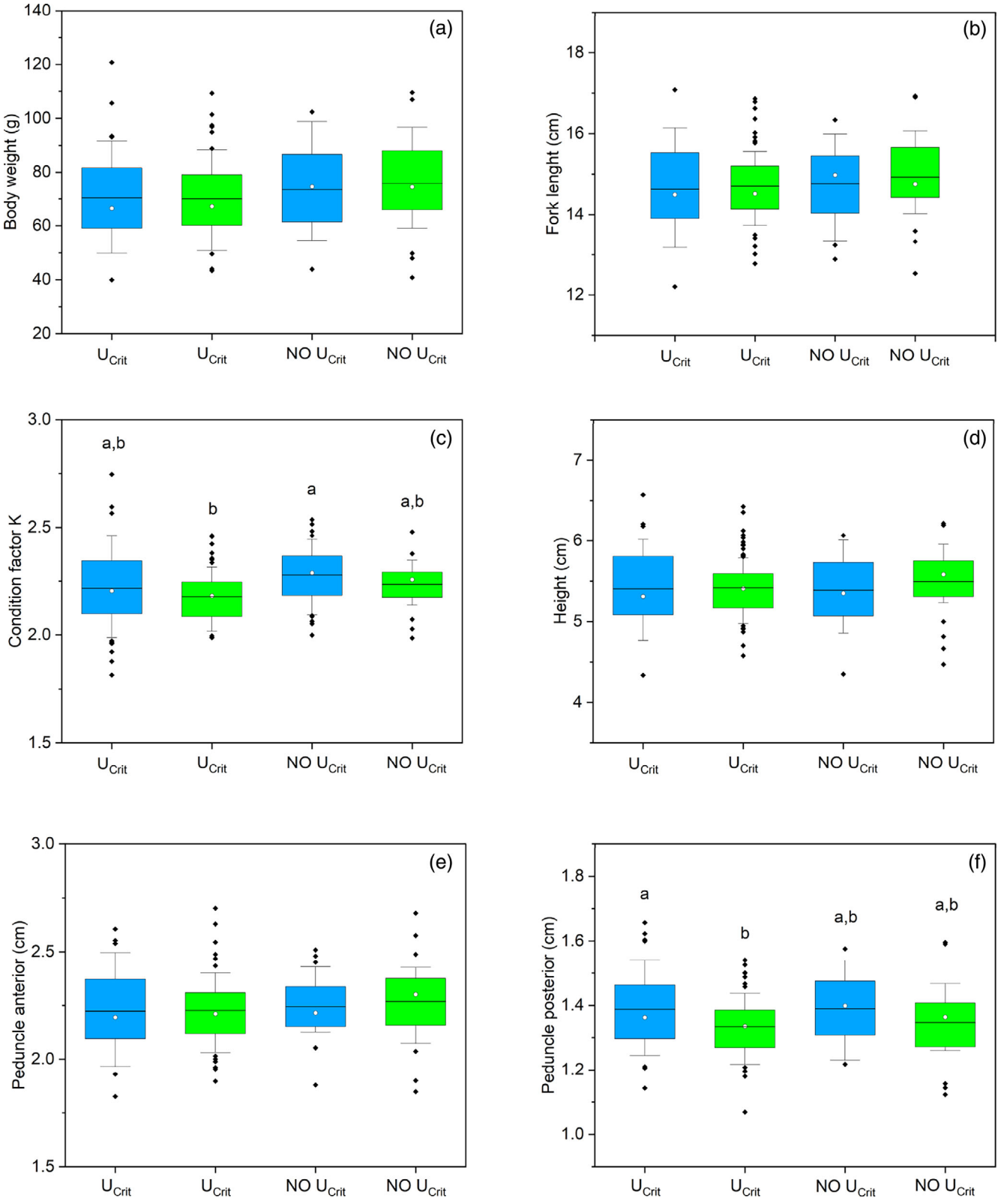

FIGURE 2 Selected biometric parameters of snapper from the F_4 (blue) and F_1 (green) cohorts were tested, distinguishing between these individuals reaching critical swimming speed (U_{Crit}) or not (NO U_{Crit}). (a) Body weight (g); (b) fork length (= BL, cm); (c) condition factor K; (d) height (cm); (e) peduncle anterior (cm); and (f) peduncle posterior (cm). A total of 80 naive individuals were used in eight independent tests per cohort, with 10 fish per swimming test. Parameters are detailed in the "Materials and Method" section and Figure 1. Boxes are the upper 75th and lower 25th percentiles, the whisker bars indicate the 90th and 10th percentiles, and the black dots are values beyond the 90th and 10th percentiles. Within each box, the white dot represents the median, and the line the mean value. The number of fish reaching Ucrit was 51 and 60 for cohorts F_4 and F_1, respectively, whereas the number of fish not reaching Ucrit was 29 and 20 for cohorts F_4 and F_1, respectively. Different letters indicate significant differences between groups (one-way ANOVA, followed by Tukey's post hoc test, $p < 0.05$).

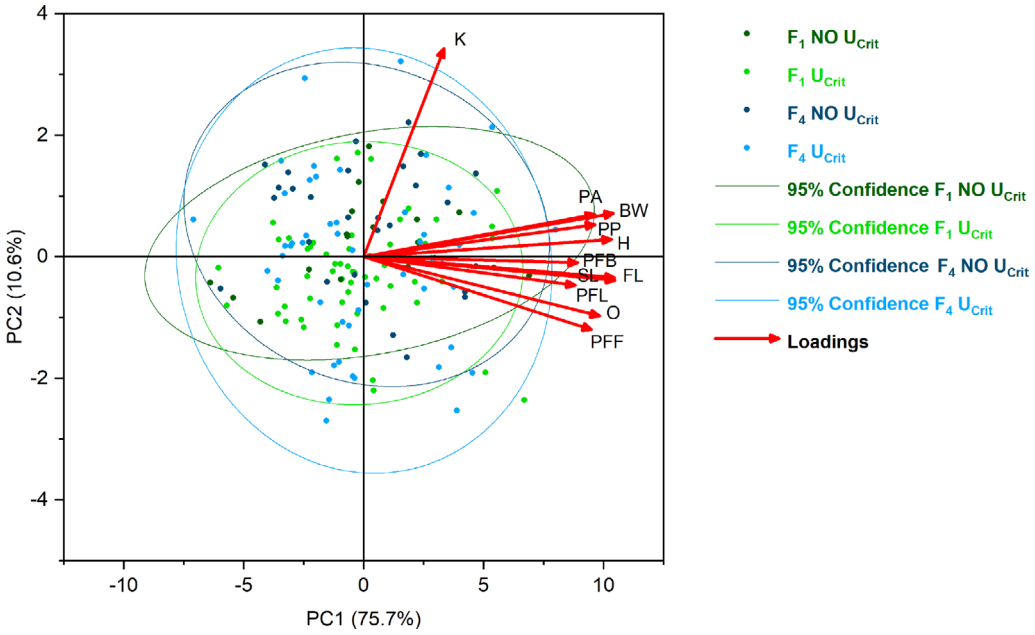

FIGURE 3 The outcome of principal component analysis (PCA) shows the relationship between biometric characteristics of snapper from the F_4 (blue) or F_1 (green) cohorts subjected to swimming tests and reaching U_{Crit} or not. The axes represent the explained variance due to the factors 1 (PC1) and 2 (PC2). The loadings and the scores for each component contributing to PC1 and PC2 are represented by arrows, along with the 95% confidence ellipsoids generated for each group. BW, body weight; FL, fork length (= BL); H, height; K, condition factor K; O, operculum; PP, peduncle posterior; PA, peduncle anterior; PFF, pectoral-fin front; PFB, pectoral-fin base; PFL, pectoral-fin length; SL, standard length.

The average absolute U_{Crit} measured in the snapper from the F_1 cohort was 0.713 ± 0.006 $m{\cdot}s^{-1}$ (mean ± SE) and was not statistically significantly different from 0.709 ± 0.009 $m{\cdot}s^{-1}$, measured in the F_4 cohort (*t*-test, $p = 0.115$). Similarly, the relative U_{Crit} measured in snapper from the F_1 cohort was 4.893 ± 0.049 $BL{\cdot}s^{-1}$ (mean ± SE) and was not statistically significantly different from 4.779 ± 0.090 $BL{\cdot}s^{-1}$, measured in the F_4 cohort (*t*-test, $p = 0.321$). Figure 4c shows the proportion of snapper reaching U_{Crit} for each of the tests implemented. The proportion of fish from the F_1 cohort reaching U_{Crit} was 0.750 ± 0.046 (mean ± SE), higher than in the F_4 cohort (0.638 ± 0.046), although it was not significantly different between both groups (approximate χ^2, $p = 0.122$).

The relationships between the absolute U_{Crit} ($m{\cdot}s^{-1}$) and several biometric parameters of snapper from both cohorts are presented in Figure 5. No linear relationship was detected between U_{Crit} and BW in individuals of either the F_4 or F_1 cohorts (Figure 5a,b, ANOVA, $p = 0.781$, and $p = 0.101$, respectively). Similarly, no linear relationship was detected between U_{Crit} and BL in individuals of either the F_4 or F_1 cohorts (Figure 5c,d, ANOVA, $p = 0.094$, and $p = 0.139$, respectively). In line with these findings, no linear relationship was detected between U_{Crit} and K in individuals of the F_1 cohort (Figure 5f, ANOVA, $p = 0.275$). However, a positive linear relationship ($y = 0.36 + 0.15\,x$, Pearson's r = 0.414) was found between U_{Crit} and K in individuals of the F_4 cohort (Figure 5e, ANOVA, $p = 0.003$). The slopes of the linear regressions between U_{Crit} and K were significantly different between both cohorts (F-test, $p = 0.047$).

The relationship between the relative U_{Crit} ($BL{\cdot}s^{-1}$) and several biometric parameters of snapper from both cohorts are presented in Figure 6. A negative linear relationship was detected between U_{Crit} and BW in individuals of both the F_4 or F_1 cohorts (Figure 6a,b, Pearson's r = −0.501, and −0.544, ANOVA, $p < 0.001$, *and* $p < 0.001$, respectively). The slopes of the linear regressions between U_{Crit} and BW were not significantly different between both cohorts (F-test, $p = 0.355$). Similarly, a negative linear relationship was detected between U_{Crit} and BL in individuals of both the F_4 or F_1 cohorts (Figure 6c,d, Pearson's r = −0.682, and −0.589, ANOVA, $p < 0.001$, and $p < 0.001$, respectively). The slopes of the linear regressions between U_{Crit} and BL were significantly different between both cohorts (F-test, $p = 0.016$). On the contrary, no linear relationship was detected between U_{Crit} and K in individuals of either the F_4 or F_1 cohorts (Figure 6e,f, $p = 0.095$, and $p = 0.514$, respectively).

3.3 | Metabolic traits and their relationship with swimming performance and morphology

Figure 7 displays the plasma metabolite concentrations measured in snapper after implementing the critical swimming speed test, whether individuals reached fatigue or not (U_{Crit} and NO U_{Crit}, respectively). Figure 7a shows that lactate concentration in the plasma was higher in snapper reaching fatigue in the F_4 cohort than in the F_1 individuals, displaying mean values of 4.685 ± 0.212 mM and 2.802 ± 0.475 mM, respectively (Tuckey's post hoc test, $p < 0.001$). Additionally, plasma lactate concentration in snapper from the F_4 cohort reaching U_{Crit} was significantly higher than in those not reaching fatigue (NO U_{Crit}) during the test (Tuckey's post hoc test, $p < 0.001$). No statistically

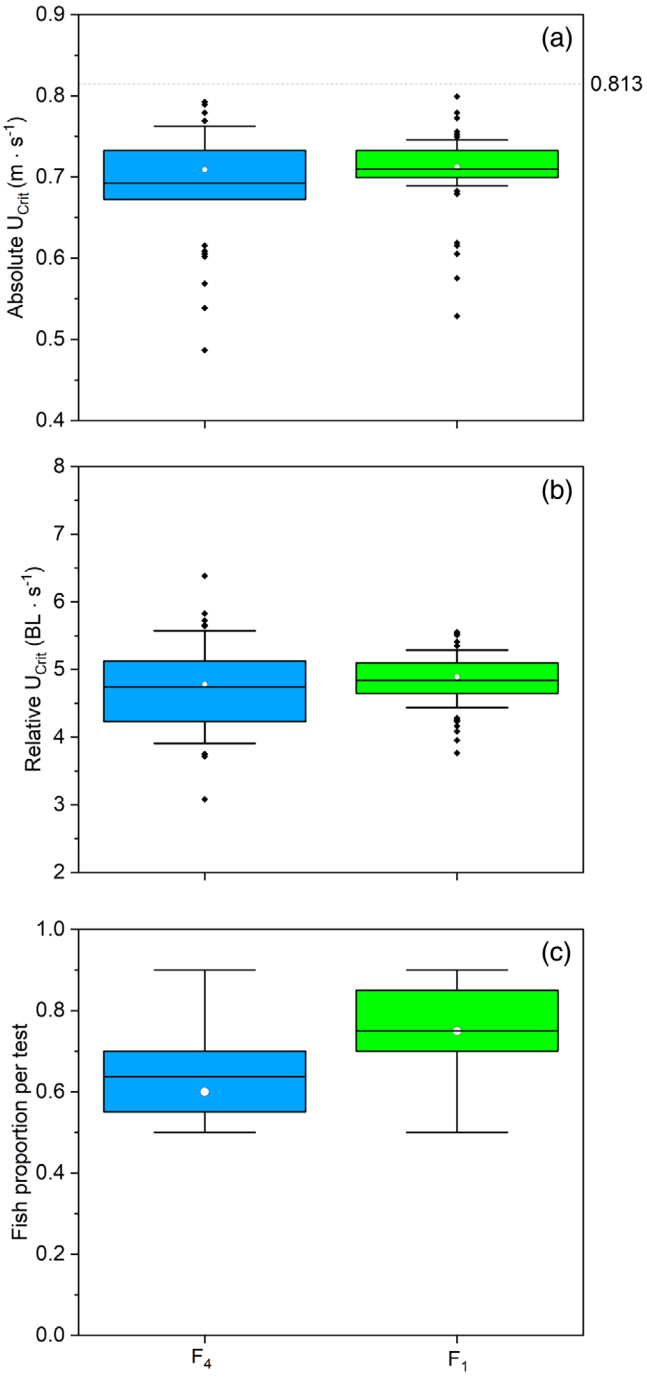

FIGURE 4 Critical swimming speed (U_{Crit}) of the snapper in F_4 (blue) and F_1 (green) cohorts expressed in absolute value (a, meters per second), relative value (b, body lengths, BL, per second), and the proportion of individuals reaching fatigue in each test (c). A total of 80 naive fish were used in eight independent tests per cohort, with 10 snapper per swimming test. The horizontal dotted line in panel a indicates the maximal swimming speed achievable under the experimental conditions applied. Boxes show the upper 75th and lower 25th percentiles, the whisker bars indicate the 90th and 10th percentiles, and the black dots are values beyond the 90th and 10th percentiles. Within each box, the white dot represents the median, and the line the mean value. The number of fish reaching U_{Crit} was 51 and 60 for cohorts F_4 and F_1, respectively. No statistically significant differences were found between the two snapper cohorts (*t*-test for U_{Crit} values, approximate χ^2 for proportions, $p > 0.05$).

significant differences were detected in the plasma lactate concentration of snapper of either cohort not reaching U_{Crit} (Tukey's post hoc test, $p = 0.476$), or between fish reaching U_{Crit} or not in the F_1 cohort (Tukey's post hoc test, $p = 0.349$).

Similar to that shown for plasma lactate concentration, plasma glucose concentration was higher in snapper reaching fatigue in the F_4 cohort than in the F_1 individuals (Figure 7b), displaying mean values of 6.340 ± 0.219 mM and 5.564 ± 0.224 mM, respectively (Tukey's post hoc test, $p = 0.040$). On the contrary, the concentration of this metabolite in plasma in snapper of the F_4 cohort reaching fatigue or not was similar (Tukey's post hoc test, $p = 0.428$). Additionally, no differences were revealed in plasma concentration of this metabolite in individuals of the F_1 cohort reaching fatigue or not (Tukey's post hoc test, $p = 0.290$). Also, no differences were detected in plasma glucose concentration between individuals of either the F_4 or F_1 cohorts not reaching fatigue (Tukey's post hoc test, $p = 0.159$).

Figures S3 and S4 (Supporting Information) show the relationship between plasma metabolite concentrations and absolute U_{Crit} or relative U_{Crit}, respectively, in fish from both cohorts. Plasma lactate concentration and U_{Crit} were not correlated in individuals of the F_4 (Figures S3A and S4A) or F_1 cohorts (Figures S3B and S4B). Also, plasma glucose concentration and U_{Crit} were not correlated in individuals of the F_4 (Figures S3C and S4C) or F_1 cohorts (Figures S3D and S4D).

Figures S5 and S6 (Supporting Information) show the relationships between plasma metabolite concentration and biometric parameters (BW, BL, and K) in fish from both cohorts. Plasma lactate concentration and these biometric parameters were not correlated in individuals of the F_4 (Figure S5A,C,E) or F_1 cohorts (Figure S5B,D,F). Also, plasma glucose concentration was not correlated with these biometric parameters in individuals of the F_4 cohort (Figure S6A,C,E). However, a positive correlation was observed between glucose and BW or BL in individuals of the F_1 cohort (Figure S6B,D, Pearson's $r = 0.352$ and 0.395, ANOVA $p = 0.006$, and 0.002, respectively). No correlation was observed between glucose and K in individuals of the F_1 cohort (Figure S6E).

4 | DISCUSSION

4.1 | Selective breeding changes the external morphology without changing swimming performance

Our results show that the two different snapper cohorts (F_1, derived from wild broodstock; F_4 selected for fast growth) displayed similar swimming performance, as evidenced by the lack of differences in both absolute and relative U_{Crit}. Absolute and relative U_{Crit} values of 0.72 m·s^{-1} or 5.02 BL·s^{-1} were reported in snapper with an average BL of 14.5 cm using a single individual per test (Coxon, 2014), as this method has traditionally been used to evaluate swimming performance in fish (Brett, 1964). These values were similar to the reported U_{Crit} values for snapper of both cohorts measured in this study. However, solid-blocking effects (Bell, 1970) were not measured when

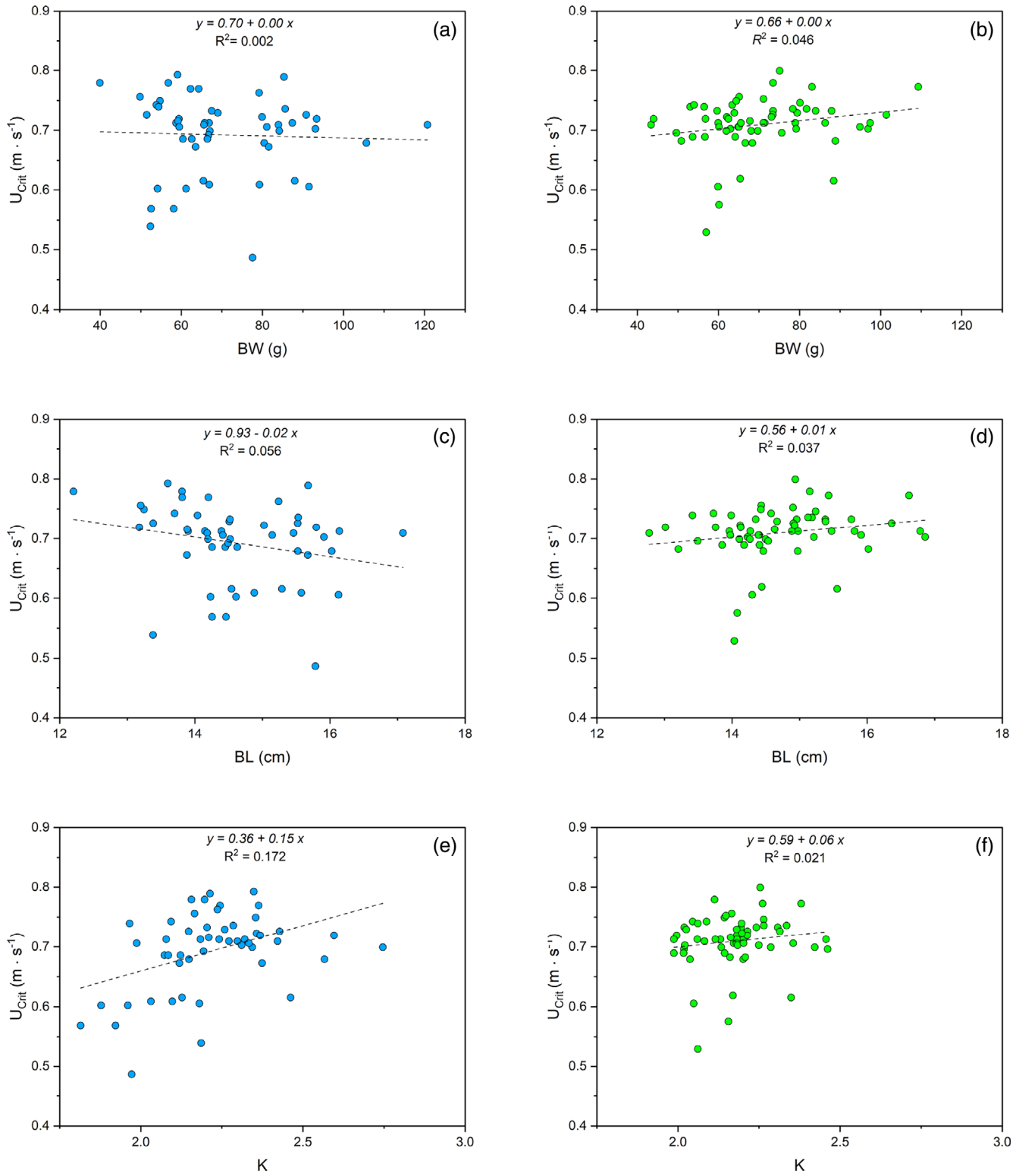

FIGURE 5 Relationships between the absolute critical swimming speed (U_{Crit}) and biometric parameters of snapper tested in the F_4 (blue dots) and F_1 (green dots) cohorts. A total of 80 naive fish were used in eight independent tests per cohort, with 10 juvenile snapper per swimming test, resulting in F_1 $n = 51$ and F_4 $n = 60$ snapper reaching U_{Crit}. A linear model was applied ($y = a + b * x$, broken line), followed by ANOVA to test if $b \neq 0$. Parameters and R^2 coefficients are included in each panel. Panels (a) and (b) show the relationship between body weight (BW) and U_{Crit} ($p = 0.781$, and $p = 0.101$, respectively). Panels (c) and (d) show the relationship between body length (BL) and U_{Crit} ($p = 0.094$, and $p = 0.139$, respectively). Panels (e) and (f) show the relationship between condition factor (K) and U_{Crit} ($p = 0.003$, and $p = 0.275$, respectively).

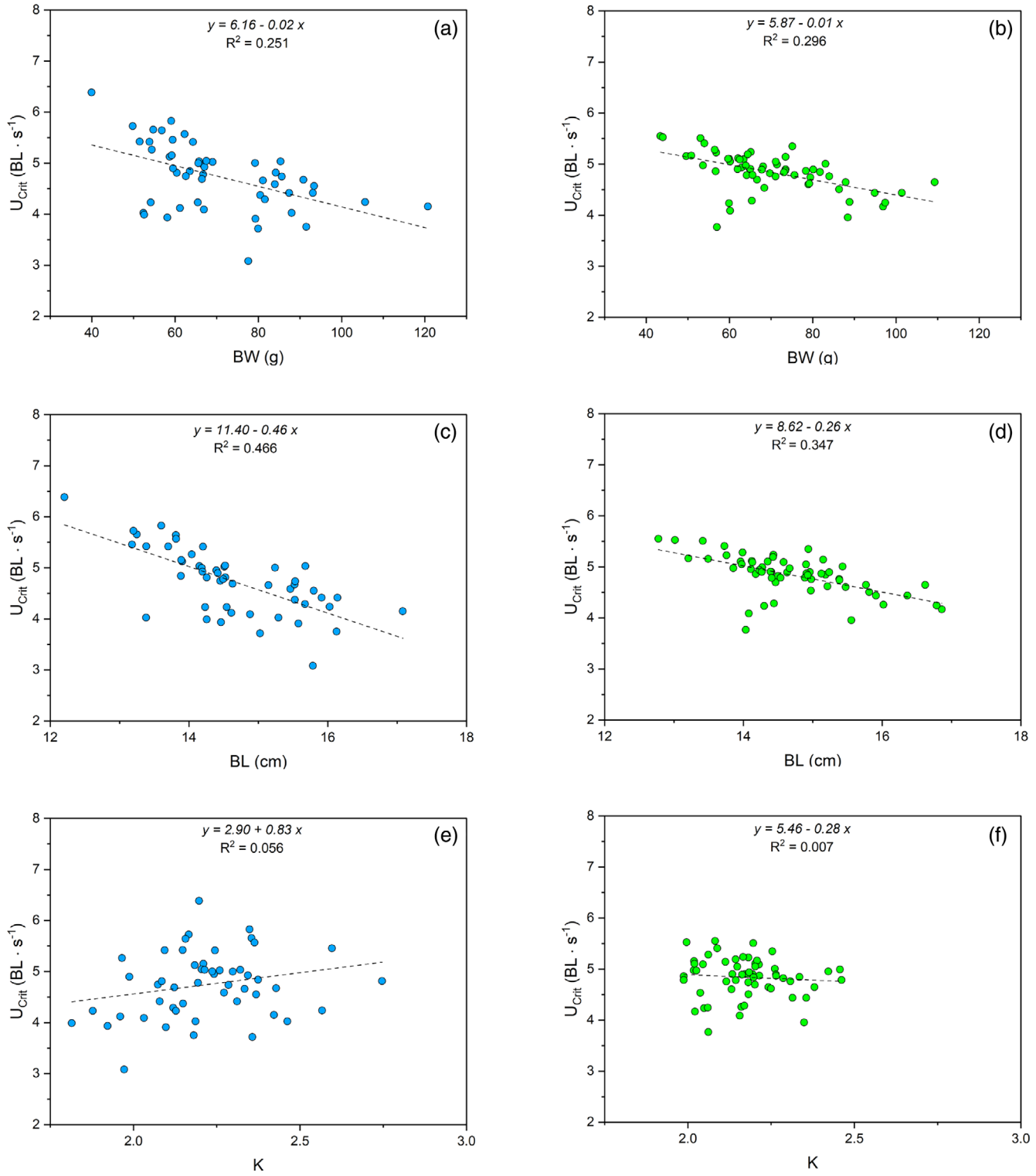

FIGURE 6 Relationships between the relative critical swimming speed (U_{Crit}) and biometric parameters of snapper tested in the F_4 (blue dots) and F_1 (green dots) cohorts. A total of 80 naive fish were used in eight independent tests per cohort, with 10 juvenile snapper per swimming test, resulting in F_1 $n = 51$ and F_4 $n = 60$ snapper reaching U_{Crit}. A linear model was applied ($y = a + b * x$, broken line), followed by ANOVA to test if $b \neq 0$. Parameters and R^2 coefficients are included in each panel. Panels (a) and (b) show the relationship between body weight (BW) and U_{Crit} ($p < 0.001$, and $p < 0.001$, respectively). Panels (c) and (d) show the relationship between body length (BL) and U_{Crit} ($p < 0.001$, and $p < 0.001$, respectively). Panels (e) and (f) show the relationship between condition factor (K) and U_{Crit} ($p = 0.095$, and $p = 0.514$, respectively).

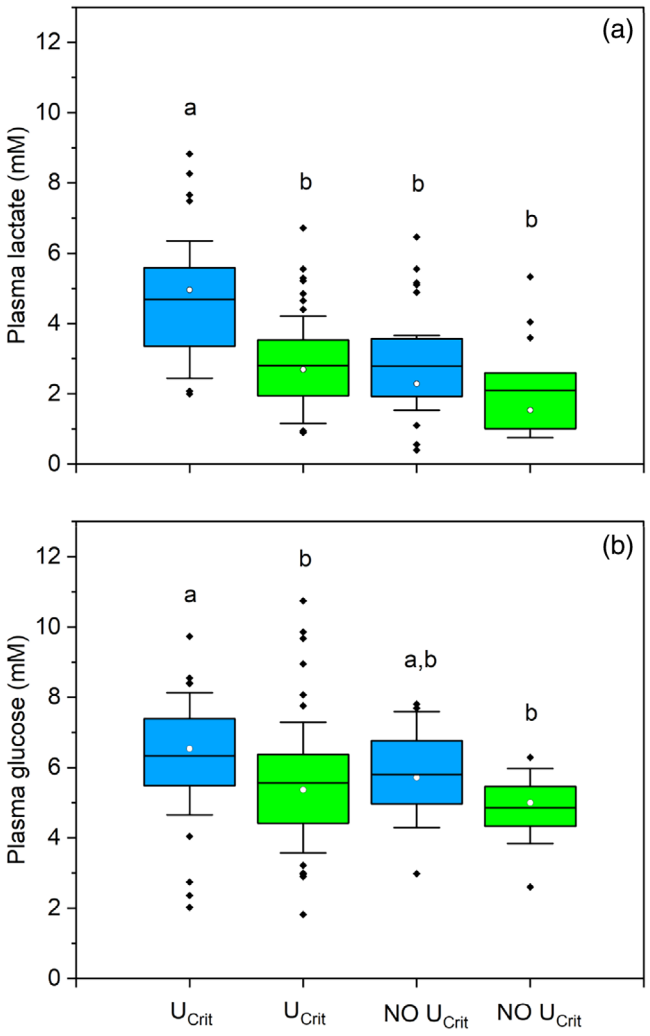

FIGURE 7 Plasma lactate (a) and glucose (b) concentrations of snapper in F_4 (blue) and F_1 (green) cohorts were tested, distinguishing between these individuals reaching critical swimming speed (U_{Crit}) or not (NO U_{Crit}). Boxes are the upper 75th and lower 25th percentiles, the whisker bars indicate the 90th and 10th percentiles, and the black dots are values beyond the 90th and 10th percentiles. Within each box, the white dot represents the median, and the line the mean value. The number of fish reaching U_{Crit} was 51 and 60 for cohorts F_4 and F_1, respectively, whereas the number of fish not reaching U_{Crit} was 29 and 20 for cohorts F_4 and F_1, respectively. Different letters indicate significant differences between groups (one-way ANOVA, followed by Tukey's post hoc test, $p < 0.05$).

evaluating the U_{Crit} of snapper in this study and in that reported by Coxon (2014). This consideration, in addition to the methodological limitation to achieve absolute U_{Crit} values above 0.813 $m \cdot s^{-1}$ in the current study, resulted in an underestimation of mean U_{Crit} in both cohorts. Therefore, our assessment may be seen as a rough appraisal of the individual value for swimming performance, although it was useful to phenotype a large number of fish in both cohorts. This was intended to investigate both the effects of selective breeding on fish phenotype and the links between morphology, swimming performance, and metabolic traits at a large scale in a relatively short time frame, therefore minimizing potential confounding effects of body size owing to differing growth rates between cohorts (Moran et al., 2023). Interestingly, a previous study has shown that the U_{Crit} in Atlantic salmon (*Salmo salar*) was higher when tests were applied to groups rather than to single individuals (Remen et al., 2016), an effect that may be attributed to the fish behavior of establishing schools or shoals when fish are in large groups (Killen et al., 2012; Killen et al., 2017; Wiwchar et al., 2018). Based on these previous studies, we were expecting a higher U_{Crit} for snapper swimming in groups compared with values reported in individuals with equivalent body size at similar temperatures (Coxon, 2014). However, U_{Crit} values were similar in snapper swimming individually or in groups, as described earlier.

Our findings suggest that two rounds of selection applied to maximize growth are not enough to induce significant changes in swimming performance, despite external morphological changes (condition factor K, and the peduncle posterior distance, PP) detected between fish in both cohorts. This was contrary to our hypothesis stating that changes in body shape resulting from the selective breeding programme in snapper could be reflected in differences in swimming performance. This comparison was applied to snapper of both cohorts reared in analogous conditions with a similar body size, aimed to minimize the scaling effect described for swimming performance (Goolish, 1989). In this regard, it has been described in snapper (Coxon, 2014) and other species (Mateus et al., 2008; Rubio-Gracia et al., 2020; Srean et al., 2017) that the absolute and relative U_{Crit} are positively and negatively related to fish body size, respectively. In agreement with that description, both cohorts of snapper in this study displayed a weak negative correlation between relative U_{Crit} and body size (BW and BL), conceivably owing to the narrow range of fish body sizes tested in this study. Interestingly, snapper selected for fast growth (F_4) displayed a positive correlation between absolute U_{Crit} and K, indicating that shorter/heavier fish performed better than longer/lighter fish. This was surprising, considering that such a relationship was not apparent in fish tested in the F_1 cohort. It may be possible that these differences could be linked to a narrow distribution of K in the F_1 cohort, reflecting less individual variability in this group than in the F_4 cohort. This appears to be contrary to the prospect of homogeneous fish body sizes (decreased variability within the cohort), as a potential outcome of selective breeding. Additionally, no positive correlations between absolute U_{Crit} and body size (BW, BL) were observed in both cohorts. This difficulty in detecting a scaling effect between absolute U_{Crit} and BW or BL across both cohorts of snapper could be related to the narrow range of fish body size used in this study.

This study has also shown that the proportion of snapper reaching U_{Crit} in each test was higher for the F_1 than for the F_4 cohort, although differences were not significant. It seems possible that this could be linked to differences in morphology, namely the higher K and the longer distance for the posterior section toward the caudal fin of the peduncle in the F_4 cohort, although additional studies may be required to confirm this possibility. In this regard, morphological differentiation has been detected in salmonids, suggesting that

phenotypic plasticity is an important strategy to cope with different environments (Pakkasmaa & Piironen, 2000). The latter authors have shown contrasting differences in body shape induced by different water flow conditions during rearing in juvenile Atlantic salmon and brown trout, with salmon being deeper-bodied and trout a more streamlined shape in fast-flowing water. Similarly, rearing conditions with fast flow and obligatory long-term swimming induce changes in the external morphology of gilthead seabream (Yu et al., 2022b) and the cyprinid *Schizothorax wangchiachii* (Lu et al., 2020), by decreasing height and shaping a streamlined body, consequently reducing drag and energy costs. In general, cultured fish are described to have greater height and condition factors than their wild conspecifics, probably related to rearing environments leading to similar morphological changes (Wringe et al., 2015). As the rearing environment was similar for both cohorts in our study, results suggest that the changes in external morphology detected could be linked to genotypic differences in snapper.

A few studies have suggested that swimming performance has a heritable component in fish, linking selective breeding with changes in body shape and swimming performance. A significant additive genetic variance for critical swimming speed has been estimated in cultured Nile tilapia (Mengistu et al., 2020). Also, a subsequent study in this species found substantial heritability for absolute U_{Crit}, although this trait displays a negative correlation in early life with growth (Yu et al., 2022a), suggesting a trade-off between swimming and growth performance. A previous study in different cohorts of European seabass showed a high heritability for swimming performance when measured in groups, defined as U_{Max}, displaying considerable genetic variability in this trait (Vandeputte et al., 2016). These authors showed that the relative U_{Max} tended to have lower values in two cohorts selected to maximize growth versus wild or F_1 fish, which could be explained by larger body size in the former groups, as the difference between any of the groups disappeared when BL was introduced as a covariate. That study also showed a weak positive correlation between absolute U_{Max} and BW, and a strong negative correlation between relative U_{Max} and BW. A negative correlation between relative U_{Crit} and BW was also observed in the two cohorts of snapper of the current study, with the F_1 fish displaying a slightly better fit to a linear regression than the F_4 fish.

4.2 | Metabolic traits in fish subjected to U_{Crit} tests are different between cohorts

Coxon (2014) has shown a significant lactate release into the circulation of snapper immediately after reaching U_{Crit} (~7 mM), which continued to increase 1 h after exercise, peaking to a concentration of 15 mM, or a 32-fold increase compared with resting concentrations (~0.5 mM). A similar response in magnitude and duration has been described in rainbow trout, peaking at concentrations of 15–20 mM at 1–2 h post-exercise (Milligan et al., 2000; Wang et al., 1994). In our current study, the blood was sampled in snapper within 5 min after reaching fatigue or finishing the experiment when fish did not attain U_{Crit}. Plasma lactate concentration was higher in snapper from the F_4 cohort when reaching the U_{Crit} compared with the F_1 cohort (4.685 ± 0.212 and 2.802 ± 0.147 mM, respectively), confirming only in part the proposed hypothesis that plasma metabolite levels are different between both cohorts when snapper reach fatigue. However, the link between these metabolic differences and the swimming performance could not be established, as the U_{Crit} value was similar between both cohorts.

A higher plasma lactate concentration was also displayed in snapper not reaching U_{Crit} in the F_4 cohort compared with F_1 during the tests. This may suggest a different anaerobic capacity in snapper selected for fast growth when exercised at or near maximal sustainable speed, indicating potential changes in lactate fluxes between cohorts when swimming at a high speed. Despite the suggested differential anaerobic capacity of the F_4 cohort, swimming performance does not appear to be a good predictor for plasma lactate concentration, as no correlation was detected between plasma lactate concentration and U_{Crit} (absolute or relative) in either cohort.

Regarding the glucose concentration present in the circulation, it has been proposed that this metabolite is important to restore glycogen content in the white muscle after exhaustive exercise (Pagnotta & Milligan, 1991). Hyperglycaemic response to high-intensity swimming has been described in several fish species (Milligan & Girard, 1993; Wells & Baldwin, 2006). In addition, glucose fluxes are stimulated in rainbow trout during U_{Crit} tests, particularly when swimming speeds reach ~80% U_{Crit} or greater (Choi & Weber, 2016). Coxon (2014) reported significant increases in glucose concentration in U_{Crit} tests in snapper immediately after fatigue, reaching values of ~7 mM compared with ~4 mM before the test. These fish showed a modest peak of ~14 mM at 1-h post-U_{Crit} and stayed elevated up to 6 h during recovery. In this study, plasma glucose concentration was significantly higher in snapper from the F_4 cohort when reaching the U_{Crit}, analogous to these changes described for plasma lactate. This may indicate a different metabolic capacity of the F_4 cohort when exercised at maximal sustainable speed, suggesting an increased reliance on glycolysis and anaerobic metabolism, which may become important in the recovery phase after exhaustion.

We can conclude that the selection for fast growth produces some changes in body shape, namely the K factor and the PP distance, although this did not result in significant differences in the U_{Crit} compared with that of the individuals from the F_1 cohort. This may imply that a longer selective programme may be required to detect differences in swimming performance. Interestingly, the proportion of fish reaching the U_{Crit} in each test suggests that the morphology may have an impact on swimming performance, which may be of relevance in finfish cultured under different conditions (e.g., open ocean vs. coastal deployments of enclosures). Selection for fast growth did not reduce the variability in U_{Crit}, although plasma lactate and glucose concentrations were consistently higher in the F_4 cohort subjected to the U_{Crit} test. Finally, higher lactate and glucose concentrations in individuals from the F_4 cohort after being induced to swim at high speed suggest a possible different metabolic flux of these key metabolites in snapper. In addition to swimming to exhaustion, these differences may be

relevant in other physiologically challenging situations, such as environmental hypoxia or higher temperatures. Future studies should explore the potential relationships between selective breeding, acute changes in dissolved oxygen concentration, and/or water temperatures along with their metabolic outcomes.

AUTHOR CONTRIBUTIONS

Conceptualization: Leonardo J. Magnoni; formal analysis: Leonardo J. Magnoni; funding acquisition: Leonardo J. Magnoni, Suzanne E. Black, and Maren Wellenreuther; methodology: Leonardo J. Magnoni, Selwyn P. Collins, Matthew J. Wylie, and Maren Wellenreuther; resources: Leonardo J. Magnoni, Suzanne E. Black, and Maren Wellenreuther; writing—original draft: Leonardo J. Magnoni; writing—review and editing: Selwyn P. Collins, Matthew J. Wylie, Suzanne E. Black, and Maren Wellenreuther.

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CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this manuscript will be made available by the authors, without undue reservation, to any qualified researcher.

INSTITUTIONAL REVIEW BOARD STATEMENT

Experiments were carried out in compliance with approved guidelines by the Nelson Marlborough Institute of Technology (NMIT) —Te Pūkenga Animal Ethics Committee, under the Code of Ethical Conduct Animal Welfare 2009 and the Aotearoa/New Zealand Animal Welfare Act 1999.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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