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Original Article

Sea-based cage culture of red tilapia (*Oreochromis* spp.) juveniles: Effects of different cyclic feeding regimes on compensatory growth, feed utilization efficiency, biochemical composition, and water quality

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Abstract: Red tilapia (*Oreochromis* spp.) is a valuable aquaculture species due to its rapid growth, salinity tolerance, and adaptability to diverse environmental conditions. A 60-day feeding trial was conducted in sea-based cages (2× 2× 2 m) at 37 fish•m^{-3} (equivalent to 296 fish•cage^{-1}) to assess the effects of cyclic feeding regimes (CFRs) on growth performance, feed utilization efficiency, biochemical composition, condition factor, survival, and water quality of red tilapia juveniles. Tilapia juveniles (10.67±0.50 g; mean ±SEM) were subjected to three feeding strategies: continuous daily feeding (control), 1:6 CFR (1-day starvation followed by 6 days refeeding), and 2:5 CFR (2-days starvation followed by 5 days refeeding). The results showed that fish subjected to 1-day starvation exhibited compensatory growth (CG), with final body weight (FBW), weight gain (WG), specific growth rate (SGR), protein efficiency ratio (PER), feed conversion ratio (FCR), and condition factor (CF) comparable to the control group. In contrast, 2-day starvation (2:5 CFR) significantly reduced growth performance compared to the control group. FCR, PER, and CF of red tilapia juveniles were not significantly affected by CFRs. Correlation analysis revealed a strongly significant negative relationship between CFRs and FBW (r = –0.91), WG (r = –0.91), and SGR (r = –0.90), while it showed a moderately significant negative correlation with FBL (r = –0.65), LI (r = –0.65), and PER (r = –0.62). A strong positive correlation was also observed between CFR and survival rate (r = 0.90), indicating that cyclic feeding schedules significantly influence the survival of red tilapia juveniles. Biochemical analysis indicated decreased crude protein and increased lipid content with longer starvation periods. Salinity showed a moderate positive correlation with CFRs (r = 0.76) and dissolved oxygen (DO; r = 0.79), and a strong negative correlation with pH (r = –0.82). Hyperphagia during refeeding was identified as the primary mechanism for CG. Overall, short-term cyclic feeding (1:6 CFR) offers a viable management strategy to reduce feed costs while maintaining growth and sustainability in sea-based tilapia farming.

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Introduction

Red tilapia, a member of the family Cichlidae, includes hybrids such as the cross between Blue tilapia (*Oreochromis aureus*) and Mozambique tilapia (*O. mossambicus*), which are widely recognized in aquaculture (Wang et al., 2020). Red tilapia is among the few farmed finfish species that feed on natural foods at low trophic levels and exhibit omnivorous feeding behavior (Klahan et al., 2023). Globally, it has become one of the most popular cultured fish due to its palatable flavor, ease of cultivation, rapid growth, ability to withstand harsh environmental conditions, and strong resistance to diseases (Haque et al., 2016; Eissa et al., 2023). During the 1980s, tilapia production in the Philippines expanded significantly with the introduction of hybrid red tilapia (*Oreochromis* spp.). This strain gained popularity in the local Filipino–Chinese market due to its reddish-orange to pale red (pink) coloration. Compared with Nile tilapia, red tilapia exhibits greater salinity tolerance and can therefore be cultured in rearing enclosures with water salinities ranging from

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brackish to full-strength seawater (Romana-Eguia et al., 2020). Red tilapia grows as quickly as Nile tilapia and may perform even better in brackish ponds and marine cages (Romana-Eguia et al., 2020; Eguia and Romana-Eguia, 2004).

Tilapia has been referred to as the "aquatic chicken," the "fish of the 1990s," and the "food fish of the 21st century" owing to its high nutritional value (Eguia and Romana-Eguia, 2004; Painkra et al., 2026). It is one of the most widely farmed fish species in the Philippines, valued for its increasing market acceptance and remarkable adaptability to diverse environmental conditions and culture systems (Baliao et al., 2000; Yildirim-Aksoy et al., 2020; Romana-Eguia et al., 2020). Tilapia farming contributes substantially to aquaculture production in the Philippines, across Southeast Asia, and in many other countries worldwide (Eguia and Romana-Eguia, 2004). As the second most cultured species in the Philippines after milkfish (*Chanos chanos*) in terms of total aquaculture production, tilapia is currently one of the priority commodities in the aquaculture sector (Guerrero, 2019; DA-BFAR, 2022). The rapid growth of aquaculture and the tilapia industry has resulted in a significant surge in demand for aquafeeds and tremendous pressure on feed supply (Gatlin et al., 2007). Feed accounts for an enormous share of operating costs in aquaculture, comprising 75-90% of total production costs (El-Sayed et al., 2015), followed by expenditures on fish fry, land rent, electricity, and diesel (Macfadyen et al., 2011). In the Philippines, the average production cost for a one-hectare tilapia fishpond operation in 2019 amounted to PhP 302,000, with a total cash cost of PhP 256,959. Meanwhile, feed component costs PhP 173,033, accounting for 56.9% of total tilapia production costs (DA-BFAR, 2022). Hence, strategies to minimize feed inputs were of prime importance for making the aquaculture industry more profitable at a sustainable level.

Cyclic feeding, a scheme involving feed restriction or starvation followed by a refeeding period, could induce compensatory growth (Ribeiro and Tsuzuki, 2010). Compensatory growth (CG), or "catch-up" growth, is a physiological phase of accelerated growth when favorable conditions are restored after a period of food restriction or undernutrition (Hayward et al., 1997; Hornick et al., 2000; Ali et al., 2003; Cho et al., 2006). Research on the use of a cyclic feeding strategy as a management tool to elicit CG in aquatic animals has become increasingly prominent, as it not only helps reduce feed costs but also enhances feed efficiency and minimizes the loading of waste from aquaculture effluents into the aquatic environment (Shao et al., 2020).

Earlier reports on the CG phenomenon resulting from refeeding after food restriction or starvation had been documented in several cold and warm water fish species (Wang et al., 2000; Tian and Qin, 2003; Nikki et al., 2004; Cho et al., 2006; Oh et al., 2007-2008; Känkänen and Pirhonen, 2009). Moreover, numerous studies on a feeding strategy using cyclical fasting and re-feeding to save feed costs were documented in Atlantic salmon, *Salmo salar* (Johansen et al., 2001), Atlantic cod, *Gadus morhua* (Hanssen et al., 2012), black sea bream, *Acanthopagrus schlegelii* (Xiao et al., 2013), Amazon fish Matrinxã, *Brycon amazonicus* (Urbinati et al., 2014), walleye, *Sander vitreus* (Hayward et al., 2015), longfin yellowtail, *Seriola rivoliana* (Argüello-Guevara et al., 2018), and a carnivorous Neotropical catfish, *Lophiosilurus alexandri* (Silva et al., 2019). These studies applied different periods of feed deprivation to elicit a CG response in fish, followed by periods of refeeding (i.e., cyclic feeding), thereby enhancing feed efficiency without deleterious effects on weight gain. Thus, a suitable feeding strategy was crucial for enhancing feed efficiency, reducing feed costs, and increasing tilapia farmers' income. Feeding strategies that minimize feed input and overall production costs are essential for achieving economically viable and environmentally sustainable fish farming. Several scientific studies have documented feed restriction–refeeding cycles in several fish species to induce CG. However, the potential of different cyclic feeding regimes (CFRs) to elicit a CG response in red tilapia (*Oreochromis* spp.) reared in marine cages has not yet been determined. Hence, this study was conducted to assess the effects of various CFRs on the survival, growth performance, feed utilization efficiency, biochemical composition, and water quality of red tilapia subjected to different periods of food restriction or starvation followed by refeeding in marine cages.

Materials and Methods

Experimental animals, acclimatization, and maintenance: Red tilapia (*Oreochromis* spp.) juveniles were sourced from the Freshwater Hatchery of the Bureau of Fisheries and Aquatic Resources–National Mariculture Center (BFAR-NMC) in Southern Davao, Panabo City, Davao del Norte, Philippines. Before the start of the experiment, only healthy and active fish with no visible signs of deformities, injuries, or disease symptoms were selected for the feeding trial. The experimental animals were then transported to the BFAR-NMC Acclimatization Facility Center, Coastal Road, Cagangohan, Panabo City, Davao del Norte, in oxygen-saturated seawater. Upon arrival, the juveniles were briefly acclimatized by allowing the oxygenated polyethylene bags containing the fish to float in a rectangular fiberglass tank with a capacity of 1.5 tons. Once the water temperatures in both media were similar, the fish were slowly released into the tank. Fish were initially stocked in a rectangular fiberglass tank with a 1.5-ton capacity and freshwater, and subsequently acclimated to seawater at a salinity adjustment rate of 3 ppt per day. After acclimatization, the fish were maintained in seawater salinity for two weeks and fed twice daily with a commercial pellet diet containing 36% crude protein and 7.0% crude lipid. Optimal water quality parameters conducive to the growth and survival of red tilapia juveniles were monitored and maintained throughout the feeding trial (dissolved oxygen: >5 ppm; pH: 7.67–7.97; salinity: 32.35–35.03 ppt; temperature: 27.54-28.40°C).

Study site and sea-based cage culture set-up: The study was conducted at the Panabo City Mariculture Park (PCMP) in Cagangohan, Panabo City, Davao del Norte, approximately 31.3 km from Davao City on the island of Mindanao, Southern Philippines. At the end of the acclimatization period, 2,664 healthy and homogeneously sized mixed-sex red tilapia juveniles (10.67±0.50 g and 8.21±0.10 cm; mean±SEM) were transported in plastic bags with oxygenated seawater to the Panabo City Mariculture Park (PCMP), Cagangohan, Panabo City, Davao del Norte, Philippines. Upon arrival, the experimental animals were randomly distributed among the nine pre-conditioned units of fish cages at a density of 37 fish$\cdot$m^{-3} (i.e., 296 fish$\cdot$cage^{-1}). Each fish cage enclosure is made of green polyethylene (PE) net (~23.45 mm mesh size) fabricated into an 8 m^3 bag with dimensions of 2×2×2 m (length×width×depth).

Experimental treatments and design: Following the acclimation period, each marine cage enclosure was randomly assigned to one of three CFRs (Table 1), namely, a control (T1), fed continuously, one day fasting followed by 6 days refeeding (1:6, days starved: days fed; T2), and two days fasting followed by 5 days refeeding (2:5, days starved: days fed; T3). These treatments were randomly assigned to 9 cages with three replicates following a completely randomized design (CRD).

Feeding and water management: The experimental animals were fed commercial feeds (31-36% crude protein) three times daily at 08:00, 12:00, and 16:00 h using a 6-5% feeding rate (0-30 days 6%; and 30-60 days 5%) throughout the 60-day culture period in marine fish cages. The stock was fed pre-starter pellets from 0 to 15 days old, starter pellets from 16 to 30 days old, and grower pellets from 31 to 60 days old. The proximate composition of commercial feed, as indicated on its label, is shown in Table 2. The daily feed ration was adjusted every 15 days based on the average body weight (ABW) of the fish during each sampling period.

The water quality parameters were monitored every morning using the multi-parameter water quality equipment (YSI). Daily check-ups of the net cages and frames were conducted before the first feeding session, and floating debris was removed to prevent damage to cages and stocks. Regular monitoring of the red tilapia in marine fish cages was conducted to ensure the smooth implementation of the research study.

Water quality parameters: The water parameters,

Table 1. Description of the different cyclical feeding strategies used in the study.

Parameters	Treatments		
	T1 (control)	T2 (1:6)	T3 (2:5)
Fasting (day·week^{-1})	0	1	2
Refeeding (day·week^{-1})	7	6	5
Number of fish·cage^{-1}	296	296	296
Density (fish·m^{-3})	37	37	37
Number of replicates (n)	3	3	3

Table 2. Proximate composition of commercial diets as indicated on the label.

Proximate analysis	Pre-starter [a]	Starter [a]	Grower [a]
Crude protein (%)	36	34	31
Crude lipid (%)	7	7	6
Crude fiber (%)	5	5	6
Crude ash (%)	12	12	12
Moisture (%)	12	12	12
NFE[b]	40	42	45
Gross energy (KJ·g^{-1}) [c]	18.1	17.96	17.37

[a] Tateh Malaga Feeds, Santeh Feeds Corporation, Philippines; [b] Nitrogen-free extract, computed by difference; [c] Computed using gross calorific values of 17, 24, and 38 KJ·g^{-1} for carbohydrate, protein, and lipid, respectively (Jobling, 1993).

including dissolved oxygen (DO), temperature, salinity, and pH, were monitored once daily at approximately 9:00 AM throughout the experimental period using a calibrated YSI Pro Plus multiparameter meter. Prior to data collection, the probe was immersed at a depth of approximately 1 meter for 1-2 minutes to allow the readings to stabilize. Instrument calibration was performed in accordance with the manufacturer's standard operating procedures prior to water quality monitoring. The recorded water quality parameters were then compared with the acceptable standards for tilapia culture as recommended by DENR-DAO (2016) and Balarin and Haller (1982) to assess the suitability of the culture environment throughout the study.

Biochemical proximate composition analysis of the whole-fish body: The whole-fish body composition was analyzed at the start of the experiment (10 fish per stock) and at the termination of the study (5 fish per cage). Samples were assessed for moisture, crude protein, crude fat, and total ash following standard laboratory procedures (AOAC, 2000). Samples of five fish per treatment were taken for the analysis of initial body composition. Proximate composition of the fish carcass (initial and final) was analyzed following standard methods (AOAC, 2000). Crude protein (N x 6.25) was determined using the Kjeldahl method. Crude lipid was determined by the Soxhlet method (AOAC 920.39); crude fiber was determined with the Fibertic system heat extractor; moisture content was determined by drying to constant weight in an oven at 135 °C (AOAC 930.15); and ash content was determined by ignition (AOAC 942.05).

Growth, feed utilization efficiency, and body condition indices: Periodic sampling of the experimental animals was carried out at 15-day intervals to adjust the feeding ration. During each sampling, 10% or 30 individuals of the total stock from each cage enclosure were weighed individually. Immediately after weighing, the fish were returned to their respective cage enclosure to minimize stress. Following the termination of the study, growth indices and feed utilization efficiency parameters were assessed in relation to the experimental cyclic feeding regimes using the following biometric measurements.

The growth performance, feed utilization efficiency, and Fulton's condition factor (CF), including final body weight (FBW), final body length (FBL), weight gain (WG), length increment (LI), specific growth rate (SGR), feed conversion ratio (FCR), protein efficiency ratio (PER), and survival, were calculated following the formula of Cho et al. (2006) and Ribeiro and Tsuzuki (2010). WG was calculated as WG = FBW (g) − IBW (g). LI was

Table 3. Growth, condition index, and survival of red tilapia reared in sea-based cage enclosures at different cyclic feeding regimes (CFRs). Values are the mean of three replicates.

Parameters	Treatments			*P*-value
	T1 (control)	T2 (1:6)	T3 (2:5)	
FBW (g)	193.33±0.3.84[a]	183.33±1.86[a]	158.33±5.17[b]	0.002
FBL (cm)	22.07±0.72 [a]	19.82±1.75 [a]	18.73±0.27 [a]	0.175
WG (g)	182.66±3.84[a]	172.66±1.86[a]	147.66±5.17[b]	0.002
LI (cm)	13.86±0.72[a]	11.61±1.75[a]	10.52±0.27[a]	0.175
SGR (%/day)	4.83±0.03[a]	4.74±0.02[a]	4.49±0.06[b]	0.002
CF	1.83±0.19 [a]	2.61±0.76 [a]	2.41±0.02 [a]	0.488
Survival (%)	21.73±1.00[b]	31.42±3.21[b]	45.72±4.58 [a]	0.006

* Mean values (expressed as means ±SEM) with different superscripts in the same column are significantly different (P<0.05). FBW=final body weight; FBL=final body length; WG = weight gain; LI=length increment; SGR=specific growth rate; CF=condition factor; Control=fed continuously; 1:6= 1-day feed deprivation followed by 6 days of feeding; 2:5= 2-day feed deprivation followed by 5 days of feeding.

Table 4. Feed and nutrient utilization efficiency of red tilapia reared in sea-based cage enclosures at different cyclic feeding regimes (CFRs). Values are the mean of three replicates.

Parameters	Treatments			*P*-value
	T1 (control)	T2 (1:6)	T3 (2:5)	
FC	257.79±12.04 [a]	262.66±16.53 [a]	242.91±13.13[a]	0.610
FCR	1.41±0.09 [a]	1.52±0.11[a]	1.64±0.04 [a]	0.227
PER	2.12±0.17 [a]	1.97±0.16 [a]	1.81±0.05 [a]	0.230

* Mean values (expressed as means ±SEM) with different superscripts in the same column are significantly different (P<0.05). FC=feed consumed; FCR= feed conversion ratio; PER=protein efficiency ratio; Control=fed continuously; 1:6= 1-day feed deprivation followed by 6 days of feeding; 2:5= 2-day feed deprivation followed by 5 days of feeding.

calculated as FBL (cm) −IBL (cm). SGR was calculated as SGR ($\%day^{-1}$) = 100 (ln FBW−ln IBW)/60 days, where ln is the natural logarithm. FCR was calculated as FCR = FC (g)/ WG (g), where FC was the feed consumed. PER was computed as PER = WG (g)/ PC (g), where PC was the protein consumed. CF was calculated as CF = 100 * FBW (g)/L^3, where L was the total length in cm.

Statistical analysis: Before the analysis, all recorded measurements and computed data were first tested for normality using the Shapiro–Wilk test and for homogeneity of variances using Levene's test. Differences among treatment means were analyzed through one-way analysis of variance (ANOVA), followed by Tukey's HSD post hoc test to identify significant differences among treatments at P<0.05. Pearson correlation analysis was also performed to evaluate the relationships between growth performance, feed utilization efficiency, water quality, and survival of red tilapia juveniles under different cyclic feeding regimes. ANOVA and Tukey's HSD tests were conducted using IBM SPSS Statistics Version 20 for Windows, while correlation analysis was carried out with PAST Version 5.2.1. Data were expressed as mean ± SEM (standard error of the mean).

Results

Growth, feed utilization efficiency, condition factor, and survival: Growth curves of red tilapia juveniles subjected to different cyclic feeding regimes (CFRs) over a 60-day culture period, based on periodic samplings and final weight measurements, are presented in Figure 1. The growth performance (FBW, FBL, WG, LI, and SGR), feed utilization efficiency (FCR and PER), condition factor, and survival of red tilapia juveniles after a 60-day culture period at CFR are presented in Tables 3 and 4. The potential CG of fish in the two starved treatment groups (1:6 and 2:5 CFRs) was assessed by comparing the growth performance and feed utilization efficiency with those of the control group during the feeding days.

The CFRs significantly influenced the growth performance of the starved red tilapia juveniles (P<0.05). At the termination of the feeding trial, the highest FBW, FBL, WG, LI, and SGR (193.33±0.3.84 g, 22.07±0.72 cm, 182.66±3.84 g, 13.86±0.72 cm, and

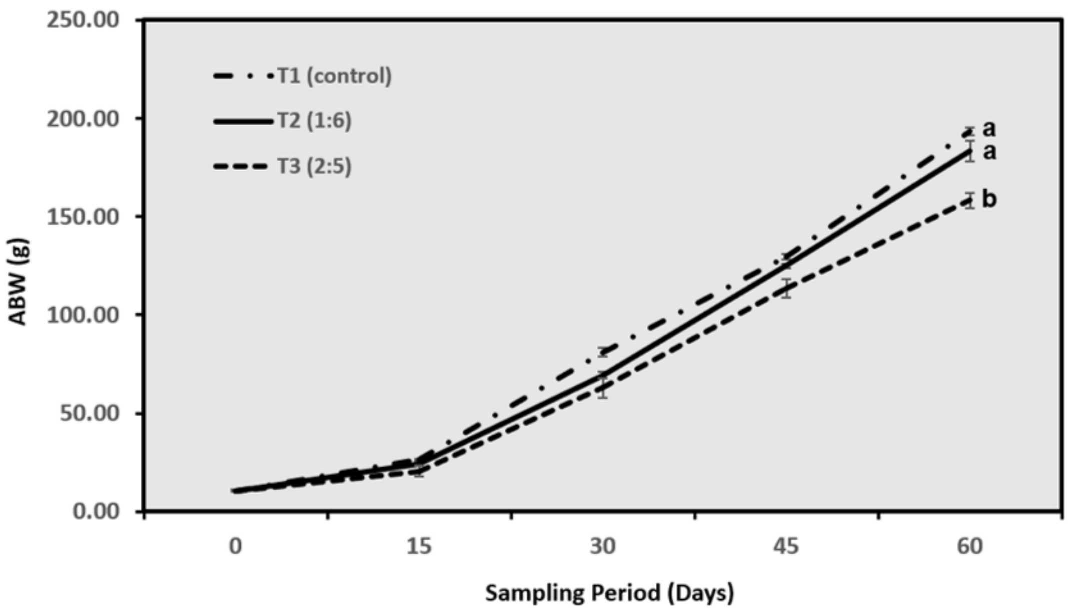

Figure 1. Periodic final weight of red tilapia juveniles reared in sea-based cage enclosures at different cyclic feeding regimes (CFRs).

4.83±0.03%, respectively) were significantly obtained by the red tilapia juveniles fed continuously without fasting (control) among all treatments (P<0.05). However, the starved tilapia juveniles fed T2 (1:6 CFR) exhibited growth comparable to that of the T1 (control). Juvenile tilapia subjected to treatment 2 (1:6 CFR; 1-day starvation) were found to recover fast enough once feeding was continued and exhibited an accelerated growth response similar to the control (no starvation) treatment (P>0.05). Table 3 shows that fish in T2 (1-day starvation) increased in growth (FBW, WG, and SGR) comparable to T1 (no starvation), but significantly higher than in T3 (2-day starvation). Moreover, the FBL and LI of the red tilapia juveniles were similar in all tested CFRs (P>0.05). On the contrary, the lowest FBW, FBL, WG, LI, and SGR (158.33±5.17g, 18.73±0.27 cm, 147.66±5.17 g, 10.52±0.27 cm, and 4.49±0.06%, respectively) values of red tilapia juveniles were significantly observed in T3, where the fish were exposed to 2 days of food deprivation (Table 4; P<0.05).

The FCR (mean±SEM, n=3) of red tilapia juveniles ranged from 1.41±0.09 to 1.64±0.04, with the best FCR (i.e., the lowest value) being observed in control (no starvation) compared to that of starved tilapia juveniles (1:6 or 2:5 CFRs). However, no significant difference was observed in the FCR of starved tilapia juveniles after 1 or 2 days of starvation (P>0.05). Moreover, no significant treatment effects were detected in the FC (P=0.610), PER (P=0.230), and Fulton's CF (P=0.488) of red tilapia juveniles at various CFRs (P>0.05; Tables 3-4).

Survival of red tilapia juveniles differed significantly among treatments (P=0.006), indicating that feeding regimes strongly influenced survival (Table 3). Tilapia juveniles fed T3 (2-day starvation) exhibited significantly higher survival (45.72±4.58%) than those fed continuously without fasting (control) or T3 (1-day starvation). However, no significant difference was observed in the survival of starved tilapia juveniles after 1 day of starvation (T2) compared with the control treatment (no starvation).

The correlations between growth performance (FBW, FBL, WG, LI, and SGR), feed utilization (FCR and PER) efficiency, and condition factor of red tilapia juveniles at different cyclic feeding regimes are shown in Figure 2. Correlation analysis revealed a strongly significant negative association between cyclic feeding regimes and FBW (r = –0.91), WG (r = –0.91), and SGR (r = –0.90), while it showed moderately significant negative correlation with FBL (r = –0.65), LI (r = –0.65), and PER (r = –0.62). FCR also exhibited significant negative correlations with FBW (r = –0.65), FBL (r = –0.74), WG (r = –0.65),

Table 5. Whole-body proximate biochemical composition (% dry matter) of red tilapia during and after the termination of the study.

Proximate composition [a]	Initial	Treatments		
		T1 (control)	T2 (1:6)	T3 (2:5)
Crude protein (%)	48.92	45.66	45.92	45.83
Crude lipid (%)	10.81	10.64	11.06	11.27
Crude fiber (%)	0.84	0.41	1.47	0.58
Moisture	11.46	14.00	14.23	13.52
Ash	24.93	28.10	26.08	26.66

[a] Analyzed values from the Department of Agriculture-Bureau of Animal Industry, Chemical and Feed and Analysis Section, CFAS Bldg., 5 Visayas Avenue, Diliman, Quezon City, Philippines.

Table 6. Water quality parameters of red tilapia reared in sea-based cage enclosures at different cyclic feeding regimes (CFRs). Values are the mean of three replicates.

Parameters	Treatments			*P*-value	Accepted level
	T1 (Control)	T2 (1:6)	T3 (2:5)		
DO (ppm)	6.04±0.02^{b}	6.02±0.01^{b}	6.24±0.02^{a}	0.0003	>5.0[1]
pH	7.86±0.00^{a}	7.85±0.01^{a}	7.81±0.04^{a}	0.306	6.5-9.0[1]
Salinity (ppt)	33.33±0.00^{b}	33.35±0.01^{ab}	33.40±0.02^{a}	0.045	20-35[2]
Temperature (^{0}C)	28.00±0.00^{a}	28.07±0.02^{a}	28.00±0.02^{a}	0.052	25-31[1]

* Mean values (expressed as means ±SEM) with different superscripts in the same column are significantly different (P<0.05).
[1] Water quality requirement for the propagation and growth of fish and other aquatic resources (DENR-DAO, 2016).
[2] Water quality requirements of farmed tilapia (Balarin and Haller, 1982).

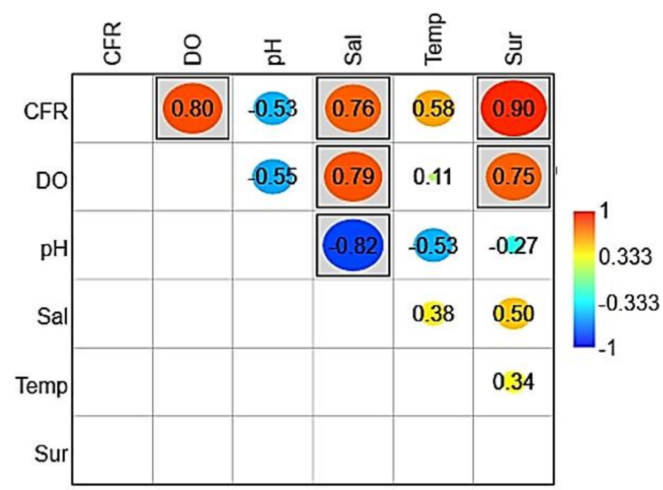

Figure 2. Correlogram of the water quality parameters and survival rate of red tilapia juveniles at various cyclic feeding regimes. Darker circles indicate stronger correlations (i.e., the color intensity ranging from −1 to 1), with red representing positive correlations and blue signifying negative correlations. Boxed values signify a significant correlation (P<0.05). Legend: CFR – Cyclic Feeding Regime, DO – Dissolved Oxygen, pH, Temp – Temperature, Sur – Survival Rate.

SGR (r = −0.63), and LI (r = −0.74). Further analysis indicated strong positive correlations of FBW with WG (r = 1.00) and SGR (r = 1.00). Similarly, FBL was strongly correlated with LI (r = 1.00). In addition, WG was strongly correlated with SGR (r = 1.00). Conversely, the PER demonstrated moderately significant positive correlations with FBW (r = 0.67), FBL (r = 0.69), WG (r = 0.67), SGR (r = 0.64), and LI (r = 0.69).

Fish carcass biochemical composition: The whole-body proximate composition of red tilapia juveniles subjected to different cyclic feeding regimes is presented in Table 5. Crude protein content decreased with increasing periods of starvation, ranging from 48.92 to 45.83% in T3 (Table 5). At the end of the study, crude protein levels in red tilapia following successive feed-deprivation periods appeared similar across treatments; however, this observation is inconclusive because statistical analysis was not performed due to insufficient replication. In contrast, crude fat (lipid) content increased with longer starvation periods, while ash tended to decrease at the end of the experiment. Fat levels returned to normal, with the highest value recorded in T3 (11.27%), exceeding the initial level, and the lowest in the control group (10.64%; Table 5). Moisture content also increased slightly as starvation duration increased, from 11.46 to 13.52%. Crude protein, crude lipid, and moisture data were not subjected to statistical analysis because of insufficient sample replication.

Water quality parameters: Daily mean values

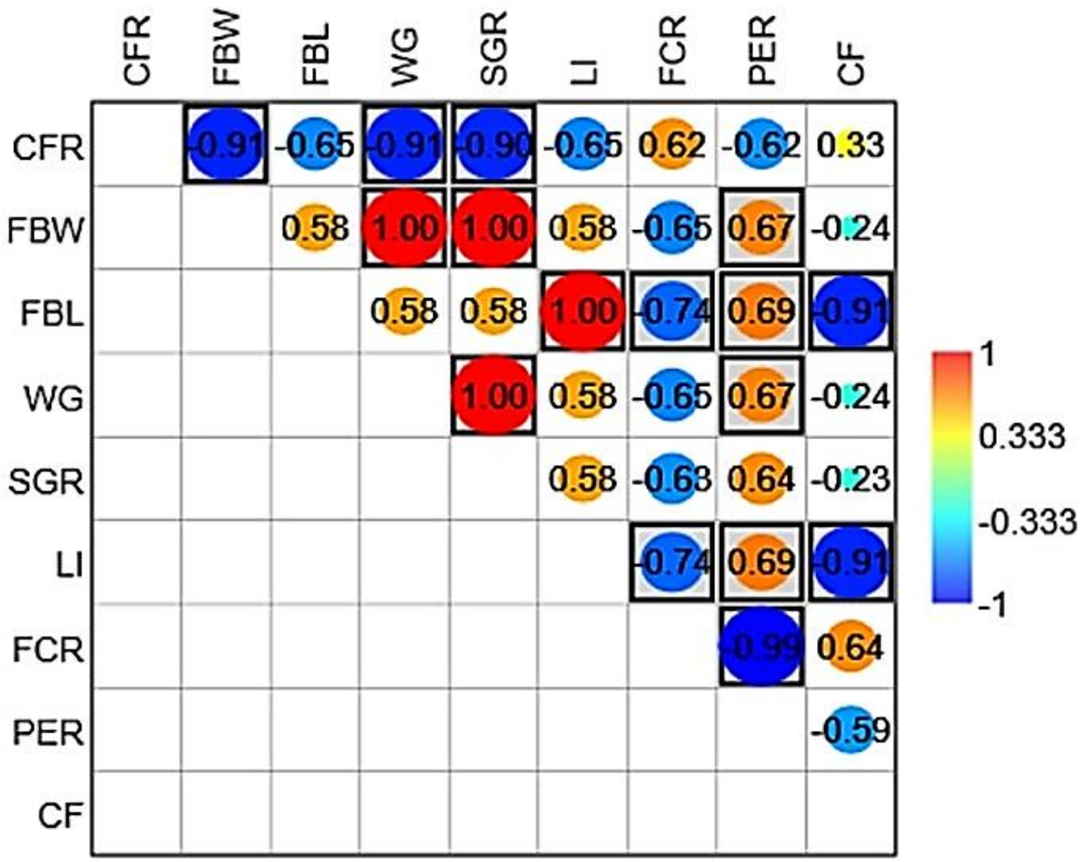

Figure 3. Pearson correlation matrix between growth performance and feed utilization efficiency of red tilapia juveniles at various cyclic feeding regimes. Darker circles indicate stronger correlations (i.e., the color intensity ranging from −1 to 1), with red representing positive correlations and blue signifying negative correlations. Boxed values signify a significant correlation (*P*<0.05). Legend: CFR – Cyclic Feeding Regime, FBW – Final Body Weight, FBL – Final Body Length, WG – Weight Gain, SGR – Specific Growth Rate, LI – Length Increment, FCR – Feed Conversion Ratio, PER– Protein Efficiency Ratio, and CF – Condition Factor.

(±SEM) and ranges of DO, pH, salinity, and temperature during the sea-based nursery production of red tilapia juveniles at various cyclic feeding regimes are summarized in Table 6. Water DO and salinity levels of red tilapia juveniles significantly differed among treatments (*P*<0.05). However, no significant differences were observed in water pH and temperature among various CFRs (*P*>0.05). DO was lowest in T2 than in the control; however, no significant differences were detected between the control and T2. As the period of starvation increased, pH declined, though the differences were not statistically significant (Table 6).

Correlation between survival rate and water quality parameters: The correlation between water quality parameters (DO, pH, salinity, and temperature) and the survival rates of red tilapia juveniles under different CFRs is presented in Figure 3. A strong positive correlation was observed between CFR and survival rate (r = 0.90), indicating that cyclic feeding schedules significantly influence juvenile survival. Moderate positive correlations were also found with dissolved oxygen (r = 0.80) and salinity (r = 0.76), suggesting that higher DO levels and stable salinity conditions may enhance survival during short-term feed deprivation. Salinity exhibited a moderate positive correlation with CFR (r = 0.76) and DO (r = 0.79), while showing a strong negative correlation with pH (r = –0.82). These relationships suggest that fluctuations in salinity and DO, coupled with reduced pH, can adversely affect survival. Thus, careful regulation of these parameters is essential to mitigate stress and mortality risks. Overall, the significant correlations (*P*<0.05) underscore the importance of managing both feeding regimes and water quality parameters in the sea-based production of red tilapia juveniles. Optimizing these factors can maximize survival, improve resilience during feed restriction, and support the sustainable culture of red tilapia juveniles in marine cages.

Discussions

Feeding is the primary means by which fish acquire external energy necessary for normal growth and development in aquaculture (Hidalgo et al., 2017). However, starvation followed by refeeding has been shown to exert strong effects on fish physiology and muscle growth (Navarro and Gutiérrez, 1995). In this study, the effects of starvation and subsequent CG through refeeding were evaluated by comparing the growth and feed utilization indices of the feed-restricted treatment groups during non-feeding days with those of the control group in red tilapia juveniles. Growth performance indices (FBW, WG, and SGR) of tilapia juveniles fed with T2 (1-day starvation) were comparable to those of fish fed continuously without fasting (control), but significantly higher than those of fish fed with T3 (2-day starvation). These results indicated that red tilapia juveniles in marine cages exhibited CG within one day of feed restriction once refeeding was initiated. No significant differences were observed in the FBW, WG, and SGR of tilapia juveniles in T2 and T1 (control) groups, but significantly higher than those of fish fed in T3, indicating that this species is capable of a full CG response following a short period (one day) of feed restriction. This growth pattern, commonly referred to as compensatory or “catch-up” growth (Russell and Wootton, 1992), enables the fish to attain a body size comparable to that of the control group.

The condition factor (CF) is a quantitative measure of fish health and overall physiological well-being, reflecting its influence on growth, reproduction, and survival (Richter, 2007); higher CF values generally indicate better physiological condition and greater growth potential (Froese, 2006; Keivany et al., 2015; Mouludi-Saleh and Eagderi, 2019; Abbasi et al., 2019). The CF of red tilapia juveniles was comparable across treatments, with starved groups exhibiting slightly higher CF values than the control. The absence of a significant difference in CF among all experimental groups further supports the occurrence of compensatory mechanisms (Känkänen and Pirhonen, 2009). CG typically follows a period of food restriction (Hayward et al., 1997). Feed restriction in fish often elicits a compensatory growth response, manifested as increased SGR, improved FCR, or both during the refeeding period (Ali et al., 2003). Such responses across various fish species have resulted in partial (Miglavs and Jobling, 1989b; Paul et al., 1995; Wang et al., 2005) or complete growth compensation (Jobling et al., 1999; Johansen et al., 2001; Maclean and Metcalfe, 2001; Ribeiro and Tsuzuki, 2010; Ali et al., 2016), with one study reporting overcompensation in hybrid bluegill, which significantly outgrew continuously fed controls after repeated two-day starvation and refeeding cycles (Hayward et al., 1997). However, no compensatory growth response was observed in common carp (*Cyprinus carpio*) after refeeding following a period of food restriction (Schwarz et al., 1985). Similarly, varying results have been reported in tilapia species, including complete CG in *O. niloticus* (Passinato et al., 2015), partial compensation in hybrid tilapia (*O. mossambicus* × *O. niloticus*) (Wang et al., 2000), and no CG in *O. niloticus* (Gao et al., 2015).

In the present study, following a 60-day feeding trial, no significant differences were observed in feed utilization efficiency (FCR and PER) between the control and T2. This result has important cost-saving implications, as it indicates reduced feed input without compromising growth, given that the FBW, WG, and SGR of the control group were not significantly different from those of fasted fish (i.e., 1:6). These findings clearly demonstrate complete growth compensation, as evidenced by similar FBW, WG, SGR, and FCR between T1 and T2, but relatively superior than T3. Complete compensation occurs when fish previously subjected to food restriction attain the same body weight as those that were continuously fed (Kim and Lovell, 1995; Nicieza and Metcalfe, 1997; Jobling et al., 1999; Ribeiro &and

Tsuzuki, 2010). Consistent with the present findings, Abdel-Hakim et al. (2009) observed full CG in hybrid tilapia (*O. niloticus* × *O. aureus*) subjected to one- or two-day weekly feed deprivation. These researchers further noted that moderate feed restriction (1-2 days per week) significantly reduced feeding costs without impairing growth compared to continuous feeding. Likewise, complete CG has been documented in Nile tilapia (*O. niloticus*) (Cuvin-Aralar et al., 2012; Passinato et al., 2015) and in barramundi (*Lates calcarifer*) under various feed restriction–refeeding regimes (Tian and Qin, 2003, 2004).

Although the selected treatment groups experienced periods of starvation, red tilapia juveniles' feed consumption remained relatively consistent across treatments, with no significant differences from the control. This finding indicates that additional feed was consumed during episodes of hyperphagia; however, the extra intake did not translate into enhanced growth, unlike observations reported in other studies (Hayward et al., 1997). Higher daily feed consumption in starved fish (T2) than in the control (T1) upon resumption of feeding is a behavioral trait known as hyperphagia, in which previously starved animals consume excessively beyond normal levels (Jobling, 1994). In this study, hyperphagia was observed only in the short term, lasting about one day. Feed consumed in T2 was higher than in the control. This suggests that fish starved for one day require a 1% higher feed ration than is normally provided to catch up with the growth of continuously fed fish. Hyperphagia is commonly observed during CG (Rueda et al., 1998; Saether and Jobling, 1999; Wang et al., 2000; Tian and Qin, 2003) and is often accompanied by rapid growth and improved feed efficiency. In some cases, however, starved animals have demonstrated improved feed efficiency without exhibiting hyperphagia (Jobling, 1994). In some cases, fish have responded to various feed deprivation–refeeding protocols by improving feed efficiency (Jobling et al., 1994; Qian et al., 2000; Li et al., 2005). However, in most studies, no significant differences in feed efficiency were observed between treatment groups and controls (Hayward et al., 1997; Miglavs and Jobling, 1989a; Xie et al., 2001; Nikki et al., 2004; Wang et al., 2005). In some instances, improvements in feed efficiency were only temporary (Miglavs and Jobling, 1989b; Hayward et al., 1997), variable depending on the duration of feed restriction (Eroldogan et al., 2006a), or were even lower than those of control fish (Eroldogan et al., 2006b).

In this study, the red tilapia juveniles showed no differences in overall feed utilization efficiency indices (PER and FCR), indicating that compensation for feed deprivation occurred primarily through increased consumption when feed was available. However, unlike the earlier findings of Cho (2005), improvements in feed efficiency during CG were not detected in this study. Similarly, no enhancement in feed efficiency was observed in fish that achieved CG, consistent with previous reports in other fish species (Wang et al., 2000; Tian and Qin, 2003; Zhu et al., 2004). Hyperphagia has also been cited as a primary mechanism for growth compensation in previous studies (Jobling et al., 1994; Rueda et al., 1998; Wang et al., 2000, 2004; Tian and Qin, 2004; Cho et al., 2006), with the hyperphagic response being most pronounced during the first day of refeeding and particularly after multiple cycles of feed restriction and refeeding (Hayward et al., 1997; Ali and Wootton, 2001; Wu et al., 2002). This pattern was likewise evident in the red tilapia juveniles exposed to T2 (starved for one day) in the present experiment. In this study, feed consumption of starved red tilapia juveniles did not differ significantly from that of the control, likely due to hyperphagic behavior in the fed-deprived groups. Similar hyperphagic responses have been documented in other fish species attaining CG (Wang et al., 2000, 2004; Tian and Qin, 2004; Zhu et al., 2004; Cho, 2005; Cho et al., 2006). The present study corroborates earlier findings on CG in tilapia subjected to feed deprivation, confirming that hyperphagia is the primary mechanism underlying this species' CG response (Wang et al., 2000, 2004; Tian and Qin, 2004).

The duration of feed deprivation also influenced the extent of CG in this study. Fish subjected to longer periods of starvation exhibited slower growth compared to those deprived for shorter durations (i.e., 1:6 cyclic feeding). Previous studies have demonstrated that CG depends on both the severity and duration of feed restriction (Jobling et al., 1993). Larger fish may require extended periods of nutritional stress before the deprivation becomes sufficiently severe to induce a CG response (Jobling et al., 1994). Shorter periods of feed deprivation and longer refeeding durations have been shown to result in full growth compensation (Miglavs and Jobling, 1989a; Chatakondi and Yant, 2001; Hayward and Wang, 2001; Johansen et al., 2001). In the current experiment, the red tilapia juveniles exposed to a shorter deprivation period (1:6 CFR) exhibited growth (FBW, WG, and SGR) and feed utilization efficiency (FCR and PER) values that were statistically comparable to those of the control group at the end of the feeding trial. Thus, a single day of feed deprivation was sufficient to elicit a measurable CG in red tilapia juveniles. CG offers a practical strategy to enhance fish growth rates by appropriately alternating periods of feed deprivation with subsequent phases of satiation. When properly implemented, this technique can offset growth losses incurred during starvation and provides an opportunity for fish to recover once feeding resumes (Ali et al., 2016).

A decline in carcass protein among starved fish at the end of the experiment was similarly reported by Satoh et al. (1984) in adult Nile tilapia (*O. niloticus*) fasted for 60 days. Crude lipid and moisture content did not follow a consistent pattern, but they tended to increase with longer periods of feed deprivation. This suggests that muscle lipids were progressively replaced by water as starvation duration increased (Ali et al., 2016). In some previous studies, lipid percentages of fish have been reported to increase during the first two weeks of starvation (Martinez et al., 1994; Rueda et al., 1998). Moreover, similar to these studies, the body lipid content of barramundi, *Lates calcarifer*, increased with longer feeding durations or higher feed allowances (Tian and Qin, 2004). Rueda et al. (1998) reported that during the early phase of starvation (up to two weeks), red porgy, *Pagrus pagrus*, appeared to mobilize protein to a greater extent than lipids. In later stages, however, lipid mobilization became more pronounced when fish were refed following 1-, 2-, 3-, or 4-week periods of feed deprivation. The increase in lipid content observed in fish exposed to prolonged fasting may be associated with physiological and metabolic adjustments that occur during starvation and compensatory refeeding. During feed deprivation, fish utilized stored energy reserves to maintain essential physiological functions. Upon refeeding, compensatory metabolic responses may enhance lipid deposition as the fish attempt to restore depleted energy reserves. Similar findings were reported by Rueda et al. (1998) and Ali et al. (2016), who observed increased lipid accumulation following periods of feed restriction and subsequent refeeding.

High mortalities across all treatments, including the control, may be attributed to elevated salinity levels (33.33-33.40 ppt) at the experimental sites, as well as cyclic feeding schedules, which significantly affect the survival of red tilapia juveniles. Red tilapia has been reported to tolerate full-strength seawater with salinity levels up to 32 ppt (Jaspe and Caipang, 2011). Mortality could also have been influenced by stress associated with frequent physical handling during periodic weighing. In this study, tilapia juveniles exposed to T3 (2-day starvation) exhibited significantly higher survival than those fed continuously (control) or under T1 (1-day starvation). Fish exposed to 2:5 CFR and receiving suboptimal feed exhibited reduced growth, as stored energy was mobilized to extend their survival (El-Araby et al., 2020). Previous studies have documented that fish reallocate their energy reserves to sustain essential tissue functions and survival during periods of starvation (Finstad et al., 2010; Stallings et al., 2010; Giacomini and Shuter, 2013). This energy was replenished after refeeding, leading to compensatory growth and recovery of body weight (Yang et al., 2019). However, no significant difference in survival was observed between tilapia juveniles subjected to one day of starvation (T2) and those in the control group (continuous feeding), indicating that 1-day starvation did not compromise the survival or growth of tilapia juveniles.

Conclusion

Cyclic feeding successfully elicited a CG response in red tilapia juveniles under short-term feeding deprivation (1-day starvation) and refeeding (6 days), comparable to the continuously fed control group. Fish exposed to the 1:6 CFR exhibited final weight, weight gain (WG), specific growth rate (SGR), and feed conversion ratio (FCR) values that were statistically comparable to those of the continuously fed control group. Based on the results of the present study, complete growth compensation was observed in the 1:6 CFR. Catch-up growth occurred earlier and progressed more rapidly in fish exposed to shorter starvation periods than in those exposed to longer periods. Juveniles recovered from short-term starvation without reductions in FBW, WG, SGR, or FCR. These findings suggest that red tilapia juveniles can withstand a one-day feed deprivation without significant adverse effects on growth performance and feed utilization efficiency. However, studies extending beyond 60 days are necessary to validate this observation. The capacity of tilapia juveniles to adapt to CG after a short period of feed deprivation may prove advantageous and cost-effective for aquaculture operations, especially in unforeseen circumstances (e.g., severe weather events or feed shortages) that temporarily disrupt continuous feeding. This cyclical feeding strategy enables fish farmers to achieve comparable harvest yields while reducing feed input. This practice can enhance the economic efficiency of fish culture by lowering production costs (e.g., labor and feed) without compromising fish growth performance. Therefore, in commercial fish farms, feed delivery may be restricted to one working day per week, followed by six consecutive days of feeding. This strategy offers clear economic benefits, as total feed consumed after the refeeding period can be comparable between feed-restricted and unrestricted treatments. However, overall operational expenses are reduced, particularly labor and feed costs associated with daily feeding activities.

Ethics statement

Ethical review and approval were not required for this study involving fish, as it adheres to internationally accepted ethical standards, local legislation, and institutional requirements for the humane handling and treatment of aquatic animals in research. All experimental procedures were conducted following the Philippine National Standard (PNS) on the Code of Good Aquaculture Practices (GAqP) for Milkfish and Tilapia (PNS/BAFS 196:2017; BAFS, 2017). Rearing, handling, and animal welfare protocols were strictly followed in accordance with the ethical standards set forth in the Philippine Republic Act Number 8485, otherwise known as the Animal Welfare Act of 1998. Moreover, the study adhered to standard protocols to safeguard animals from unnecessary harm or distress (American Psychological Association, 1986).

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