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Aquaculture Reports 17 (2020) 100349

Contents lists available at ScienceDirect

Aquaculture Reports

journal homepage: www.elsevier.com/locate/aqrep

Can individual feed conversion ratio at commercial size be predicted from juvenile performance in individually reared Nile tilapia *Oreochromis niloticus*?

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ARTICLE INFO

Keywords:
Feed efficiency
GIFT tilapia
Individual rearing
Selective breeding

ABSTRACT

Feed conversion ratio (FCR), the ratio between feed intake and body weight gain, is of major interest for improving aquaculture sustainability through reduced feed costs and environmental impacts. Demonstrating whether FCR measured in juvenile fish is an accurate predictor of their performance during the whole rearing period is critical to developing genetic improvement programs for this trait. This is especially true for estimates obtained in individually reared fish, for which this has high implications regarding the size of the necessary rearing structures. We obtained individual FCR from 30 male Nile tilapia *Oreochromis niloticus* from the GIFT strain individually reared in a recirculating system, from 36 to 260 g mean weight. They were fed twice a day and uneaten pellets were counted every day to determine the feed intake of each fish. Individual growth was monitored every week. Feed conversion ratio was estimated over two-week periods and over the whole rearing period (210 days). Phenotypic correlations between the two-week FCRs and global FCR estimations were mostly significant (ranged from 0.38 to 0.64). A significant phenotypic correlation between growth and FCR was also found: faster-growing fish had a better (lower) FCR. Individual breeding values for global FCR were estimated using FCR phenotypes from the present study and previously published heritabilities for FCR in Nile tilapia. Potential estimated genetic gain for global FCR was 2.2% per generation with 50% selection intensity. When selecting fish on their FCR from only a two-week period, approximately 50% of the reference genetic gain could be obtained with the same selection intensity. FCR measured during a two-week period at juvenile stage could be a moderately accurate approximation of the whole rearing period FCR, and could be used as a lower cost criterion to select for FCR in future genetic improvement programs using individual rearing of fish.

1. Introduction

Continuing to feed the increasing world's human population while reducing food production pressure on the environment is a major challenge. Fish is seen as a key component of sustainable future diets (Froehlich et al., 2018). Since fisheries production stagnates, meeting the future demand for products of aquatic origin will rely on aquaculture (FAO, 2016). However, increasing aquaculture production will require an increase in fish feed production which will compete for access to ingredients with agriculture and direct human consumption (Troell et al., 2014). Improving the ability of cultured fish to convert feed intake into biomass could play a significant role in reducing feed use in aquaculture and improving its sustainability through reduced costs and environmental impacts (Besson et al., 2014, 2016; de Verdal et al., 2018a). The ability to convert feed intake into body weight gain can be measured by the feed conversion ratio (FCR) which is the ratio between feed intake (FI) and body weight gain (BWG) over a given time period. Feed conversion ratio can be improved through changes in feed

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https://doi.org/10.1016/j.aqrep.2020.100349
Received 26 February 2020; Received in revised form 20 April 2020; Accepted 25 April 2020
Available online 11 May 2020

composition and husbandry (NRC, 2011) and through selective breeding (de Verdal et al., 2018a). The main challenge to improving FCR in breeding programs is the capacity to accurately measure FCR at the individual level on a large number of fish.

Measuring the individual FI of a large number of fish is particularly difficult as fish are reared in groups, and the share of a meal eaten by each individual is not easily recorded. Various methods have been proposed to measure individual FI, such as X-radiography with radio-opaque pellets (Kause et al., 2006; Grima et al., 2008) or using video recording of small groups of fish distinguished by colored T-bar tags (de Verdal et al., 2017, 2018b). Another option is the rearing of individual fish in aquaria with collection of all uneaten pellets (Silverstein, 2006; Martins et al., 2011; Besson et al., 2019). This method is tedious, but has potential to be used for selective breeding through the identification of Quantitative Trait Loci (QTLs) or the use of genomic selection (Lu et al., 2017; Besson et al., 2019).

Estimating individual fish FCR beyond juvenile stages is particularly important as the amount of feed consumed during the later stages of growth is higher than during the younger stages (Alanärä et al., 2001). In broiler chicken, de Verdal et al. (2013) made a long-term FCR evaluation and showed that selection for FCR undertaken at a given age improves offspring FCR much more at that selection age than at other ages. That work demonstrated it is essential to estimate the correlations between FCRs measured at different development stages, in order to assess the ability to use data from one given stage to select efficiently for FCR over the whole rearing period. Due to the rearing infrastructures needed and to rearing costs, it would be much more convenient to select for juvenile fish than for fish at commercial size, especially when individual rearing is used. Whether FCR estimated at early stages gives a reliable picture of FCR at older stages is thus critical information in this respect.

The objective of the present study was to assess the changes over time of three key performance traits (*i.e.* BWG, FI and FCR), to estimate whether fish with the best (lowest) FCR at juvenile stage also had the best FCR during the whole rearing period. Nile tilapia (*Oreochromis niloticus)* was used as this is the second most farmed aquaculture species in the world (FAO-FIGIS, 2019). We used the GIFT (Genetically Improved Farmed Tilapia) strain (Ponzoni et al., 2010), for which phenotypic and genetic data on individual FCR are available (de Verdal et al., 2018b). In the present study, male Nile tilapia were reared individually in aquaria, in order to measure individual BWG, FI and FCR from the juvenile stage (36 g) up to commercial size (250 − 300 g), and to evaluate the relevance of FCR estimated over short periods to predict FCR over the whole grow-out period.

2. Material and methods

2.1. Ethics statement

This study utilised phenotypic data collected as part of the GIFT selective breeding program managed by WorldFish at Jitra, Kedah State, Malaysia (6°15′32 °N; 100°25′47 °E). All fish in the GIFT breeding population are managed in accordance with the Guiding Principles of the Animal Care, Welfare and Ethics Policy of the WorldFish.

2.2. Biological material

Forty individual Nile tilapia were used in the experiment, taken from two families (20 full-sibs from each family) from the 17th generation of GIFT produced on the 27th of December 2017 at WorldFish Aquaculture Extension Centre in Jitra. Fish were reared in two distinct hapas in the same pond and transferred to 1500 L holding tanks (3 × 1 × 0.5 m) at 110 days post hatching (dph). During this period, PIT-tags were injected to identify each fish individually. These 40 fish were initially sorted from a larger group at 131 dph to have a similar body weight at the beginning of the experiment, allowing easier comparisons between individuals.

At 145 dph, fish were too young to be sexed. Fish were sexable only after seven weeks of experiment (at 201 dph). Among these 40 fish, nine were females and 31 were males, one of which jumped and died after the beginning of the experiment. Although females were kept in the rearing system, the study focused on the 30 remaining males (18 coming from the first family and 12 from the second one). The first objective was to study both sexes, but the number of females was too small to ensure a reliable statistical analysis including both sexes.

2.3. Rearing system

The rearing system consisted of two recirculating water systems, in the same room, each including 20 aquaria, a sand and a biological filter. Each fish was placed into a 60 L (61 × 30 × 33 cm) single plastic aquarium at 145 dph and left for one week of acclimation time. The experiment started at 152 dph with males weighing 36.3 ± 5.9 g (mean ± standard deviation). The initial coefficient of variation ($CV = 100 * (Standard\ deviation . Mean^{-1})$) of body weight was thus 16.3%. The 30 males were shared equally (15 and 15) between both recirculating water systems even if fish were distributed by a random draw.

Water renewal rate was 240% per hour and each aquarium included a constant aeration system. Water temperature was 29.1 ± 1.2 °C, water oxygen saturation rate was on average 7.1 mg/L (92.1% of saturation), water pH was 7.0 and photoperiod was natural, around 12 h light/12 h dark. The feed used was the same during all the experiment: a commercial tilapia feed (Cargill®, “Starter tilapia 6113”) with 34.0% crude protein, 5.0% crude fat, 5.0% crude fibre and 12.0% moisture, with constant pellet size (2 mm diameter). The 100% daily feed ration (DFR; in percentage of body weight) was calculated based on the formula published by Mélard et al. (1997):

$DFR = 14.23 * BW^{-0.322}$ with BW the body weight of each fish (in g).

Throughout the experiment, fish were fed 90% of the calculated DFR, shared equally in two meals. Fish were fed by hand twice a day at 9 a.m. and 2 p.m. (all fish were fed in less than 10 min), except on days of body weight measurements where fish were fed only at 2 p.m. The fish were fed 90% rather than 100% of the DFR in order to reduce the amount of uneaten feed and thus the time needed for counting uneaten pellets. With this feeding rate, fish were generally wasting a few pellets at each meal, indicating that they were close to *ad libitum*. Furthermore, while the equation developed by Mélard et al. (1997) was not developed on the same feed and on the same tilapia strain, a calculated ration was preferred to an “*ad libitum”* feed ration. Several people were involved in the management of the experiment, and from one experimenter to another, the amount of feed given to a fish as “*ad libitum”* can fluctuate widely, reducing repeatability of the FI measurement.

2.4. Feed intake measurement and FCR calculation

Each fish was anaesthetized with clove oil (0.5 mL per litre of water) and weighed once a week. The DFR was updated every week for each fish. Every day, feed given to the fish was weighed and the uneaten pellets were counted and removed from the aquaria at least two h after the last meal of the day. The uneaten feed weight was estimated every day, considering that all pellets had the same weight (16.2 ± 1.8 mg). Daily feed intake (DFI) was calculated for each fish as the difference between daily feed weight given and daily feed weight uneaten.

The FI, BWG and FCR for individual fish were calculated on two-week time steps. Two-week periods were chosen instead of one-week periods to smooth the strong weekly variation of individual BWG (Supplementary Material 1). Bi-weekly FI values were calculated for each fish as the sum of the DFI during two full consecutive weeks. Bi-weekly BWG was calculated for each fish as $BWG = BW_f - BW_i$, with BW_i and BW_f the body weights at the beginning and at the end of the two-week period, respectively. Each fish was measured for FI and BWG

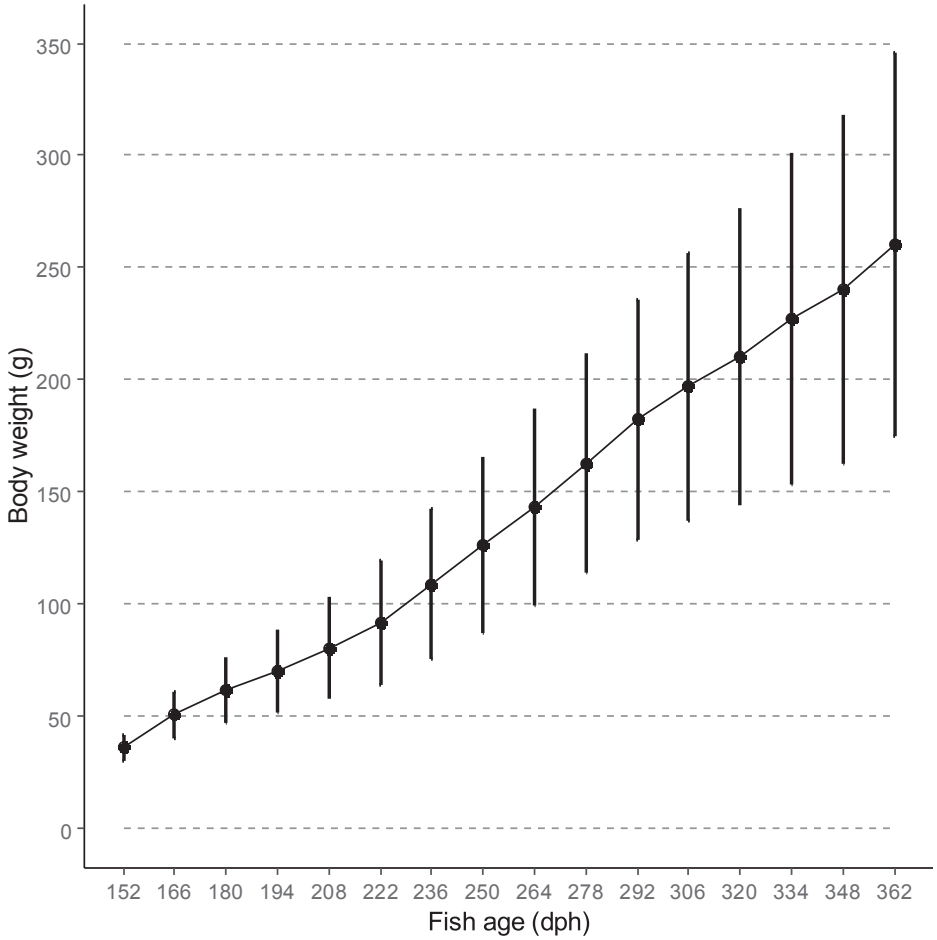

Fig. 1. Mean body weight (g) over the duration of the experiment (error bars represent standard deviation).

over 15 consecutive two-week periods (30 weeks of experiment in total), from 152 to 362 dph. Global FI (FIg) and BWG (BWGg) were calculated for each fish over the whole experimental period, as the sum of all DFI values and as the difference between body weights at the end and at the beginning of the experiment, respectively, in order to estimate global FCR ($FCRg = FIg.\ BWGg^{-1}$).

2.5. Statistical analysis

All statistical analyses were performed using R software (R Core Team, 2018). Negative and outlier bi-weekly FCR values (10 data points out of 450) were not included in the statistical analysis. Over each period, FCR values were considered outliers when not between M – 3 * Sd and M + 3 * Sd, with M the mean FCR and Sd the standard deviation of FCR over the period. Negative FCR were due to fish losing weight and outlier (high) FCR to fish gaining very little weight. The family and the recirculating water system effects were not significant for any trait in any period, and are thus not reported in the analyses.

2.5.1. Linear mixed models

The aim was to determine how fish performance traits (FI, BWG and FCR) changed through time. Firstly, whether they could be modelled as a function of time with only one linear regression through the whole experiment was tested. Otherwise, a segmented regression was used in the case of performance with sequences of increase and decrease. Potential breakpoints and segments in fish performance were detected using Chow test with the R package "strucchange" (Zeileis et al., 2002) that can handle repeated measures on the same individuals. Then, performance traits were analyzed on each separate segment with the following repeated measures linear mixed model:

$$Y_{ij} = \mu + \beta * T_i + A_j + \varepsilon_{ij}$$

where Y_{ij} is the phenotype (FI, BWG, FCR) of individual j measured for the two-week measurement period i (i between 1 and 15), μ is the general mean, β is the fixed effect of time T for every period i, A_j the random effect of the animal j with $A_j \sim N(0;\sigma^2_a)$, and ε_{ij} the residual ($\varepsilon_{ij} \sim N(0;\sigma^2_e)$). The normality of residuals was checked using the quantile-quantile method (comparing residuals quantiles with theorical normal quantiles), and their homoscedasticity and independence by comparing residuals with the model fitted values. Linear mixed models and Student tests associated to these models were realized using R packages "lme4" (Bates et al., 2015) and "lmerTest" (Kuznetsova et al., 2017).

2.5.2. Correlation estimates and correlation temporal patterns

Individual values of FI, BWG and FCR were log-transformed (lnFI, lnBWG, lnFCR) to achieve normal distribution, allowing Pearson correlation analyses. Correlations between lnFIg, lnBWGg and lnFCRg allowed the estimation of phenotypic links between the three traits over the whole rearing period. Then, for each trait, the correlation between each two-week period and the whole rearing period was estimated. For each trait, pairwise correlations between the different two-week periods were submitted to a Mantel test (R "ape" package; Paradis and Schliep, 2018) to assess whether they were significantly structured along a temporal gradient. The Mantel test was performed between the matrix of between-periods correlations and the matrix of time lapse between periods.

The relevance of measuring FCR during a two-week period rather than during the whole rearing period was then assessed. To this end, the

potential genetic gain on FCRg using direct mass selection on FCRg was compared to the potential genetic gain on FCRg using mass selection on FCR measured during the two-week periods which showed 1) the highest and 2) the lowest correlation with FCRg. For each fish, an estimated breeding value for FCRg was obtained with the following equation (Falconer and Mackay, 1996):

$$EBV_i = h^2 * (FCRg_i - \bar{FCRg})$$

with EBV_i the estimated breeding value of fish i for FCRg, h^2 the heritability of FCRg, $FCRg_i$ the FCRg of fish i and $\bar{FCRg}$ the mean FCRg of the 30 fish. Heritability was set to 0.32, the estimate for juvenile FCR in GIFT Nile tilapia from de Verdal et al. (2018b).

In mass selection, the best fish are selected based on their own phenotypes. So, the fish were ranked with three alternative methods: with FCRg (reference method), with FCR on the two-week period having the best correlation with FCRg, and with FCR on the two-week period having the worst correlation with FCRg. In each case, the fifteen best fish were identified, corresponding to a selection intensity of 50%. These best fish were the ones that would be selected in a mass selection program. Thus, the mean EBVs for FCRg of the fifteen best fish obtained with each of the three methods were estimated.

3. Results

3.1. Temporal patterns of growth, BWG, FI and FCR

Fish reached commercial size (260.5 ± 85.4 g) at 362 dph and the variability of body weight increased through time (Fig. 1). The mean BWGg over the full experiment was 224.5 ± 84.4 g. The corresponding mean FIg was 385.0 ± 128.6 g, resulting in a mean FCRg of 1.76 ± 0.19.

Performance traits were modelled with segmented linear mixed regressions as, according to the Chow test, the changes in FI, BWG and FCR over time were best modelled with breakpoints (Fig. 2). The CV of FCR was ranged from 11.3 to 36.2% with an average of 23.7 ± 7.7% (Fig. 3).

3.2. Correlation among traits and time periods

3.2.1. Correlation among traits

Over the whole experiment, the correlation between lnBWGg and lnFIg was high and significant ($r = 0.98$). The correlation between lnBWGg and lnFCRg was significant and negative ($r = -0.63$). Finally, the correlation between lnFIg and lnFCRg was also significant and negative ($r = -0.44$).

3.2.2. Correlation among time periods within traits

All two-week lnBWG were significantly and moderately to highly correlated with lnBWGg ($r = 0.55-0.94$). The same results were observed for lnFI ($r = 0.67-0.97$ with lnFIg). Global FCR (lnFCRg) was significantly and positively correlated with lnFCR recorded in 11 out of the 15 two-week periods, with correlations ranged from 0.38 to 0.64 (Fig. 4). Significant and higher correlations were mainly seen during the first half of the experiment (between 152 and 250 dph).

For each trait, the period to period correlation matrix was significantly structured along a temporal gradient, with higher correlations for closer periods (Mantel test, $P < 0.001$ for lnBWG and lnFI and $P < 0.05$ for lnFCR). However, only 19 out of 105 pairwise correlations were significant for lnFCR (only 7 out of 14 considering exclusively consecutive periods pairs).

3.3. Potential genetic gain for FCR

Estimated improvement in FCRg was 2.2% per generation with 50% of selection intensity on FCRg itself. This reference genetic gain for FCRg was compared with that projected using FCR from two-week periods to rank the fish. When using FCR from 152 to 166 dph to rank the fish (the period for which FCR was best correlated with FCRg, $r = 0.64$), the estimated genetic gain was 1.0%. When using FCR from 334 to 348 dph to rank the fish ($r = 0.38$ with FCRg, the worst period) the estimated genetic gain was 1.2%. Globally, when using a two-week period to rank the fish, approximately 50% of the reference genetic gain can be obtained with 50% selection intensity.

4. Discussion

4.1. Temporal variation in parameters

The aim of the present study was to determine whether FCR measured in young fish would reflect their performance during the whole rearing period. Feed intake, BWG and FCR globally increased with time but also fluctuated through time. Two major fluctuations in the measured performance occurred, which might result from physiological changes in the fish, since abiotic parameters were constant over time.

First, the decrease in BWG and FI between 152 and 194 dph might be explained by sexual maturation. The mean weights during this period (36.0 g at 152 dph and 70.3 g at 194 dph) correspond to the weight at onset of maturity in Nile tilapia reported in the literature (30 − 60 g, Galemoni de Graaf and Huisman, 1999; Gómez-Márquez et al., 2003; Hussain, 2004). Decrease in FI linked with male maturation has been demonstrated in several fish species (Kelly and Peter, 2006; Leal et al., 2009; Nishiguchi et al., 2012).

Until 292 dph, FI and BWG changes through time were simultaneous and in similar proportions, FCR did not change strongly during that period. However, BWG decreased between 292 and 348 dph, without related FI decrease, leading to a significant increase in FCR during this time frame. Even though fish were reared individually, pheromones from the few females kept in the same water system could be transmitted through the water exchange between tanks (Stacey and Sorensen, 2002). Female pheromones may induce an increased allocation of energy to gonad development in male fish (Miranda et al., 2005) and aggressive behavior (Giaquinto and Volpato, 1997), reducing investment in growth. Reports that male tilapia in a monosex group grew faster than in a mixed-sex group may provide indirect evidence to support this hypothesis (Macintosh and Little, 1995; Green et al., 1997; Dan and Little, 2000; Hafeez-ur-Rehman et al., 2008). However, individual rearing may have impeded behavioral aspects of tilapia reproductive functions, and present observations may not be completely comparable to large populations with mixed-sex rearing systems.

4.2. Correlations among traits and time periods

For lnFI and lnBWG, the closer two two-week periods were in time, the higher the correlation between them, meaning that a measurement at a given period would better predict performance at adjacent periods. A similar result was observed for body weight in a GIFT-derived strain of Nile tilapia when reared in mixed-sex groups (He et al., 2017). For lnFCR, the correlation was also greater between closer measurements in time, but these correlations were generally low and not significant, showing that FCR measured at a given two-week period is a poor predictor of FCR at any other two-week period. However, lnFCRs for 11 out of 15 two-week periods were significantly correlated with the global FCRg measured over the whole experiment, suggesting that a two-week FCR assessment may efficiently predict global FCR. Among the four two-week periods that were not significantly correlated with FCRg, three occurred just before or during the second BWG decrease.

A significant but moderate correlation was observed between lnFCRg and lnBWGg ($r = 0.63$), showing that faster-growing fish had a better (lower) FCR. This is in accordance with phenotypic correlations found in the literature between FCR and growth traits of fish reared in groups, whose values are ranged between −0.6 and −0.9 (de Verdal

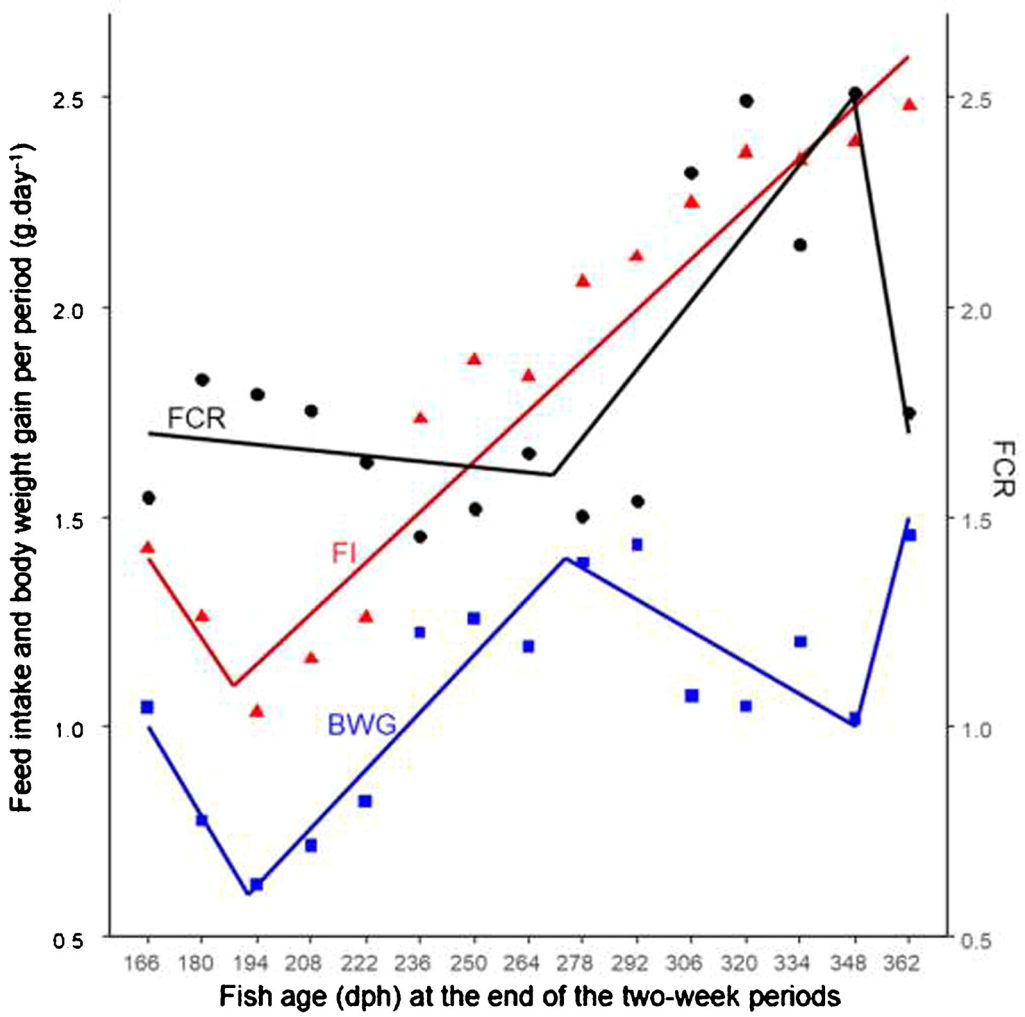

Fig. 2. Feed intake (FI, g day^{-1}), body weight gain (BWG, g day^{-1}) and feed conversion ratio (FCR) measured over the course of the experiment (dots), with segmented linear regressions associated (regression lines were extended until intersection).

et al., 2018a). However, at genetic level, de Verdal et al. (2018b) did not find a significant correlation between FCR and BWG (0.07 ± 0.24) with fish around 20 − 30 g. The negative phenotypic correlation observed here should thus be interpreted with care in a selective breeding context as this is a phenotypic but not a genetic correlation: selection for BWG may improve FCR, or not, depending on the (unknown) value of the genetic correlation.

4.3. Implications for genetic improvement programs

The genetic gain estimated for FCRg when ranking fish based on a two-week FCR provided a substantial proportion (around 50%) of that estimated using FCRg itself to rank the fish. The estimated genetic gain in FCRg, when selecting fish with two-week FCR values, ranged between 1.0% and 1.2% per generation with a selection intensity of 50%. Since FCR is tedious and expensive to estimate, applying such a low selection intensity would allow a sufficient number of breeders for the next generation to be obtained with the evaluation of a relatively small number of fish, reducing the number of fish to phenotype.

As first FCR measurements (before 250 dph) were the most correlated with FCRg, early measurements between 36 and 70 g (between 152 and 194 dph) would be appropriate. This would save 24–28 weeks of fish maintenance compared to the measurement of FCRg. The benefit of saving in time and money would need to be balanced against the reduced selection gain in comparison with using FCRg directly to rank the fish.

Large phenotypic variability contributes to genetic gain in a breeding program. In the present study, the average CV of FCR (23.7%) is in line with literature estimates for GIFT tilapia, ranging from 22.1%–23.4% (de Verdal et al., 2017, 2018b), and for other species like European sea bass *Dicentrarchus labrax* (21.9%, Besson et al., 2019). The CV of FCR was above average (between 27.5% and 36.2%) during the three periods between 152 and 194 dph, suggesting a potentially higher genetic gain if selection was done at that stage, provided a constant level of heritability.

The present results suggest it could be relevant to record FCR before 250 dph, as it is more variable and better correlated to FCRg than in later periods, thus increasing the likely response to selection. This will need to be confirmed in additional experiments. Further work is also needed to increase the accuracy of the approach, especially regarding heritability estimates at the different periods, which were considered constant and equal to the one estimated on a one-week period by de Verdal et al. (2018b).

The need to obtain individual information to enable selection for FCR led us to use individual rearing in the present experiment. This method has the major advantage to allow recording individual FI every consecutive day for several months. However, in aquaculture, fish are always held in social groups. Studies on several species has suggested group rearing affects FI and FCR, *e.g.* bluegill sunfish (*Lepomis macrochirus*, McComish, 1971); Atlantic salmon (*Salmo salar*, Nicieza and

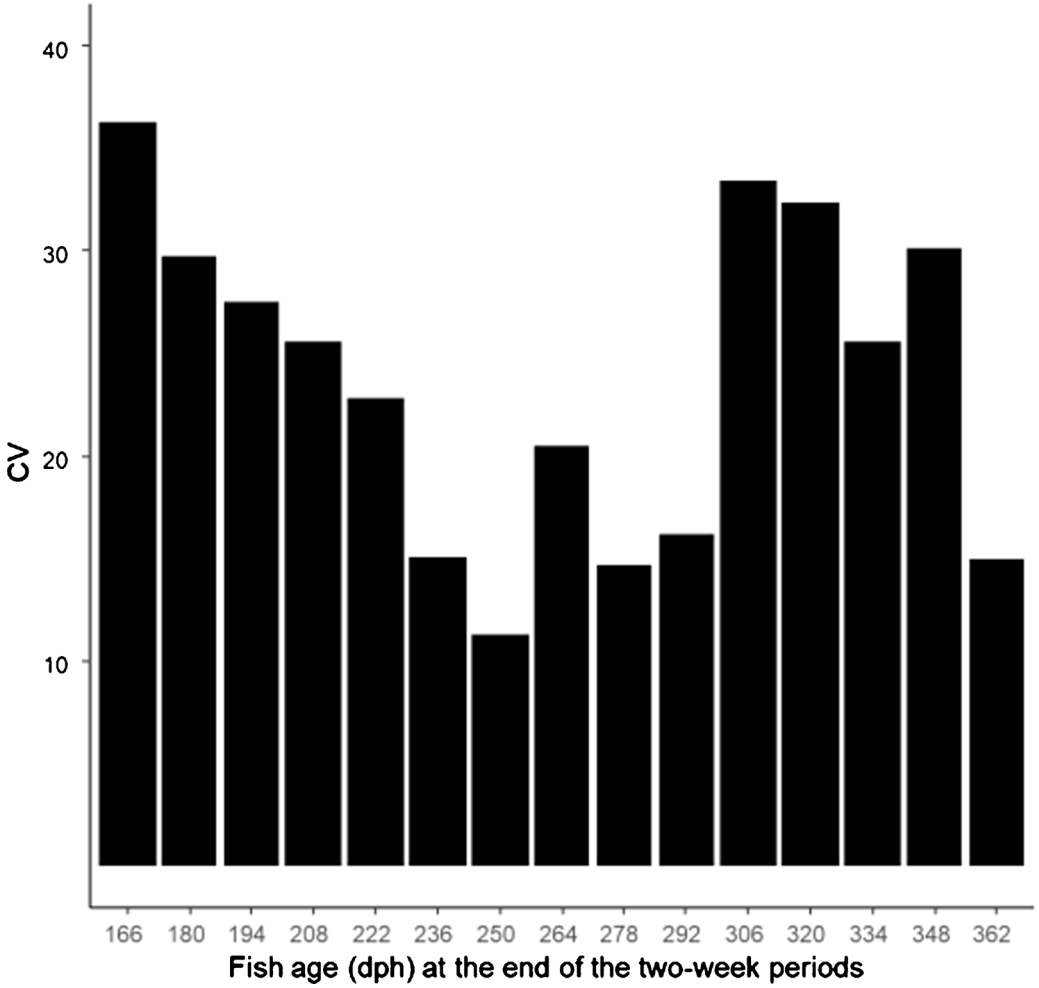

Fig. 3. The coefficients of variation (CV) of individual feed conversion ratio over time.

Metcalfe, 1999) and Nile tilapia (Schreiber et al., 1998). In the case of Nile tilapia, Schreiber et al. (1998) suggested that individual rearing led to better access to feed and to better growth performance. Still, using the same GIFT strain as the present experiment, de Verdal et al. (2019) found that agonistic behaviors were not phenotypically correlated with growth or FCR. Even if group rearing can create competition for feed among fish, individual rearing may induce stress, and thus be even more detrimental to fish performance. Here, fish could not come in contact with fellows and were disturbed every day when the uneaten pellets were removed, and every week to be weighed. Nevertheless, other evidence may suggest little difference between group and individual rearing. In group rearing, phenotypic correlations between BWG and FCR or between BWG and FI were rather similar to the ones observed in the present study (Kolstad et al., 2004; Doupé and Lymbery, 2004; de Verdal et al., 2017).

The impact of individual rearing on fish performance remains debatable and probably dependent on the species, the rearing conditions and the measurement methodology used. To our knowledge, no experiment has compared individual FCRs of the same fish successively reared as a group (but assessed individually) and isolated. Such an experiment would be very relevant for the evaluation of the reliability of assessing individual FCR with an individual rearing design. Some clues were provided by Besson et al. (2019) who have shown that the average individual FCR of European sea bass was partly reflected in subsequent group FCR differences. Beyond biological aspects, Besson et al. (2019) also demonstrated that individual rearing is a method that permits phenotyping several hundreds of juvenile fish in very short periods (two weeks) with a favorable cost-benefit ratio, and is therefore potentially promising for large-scale commercial practice.

5. Conclusion

Our results suggest that the use of FCR estimates of juveniles over short time periods should be adequate to perform selection for FCR until commercial size in male tilapia. Despite fluctuations of FI, BWG and FCR over time, most of the FCR values obtained over two-week periods were positively correlated with FCRg calculated over the whole rearing period. This was especially true for measurements performed at juvenile stage (around 152–194 dph, 36 − 70 g). Under the hypotheses made, potential genetic improvement of FCR of approximately 1% per generation, with 50% selection intensity, could be within reach.

Author statement

CR, BC, MV, JAHB and HV conceptualized the experiment, CR and TQT conducted the experiment; CR, MV and HV analyzed the data and CR wrote the manuscript and all the co-authors worked on the writing and editing process; JAHB, BC and HV acquired the financial support for the experiment and the publication.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

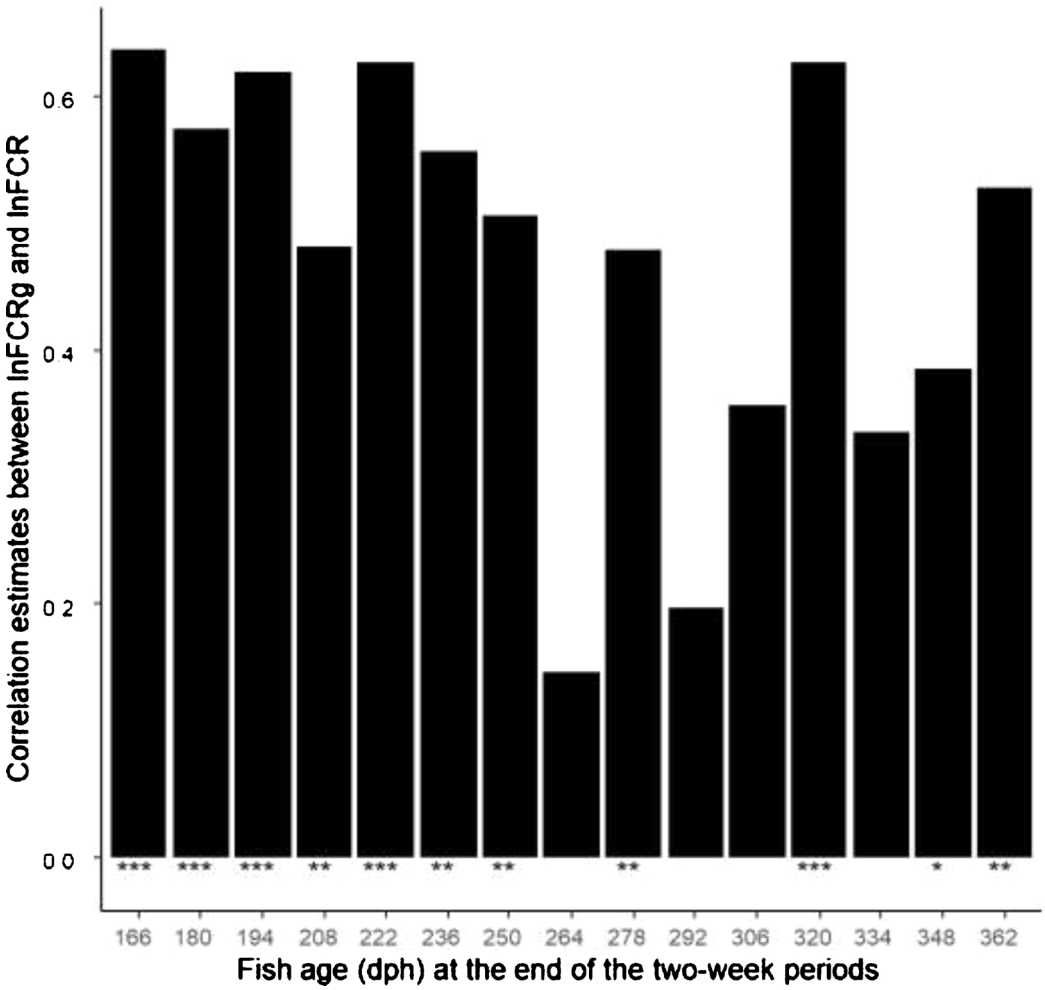

Fig. 4. Correlation estimates between log-transformed feed conversion ratio for the whole rearing period (lnFCRg) and log-transformed feed conversion ratio for each two-week period (lnFCR) with significant correlations indicated as follows (*P < 0.05; **P < 0.01; ***P < 0.001).

Acknowledgments

We thank all the technicians from WorldFish Aquaculture Extension Centre in Jitra for their support, in particular Khairul Rizal Abu-Bakar, Mohd Aznan Bin Aziz, Nor Azam Bin Amhad and Yee Hoong Yip. This publication was made possible through support provided by CIRAD (France) and the CGIAR Research Program on Fish Agrifood Systems (FISH) and the International Fund for Agricultural Development (IFAD).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aqrep.2020.100349.

References

Alanärä, A., Kadri, S., Paspatis, M., 2001. Feeding management. In: Houlihan, D., Boujard, T., Jobling, M. (Eds.), Food Intake in Fish. Blackwell Science Ltd, Oxford, UK, pp. 332–353.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.

Besson, M., Komen, H., Aubin, J., de Boer, I.J., Poelman, M., Quillet, E., Vancoillie, C., Vandeputte, M., van Arendonk, J.A., 2014. Economic values of growth and feed efficiency for fish farming in recirculating aquaculture system with density and nitrogen output limitations: a case study with African catfish (*Clarias gariepinus*). J. Anim. Sci. 92, 5394–5405.

Besson, M., Aubin, J., Komen, H., Poelman, M., Quillet, E., Vandeputte, M., van Arendonk, J.A.M., de Boer, I.J.M., 2016. Environmental impacts of genetic improvement of growth rate and feed conversion ratio in fish farming under rearing density and nitrogen output limitations. J. Clean. Prod. 116, 100–109.

Besson, M., Allal, F., Chatain, B., Vergnet, A., Clota, F., Vandeputte, M., 2019. Combining individual phenotypes of feed intake with genomic data to improve feed efficiency in sea bass. Front. Genet. 10, 219.

Dan, N.C., Little, D.C., 2000. The culture performance of monosex and mixed-sex new-season and overwintered fry in three strains of Nile tilapia *Oreochromis niloticus* in northern Vietnam. Aquaculture 184, 221–231.

de Verdal, H., Mignon-Grasteau, S., Bastianelli, D., Même, N., Le Bihan-Duval, E., Narcy, A., 2013. Reducing the environmental impact of poultry breeding by genetic selection. J. Anim. Sci. 91, 613–622.

de Verdal, H., Mekkawy, W., Lind, C.E., Vandeputte, M., Chatain, B., Benzie, J.A.H., 2017. Measuring individual feed efficiency and its correlations with performance traits in Nile tilapia, *Oreochromis niloticus*. Aquaculture 468, 489–495.

de Verdal, H., Komen, H., Quillet, E., Chatain, B., Allal, F., Benzie, J.A.H., Vandeputte, M., 2018a. Improving feed efficiency in fish using selective breeding: a review. Rev. Aquac. 10, 833–851.

de Verdal, H., Vandeputte, M., Mekkawy, W., Chatain, B., Benzie, J.A.H., 2018b. Quantifying the genetic parameters of feed efficiency in juvenile Nile tilapia *Oreochromis niloticus*. BMC Genet. 19, 105.

de Verdal, H., O'Connell, C.M., Mekkawy, W., Vandeputte, M., Chatain, B., Bégout, M.-L., Benzie, J.A.H., 2019. Agonistic behaviour and feed efficiency in juvenile Nile tilapia *Oreochromis niloticus*. Aquaculture 505, 271–279.

Doupé, R.G., Lymbery, A.J., 2004. Indicators of genetic variation for feed conversion efficiency in black bream. Aquac. Res. 35, 1305–1309.

Falconer, D.S., Mackay, T.F.C., 1996. Selection: I. The response and its prediction. In: Falconer, D.S., Mackay, T.F.C. (Eds.), Introduction to Quantitative Genetics, fourth ed. Longman, Harlow, UK, pp. 184–207.

FAO, 2016. The State of world fisheries and aquaculture 2016. Contributing to Food Security and Nutrition for All. Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO-FIGIS (Fisheries Global Information System), 2019. FAO Fisheries and Aquaculture Department. (accessed 11 January 2019). http://www.fao.org/fishery/statistics/global-aquaculture-production/query/.

Froehlich, H.E., Runge, C.A., Gentry, R.R., Gaines, S.D., Halpern, B.S., 2018. Comparative

terrestrial feed and land use of an aquaculture-dominant world. Proc. Natl. Acad. Sci. 115, 5295–5300.
Galemoni de Graaf, G.J.F., Huisman, E.A., 1999. Reproductive biology of pond reared Nile tilapia, *Oreochromis niloticus* L. Aquac. Res. 30, 25–33.
Giaquinto, P.C., Volpato, G.L., 1997. Chemical communication, aggression, and conspecific recognition in the fish Nile tilapia. Physiol. Behav. 62, 1333–1338.
Gómez-Márquez, J.L., Peña-Mendoza, B., Salgado-Ugarte, I.H., Guzmán-Arroyo, M., 2003. Reproductive aspects of *Oreochromis niloticus*(Perciformes: Cichlidae) at Coatetelco lake, Morelos, Mexico. Rev. Biol. Trop. 51, 221–228.
Green, B.N.W., Veverica, K.L., Fitzpatrick, M.S., 1997. Fry and fingerlings production. In: Egna, H.S., Boyd, C.E. (Eds.), Dynamics of Pond Aquaculture. CRC Press, Boca Raton, Florida, USA, pp. 215–243.
Grima, L., Quillet, E., Boujard, T., Robert-Granié, C., Chatain, B., Mambrini, M., 2008. Genetic variability in residual feed intake in rainbow trout clones and testing of indirect selection criteria. Genet. Sel. Evol. 40, 607–624.
Hafeez-ur-Rehman, M., Ahmed, I., Ashraf, M., Khan, N., Rasool, F., 2008. The culture performance of mono-sex and mixed-sex tilapia in fertilized ponds. Int. J. Agric. Biol. 10, 352–354.
He, J., Zhao, Y., Zhao, J., Gao, J., Han, D., Xu, P., Yang, R., 2017. Multivariate random regression analysis for body weight and main morphological traits in genetically improved farmed tilapia (*Oreochromis niloticus*). Genet. Sel. Evol. 49, 80.
Hussain, M.G., 2004. Farming of Tilapia: Breeding Plans, Mass Seed Production and Aquaculture Techniques. Bangladesh Fisheries Research Institute, Mymensingh, Bangladesh.
Kause, A., Tobin, D., Dobly, A., Houlihan, D., Martin, S., Mäntysaari, E.A., Ritola, O., Ruohonen, K., 2006. Recording strategies and selection potential of feed intake measured using the X-ray method in rainbow trout. Genet. Sel. Evol. 38, 389–409.
Kelly, S.P., Peter, R.E., 2006. Prolactin-releasing peptide, food intake, and hydromineral balance in goldfish. Amer. J. Physiol. Regul. Integr. Comp. Physiol. 291, 1474–1481.
Kolstad, K., Grisdale-Helland, B., Gjerde, B., 2004. Family differences in feed efficiency in Atlantic salmon (*Salmo salar*). Aquaculture 241, 169–177.
Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82, 1–26.
Leal, E., Sánchez, E., Muriach, B., Cerdá-Reverter, J.M., 2009. Sex steroid-induced inhibition of food intake in sea bass (*Dicentrarchus labrax*). J. Comp. Physiol. Biochem. Syst. Environ. Physiol. 179, 77–86.
Lu, C., Laghari, M.Y., Zheng, X., Cao, D., Zhang, X., Kuang, Y., Li, C., Cheng, L., Mahboob, S., Al-Ghanim, K.A., Wang, S., Wang, G., Sun, J., Zhang, Y., Sun, X., 2017. Mapping quantitative trait loci and identifying candidate genes affecting feed conversion ratio based onto two linkage maps in common carp (*Cyprinus carpio* L). Aquaculture 468, 585–596.
Macintosh, D.J., Little, D.C., 1995. Nile tilapia (*oreochromis niloticus*). In: Bromage, N.R., Roberts, R.J. (Eds.), Broodstock Management and Egg and Larval Quality. Blackwell Science Ltd, Oxford, UK, pp. 277–320.
Martins, C.I.M., Conceição, L.E.C., Schrama, J.W., 2011. Feeding behavior and stress response explain individual differences in feed efficiency in juveniles of Nile tilapia *Oreochromis niloticus*. Aquaculture 312, 192–197.
McComish, T.S., 1971. Laboratory Experiments on Growth and Food Conversion by the Bluegill. University of Missouri, Columbia, USA.
Mélard, C., Baras, E., Desprez, D., 1997. Compensatory growth of Nile tilapia *Oreochromis niloticus*. In: Fitzsimmons, K. (Ed.), Proceedings from the Fourth International Symposium on Tilapia in Aquaculture. Northeast Regional Agricultural Engineering Service, Orlando, Florida, USA, pp. 178–185.
Miranda, A., Almeida, O.G., Hubbard, P.C., Barata, E.N., Canário, A.V.M., 2005. Olfactory discrimination of female reproductive status by male tilapia (*Oreochromis mossambicus*). J. Exp. Biol. 208, 2037–2043.
Nicieza, A.G., Metcalfe, N.B., 1999. Costs of rapid growth: the risk of aggression is higher for fast-growing salmon. Funct. Ecol. 13, 793–800.
Nishiguchi, R., Azuma, M., Yokobori, E., Uchiyama, M., Matsuda, K., 2012. Gonadotropin-releasing hormone 2 suppresses food intake in the zebrafish, *Danio rerio*. Front. Endocrinol. (Lausanne) 3, 122.
NRC, 2011. Nutrient Requirements of Fish and Shrimp. Animal Nutrition Series. National Research Council of the National Academies. The National Academies Press, Washington, DC, USA.
Paradis, E., Schliep, K., 2018. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35, 526–528.
Ponzoni, R.W., Ling Khaw, H., Yip Yee, H., 2010. GIFT: The story since leaving ICLARM (Now Known as the WorldFish Center). Socioeconomic, Access and Benefit Sharing and Dissemination Aspects. The WorldFish Center, Penang, Malaysia.
R Core Team, 2018. R: A Language and Environment for Statistical Computing. URL. R foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.
Schreiber, S., Focken, U., Becker, K., 1998. Individually reared female Nile tilapia (*Oreochromis niloticus*) can grow faster than males. J. Appl. Ichthyol. 14, 43–47.
Silverstein, J.T., 2006. Relationships among feed intake, feed efficiency, and growth in juvenile rainbow trout. N. Am. J. Aquac. 68, 168–175.
Stacey, N.E., Sorensen, P.W., 2002. Fish hormonal pheromones. In: In: Pfaff, D.W., Arnold, A.P., Etgen, A.M., Fahrbach, S.E., Rubin, R.T. (Eds.), Hormones, brain, and behaviour: Non-Mammalian Hormone-Behaviour Systems 2. Academic Press, New York, USA, pp. 375–435.
Troell, M., Naylor, R.L., Metian, M., Beveridge, M., Tyedmers, P.H., Folke, C., Arrow, K.J., Barrett, S., Crépin, A.-S., Ehrlich, P.R., Gren, Å., Kautsky, N., Levin, S.A., Nyborg, K., Österblom, H., Polasky, S., Scheffer, M., Walker, B.H., Xepapadeas, T., de Zeeuw, A., 2014. Does aquaculture add resilience to the global food system? Proc. Natl. Acad. Sci. USA. 111, 13257–13263.
Zeileis, A., Leisch, F., Hornik, K., Kleiber, C., 2002. Strucchange: an R package for testing for structural change in linear regression models. J. Stat. Softw. 7, 1–38.