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RESEARCH

Effect of restricted feeding regimes on growth, lipid metabolism and stress related genes in Nile tilapia (*Oreochromis niloticus*, Linnaeus 1758) cultured in a biofloc-aquaponic basil (*Ocimum basilicum*) system

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Abstract

The objective of this study was to evaluate the productive performance and expression levels of growth-related (IGF1, mTOR), lipid metabolism-related (FAS), and oxidative stress-related (hsp70) genes in Nile tilapia (*Oreochromis niloticus*) subjected to different feed restriction regimes in a biofloc-aquaponics system. The experiment included a restriction phase of 84 days with different feeding schedules (Control: daily; T1: 5 days of feeding/2 days of restriction; T2: 3 days of feeding/4 days of restriction; T3: 1 day of feeding/6 days of restriction), followed by a 28-day refeeding period. T1 showed the highest weight gain, and Specific Growth Rate (SGR), indicating complete compensatory growth. More severe restrictions resulted in lower Feed Conversion Ratio (FCR) values. Short-term restrictions did not significantly alter IGF1, mTOR, or hsp70 expression; however, long-term restrictions resulted in a marked downregulation of mTOR and an upregulation of hsp70 in treatments T2 and T3. Notably, FAS expression appeared responsive to moderate restriction. In basil plants (*Ocimum basilicum*), no significant differences were found in biometric variables or total phenolic content among treatments. Overall, the results indicate that moderate feed restriction can be applied in integrated biofloc–aquaponic systems without compromising fish survival or plant performance, while inducing distinct metabolic and physiological responses in Nile tilapia.

Keywords Compensatory growth · Feed restriction · Gene expression · Biofloc-aquaponics · Basil plant · Nile tilapia

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Introduction

In economic terms, one of the major expenses in aquaculture is feeding, which represents more than 60% of total production costs (Zhang et al. 2023). This proportion tends to be particularly high in tilapia culture due to the need for nutritionally balanced formulated diets to sustain rapid growth and stable feed conversion ratios (El-Sayed 2020). In biofloc technology (BFT) systems, feed inputs also serve as the primary source of organic carbon and nitrogen for microbial floc development, which may further increase the economic importance of feeding strategies (Azim and Little 2008; Emerenciano et al. 2017). Consequently, improving feed efficiency is a key objective for enhancing the sustainability and profitability of intensive aquaculture systems.

Feed restriction has been proposed as a management strategy to reduce feed waste and production costs while potentially improving water quality (Aljehani et al. 2025; Favero et al. 2021; Turano et al. 2008). When aquatic organisms undergo periods of feed deprivation, physiological compensatory responses are activated, which often result in hyperphagia once normal feeding resumes. (Debbarma et al. 2019; Gallardo-Collí et al. 2020; Mankiewicz et al. 2022; Xu et al. 2020). This phenomenon, known as compensatory growth, is characterized by an accelerated growth rate following a period of restricted nutrition (Ali et al. 2003; Poot-López et al. 2020).

Several studies have reported positive outcomes from feed restriction, especially in shrimp and tilapia. However, evidence of its effectiveness in production systems using biofloc technology remains scarce (Aboseif et al. 2022; Gallardo-Collí et al. 2020; Maciel et al. 2018; Prates et al. 2023). It is therefore important to evaluate different feeding/restriction regimes in economically important species such as Nile tilapia (*Oreochromis niloticus*) (FAO 2024), particularly within systems that provide a continuous supply of live microbial feed (El-Sayed 2020), which may support more aggressive restriction strategies. Nonetheless, biofloc systems face certain challenges, such as their sensitivity to water quality fluctuations and the requirement for intense aeration to maintain optimal oxygen levels (Khanjani et al. 2024).

The integration of BFT with aquaponic systems offers an additional opportunity to enhance system efficiency and environmental sustainability. In aquaponics, nutrients derived from fish metabolism are reused for plant cultivation, while plants contribute to water quality improvement through nutrient uptake (Goddek et al. 2015; Wong et al. 2020; Yu et al. 2023a, b). Among the most cultivated species in aquaponics is basil (*Ocimum basilicum*), due to its rapid growth, adaptability to hydroponic systems, high market demand, favorable economic value and strong capacity to take up dissolved nutrients from fish effluents, thereby functioning as an efficient biofilter (Polyakova et al. 2015; Sipos et al. 2021). Several studies have shown that basil cultured in aquaponics can help to maintain suitable water quality for warm-water fish species, including Nile tilapia (Espinosa-Moya et al. 2018; Hundley et al. 2018; Hussain and Brown 2025; Selek et al. 2017).

Beyond productive performance, understanding the physiological responses of fish to feed restriction in integrated biofloc–aquaponic systems requires molecular-level evaluation. Insulin-like growth factor 1 (IGF1) is a central regulator of somatic growth and compensatory responses (Debbarma et al. 2019; Elbialy et al. 2022; Nebo et al. 2017), while the mechanistic target of rapamycin (mTOR) functions as a key nutrient-sensing pathway linking dietary inputs to protein synthesis (Ali et al. 2022; Han et al. 2020). Lipid metabolism during restriction and refeeding can be assessed through the expression

of fatty acid synthase (FAS) (Tian et al. 2013; Xu et al. 2022; Zuo et al. 2017), whereas heat shock protein 70 (hsp70) serves as an indicator of cellular stress associated with nutritional or environmental challenges (Shi et al. 2015; Wang et al. 2019). Together, these molecular markers provide insight into the balance between growth, metabolism, and stress under variable feeding regimes.

In this context, the objective of the present study was to evaluate the productive performance and the expression of mTOR, FAS, hsp70, and IGF1 genes in *Nile tilapia* subjected to different feed restriction and refeeding regimes in an aquaponic-biofloc integrated system.

Materials and methods

The experiment was conducted at the Live Feed Laboratory of the Universidad Autónoma Metropolitana, Unidad Xochimilco, Mexico City, Mexico. This facility provides controlled environmental conditions suitable for aquaculture experimentation and specialized infrastructure for aquaponic and biofloc research. Animal care and treatment procedures were carried out in strict accordance with the ethical requirements of the Universidad Autónoma Metropolitana approved by the Ethics Committee of the División de Ciencias Biológicas y de la Salud (Session 70/20).

Experimental design

A completely randomized design was employed, consisting of four feeding treatments applied simultaneously, each with three independent replicates: Control (daily feeding), T1 (5 days feeding followed by 2 days of feed restriction), T2 (3 days feeding followed by 4 days of feed restriction), and T3 (1 day feeding followed by 6 days of feed restriction). Each replicate constituted an independent experimental unit and consisted of a 200-L tank stocked with 20 Nile tilapia fingerlings with an initial mean weight of 2.19 ± 0.2 g, integrated with a hydroponic channel containing 20 basil plants. All experimental units, including the control treatment, were operated under identical integrated aquaponic conditions, and the control group differed from the restricted-feeding treatments only in feeding frequency. All treatments were maintained under the same environmental and management conditions. The experimental trial lasted 112 days and was divided into two consecutive phases: an 84-day feed-restriction phase, during which the feeding regimes were implemented, followed by a 28-day refeeding phase.

Experimental system

The experiment was conducted outdoors using 12 aquaponic units equipped with biofloc technology. Each unit consisted of a 200 L fish tank containing 20 fingerlings Nile tilapia previously acclimatized for a period of two weeks in an 800 L container with clear water, at a temperature of 25 ± 2 °C, pH of 7.5 ± 1. Tanks were connected to hydroponic systems based on the Nutrient Film Technique (NFT), constructed from PVC and with a capacity for 20 basil plants.

Water recirculation was maintained by submersible pumps programmed via a digital timer (GE® Digital Heavy Duty Timer 15,079, China) to operate at 20-min intervals every two hours, ensuring a constant flow of 6 L min^{-1}. Aeration was provided by a ¼ hp

blower to maintain continuous water movement. Water temperature was kept at 25 ± 2 °C using heaters (Thermal PRO 300 W Lomas®, México). The experiment was divided into two phases: (1) a feed restriction phase lasting 84 days, and (2) a refeeding phase lasting 28 days.

Feeding protocols for Nile tilapia

During the restriction phase, four feeding regimes were applied: Control: daily feeding; T1: 5 days feeding/2 days restriction; T2: 3 days feeding/4 days restriction; T3: 1 day feeding/6 days restriction.

In the refeeding phase, all treatments were fed daily. Feeding three times a day (9:00, 13:00 and 17:00 h) using commercial tilapia feed El Pedregal Silver Cup (crude protein 32% min., crude fat 5% min, crude fiber 3.5% max, moisture 14% max, ash 10% max). The feeding rate was adjusted biweekly (from 8 to 2%) according to the average body weight.

Carbon supplementation and C:N ratio adjustment

To maintain the biofloc microbiota, we followed the carbon–nitrogen adjustment procedure described by Emerenciano et al. (2017), targeting a C:N ratio of 15:1. The amount of carbon and nitrogen released into the water were first estimated based on the composition of the commercial feed (32% crude protein, 95% dry matter), assuming that approximately 70% of this nitrogen is excreted into the water as inorganic nitrogenous metabolites available for heterotrophic assimilation. The estimated excreted nitrogen (g N) was then multiplied by 15 to determine the total carbon requirement needed to achieve the desired C:N ratio. This carbon demand was converted into grams of *Egregia* sp. flour by considering its proximate composition (27% carbohydrates and 1.7% protein), where the carbohydrate fraction represented the primary source of organic carbon available for microbial growth. The amount of flour added was recalculated and adjusted every 14 days.

Water quality monitoring

Water samples (100 mL) were collected every 14 days from each tank to assess water quality. Ammonia (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), and pH were measured using a HANNA® multiparameter photometer (HI-83300, USA). Settleable solids were quantified using Imhoff cones (Kartell®, Italy) after 20 min of sedimentation (Emerenciano et al. 2017).

Fish growth performance

Every 14 days all fish were individually weighed using a digital scale (OHAUS® Scout Pro SP402, USA) and their standard length was measured with a digital Vernier (General® UltraTech®, USA). With biometric data, the length and weight gain of Nile tilapia was obtained using the following formulas:

Height and weight gain (Hopkins 1992):

$$G = W_2 - W_1$$

where:

W_2 Final weight (g).
W_1 Initial weight (g).

Specific growth rate (SGR) (Hopkins 1992):

$$\mathrm{SGR} = \frac{\mathrm{LN\ Vbf} - \mathrm{LN\ Vbi}}{\mathrm{T2} - \mathrm{T1}} * 100$$

where:

LN natural logarithm.
Vbf Final value of biometric variable.
Vbi Initial value of biometric variable.
T2 Final time point (days).
T1 Initial time point (days).

Feed Conversion Ratio (FCR) (De Silva and Anderson 1994):

$$\mathrm{FCR} = \frac{\text{Feed given (g)}}{\text{Weight gain (g)}}$$

Germination of basil (O. basilicum)

Seeds were sown in 60×40×2 cm polystyrene trays using peat moss (Rekyva® Remix 0, Lithuania) as substrate, placing one seed per cavity at 0.6 cm depth. Conditions were maintained at 22.0 °C with a 12 h light/12 h dark photoperiod and daily irrigation. Transplantation was carried out after 20 days into net pots within the hydroponic system.

Basil growth parameters

Every 14 days, plant height, stem thickness, and number of leaves were recorded using a digital Vernier. At the end of the trial, wet and dry weights of plants and leaves were determined.

Total Phenolic Content (TPC) determination

Basil leaves were washed with 3% sodium hypochlorite solution, dried at room temperature and micronized. Subsequently, 150 mg of the dried samples were put in 5 mL of 70% ethanol in 14 mL screw-capped tubes, mixed at 20 rpm for 4 h and centrifuged for five minutes at 3000 rpm to extract the supernatant for analysis (Moncayo Luján et al. 2015).

To determine the content of phenolic compounds in the methanolic extract, the Folin–Ciocalteau method was used (Singleton et al. 1999). For which, 300 µL of the sample dilution was taken and mixed with 1680 µl of distilled water and 120 µL of Folin–Ciocalteau reagent, the solution was mixed in a Thermo Scientific® vortex at 2500 rpm for 10 s and allowed to stand for 30 min, 0.9 mL of 7.5% sodium carbonate was added and mixed again at 2500 rpm for 10 s, allowed to stand at room temperature for 30 min and the absorbance was read at 765 nm in a spectrophotometer (Thermo Scientific™, GENESYS 20, USA).

Tissue collection for gene expression

At the end of the experiment period, three fish per treatment were euthanized using an overdose of clove oil. Subsequently, liver and muscle samples were collected and preserved in Invitrogen® brand RNAlater™ solution and stored at −80 °C until RNA extraction (Thermo Scientific™ REVCO™ Elite Plus freezer, USA).

RNA extraction and retrotranscription of cDNA

Total RNA was extracted from liver and muscle tissue using the PureLink™ RNA Mini Kit (Invitrogen, USA), following the manufacturer's instructions. The quantity and purity of RNA were evaluated with an Eppendorf® Biophotometer (6132, USA). Only samples with an RNA Integrity Number between 1.8 and 2.2 were used for the retrotranscription synthesis.

For cDNA synthesis, 1 µg of RNA was used, using the High-Capacity cDNA Reverse Transcription kit (Applied Biosystems, USA), following the manufacturer's instructions. Quantitative PCR (qPCR) was performed using SYBR® Green Supermix (Bio-Rad, USA), in a total volume of 25 µL. The reaction mixture included 10 µL of RT-PCR solution (dilution factor: 32) and 200 nM of each oligonucleotide. It is worth mentioning that the oligonucleotides were designed using Primer3 software version 4.1.0. The *β-act* was used as the

Table 1 Primer sequences used for quantitative real-time PCR (qPCR) analysis in Nile tilapia. Forward (Fw) and reverse (Rv) primer sequences are shown in the 5′–3′ orientation, along with the corresponding GenBank accession numbers

Gen	Sequence (5'- 3')	Accesion no. GenBank
mTOR	Fw: TTGATGCCCCTGATGATGTTCCC Rv: GAATACGAGCGAGGAGGACAGGACAGGG	XM_003449131.5
FAS	Fw: GCTCCACACACACACAAGGCAAAG Rv: AAGGAATAACGCCATGCCCCCA	XM_003454056.5
hsp70	Fw: CAAGATCACCATCACCAACCAACG Rv: TCTTGTCCTCCTCCTCGCCTGATT	XM_003448890.5
IGF1	Fw: TCTGTCTCCTCTCTCTGCCTGTGTGTGT Rv: ACCTCCAATGTAAGCCCTGC	XM_019346352.2
β-act	Fw: GAGCGTGGTGGCTACTCCTTCAC Rv: GCAGGATTCCATACCAAGGA	EF026001.1

The β-actin gene (β-act) was used as the reference gene for normalization of target gene expression

reference gene, and the control treatment as an internal reference. The genes analyzed with their respective sequences are shown in Table 1.

Quantitative gene expression analysis

Determination of expression levels was performed by relative quantification using the ΔΔCT method (Livak and Schmittgen 2001), with an automated cutoff and a moving baseline to determine CT values. The procedure for PCR included: an initial denaturation and polymerase activation for 10 min at 95 °C; 40 cycles of denaturation at 95 °C for 15 s, alignment and extension at 60 °C for 45 s, and a melting curve from 60 °C to 95 °C for 20 min to check for possible dimer effects in the primers.

Statistical analysis

Data were initially evaluated for normality and homoscedasticity to determine the suitability of parametric statistical tests. Normality of residuals was assessed using the Kolmogorov–Smirnov test, and homogeneity of variances among treatments was evaluated using Levene's test. These preliminary analyses were conducted to confirm that the assumptions underlying parametric ANOVA were satisfied. Subsequently, treatment effects were analyzed using one-way ANOVA, followed by Tukey's post hoc test for multiple comparisons when significant differences were detected ($p < 0.05$). All analyses were processed in the Systat 13.0 software.

Results

Water quality parameters

Water quality remained within optimal ranges across all treatments throughout the experiment. Temperature was stable at 25 ± 2 °C, and pH mean ranged from 7.6 to 7.31.

Table 2 Water quality parameters measured in the integrated biofloc–aquaponic system under different feeding regimes (Control, T1, T2, and T3). Values are expressed as mean ± SD

	Control	T1	T2	T3
NH_3 (mg L^{-1})	0.45 ± 0.3	0.38 ± 0.34	0.54 ± 0.23	0.52 ± 0.24
NO_2^- (mg L^{-1})	2.18 ± 1.48	2.50 ± 0.92	2.05 ± 0.71	2.26 ± 1.28
NO_3^- (mg L^{-1})	61.25 ± 40.28	63.54 ± 43.74	60 ± 43.54	81.04 ± 64.28
EC (µS cm^{-1})	1032.20 ± 179.33	1040 ± 59.04	929.07 ± 97.98	842.93 ± 52.11
pH	7.06 ± 0.56	7.13 ± 0.52	7.19 ± 0.59	7.31 ± 0.53
Settleable Solids (ml L^{-1})	19.63 ± 8.85	22.13 ± 9.12	17.54 ± 8.06	15.63 ± 8.12

Parameters include total ammonia nitrogen (NH_3), nitrite (NO_2^-), nitrate (NO_3^-), electrical conductivity (EC), pH, and settleable solids. No significant differences were observed among treatments ($P > 0.05$)

Ammonia and nitrite levels stayed below critical thresholds (< 1.10 mg L^{-1} and < 5 mg L^{-1}, respectively). As for nitrates, the treatment that obtained the highest concentration was T3 with 160 ppm, while for electrical conductivity the highest value was recorded in the control group with 1476 µS/cm, followed by T1 with 1354 µS/cm, T2 with 1154 µS/cm and T3 with 956 µS/cm. Sedimentable solids remained within the operational range expected for BFT systems across all treatments, with mean values of 19.63 ± 8.85, 22.13 ± 9.12, 17.54 ± 8.06 and 15.63 ± 8.12 ml L^{-1}, for the Control, T1, T2 and T3 groups, respectively. Although numerical differences were observed, the one-way ANOVA revealed no significant differences among treatments ($P > 0.05$) (Table 2).

Growth performance and survival of Nile tilapia

All the experimental groups exhibited high survival rates. Fish in the control group showed 93% survival, while fish in the T1 treatment reached 90%. The T2 and T3 treatments achieved 100% survival. Length–weight relationships were evaluated assuming the model $W = aL^b$ (Froese 2006). The growth was considered approximately isometric, since the estimated allometric coefficient b ranged from 2.97 to 3.16 among treatments. The treatment that reached the highest weight at the end of the experiment was T1 with 66.05 ± 1.70 g, followed by the control group and T3. On the other hand, treatment T3 exhibited the lowest weight, with 21.31 ± 1.02 g. The weight growth curves are shown in Fig. 1. Regarding weight gain, the treatment with the highest gain was T1, with an average gain of 64.02 g, followed by the control group and T2. The lowest gain was recorded by treatment T3 with 18.91 g. Regarding FCR, the lowest value during the restriction period was 0.75, obtained in T3. On the other hand, the lowest FCR value at the end of the refeeding period corresponded to T2, with 1.03. In relation to final

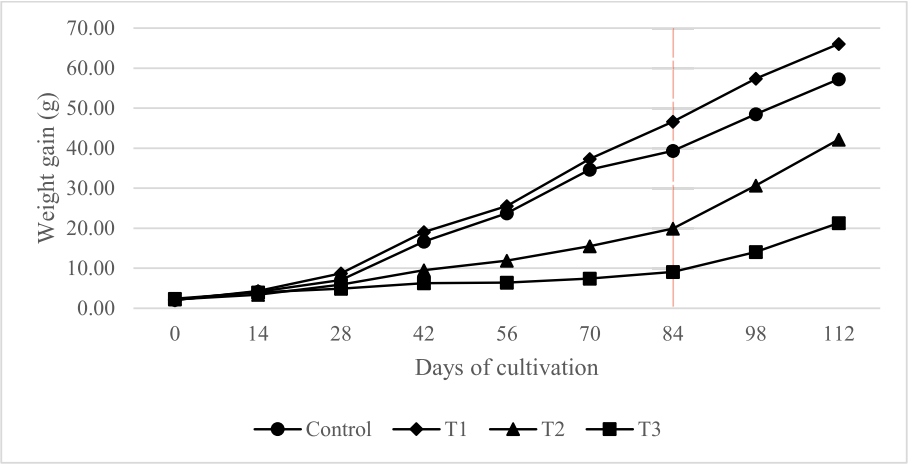


Fig. 1 Weight growth curves of Nile tilapia subjected to different feeding restriction regimes under integrated biofloc–aquaponic conditions. The dashed vertical line indicates the end of the restriction period and the beginning of the refeeding phase. Fish under the moderate restriction regime (T1: 5 days feeding/2 days fasting) exhibited full compensatory growth, reaching higher final weights than the control group. In contrast, more severe restriction schedules (T2: 3 days feeding/4 days fasting; T3: 1 day feeding/6 days fasting) resulted in partial compensatory growth

Table 3 Growth performance and feed utilization parameters of Nile tilapia subjected to different feeding restriction regimes (Control, T1, T2, and T3) under integrated biofloc–aquaponic conditions

Variable	Control	T1	T2	T3
Initial weight (g)	2.13 ± 0.10^{a}	2.04 ± 0.17^{a}	2.21 ± 0.13^{a}	2.40 ± 0.17^{a}
Final weight (g)	57.24 ± 1.57^{a}	66.05 ± 1.70^{b}	42.17 ± 1.20^{c}	21.31 ± 1.02^{d}
Weight gain (g)	55.11 ± 1.60^{a}	64.02 ± 1.69^{b}	39.96 ± 1.22^{c}	18.91 ± 1.02^{d}
SGR (% day^{-1})	3.57 ± 0.03^{a}	3.70 ± 0.02^{b}	3.27 ± 0.03^{c}	2.58 ± 0.05^{d}
FCR Restriction	1.38 ± 0.01^{a}	1.06 ± 0.01^{b}	1.06 ± 0.01^{c}	0.74 ± 0.01^{d}
FCR Refeeding	1.44 ± 0.01^{a}	1.29 ± 0.01^{b}	1.03 ± 0.01^{c}	1.14 ± 0.01^{d}
FCR Total	1.40 ± 0.01^{a}	1.13 ± 0.01^{b}	1.04 ± 0.01^{c}	1.00 ± 0.01^{d}

Values are expressed as mean ± SD. Different superscript letters within the same row indicate statistically significant differences among treatments ($P < 0.05$). Parameters include initial weight, final weight, weight gain, specific growth rate (SGR), feed conversion ratio during the restriction period (FCR Restriction), during the refeeding period (FCR Refeeding), and over the entire experimental period (FCR Total)

Table 4 Length-based growth performance of Nile tilapia subjected to different feeding restriction regimes (Control, T1, T2, and T3) under integrated biofloc–aquaponic conditions

	Control	T1	T2	T3
Initial length (cm)	4.55 ± 0.16^{a}	4.21 ± 0.20^{a}	4.27 ± 0.21^{a}	4.26 ± 0.21^{a}
Final length (cm)	12.90 ± 0.86^{a}	13.61 ± 0.81^{b}	11.00 ± 0.96^{c}	8.60 ± 0.80^{d}
Gain (cm)	8.35 ± 0.9^{a}	9.4 ± 0.86^{b}	6.74 ± 0.9^{c}	4.34 ± 0.93^{d}
SGR (% day^{-1})	2.45 ± 0.13^{a}	2.51 ± 0.1^{b}	2.27 ± 0.16^{c}	1.99 ± 0.33^{d}

Values are expressed as mean ± SD. Different superscript letters within the same row indicate statistically significant differences among treatments ($P < 0.05$). Parameters include initial length, final length, length gain, and specific growth rate (SGR)

weight, weight gain and FCR all treatments showed significant differences ($P < 0.05$) (Table 3).

The treatment that obtained the greatest length at the end of the experiment was T1 with 13.61 ± 0.81 cm, followed by the control group and T2, while T3 obtained the lowest length with 8.60 ± 0.80 cm. Table 4 shows the values of initial length, final length, length gain and Specific Growth Rate (SGR) of fish length. The treatment with the highest average length gain was T1, with 9.4 cm, while the treatment with the lowest length gain and the lowest SGR was T3. In relation to final length, length gain and SGR, there was significant differences among all treatments ($P < 0.05$).

Relative gene expression

At the end of the restriction phase, the highest IGF1 expression was observed in T1. However, all treatments showed an increase in IGF1 expression following the refeeding period, suggesting a common post-restriction upregulation. No significant differences were found between treatments at the end of refeeding ($P > 0.05$), although the trend was more pronounced in T1 (Fig. 2).

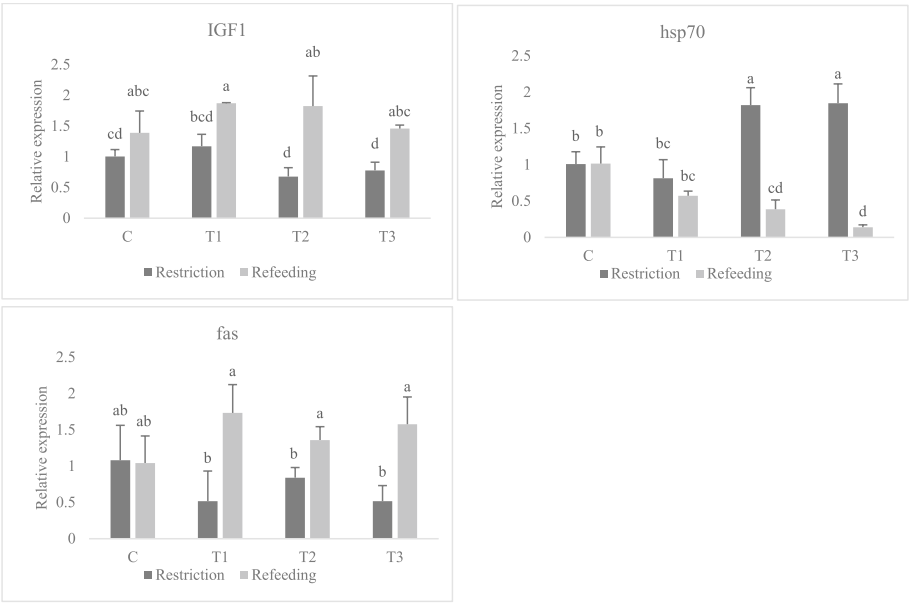


Fig. 2 Effect of restriction and refeeding treatments on the hepatic gene expression of IGF1, hsp70 and FAS of Nile tilapia at different times. Data are expressed as averages ± SD. Different letters indicate differences between treatments at different times ($P < 0.05$)

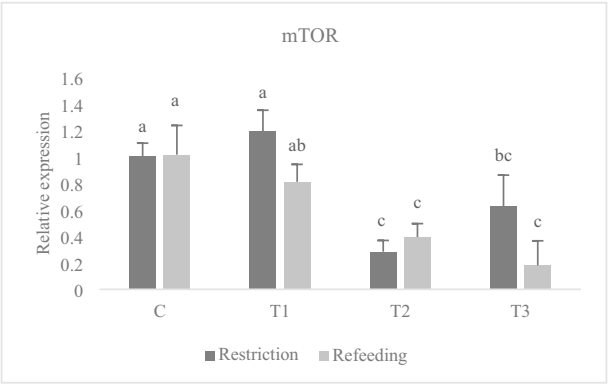


Fig. 3 Effect of restriction and refeeding treatments on the gene expression of mTOR in muscle, of Nile tilapia at different times. Data are expressed as averages ± SD. Different letters indicate differences between treatments at different times ($P < 0.05$)

In the case of FAS, expression levels increased significantly in all treatments after refeeding, indicating a consistent metabolic response to nutritional recovery. However, differences between treatments and the control were not statistically significant ($P > 0.05$). Expression of hsp70 remained unchanged in T1 and the control group throughout both phases ($P > 0.05$). In contrast, T2 and T3 exhibited significant upregulation of hsp70 during the restriction period ($P < 0.05$), followed by a marked decrease

after refeeding, suggesting stress recovery dynamics in those groups. Regarding mTOR, no significant differences were observed between T1 and the control group at any stage ($P > 0.05$). However, expression levels in T2 and T3 decreased after the restriction phase and remained low after refeeding, indicating a possible suppression of anabolic signaling under more severe restriction regimes (Fig. 3).

Basil growth and phenolic content

No significant differences were detected among treatments in any of the evaluated plant growth parameters ($P > 0.05$). Nevertheless, some trends were observed. The highest stem length gain was recorded in the control group, followed closely by T1 and T3, while T2 showed the lowest value. Although not statistically significant, T1 plants developed the highest average number of leaves per plant, slightly surpassing T3. Similarly, T1 recorded the highest average dry weight of leaves, while T2 had the lowest. As for total phenolic content (TPC), values ranged from 15.48 to 16.18 mg GAE g. The highest TPC was observed in T3, while the control group had the lowest value. Despite these variations, no significant differences were found in TPC among treatments ($P > 0.05$) (Table 5).

Discussion

Water quality and integration of biofloc-aquaponic systems

Maintaining adequate water quality is essential for the success of recirculating aquaculture systems, especially those based on biofloc technology (BFT), where water exchange is minimal and nitrogen accumulation can be a limiting factor (Lindholm - Lehto 2023). In this study, parameters such as pH, ammonia, and nitrite remained within suitable ranges for Nile tilapia culture (Abd El-Hack et al. 2022). Previous reports have shown that BFT supports the rapid assimilation of ammonia and nitrite by bioflocs, leading to improved water

Table 5 Growth, biomass production, and phytochemical characteristics of basil cultivated in an integrated biofloc–aquaponic system under different fish feeding regimes (Control, T1, T2, and T3)

	Control	T1	T2	T3
Initial length (cm)	8.35 ± 2.83	10.97 ± 1.95	9.58 ± 3.52	9.45 ± 3.38
Final length (cm)	40.88 ± 11.22	42.09 ± 10.28	38.54 ± 11.43	39.94 ± 12.72
Gain (cm)	32.35 ± 12.24	31.11 ± 10.94	28.96 ± 11.5	30.49 ± 12.46
SGR (% day^{-1})	3.61 ± 0.38	3.63 ± 0.33	3.54 ± 0.39	3.58 ± 0.41
Number of leaves	51.28 ± 21.42	57.83 ± 22.92	51.17 ± 24.68	59.28 ± 23.01
Wet weight leaves (g)	12.3 ± 3.95	13.31 ± 4.2	10.26 ± 3.75	12.91 ± 5.03
Dry weight leaves (g)	1.5 ± 0.76	1.95 ± 0.64	1.24 ± 0.31	1.88 ± 1.03
Leaf area (cm^2)	487.27 ± 37.91	504.44 ± 21.81	522.83 ± 39.68	544.58 ± 38.22
TPC (mg GAE g)	15.49 ± 0.07	16.04 ± 0.46	15.63 ± 0.33	16.18 ± 0.50

Values are expressed as mean ± SD. Evaluated parameters include plant length (initial, final, and gain), specific growth rate (SGR), number of leaves, wet and dry leaf biomass, leaf area, and total phenolic content (TPC). No significant differences were observed among treatments ($P > 0.05$)

stability (Khanjani and Sharifinia 2020). This recycling of nitrogen compounds is generally associated with the activity of heterotrophic bacteria (Ramasubburayan et al. 2024).

The lack of significant differences among treatments indicates that feed restriction did not markedly influence floc accumulation under the conditions of this study. Comparable levels of sedimentable solids have been reported as operationally acceptable in tilapia BFT systems, where ranges between 5–20 ml L^{-1} are considered suitable for maintaining water quality and microbial activity (Collazos-Lasso et al. 2022; Emerenciano et al. 2017). The stability of solids across treatments suggests that the biofloc community was able to adjust to fluctuations in feed input, a response previously described in BFT systems due to the high resiliency and rapid turnover of heterotrophic microbial aggregates (Avnimelech 2015).

The integration of aquaponics with BFT not only mitigated potential water quality issues but also allowed the reuse of nitrate-rich water for plant cultivation. The high nitrate levels, were efficiently absorbed by the basil plants, supporting the dual role of plants as nutrient sinks and biofilters (Deswati et al. 2020; Pinho et al. 2021; Souri et al. 2009; Yu et al. 2023a, b). Electrical conductivity values observed in this study (956–1476 µS/cm) were higher than typical aquaponic systems (300–600 µS/cm) (Rakocy 2012), but well within the recommended range for basil grown hydroponically (1000–1600 µS/cm) (Sharma et al. 2018). This suggests that the system achieved a favorable electrical conductivity suitable for both fish and plant components (Bhatnagar and Devi 2013; Pinho et al. 2021; Rakocy 2012; Sharma et al. 2018; Ujjania et al. 2021).

Growth performance and compensatory response in Nile tilapia

Moderate feed restriction (T1: 5 days feeding/2 days fasting) resulted in full compensatory growth in Nile tilapia, with fish achieving even higher final weights than those in the control group. This finding supports previous studies in hybrid tilapia and other species where short-term or moderate restriction stimulated growth recovery mechanisms without compromising performance (Abdel-Hakim et al. 2009; Chareo-Benítez et al. 2023; Oliveira et al. 2023; Wang et al. 2025).

In contrast, more severe restriction schedules (T2 and T3) led to only partial compensation, with significantly lower final weights and growth rates. This pattern aligns with reports by Braz et al. (2022), who found that compensatory growth occurs in tilapia subjected to short fasting periods, while prolonged restriction reduces growth, feed conversion, and survival. It should be noted, however, that the study of Braz et al. was conducted in a water recirculation system at low temperatures and not under biofloc technology conditions. Similar patterns of partial compensation under severe restriction have been documented in juvenile Nile tilapia cultured in biofloc systems (Oliveira et al. 2023).

Notably, all treatments exhibited high survival rates, even under the most severe restriction (T3), which achieved 100% survival. This suggests that the biofloc provided a nutritional and functional buffer that mitigated fasting stress (Adineh et al. 2019; Azim and Little 2008; Emerenciano et al. 2017; Liu et al. 2018; Wasielesky et al. 2013). The continuous presence of flocs may support not only compensatory growth but also overall physiological stability.

The superior performance of T1 in both growth and survival indicates that moderate restriction can stimulate efficient nutrient use, supported by the endogenous capacity for compensation. However, in more aggressive restriction schedules, although survival remained high, the reduction in growth highlights a trade-off between feed savings and performance.

Feed conversion efficiency and survival

Feed conversion ratio (FCR) is a key indicator of production efficiency and cost-effectiveness in aquaculture systems. In this study, fish under the most restrictive feeding schedule (T3) achieved the lowest FCR during the restriction phase, while T2 recorded the best FCR after refeeding. These results suggest that more severe restriction can enhance feed efficiency, likely due to increased metabolic efficiency and the compensatory use of biofloc-derived nutrients.

The improved FCR observed in restricted treatments may be attributed to the ingestion of microbial aggregates, which are known to be rich in essential amino acids, fatty acids, vitamins, and trace elements (Avnimelech 2007; Azim and Little 2008; Emerenciano et al. 2017; Liu et al. 2018; Najdegerami et al. 2016; Ramasubburayan et al. 2024). Similar trends were reported by Islam et al. (2021), who found improved FCR in restricted-feeding treatments of monosex tilapia, accompanied by lower feed costs. Elnady et al. (2023) also documented improvements in feed performance metrics of Nile tilapia under restricted feeding regimes in biofloc culture during the fattening stage.

Expression of growth, lipid metabolism, and stress-related genes

IGF1 expression increased in all treatments after refeeding, particularly in T1, indicating activation of anabolic pathways associated with compensatory growth. Similar post-refeeding responses have been documented in Nile tilapia (Elbialy et al. 2022; Nebo et al. 2017), *Oncorhynchus mykiss* (Montserrat et al. 2007), *Sparus aurata* (Lavajoo et al. 2020), and *Sebastes* spp. (Hack et al. 2018, 2019), However, unlike the results of the present work, these studies also reported a significant decrease in igf1 levels after the different restriction periods. Some other studies in Oreochromis mossambicus (Breves et al. 2014), Salmo salar (Breves et al. 2016), and Scorpaenichthys marmoratus (Strobel et al. 2020), also did not show a decrease in igf1 after starvation which is in agreement with our results, these differences in igf1 expression may be attributable to variation in restriction times, taxonomic variation, dietary nutrients but also culture conditions (Ndandala et al. 2022; Strobel et al. 2020). In the case of this research, the constant presence of food allowed by biofloc technology could have influenced that igf1 expression levels did not decrease drastically after the fasting period. On the other hand, the increase in igf1 expression at the end of refeeding coupled with the increase in growth curves after the restriction period suggest an important role of igf1 in promoting compensatory growth as it appears to be mainly regulated by feeding and refeeding and probably has differential effects in promoting muscle growth during recovery from starvation (Elbialy et al. 2022; Ndandala et al. 2022; Won and Borski 2013).

Regarding mTOR, a central kinase in cellular growth and metabolism, expression levels were higher in T1 and the control group, while significantly lower values were recorded in T2 and T3, especially after restriction. This pattern indicates that mTOR activation is sensitive to restriction duration, with short-term fasting maintaining anabolic signaling, and prolonged deprivation resulting in suppression (Bu et al. 2021; Perez et al. 2022). The persistent inhibition of mTOR in T2 and T3 even after refeeding seems to indicate that in short periods of fasting it is feasible for cells to maintain muscle mass and increase mtor expression to activate anabolic processes, on the contrary, in more severe periods of fasting, mtor expression is inhibited and this inhibition is maintained after refeeding, this inhibition is generally found to be related to increased lipid catabolism and autophagy (Johnson et al. 2013; Kennedy and Lamming 2016; Paula et al. 2017).

About fas expression, in the present study there was lower expression in the treatments subjected to restriction, which subsequently significantly increased its expression at the end of refeeding, which is in agreement with several studies in *O. niloticus* (Tian et al. 2013), *Onychostoma macrolepis* (Gou et al. 2023), *Ctenopharyngodon idellus* (Gong et al. 2017), *Lateolabrax maculatus* (Huang et al. 2018), *Synechogobius hasta* (Cui et al. 2024), which reported a decrease in fas expression in liver after a period of dietary restriction. However, Tian et al. (2013) and Gou et al. (2023) reported an increase in fas expression triggered by refeeding organisms undergoing restriction. This trend suggests a mechanism to conserve energy by reducing fat synthesis de novo when food is in short supply (Huang et al. 2018), whereas, during refeeding, fas expression was likely up-regulated to maintain metabolic homeostasis, and to facilitate lipid re-accumulation after a period of energy deficit (Gou et al. 2023).

Finally, in this study, dietary stress was reflected in T2 and T3 treatments as they showed a significant increase in hsp70 expression in the restriction period followed by a significant decrease in hsp70 at the end of refeeding, similar results were reported by Sakyi et al. (2020), who induced fasting in *O. niloticus* organisms and observed a linear increase in hsp70 expression in the liver of fasting organisms. However, these hsp70 expression levels gradually decreased with refeeding after 21 days. Likewise, Dar et al. (2019), reported a significant increase in hsp70 expression in the liver and gills of *Labeo rohita* after seven days of restriction that gradually decreased after 15 days of refeeding. On the other hand, Wang et al. (2019), found no differences in hsp70 expression in the liver of organisms subjected to one, two and three days of restriction per week, mentioning that possibly the degree of food restriction was not severe enough to induce the heat shock response in that tissue. This indicates that stress response mechanisms were only triggered under prolonged restriction, while moderate fasting (T1) did not elicit significant cellular stress (Balakrishnan et al. 2025; Hu et al. 2019; Lu et al. 2024; Nie et al. 2018).

Collectively, these gene expression patterns reflect the degree of physiological stress and metabolic adaptation under each feeding regime. Moderate restriction (T1) maintained anabolic activity with minimal stress, while prolonged fasting (T2 and T3) induced cellular protection pathways and delayed metabolic recovery.

Basil growth and phenolic content under aquaponic conditions

Although no statistically significant differences were observed among treatments ($P > 0.05$), the basil plants cultivated in the integrated biofloc-aquaponic system showed favorable biometric values and secondary metabolite content. The stem elongation, leaf number, and dry leaf biomass observed in the present study were comparable to or exceeded those reported for soil-based basil production. Colorado et al. (2013) documented an average plant height of 37.5 cm after 60 days in soil, while Yepez-Hernandez et al. (2016) and Ronzón-Ortega et al. (2012) reported lower leaf counts than the recorded in this study. Although higher values have been documented in some aquaponic systems—such as those by Pasch et al. (2021), who reported up to 120 leaves per plant with African catfish effluent—those systems involved higher electrical conductivity and possibly supplemental fertilization. In the current study, plant growth was achieved without added fertilizers, suggesting that nutrient availability derived from the biofloc-aquaponic system was sufficient to support healthy development (Pinho et al. 2021; Yu et al. 2023a, b).

Regarding total phenolic compounds (TPC), values ranged from 15.48 to 16.18 mg GAE g^{-1}, which are consistent with those reported by Nguyen et al. (2021) and Kwee and Niemeyer (2011) for basil grown in controlled systems, and notably higher than the values obtained in conventional hydroponic systems without biofloc support (e.g., 1.57–7.60 mg

GAE g^{-1}, Aghamirzaei et al. (2024)). This suggests that the combination of aquaponic cultivation and biofloc-derived nutrients may enhance the synthesis of antioxidant compounds, even under varying feed regimes for the fish component.

The absence of significant differences among treatments indicates that changes in feeding frequency did not negatively affect plant performance. This reinforces the potential of biofloc-aquaponic systems to maintain stable plant productivity even under fish feeding restrictions, which could reduce feed costs without compromising vegetable yield or quality (Pinho et al. 2021).

Implications and perspectives for integrated aquaculture systems

The results of this study highlight the feasibility of combining feed restriction strategies with integrated biofloc-aquaponic systems without compromising fish survival, plant productivity, or water quality. The high survival rates observed under severe feed restriction indicate the capacity of bioflocs to function as a continuous source of nutritional and immunological support, thereby mitigating physiological stress (Khanjani and Sharifinia 2020; Ramasubburayan et al. 2024).

Moreover, the differential gene expression patterns indicate that moderate restriction (T1) supports growth and metabolic homeostasis, while more severe protocols (T2, T3) trigger adaptive responses such as suppression of anabolic signaling and upregulation of stress-related genes. These findings offer insights into the physiological thresholds of tilapia in constrained feeding environments and underscore the importance of balancing restriction intensity with system support capacity.

On the plant side, stable biometric and phytochemical performance across treatments reinforces the robustness of basil as a horticultural component in aquaponic modules, even when nutrient input from fish is reduced. This contributes to the year-round viability of integrated systems, especially in resource-limited settings.

From a practical standpoint, the results of this study suggest that moderate feed restriction can be safely implemented in integrated biofloc–aquaponic systems as a cost-reduction strategy without compromising fish growth, survival, water quality, or plant productivity. A moderated feed restriction proved to be the most balanced strategy, promoting full compensatory growth, stable anabolic signaling, and minimal physiological stress. More severe restriction schedules, although improving feed conversion efficiency, resulted in reduced growth performance and activation of stress-related pathways, indicating a trade-off that may not be desirable for commercial production.

Therefore, for producers operating biofloc–aquaponic systems, moderate restriction protocols are recommended, particularly in contexts where biofloc availability and plant integration can buffer nutritional deficits. These findings provide a practical guideline for optimizing feed management while enhancing sustainability and reducing operational costs under controlled intensive production conditions.

Conclusions

Moderate feed restriction in Nile tilapia cultured under integrated biofloc–aquaponic conditions resulted in complete compensatory growth, whereas prolonged restriction led to partial compensation accompanied by improved feed conversion efficiency. High survival

rates across all treatments indicate that biofloc-based systems can maintain adequate physiological support under reduced feeding input. Gene expression analyses revealed that moderate did not significantly alter IGF1, mTOR, or hsp70 expression; however, long-term restrictions resulted in a marked downregulation of mTOR and an upregulation of hsp70. Notably, FAS expression appeared responsive to moderate restriction. Basil growth and phenolic content were not adversely affected by fish feeding regimes, demonstrating stable plant performance within the integrated system. Therefore, moderate feed restriction represents a balanced and practical option for producers seeking to optimize feed efficiency and sustainability under intensive biofloc–aquaponic conditions. Collectively, these findings indicate that controlled feed-restriction strategies can be implemented in integrated biofloc–aquaponic systems to improve feed efficiency without compromising fish survival or plant productivity, within the experimental conditions evaluated in this study.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Arnulfo Misael Martinez-Meingüer, Jorge Castro-Mejía, José María del Carmen Monroy-Dosta, Carlos Iván Pérez-Rostro, Antonio Mata-Sotres, Germán Castro-Mejía, Andrés Elías Castro-Castellón. The first draft of the manuscript was written by Arnulfo Misael Martinez-Meingüer and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The data are contained in the article and are also recorded in the logbook of the Laboratorio de Alimento Vivo of Universidad Autónoma Metropolitana Xochimilco and may be made available upon request.

Declarations

Disclosure The only ones responsible for the content and writing of the article are the authors.

Ethics Statement Animal care and treatment procedures were carried out in strict accordance with the ethical requirements of the División de Ciencias Biológicas y de la Salud of the Universidad Autónoma Metropolitana (Session 70/20).

Competing interests The authors declare no competing interests.

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References

Abd El-Hack ME, El-Saadony MT, Nader MM, Salem HM, El-Tahan AM, Soliman SM, Khafaga AF (2022) Effect of environmental factors on growth performance of Nile tilapia (*Oreochromis niloticus*). Int J Biometeorol 66:2183–2194. https://doi.org/10.1007/s00484-022-02347-6

Abdel-Hakim NF, State HAA, Al-Azab AA, El-Kholy KF (2009) Effect of feeding regimes on growth performance of juvenile hybrid tilapia (*Oreochromis niloticus* × *Oreochromis aureus*). World J Agric Sci 5:49–54

Aboseif AM, Flefil NS, Taha NK, Tahoun UM, Abdel HR, El-Hammady AK (2022) Feed restriction and compensatory growth of the Nile tilapia, *Oreochromis niloticus* under Biofloc system condition. Egypt J Aquat Biol Fish 26:1171–1191. https://doi.org/10.21608/ejabf.2022.256394

Adineh H, Naderi M, Hamidi MK, Harsij M (2019) Biofloc technology improves growth, innate immune responses, oxidative status, and resistance to acute stress in common carp (*Cyprinus carpio*) under high stocking density. Fish Shellfish Immunol 95:440–448. https://doi.org/10.1016/j.fsi.2019.10.057

Aghamirzaei H, Mumivand H, Nia AE, Raji MR, Maroyi A, Maggi F (2024) Effects of micronutrients on the growth and phytochemical composition of basil (*Ocimum basilicum* L.) in the field and greenhouse (hydroponics and soil culture). Plants 13:2498. https://doi.org/10.3390/plants13172498

Ali A, Shaalan WM, Al-Tobasei R, Salem M (2022) Coding and noncoding genes involved in atrophy and compensatory muscle growth in Nile Tilapia. Cells 11(16):2504. https://doi.org/10.3390/cells11162504

Ali M, Nicieza A, Wootton JR (2003) Compensatory growth in fishes: a response to growth depression. Fish Fish 4:147–190. https://doi.org/10.1046/j.1467-2979.2003.00120.x

Aljehani F, N'Doye I, Laleg-Kirati TM (2025) Feeding control and water quality monitoring in aquaculture systems: opportunities and challenges. Aquac Eng 109:102511. https://doi.org/10.1016/j.aquaeng.2024.102511

Avnimelech Y (2007) Feeding with microbial flocs by tilapia in minimal discharge bio-flocs technology ponds. Aquaculture 264:140–147. https://doi.org/10.1016/j.aquaculture.2006.11.025

Avnimelech Y (2015) Biofloc Technology-a Practical Guide Book, 3rd edn. The World Aquaculture Society, Baton Rouge

Azim ME, Little DC (2008) The biofloc technology (BFT) in indoor tanks: water quality, biofloc composition, and growth and welfare of Nile tilapia (*Oreochromis niloticus*). Aquaculture 283:29–35. https://doi.org/10.1016/j.aquaculture.2008.06.036

Balakrishnan S, Sajeevan AKM, PS A, Singh IS, Puthumana J (2025) A laboratory-scale recirculating aquaculture system for long-term experimental rearing of bivalves under minimal stress conditions for aquatic animal research. Aquac Int 33:1–12. https://doi.org/10.1007/s10499-025-01941-w

Bhatnagar A, Devi P (2013) Water quality guidelines for the management of pond fish culture. Int J Environ Sci 3:1980–2009. https://doi.org/10.6088/ijes.2013030600019

Braz JM, Marques AG, Honorato CA, De Almeida FLA, Neu DH (2022) Compensatory growth of Nile tilapia fingerlings subjected to food restriction and re-feeding at low temperatures. Rev Ciênc Agroveterin 21:481–488. https://doi.org/10.5965/223811712142022481

Breves JP, Phipps-Costin SK, Fujimoto CK, Einarsdottir IE, Regish AM, Björnsson BT, McCormick SD (2016) Hepatic insulin-like growth-factor binding protein (igfbp) responses to food restriction in Atlantic salmon smolts. Gen Comp Endocrinol 233:79–87. https://doi.org/10.1016/j.ygcen.2016.05.015

Breves JP, Tipsmark CK, Stough BA, Seale AP, Flack BR, Moorman BP, Lerner DT, Grau EG (2014) Nutritional status and growth hormone regulate insulin-like growth factor binding protein (*igfbp*) transcripts in Mozambique tilapia. Gen Comp Endocrinol 207:66–73. https://doi.org/10.1016/j.ygcen.2014.04.034

Bu T, Xu L, Zhu X, Cheng J, Li Y, Liu L, Chu W (2021) Influence of short-term fasting on oxidative stress, antioxidant-related signaling molecules and autophagy in the intestine of adult *Siniperca chuatsi*. Aquac Rep 21:100933. https://doi.org/10.1016/j.aqrep.2021.100933

Chareo-Benítez B, Juárez-Barrientos JM, Álvarez-González CA, Kido-Cruz, MT, Alcántar-Vázquez, JP (2023) Chemical composition, productive and economic performance of Nile tilapia under different feeding regimes. Ecosistemas y recursos agropecuarios 10(3). https://doi.org/10.19136/era.a10n3.3779

Colorado F, Montañez I, Bolaños C, Rey J (2013) Growth and development of basil (*Ocimum basilicum* L.) under cover in the sabana of bogotá. Rev. U.D.C.A. Act. & Div. Cient. 16:121–129. https://doi.org/10.31910/rudca.v16.n1.2013.866

Cui X, Huang X, Chen X, Li H, Wu Y, Yang Z, Liu Z, Feng R, Xu J, Wei C, Ding Z, Cheng H (2024) Influence of starvation on biochemical, physiological, morphological, and transcriptional responses associated with glucose and lipid metabolism in the liver of javelin goby (*Synechogobius hasta*). Animals 14:2734. https://doi.org/10.3390/ani14182734

Dar SA, Srivastava PP, Varghese T, Nazir MI, Gupta S, Krishna G (2019) Temporal changes in superoxide dismutase, catalase, and heat shock protein 70 gene expression, cortisol and antioxidant enzymes

activity of *Labeo rohita* fingerlings subjected to starvation and refeeding. Gene 692:94–101. https://doi.org/10.1016/j.gene.2018.12.058

De Silva SS, Anderson TA (1994) *Fish nutrition in aquaculture* (Vol. 1). Springer Science & Business Media

Debbarma S, Tiwari VK, Reddy AK, Pavan Kumar A, Babitha Rani AM (2019) Short term ration restriction and re-alimentation: Effect on compensatory growth, body composition and insulin like growth factor gene expression in *Cyprinus carpio*. Turk J Fish & Aquat Sci 20:499–505. https://doi.org/10.4194/1303-2712-v20_6_08

Deswati D, Yani E, Safni S, Norita Tetra O, Pardi H (2020) Development methods in aquaponics systems using biofloc to improve water quality (ammonia, nitrite, nitrate) and growth of tilapia and samhong mustard. Int J Environ Anal Química 102:7824–7834. https://doi.org/10.1080/03067319.2020.1839437

Elbialy ZI, Gamal S, Al-Hawary II, Shukry M, Salah AS, Aboshosha AA, Assar DH (2022) Exploring the impacts of different fasting and refeeding regimes on Nile tilapia (*Oreochromis niloticus* L.): growth performance, histopathological study, and expression levels of some muscle growth-related genes. Fish Physiol Biochem 48:973–989. https://doi.org/10.1007/s10695-022-01094-0

Elnady MA, Abdel-Wahed RK, Helal AM, Mansour DH (2023) Growth and feed performances of the nile tilapia during the fattening stage under restricted feeding in biofloc culture. Egypt J Aqua Biol Fish 27(6):1203–1217. https://doi.org/10.21608/ejabf.2023.299577

El-Sayed AFM (2020) Tilapia Culture, 2nd edn. Academic Press. 297–328. https://doi.org/10.1016/B978-0-12-816509-6.00013-6

Emerenciano MGC, Martínez-Córdova LR, Martínez-Porchas M, Miranda-Baeza A (2017) Biofloc technology (BFT): a tool for water quality management in aquaculture. Water Qual 5:91–109. https://doi.org/10.5772/66416

Espinosa-Moya A, Álvarez-González A, Albertos-Alpuche P, Guzmán-Mendoza R, Martínez-Yáñez R (2018) Growth and development of herbaceous plants in aquaponic systems. Acta Univ 28(2):1–8. https://doi.org/10.15174/au.2018.1387

FAO (2024) The state of world fisheries and aquaculture 2024 - Blue transformation in action. Rome. https://doi.org/10.4060/cd0683en

Favero GC, dos Santos FAC, da Costa Júlio GS, Pedras PPC, Ferreira AL, e Silva WDS, Ferreira NS, Neves LC, Luz RK (2021) Effects of short feed restriction cycles in *Piaractus brachypomus* juveniles. Aquaculture 536:736465. https://doi.org/10.1016/j.aquaculture.2021.736465

Froese R (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. J Appl Ichthyol 22(4):241–253. https://doi.org/10.1111/j.1439-0426.2006.00805.x

Gallardo-Collí A, Pérez-Fuentes M, Pérez-Rostro CI, Hernández-Vergara MP (2020) Compensatory growth of Nile tilapia *Oreochromis niloticus*, L. subjected to cyclic periods of feed restriction and feeding in a biofloc system. Aquac Res 51:1813–1823. https://doi.org/10.1111/are.14530

Goddek S, Delaide B, Mankasingh U, Ragnarsdottir KV, Jijakli H, Thorarinsdottir R (2015) Challenges of sustainable and commercial aquaponics. Sustainability 7:4199–4224

Gong Y, Chen W, Han D, Zhu X, Yang Y, Jin J, Xie S (2017) Effects of food restriction on growth, body composition and gene expression related in regulation of lipid metabolism and food intake in grass carp. Aquaculture 469:28–35. https://doi.org/10.1016/j.aquaculture.2016.12.003

Gou N, Wang K, Jin T, Yang B (2023) Effects of starvation and refeeding on growth, digestion, nonspecific immunity and lipid-metabolism-related genes in *Onychostoma macrolepis*. Animals 13:1168. https://doi.org/10.3390/ani13071168

Hack NL, Cordova KL, Glaser FL, Journey ML, Resner EJ, Hardy KM, Lema SC (2019) Interactions of long-term food ration variation and short-term fasting on insulin-like growth factor-1 (IGF-1) pathways in copper rockfish (*Sebastes caurinus*). Gen Comp Endocrinol 280:168–184. https://doi.org/10.1016/j.ygcen.2019.04.025

Hack NL, Strobel JS, Journey ML, Beckman BR, Lema SC (2018) Response of the insulin-like growth factor-1 (*Igf1*) system to nutritional status and growth rate variation in olive rockfish (*Sebastes serranoides*). Comp Biochem Physiol A Mol Integr Physiol 224:42–52. https://doi.org/10.1016/j.cbpa.2018.05.025

Han SL, Wang J, Li LY, Lu DL, Chen LQ, Zhang ML, Du ZY (2020) The regulation of rapamycin on nutrient metabolism in Nile tilapia fed with high-energy diet. Aquaculture 520:734975. https://doi.org/10.1016/j.aquaculture.2020.734975

Hopkins KD (1992) Reporting fish growth: a review of the basics 1. J World Aquac Soc 23(3):173–179. https://doi.org/10.1111/j.1749-7345.1992.tb00766.x

Hu B, Li M, Yu X, Xun X, Lu W, Li X, Li Y, Lou J, Wang S, Zhang L, Cheng J, Hu X, Bao Z (2019) Diverse expression regulation of *Hsp70* genes in scallops after exposure to toxic *Alexandrium* dinoflagellates. Chemosphere 234:62–69. https://doi.org/10.1016/j.chemosphere.2019.06.034

Huang H, Zhang Y, Cao M, Xue L, Shen W (2018) Effects of fasting on the activities and mRNA expression levels of lipoprotein lipase (LPL), hormone-sensitive lipase (HSL) and fatty acid synthetase (FAS) in

spotted seabass *Lateolabrax maculatus*. Fish Physiol Biochem 44:387–400. https://doi.org/10.1007/s10695-017-0442-4

Hundley GC, Navarro FKSP, Ribeiro Filho OP, Navarro RD (2018) Integration of Nile tilapia (*Oreochromis niloticus* L.) production *Origanum majorana* L. and *Ocimum basilicum* L. using aquaponics technology. Acta Sci Technol. https://doi.org/10.4025/actascitechnol.v40i1.35460

Hussain AS, Brown PB (2025) Current status of the propagation of basil in aquaponic systems: a literature review. Aquacult Res. https://doi.org/10.1155/are/1320019

Islam MR, Ali MZ, Hasanuzzaman AFM, Golder MR (2021) Effect of skip-feeding and re-feeding regimes on compensatory growth, body composition, feed utilization, feeding cost and survival of monosex tilapia (*Oreochromis niloticus*) in pond aquaculture system. Bangladesh J Fish. 33:225–233. https://doi.org/10.52168/bjf.2021.33.25

Johnson SC, Rabinovitch PS, Kaeberlein M (2013) mTOR is a key modulator of ageing and age-related disease. Nature 493:338–345. https://doi.org/10.1038/nature11861

Kennedy BK, Lamming DW (2016) The mechanistic target of rapamycin: the grand conductor of metabolism and aging. Cell Metab 23:990–1003. https://doi.org/10.1016/j.cmet.2016.05.009

Khanjani MH, Sharifinia M (2020) Biofloc technology as a promising tool to improve aquaculture production. Rev Aquac 12:1836–1850. https://doi.org/10.1111/raq.12412

Khanjani MH, Sharifinia M, Emerenciano MG (2024) Biofloc technology (BFT) in aquaculture: what goes right, what goes wrong? a scientific-based snapshot. Aquac Nutr 2024:7496572. https://doi.org/10.1155/2024/7496572

Kwee EM, Niemeyer ED (2011) Variations in phenolic composition and antioxidant properties among 15 basil (*Ocimum basilicum* L.) cultivars. Food Chem 128:1044–1050. https://doi.org/10.1016/j.foodchem.2011.04.011

Lavajoo F, Perelló-Amorós M, Vélez EJ, Sánchez-Moya A, Balbuena-Pecino R, Riera-Heredia N, Fernández-Borràs J, Blasco J, Navarro I, Capilla E, Gutiérrez J (2020) Regulatory mechanisms involved in muscle and bone remodeling during refeeding in gilthead sea bream. Sci Rep 10:184. https://doi.org/10.1038/s41598-019-57013-6

Lindholm - Lehto P (2023) Water quality monitoring in recirculating aquaculture systems. Aquac Fish Fish 3:113–131. https://doi.org/10.1002/aff2.102

Liu G, Ye Z, Liu D, Zhao J, Sivaramasamy E, Deng Y, Zhu S (2018) Influence of stocking density on growth, digestive enzyme activities, immune responses, antioxidant of *Oreochromis niloticus* fingerlings in biofloc systems. Fish Shellfish Immunol 81:416–422. https://doi.org/10.1016/j.fsi.2018.07.047

Livak KJ, Schmittgen TD (2001) Analysis of relative gene expression data using real-time quantitative PCR and the 2− ΔΔCT method. Methods 25:402–408. https://doi.org/10.1006/meth.2001.1262

Lu H, Liu C, Yang C, He Z, Wang L, Song L (2024) Genome-wide identification of the *HSP70* genes in Pacific oyster *Magallana gigas* and their response to heat stress. Cell Stress Chaperones 29:589–602. https://doi.org/10.1016/j.cstres.2024.06.002

Maciel JC, Francisco CJ, Miranda-Filho KC (2018) Compensatory growth and feed restriction in marine shrimp production, with emphasis on biofloc technology. Aquac Int 26:203–212. https://doi.org/10.1007/s10499-017-0209-z

Mankiewicz JL, Picklo MJ, Idso J, Cleveland BM (2022) Leptin receptor deficiency results in hyperphagia and increased fatty acid mobilization during fasting in rainbow trout (*Oncorhynchus mykiss*). Biomolecules 12:516. https://doi.org/10.3390/biom12040516

Moncayo Luján MDR, Álvarez Reyna VDP, González Cervantes G, Salas Pérez L, Chávez Simental JA (2015) Producción orgánica de albahaca en invernadero en Comarca Lagunera. Terra Latinoamericana 33:69–77. ISSN 2395–8030. https://www.terralatinoamericana.org.mx/index.php/terra/article/view/46

Montserrat N, Gabillard JC, Capilla E, Navarro MI, Gutiérrez J (2007) Role of insulin, insulin-like growth factors, and muscle regulatory factors in the compensatory growth of the trout (*Oncorhynchus mykiss*). Gen Comp Endocrinol 150:462–472. https://doi.org/10.1016/j.ygcen.2006.11.009

Najdegerami EH, Bakhshi F, Lakani FB (2016) Effects of biofloc on growth performance, digestive enzyme activities and liver histology of common carp (*Cyprinus carpio* L.) fingerlings in zero-water exchange system. Fish Physiol Biochem 42:457–465. https://doi.org/10.1007/s10695-015-0151-9

Ndandala CB, Dai M, Mustapha UF, Li X, Liu J, Huang H, Li G, Chen H (2022) Current research and future perspectives of *GH* and *IGFs* family genes in somatic growth and reproduction of teleost fish. Aquac Rep 26:101289. https://doi.org/10.1016/j.aqrep.2022.101289

Nebo C, Overturf K, Brezas A, Dal-Pai-Silva M, Portella MC (2017) Alteration in expression of atrogenes and *IGF-1* induced by fasting in Nile tilapia *Oreochromis niloticus* juveniles. Int Aquat Res 9:361–372. https://doi.org/10.1007/s40071-017-0182-1

Nguyen VT, Nguyen NQ, Thi NQN, Thi CQN, Truc TT, Nghi PTB (2021) Studies on chemical, polyphenol content, flavonoid content, and antioxidant activity of sweet basil leaves (*Ocimum basilicum* L.). IOP Conf Ser Mater Sci Eng 1092:012083. https://doi.org/10.1088/1757-899X/1092/1/012083

Nie H, Liu L, Wang H, Huo Z, Yan X (2018) Stress levels over time in *Ruditapes philippinarum*: the effects of hypoxia and cold stress on *hsp70* gene expression. Aquac Rep 12:1–4. https://doi.org/10.1016/j.aqrep.2018.08.006

Oliveira LK, Krummenauer D, Wasielesky W, Tesser MB (2023) Can cyclical food restriction support growth of juvenile Nile tilapia (*Oreochromis niloticus*) in brackish water biofloc? Aquacult Int 32:1557–1571. https://doi.org/10.1007/s10499-023-01373-4

Pasch J, Appelbaum S, Palm HW, Knaus U (2021) Growth of basil (*Ocimum basilicum*) in aeroponics, DRF, and raft systems with effluents of African catfish (*Clarias gariepinus*) in decoupled aquaponics (ss). AgriEngineering 3:559–574. https://doi.org/10.3390/agriengineering3030036

Paula TGD, Zanella BTT, Fantinatti BED, Moraes LND, Duran BODS, Oliveira CBD, Dal-Pai-Silva M (2017) Food restriction increase the expression of *mTORC1* complex genes in the skeletal muscle of juvenile pacu (*Piaractus mesopotamicus*). PLoS ONE 12:e0177679. https://doi.org/10.1371/journal.pone.0177679

Perez ES, Cury SS, Zanella BTT, Carvalho RF, Duran BOS, Dal-Pai-Silva M (2022) Identification of novel genes associated with fish skeletal muscle adaptation during fasting and refeeding based on a meta-analysis. Genes 13:2378. https://doi.org/10.3390/genes13122378

Pinho SM, Lima JP, David LH, Emerenciano MGC (2021) Flocponics: the integration of biofloc technology with plant production. Rev Aquac 13(3):1647–1679. https://doi.org/10.1111/raq.12539

Polyakova MN, Martirosyan YT, Dilovarova TA, Kosobryukhov AA (2015) Photosynthesis and productivity of basil plants (*Ocimum basilicum* L.) under different irradiation. Сельскохозяйственная биология. (Agric Biol) 1(eng):124–130. https://doi.org/10.15389/agrobiology.2015.1.124eng

Poot-López GR, Gasca-Leyva E, González-Salas C, Guillen-Hernández S, Domínguez-May R (2020) Compensatory growth in Nile tilapia *Oreochromis niloticus*: feed conversion ratio, size heterogeneity, and proximal composition. Lat Am J Aquat Res 48:421–428. https://doi.org/10.3856/vol48-issue3-fulltext-2466

Prates E, Holanda M, Pedrosa VF, Monserrat JM, Wasielesky W (2023) Compensatory growth and energy reserves changes in the Pacific white shrimp (*Litopenaeus vannamei*) reared in different temperatures and under feed restriction in biofloc technology system (BFT). Aquaculture 562:738821. https://doi.org/10.1016/j.aquaculture.2022.738821

Rakocy JE (2012) Aquaponics—integrating fish and plant culture. Aquaculture production systems. pp 344–386. https://doi.org/10.1002/9781118250105.ch14

Ramasubburayan R, Prakash S, Immanuel G, MubarakAli D, Rajakumar G (2024) The transformative role of prebiotics, probiotics, and microbiomes in biofloc systems for sustainable aquaculture: a comprehensive review. Rev Aquac 17(1):e13000. https://doi.org/10.1111/raq.13000

Ronzón-Ortega M, Hernández-Vergara MP, Pérez-Rostro CI (2012) Producción hidropónica y acuapónica de albahaca (*Ocimum basilicum*) y langostino malayo (*Macrobrachium rosenbergii*). Trop Subtrop Agroecosyst 15:S63-S71. https://www.redalyc.org/articulo.oa?id=93924626009

Sakyi ME, Cai J, Tang J, Abarike ED, Xia L, Li P, Jian J (2020) Effects of starvation and subsequent re-feeding on intestinal microbiota, and metabolic responses in Nile tilapia, *Oreochromis niloticus*. Aquac Rep 17:100370. https://doi.org/10.1016/j.aqrep.2020.100370

Selek M, Endo M, Yiğit M, Takeuchi T (2017) The integration of fish and plant production: Nile tilapia (*Oreochromis niloticus*) and basil (*Ocimum basilicum*) culture in recirculating and aquaponic systems. J Aquac Eng Fish Res 3(1):28–43. https://doi.org/10.3153/JAEFR17005

Sharma N, Acharya S, Kumar K, Singh N, Chaurasia OP (2018) Hydroponics as an advanced technique for vegetable production: an overview. J Soil Water Conserv 17:364–371. https://doi.org/10.5958/2455-7145.2018.00056.5

Shi GC, Dong XH, Chen G, Tan BP, Yang QH, Chi SY, Liu HY (2015) Physiological responses and *HSP70* mRNA expression of GIFT strain of Nile tilapia (*Oreochromis niloticus*) under cold stress. Aquacult Res 46(3):658–668. https://doi.org/10.1111/are.12212

Singleton VL, Orthofer R, Lamuela-Raventós RM (1999) Analysis of total phenols and other oxidation substrates and antioxidants by means of folin-ciocalteu reagent. Methods Enzymol 299:152–178. https://doi.org/10.1016/S0076-6879(99)99017-1

Sipos L, Balázs L, Székely G, Jung A, Sárosi S, Radácsi P, Csambalik L (2021) Optimization of basil (*Ocimum basilicum* L.) production in LED light environments–a review. Sci Hortic 289:110486. https://doi.org/10.1016/j.scienta.2021.110486

Souri MK, Neumann G, Römheld V (2009) Nitrogen forms and water consumption in tomato plants. Hortic Environ Biotechnol 50:377–383

Strobel JS, Hack NL, Label KT, Cordova KL, Bersin TV, Journey ML, Beckman BR, Lema SC (2020) Effects of food deprivation on plasma insulin-like growth factor-1 (*Igf1*) and *Igf* binding protein

(*Igfbp*) gene transcription in juvenile cabezon (*Scorpaenichthys marmoratus*). Gen Comp Endocrinol 286:113319. https://doi.org/10.1016/j.ygcen.2019.113319
Tian J, Wen H, Zeng LB, Jiang M, Wu F, Liu W, Yang CG (2013) Changes in the activities and mRNA expression levels of lipoprotein lipase (LPL), hormone-sensitive lipase (HSL) and fatty acid synthetase (FAS) of Nile tilapia (*Oreochromis niloticus*) during fasting and re-feeding. Aquaculture 400:29–35. https://doi.org/10.1016/j.aquaculture.2013.01.032
Turano MJ, Borski RJ, Daniels HV (2008) Effects of cyclic feeding on compensatory growth of hybrid striped bass (*Morone chrysops* × *M. saxitilis*) foodfish and water quality in production ponds. Aquac Res 39:1514–1523. https://doi.org/10.1111/j.1365-2109.2008.02023.x
Ujjania VK, Sharma BK, Sharma SK, Upadhyay B (2021) Determination of water quality parameters with reference to management of aquaponics system. Environ Ecol 39:1289–129. https://doi.org/10.13140/RG.2.2.22603.46887
Wang C, Liang Y, Fang Y, Chang X (2019) Effects of cyclical short-term food deprivation and refeeding on compensatory growth and gene expression of *SOD*, *GPX* and *HSP70* in *Schizothorax wangchiachii*. Fish Shellfish Immunol 94:628–633. https://doi.org/10.1016/j.fsi.2019.09.047
Wang Y, Wang R, Yang R, Zhu S, Yao F, Zhang X, Yang Y (2025) Effects of feeding pattern on growth, immunity and intestinal flora of GIFT tilapia (*Oreochromis niloticus*) and largemouth bass (*Micropterus salmoides*). Aquac Rep 42:102764. https://doi.org/10.1016/j.aqrep.2025.102764
Wasielesky W Jr, Froes C, Fóes G, Krummenauer D, Lara G, Poersch L (2013) Nursery of *Litopenaeus vannamei* reared in a biofloc system: the effect of stocking densities and compensatory growth. J Shellfish Res 32:799–806. https://doi.org/10.2983/035.032.0323
Won ET, Borski RJ (2013) Endocrine regulation of compensatory growth in fish. Front Endocrinol 4:74. https://doi.org/10.3389/fendo.2013.00074
Wong CE, Teo ZWN, Shen L, Yu H (2020) Seeing the lights for leafy greens in indoor vertical farming. Trends Food Sci Technol 106:48–63. https://doi.org/10.1016/j.tifs.2020.09.031
Xu C, Liu WB, Wang BK, Li XF (2020) Restricted feeding benefits the growth performance and glucose homeostasis of blunt snout bream *Megalobrama amblycephala* fed high-carbohydrate diets. Aquac Rep 18:100513. https://doi.org/10.1016/j.aqrep.2020.100513
Xu W, Geng H, Wu L, Jin J, Han D, Zhu X, Yang Y, Liu H, Xie S (2022) Feeding restriction unalters physiological responses to dietary lipid and carbohydrate levels in juvenile gibel carp (*Carassius gibelio*). Aquac Rep 25:101273. https://doi.org/10.1016/j.aqrep.2022.101273
Yepez-Hernandez FJ, Ferrera-Cerrato R, Alarcon A, Delgadillo-Martinez J, Mendoza-López MR, Garcia-Barradas O (2016) Nitrogen fertilization effects on growth, phenolic compounds content, and antioxidant activity of Brasil. Rev Fitotec Mex 39:33–40. ISSN 0187–7380. https://www.scielo.org.mx/pdf/rfm/v39n1/v39n1a7.pdf
Yu YB, Choi JH, Lee JH, Jo AH, Han SW (2023a) Biofloc application using aquaponics and vertical aquaculture technology in aquaculture: review. Fishes 8(11):543. https://doi.org/10.3390/fishes8110543
Yu YB, Choi JH, Lee JH, Jo AH, Han SW, Han SH, Choi HJ, Choi CY, Kang JC, Min E, Kim JH (2023b) Biofloc application using aquaponics and vertical aquaculture technology in aquaculture: review. Fishes 8:543. https://doi.org/10.3390/fishes8110543
Zhang L, Li B, Sun X, Hong Q, Duan Q (2023) Intelligent fish feeding based on machine vision: a review. Biosyst Eng 231:33–164. https://doi.org/10.1016/j.biosystemseng.2023.05.010
Zuo H, Gao J, Yuan J, Deng H, Yang L, Weng S, He J, Xu X (2017) Fatty acid synthase plays a positive role in shrimp immune responses against *Vibrio parahaemolyticus* infection. Fish Shellfish Immunol 60:282–288. https://doi.org/10.1016/j.fsi.2016.11

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