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Effect of different feeding regimes in amur common carp fingerlings: compensatory growth, physio-metabolic responses, and expression of IGF-1 gene

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Abstract – The experiment was intended to evaluate the competent restricted feeding strategy for amur common carp fingerlings reared under actual pond condition. Fingerlings (2.28 ± 0.27 g) were subjected to five different restricted feeding regimes; viz. TC (daily feeding), T1/1 (1-day feeding/ 1-day starvation), T2/1 (2-days feeding/ 1-day starvation), T2/2 (2-days feeding/ 2-days starvation), and T1/2 (1-day feeding/ 2-days starvation). The results indicated significantly similar ($P > 0.05$) growth pattern in T2/1, when compared to TC. But in other feed-deprived groups the fish growth was much poor. In T2/1, the feeding strategy had no significant adverse effect on SGR; rather it supported improved nutrient utilization indices. T2/1 asserted superior digestive capacity in the starved group, with elevated ($P < 0.05$) protease and amylase activity. Reduced ($P < 0.05$) hepatic lactate dehydrogenase and malate dehydrogenase activity in T2/1 group suggests reduced stress, which might strengthen compensatory growth. Feed deprivation increased ($P < 0.05$) both alanine aminotransferase and aspartate aminotransferase activity in blood. In the current study, elevated ($P < 0.05$) level of hepatic superoxide dismutase, catalase, glutathione peroxidase activity and Insulin like growth factor 1 and reduced ($P < 0.05$) blood glucose level, parallel to the degree of starvation was also evidenced. The present study suggests that 2-day feeding followed by 1-day feed restriction (T2/1) as the best feeding strategy for pond culture of amur common carp with the highest net return without compromising the growth, yield and antioxidative status.

Keywords: Amur common carp / feeding strategy / periodic starvation / nutritional stress / antioxidative status / compensatory growth

1 Introduction

Aquaculture provides approximately half of the world's animal-based protein requirements through the most cost-effective protein-rich product, fish (FAO, 2022). In the evolution of modern intensive fish culture practices, fish feed utilization efficacy is regarded as an important controlling factor of aquaculture production efficiency, resolving growth and nutrient deposition in fish carcass (Ali et al., 2018; Maiti et al., 2023).

Feed is the most expensive component of an aquaculture enterprise, accounting for more than 40–60% of the functional variable cost, which is determined by the intensity of fish production (Jana et al., 2022). As a result, it is crucial to optimize the feeding rate to satiate the energy demand concomitant with growth performance of fish (Jana et al., 2021a). Hence, successful fish culture cycle requires optimization of feeding practices to optimize the production of fish in a cost-effective manner (Saha et al., 2021). Frequent feeding of fish may not be cost-effective or easy for farmers due to multiplied costs from a management standpoint (Riche et al., 2004). Therefore, it is equally significant to realize the growth pattern and nutritional requirements of culture species (Jana et al., 2021b; Paul et al., 2023).

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Trimming down feed expenses for culture practices in real approach can be triumphed by grabbing the advantage of restricted feeding tactics and concept of compensatory growth (Mohanta et al., 2017). The theory assumes that there is a genetically preordained growth trail in all animals, and animals can sense rebounds from this trajectory and compensate for them by readjusting appetites and metabolism (Xie et al., 2001; Yengkokpam et al., 2014). In a far-reaching logic, feeding restriction speaks up for the compensatory growth. Despite a positive correlation between the feeding frequency and growth (Riche et al., 2004; Riche 2008), Crampton (1991) reported that it may not be mandatory to feed fish daily to achieve the highest growth rate. De Silva and Anderson (1994) observed that beyond a certain level, surplus feeding consigns no influence on fish growth and result in deprived growth. Excess feed ingestion beyond what the fish really needs triggers a worse feed conversation ratio (FCR) (Sardar et al., 2008). Expression of the phenomenon of compensatory growth utilizes a wide choice of feeding restriction and re-feeding protocols amongst fish species habitually associated with a variety of physiological responses (Yengkokpam et al., 2013; Das et al., 2016; Dar et al., 2018a; Dar et al., 2018b).

Being an improved strain of wild common carp of Hungarian origin (Basavaraju et al., 2003), amur common carp (*Cyprinus carpio haematopterus*) has a greater practical connotation in low-input aquaculture systems. Amur common carp possesses better growth performance, late maturity, and accepts artificial feed as well as bares similar food habit to that of existing stock (Basavaraju and Reddy 2013; Anand et al., 2020). In Indian freshwater aquaculture system, amur common carp has already been established as an emerging species, which has almost replaced the existing common carp (*Cyprinus carpio*) strain. With this backdrop, the present study was conducted to find out a restricted feeding strategy for the successful and sustainable culture of amur common carp based on growth metrics, physio-metabolic and antioxidative status, and mRNA expression of insulin like growth factor 1 (IGF-1) gene.

2 Materials and methods

2.1 Ethics statement

The present research undertaken complies with the current guidelines of the Animal Ethics Committee of West Bengal University of Animal and Fishery Sciences, Kolkata, West Bengal, India.

2.2 Experimental setup and feeding

The experiment was carried out for 120 days in the Hatchery Complex of Department of Aquaculture, Faculty of Fishery Sciences, West Bengal University of Animal and Fishery Sciences (22°28′46″N 88°24′4″E) with 5 different batches of treatment, viz., TC (daily feeding), T1/1 (cycle of 1-day feeding and 1-day starvation), T2/1 (cycle of 2-days feeding and 1-day starvation), T2/2 (cycle of 2-days feeding and 2-days starvation), and T1/2 (cycle of 1-day feeding and 2-days starvation) following a completely randomized block (CRD) design.

It is well understood that the natural food web in earthen ponds, including plankton and benthos, contributes to nutrition and growth of fish. However, this study aimed to evaluate the effects of a short-term restricted feeding schedule using commercial floating feed, given the increasing reliance on commercial diets in aquaculture practices in West Bengal, India. To address potential biases due to natural food, the study was designed with the following considerations.

Controlled Lab Phase:

Initial experiments were conducted in fibre glass reinforced plastic (FRP) tanks without a soil base to eliminate contributions from plankton or benthos. This ensured that the growth data solely reflected the effects of the commercial feed under different restricted feeding conditions.

Earthen Pond Phase:

In the subsequent pond trials, no fertilizers or plankton growth promoters were used during pond preparation or the study period. This was a deliberate effort to minimize the influence of primary productivity on growth data. However, effect of natural food cannot be completely eliminated in such systems, these measures significantly reduced its impact of natural food items in the present experiment.

For each treatment, one earthen freshwater pond of 150 m^2 surface area and 1.5 m depth was selected, and each pond was divided into 3 equal parts to get the result in triplicates. Two nylon nets (0.5 mm mesh size) were fixed inside the pond in such a way that no fish could pass through the nets. The ponds were fully drained and dried for 2 weeks. After that the soil was ploughed manually and the ponds were filled with ground water maintaining 1.5 m water depth. All the ponds were surrounded by nylon mosquito net at periphery and covered with monofilament bird fence.

Two thousand healthy fingerlings of amur common carp were brought from Sahu Fish Farm, Sonarpur, North 2r Parganas, West Bengal in oxygen filled plastic bags. After giving initial prophylactic treatment with potassium permanganate (5 ppm), fish were acclimatized for two weeks in 1000 L circular FRP (fiber glass reinforced plastic) tanks filled with 800 L water provided with continuous aeration. Each replicate of treatments was stocked with 50 numbers of amur common carp fingerlings (average body weight 2.28 ± 0.27 g) and fed with commercial carp diet (GROWFIN STARTER, Growel Feeds, India, 1.5 mm diameter) thrice a day at the rate of 5% of the body mass. The diet contained 28.13% crude protein, 6.42% crude lipid, 6.22% crude fibre, 3.86% ash, 5.80% moisture content and 49.57% nitrogen free elements on dry matter basis. The daily ration was split into three portions and dispersed at a certain corner of the ponds by hand broadcasting (9:00, 13:00 and 17:00 hrs) (Karmakar et al., 2021) for the entire experimental period of 120 days.

2.3 Survival and growth

Survival and growth parameters were calculated as follows (Debroy et al., 2022):

- Body weight gain (g) = FW (g) − IW (g)
- Specific growth rate (SGR, %/day) = 100 [{Ln (FW)–Ln (IW)}/D]
- Feed conversion ratio (FCR) = Dry feed consumed by fish (g)/ Wet weight gain of fish (g)
- Feed conversion efficiency (FCE) = Body weight gain (g)/ Feed intake (g)

– Protein efficiency ratio (PER) = Body weight gain (g)/ Protein fed (g)
– Survival rate (%) = Number of survived fish / Number of fish stocked.

where, FW=Final weight, IW=Initial weight, D= Duration of experiment (Day).

2.4 Sample collection

Before collecting blood and tissue samples, each fish was anesthetized with 50 µl of clove oil per litre of water. Blood was drawn from the vena caudalis with a dispovan single use 2 ml syringe without anticoagulant and allowed to clot for 2 hrs at 4°C. The supernatant was then collected with a micro-pipette and centrifuged at 5000 rpm at 4°C for 10 min using a cooling centrifuge (ThermoFisher Scientific, USA). Serum samples were collected and stored at −40 °C till analysis (Maiti et al., 2023).

Fish were sacrificed after sedation to collect liver and intestine samples. Samples were carefully collected and weighed in triplicate from each treatment and pooled. To prepare a 5% (1:19 w/v) homogenate, tissues were homogenised in a chilled 0.25 (M) sucrose solution. To avoid enzyme reactions, the tube was kept on ice at all times. To obtain the supernatant for enzyme analysis, the homogenate was centrifuged at 12000 rpm for 10 min at 4 °C. All supernatants were kept at −40 °C until further analysis (Karmakar et al., 2021).

2.5 Enzyme assay

Tissue protein was estimated according to Bradford (1976) and obtained values were employed for calculation of activity of enzymes.

To determine the protease activity, the casein digestion method was used (Drapeau. 1976). Amylase activity was assessed following the methods explained by Rick and Stegbauer (1974). Using the Di-nitro Salicylic Acid (DNS) technique, the amount of reducing sugars produced by glucoamylase and alpha amylase action on carbohydrates was calculated. The lipase activity was assayed following the method described by Cherry and Crandell (1932).

Lactate dehydrogenase (LDH) activity in liver tissues was measured using the method of Wroblewski and Ladue (1955) and expressed as units/min/mg protein. The Ochoa approach (1955) was used to measure malate dehydrogenase (MDH) activity in the liver. MDH activity was expressed as units/min/mg protein.

ALT (alanine aminotransferases) kit, Modified UV (IFCC), Kinetic assay; Span Diagnostics Ltd., India was used to measure ALT activity in blood. Whereas, aspartate aminotransferases (AST) activity was estimated by AST test kit, Modified UV (IFCC), Kinetic assay; Span Diagnostics Ltd., India. Both the activity was measured according to recommendations of the test kit manufacturer and expressed as IU/L.

The activity of superoxide dismutase (SOD) was assessed using the Misra and Fridovich (1972) method. This assay is based on the enzyme, oxidising the epinephrine–adrenochrome transition. The catalase activity was evaluated by measuring the quantities of hydrogen peroxide drop at 240 nm (Takahara et al., 1960). The enzyme activity was measured in nanomoles (nM) of H_2O_2 decomposed/min/mg of protein. Hepatic glutathione peroxidase (GPx) activity was estimated following the method of Hafeman et al. (1974). GPx activity was measured in nanomoles of H_2O_2 decomposed/min/mg of protein.

2.6 Blood serum glucose

Serum glucose level was assessed following the method of Nelson and Somogyi (1945) as defined by Oser (1965) and expressed as mg/dL.

2.7 Expression of insulin like growth factor-1 (IGF-1) gene

2.7.1 RNA extraction and synthesis of single-strand cDNA

Liver tissue (100 mg) was used for total RNA isolation by using 1 ml TRIzol (Invitrogen, USA) reagent following the manufacture's protocol. Nano-Drop spectrophotometer (Thermo scientific, USA) was used to check the concentration and purity (260/280) of RNA. Electrophoresis was done to confirm the relative quantity and integrity of RNA Before cDNA synthesis, the isolated total RNA was treated with RNase free DNase I (Invitrogen, USA). Commercial cDNA synthesis Kit (iScriptTMcDNA Synthesis Kit, BIO-RAD, USA) was used to carry out the reverse transcription by using Oligo-dT as primer. Nano-Drop spectrophotometer (Thermo-scientific, USA) was used to check the concentration and purity (260/280) of product of the single-strand cDNA synthesis and the product was stored at −80 °C until the quantitative RT-PCR (qRT-PCR) was performed.

2.7.2 Primer designing

The design of RT-qPCR primers was done using the GeneRunner software and then the stability was assessed by checking of primer-dimer formation and self-binding. As reference or housekeeping gene, β-actin was used. The primers for β-actin and insulin like growth factor-I (IGF-I) were designed from the reported sequence of common carp (Tab. 1). All the designed RT-qPCR primers were purchased from Eurofins Genomics India Pvt. Ltd (Bangalore, India).

2.7.3 Quantitative real time PCR for mRNA expression

Quantification of hepatic IGF-I gene was done in an AriaMx Real-Time PCR System (Agilent Technologies, USA). 5 µl of SYBR Green qPCR Master Mix (BIO-RAD, USA), 1 µl of each gene specific primer, 1 µl of cDNA and 3 µl of nuclease free water were mixed to make a 10 µl reaction volume for the quantification. The RT-qPCR was programmed for 40 cycle's reactions each of which includes denaturation at 95 °C for 15 s, annealing at 60 °C for 30 s and extension at 72 °C for 30 s. The quantified value of mRNA was presented in terms of CT (threshold cycle) value. At the end of each PCR reaction, melting curve analysis of the amplified products was performed. The relative expression of mRNA (IGF-1) was calculated by following $2^{-\Delta\Delta CT}$ method

Table 1. Primers used for real-time PCR.

Primer name	Forward primer (5'-3')	Reverse primer (5'-3')	Reference
Beta actin (β-actin)	AGACATCAGGGTGTCATGGTTGGT	AAGGTGTGATGCCAGATCTTCTC	Anand et al. (2020)
Insulin like growth factor-1 (IGF-1)	CAGAAAGCCGACCCAATGAG	GGCCTTTCTCCTCCATTCCT	

β-actin as housekeeping gene; IGF-1 as target gene.

Table 2. Growth metrics and feed utilization of amur common carp fingerlings reared in pond for 120 days.

Variables	Treatments[1]				
	TC	T1/1	T1/2	T2/1	T2/2
Survivability (%)	96.67 ± 1.15^{c}	94.67 ± 1.15^{bc}	91.33 ± 1.15^{a}	97.33 ± 2.31^{c}	93.33 ± 1.15^{ab}
Weight Gain (g)	204.76 ± 15.55^{c}	158.65 ± 7.49^{b}	117.63 ± 4.09^{a}	193.4 ± 16.65^{c}	154.45 ± 9.51^{b}
Length Increment (cm)	20.06 ± 0.67^{c}	17.92 ± 0.36^{b}	15.62 ± 0.26^{a}	19.56 ± 0.75^{c}	17.68 ± 0.42^{b}
SGR	3.08 ± 0.06^{cd}	2.59 ± 0.07^{b}	2.28 ± 0.05^{a}	2.97 ± 0.07^{c}	2.51 ± 0.04^{b}
FCR	1.11 ± 0.09^{d}	0.64 ± 0.06^{b}	0.45 ± 0.06^{a}	0.82 ± 0.13^{c}	0.64 ± 0.08^{b}
FCE	0.90 ± 0.07^{a}	1.57 ± 0.15^{b}	2.24 ± 0.28^{c}	1.24 ± 0.19^{ab}	1.59 ± 0.21^{b}
PER	2.22 ± 0.25^{a}	2.60 ± 0.15^{c}	2.99 ± 0.19^{d}	2.44 ± 0.07^{b}	2.68 ± 0.09^{c}

Data is expressed as Mean ± SD ($n = 30$). Row wise altered superscript statistically implies significant difference ($P < 0.05$).
[1] TC (daily feeding), T1/1 (1-day feeding/ 1-day starvation), T2/1 (2-days feeding/ 1-day starvation), T2/2 (2-days feeding/ 2-days starvation), and T1/2 (1-day feeding/ 2-days starvation).

(Livak and Schmittgen, 2001) where β-actin was used as reference gene.

ΔCT= target gene CT value − reference gene CT value

ΔΔCT value = ΔCT value of treatment group − ΔCT value of control group.

2.8 Production economics

The production economics of each treatment was analyzed by using a simple algebraic equation. A net return and profit margin analysis was performed based on the price of inputs in the market and the selling prices of fish. The equation was as follows:

Net return = Sales revenue − (Fixed cost + Variable cost + Interest on input).

2.9 Statistical analysis

After checking the homogeneity of variance, the data were subjected to one-way analysis of variance (ANOVA) using SPSS Version-22.0. Duncan's multiple range test (DMRT) with post hoc analysis was performed to find out the significant differences among means at 5% probability level ($P < 0.05$). The analysed data were expressed as arithmetic mean ± standard deviation (SD). Correlation co-efficient (r) was also determined to establish relationship between selective parameters. All analyses were performed using the statistical software SPSS 16 version.

2.10 Multi-criteria decision analysis by Analytical Hierarchy Process (AHP)

The suitability of those restricted feeding strategies was estimated following Analytical Hierarchy Process (AHP). Using Saaty (1994) technique the weightage and ranking of each criterion and sub-criteria were estimated. Pair-wise Comparison Matrix (PCM) was made on the growth parameters, enzymatic/biochemical sub-criteria and economic sub-criterion. In case of enzyme/biochemical assay, weightage of 0.2 was assigned for each sub-criterion, as they were concerned equally significant for the assessment. Since, only net profit was selected as economic criterion, there was no need for weightage assignment.

Another PCM was created to set the priority among growth, enzyme/biochemical assay, and economics. Finally, performance score was evaluated as the sum of the weighted normalised value of each criterion of the final Weighted Decision Matrix.

3 Results

3.1 Growth parameters

It was evident that periodic starvation had significant impact over survival of amur common carp fingerlings. T2/1 had the highest ($P < 0.05$) survival rate, followed by TC, T1/1, T2/2, and T1/2 (Tab. 2). However, regardless of treatment,

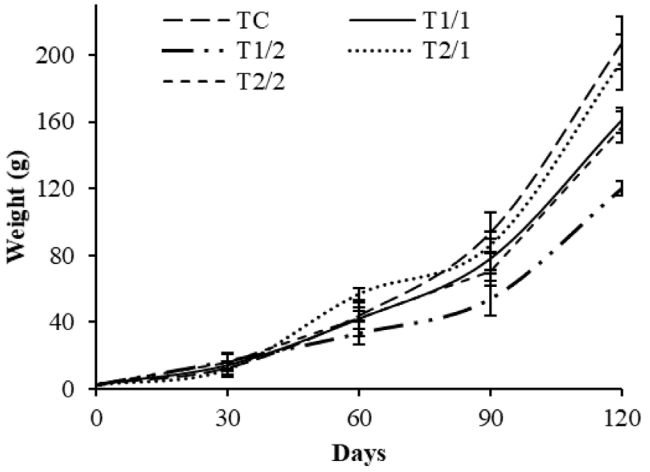

Fig. 1. Monthly alterations in body weight (g) of amur common carp fingerlings (Mean ± SD, $n = 30$) in experimental groups.

overall survivability was always greater than 90%. Monthly changes in body weight of amur common carp fingerlings are presented in Figure 1. Feed deprivation had an ample influence on growth of amur common carp fingerlings. Since, the fishes were fed on a regular basis, they grew the fastest in TC. However, when deprived groups were compared to control, growth of fish in terms of body weight gain and length increment in T2/1 was found significantly similar. In contrast, fish growth was extremely poor in other deprived groups. 1-day starvation followed by 2 consecutive days of feeding had no significantly adverse effect on SGR when compared to the fishes fed daily, as no significant disparity between TC and T2/1 was obtained (Tab. 2). FCR values in all the deprived groups were found to be lesser than in control group. T1/2 had the lowest FCR value, followed by T1/1, T2/2, T2/1, and TC, in that order. Though overall differences among the treatments remained noteworthy ($P < 0.05$), but no significant dissimilarity was evidenced between T1/1 and T2/2 during the experiment (Tab. 2). In this present investigation, the feed conversion efficiency (FCE) was truly affected by feeding strategy. All of the starved groups had higher FCE than the control group, with T1/2 having the highest FCE value (Tab. 2). The highest PER value was found in T1/2 followed by T2/2, T1/1, T2/1, and TC respectively (Tab. 2). The overall differences among the treatment groups remained significant ($P < 0.05$), but no significant difference was noticed between TC and T2/1, as well as among T1/1, T2/1 and T2/2 during the experiment.

3.2 Digestive enzyme assay

In the current experiment, starvation had a significant ($P < 0.05$) influence on protease activity, with the relationship being that the higher the starvation, the lower the protease activity. However, the highest ($P < 0.05$) level of protease activity was found in fish subjected to T2/1, followed by TC, T1/1, T2/2, and T1/2 (Tab. 3). Amylase activity was significantly influenced by periodic starvation and followed a similar trend to protease activity. But the current study did not find any evidence of a significant ($P > 0.05$) effect on lipase activity (Tab. 3).

Table 3. Digestive enzyme activity of pond reared amur common carp fingerlings for 120 days.

Treatments[1]	Protease[2]	Amylase[3]	Lipase[4]
TC	19.97 ± 1.06^{c}	10.86 ± 0.82^{c}	0.346 ± 0.021
T1/1	11.2 ± 1.17^{b}	9.53 ± 0.87^{bc}	0.333 ± 0.006
T1/2	8.38 ± 1.35^{a}	7.61 ± 0.76^{a}	0.332 ± 0.007
T2/1	24.76 ± 0.74^{d}	13.38 ± 0.86^{d}	0.347 ± 0.006
T2/2	10.71 ± 0.86^{b}	9.12 ± 0.63^{b}	0.335 ± 0.009

Data is expressed as Mean ± SD ($n = 30$). Column wise altered superscript statistically implies significant difference ($P < 0.05$).
[1] TC (daily feeding), T1/1 (1-day feeding/ 1-day starvation), T2/1 (2-days feeding/ 1-day starvation), T2/2 (2-days feeding/ 2-days starvation), and T1/2 (1-day feeding/ 2-days starvation).
[2] Protease activity is denoted as μM of tyrosine released/mg protein/min.
[3] Amylase activity is denoted as μM of maltose released/mg protein/min.
[4] Lipase activity is denoted as units/mg protein.

3.3 Metabolic enzyme assay

Various metabolic enzyme activities in liver tissue of the test fishes are portrayed in Table 4. Both hepatic LDH and MDH activity have been found to be significantly ($P < 0.05$) thematic with feeding strategies. They showed a direct relationship with starvation. TC and T2/1 did not indicate any statistical difference between them in terms of LDH activity. Whereas, no significant dissimilarities in MDH activity were found amongst T1/1, T2/1, and T2/2. ALT and AST activity were also significantly affected by periodic feed deprivation. The feed-deprived groups experienced increased ($P < 0.05$) ALT and AST activity in blood, which was proportional to the degree of feed deprivation.

3.4 Anti-oxidative enzyme assay

Periodic starvation increased ($P < 0.05$) the hepatic SOD activity of the test fishes in T2/2 and T1/2. But an inferior SOD activity was achieved in T1/1 and T2/1 when compared to control (Tab. 5). In case of catalase activity, all the feed-deprived groups experienced an elevated ($P < 0.05$) value in the liver tissue of amur common carp except T2/1 (Tab. 5). The interaction between periodic starvation and oxidative stress influenced the hepatic GPx activity of amur common carp. GPx activity exhibited a direct relationship with the degree of feed deprivation (Tab. 5). However, the statistical difference remained highly significant ($P < 0.001$) among the treatments for all the anti-oxidative enzyme activity.

3.5 Blood serum glucose

In the present study, starvation had a notable influence ($P < 0.05$) on blood glucose level of amur common carp. However, the highest blood glucose level was found in TC followed by T2/1, T1/1, T2/2, and T1/2. However, the difference among the treatments was eminently significant ($P < 0.001$) (Fig. 2).

Table 4. Metabolic enzyme activity of pond cultured amur common carp fingerlings for 120 days.

Treatments[1]	LDH[2]	MDH[3]	ALT[4]	AST[5]
TC	1.25 ± 0.11^{a}	3.59 ± 0.23^{a}	12.25 ± 0.25^{a}	50.63 ± 0.27^{a}
T1/1	2.44 ± 0.12^{b}	4.46 ± 0.34^{b}	16.39 ± 0.18^{c}	70.19 ± 0.96^{d}
T1/2	4.45 ± 0.46^{c}	5.27 ± 0.22^{c}	18.65 ± 1.12^{e}	101.09 ± 0.39^{e}
T2/1	1.63 ± 0.08^{a}	4.06 ± 0.16^{b}	14.28 ± 0.23^{b}	53.5 ± 0.44^{b}
T2/2	2.56 ± 0.11^{b}	4.48 ± 0.14^{b}	17.56 ± 0.38^{d}	63.42 ± 0.29^{c}

Data is expressed as Mean ± SD ($n = 30$). Column wise altered superscript statistically implies significant difference ($P < 0.05$).
[1] TC (daily feeding), T1/1 (1-day feeding/ 1-day starvation), T2/1 (2-days feeding/ 1-day starvation), T2/2 (2-days feeding/ 2-days starvation), and T1/2 (1-day feeding/ 2-days starvation).
[2] LDH, lactate dehydrogenase.
[3] MDH, malate dehydrogenase activity denoted as units/min/mg protein at 37 °C.
[4] ALT, alanine aminotransferase.
[5] AST, aspartate aminotransferase activity denoted as IU/L blood.

Table 5. Anti-oxidative enzyme activity of amur common carp fingerlings reared in pond for 120 days.

Treatments[1]	SOD[2]	CAT[3]	GPx[4]
TC	20.21 ± 3.03^{b}	1.61 ± 0.2^{b}	1.32 ± 0.26^{a}
T1/1	14.14 ± 1.6^{a}	1.67 ± 0.32^{b}	2.53 ± 0.27^{bc}
T1/2	43.95 ± 1.56^{d}	4.12 ± 0.62^{d}	5.09 ± 0.37^{e}
T2/1	12.41 ± 0.75^{a}	0.38 ± 0.07^{a}	2.06 ± 0.21^{b}
T2/2	24.47 ± 1.92^{c}	3.13 ± 0.75^{c}	3.95 ± 0.29^{d}

Data is expressed as Mean ± SD ($n = 30$). Column wise altered superscript statistically implies significant difference ($P < 0.05$).
[1] TC (daily feeding), T1/1 (1-day feeding/ 1-day starvation), T2/1 (2-days feeding/ 1-day starvation), T2/2 (2-days feeding/ 2-days starvation), and T1/2 (1-day feeding/ 2-days starvation).
[2] activity denoted as μmol/mg protein/min at 37 °C.
[3] CAT, catalase activity denoted as nanomoles of H_2O_2 decomposed/min/mg protein at 37 °C.
[4] GPx, glutathione peroxidase activity denoted as nanomoles of H_2O_2 decomposed/min/mg protein at 37 °C.

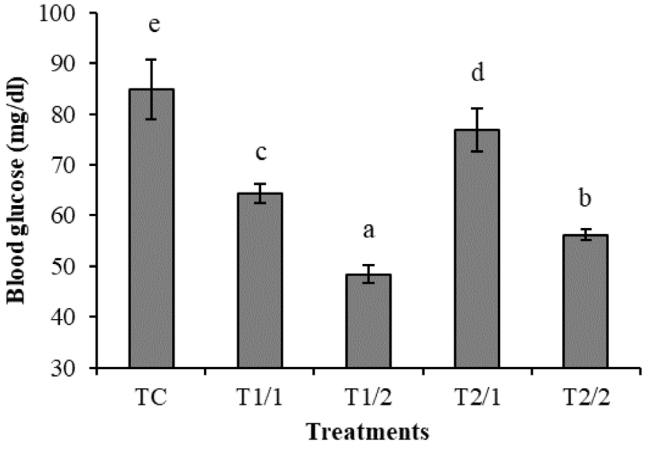

Fig. 2. Blood glucose level of amur common carp fingerlings (Mean ± SD, $n = 30$) in different experimental groups. Bars bearing different superscripts differ significantly ($P < 0.05$).

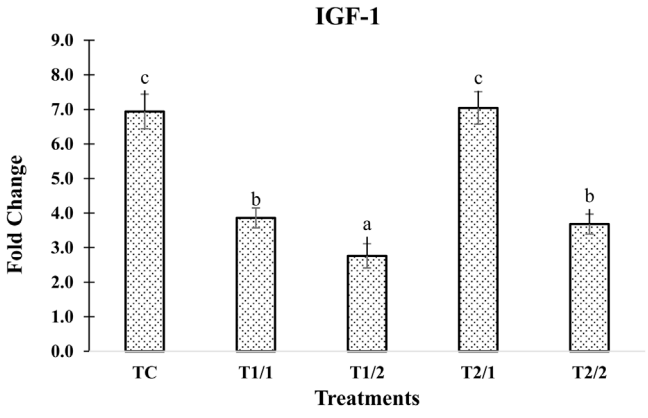

Fig. 3. Hepatic IGF-I mRNA expression of amur common carp fingerlings in different experimental groups. Bars bearing different superscripts differ significantly ($P < 0.05$).

Table 6. Economics of amur common carp pond culture for 120 days.

Variables	Treatments[1]				
	TC	T1/1	T1/2	T2/1	T2/2
Yield (Kg/ha)	2002.82 ± 156.29^{c}	1524.12 ± 72.69^{b}	1095.76 ± 36.25^{a}	1903.56 ± 128.73^{c}	1464.33 ± 103.74^{b}
Selling Price (Rs. /Kg)	90 ± 0	80 ± 0	75 ± 0	90 ± 0	80 ± 0
Feed Provided (kg/Ha)	2233.11 ± 174.26^{d}	978.49 ± 46.67^{b}	495.07 ± 16.38^{a}	1556.19 ± 105.24^{c}	988.36 ± 70.02^{b}
Total Feed Cost (Rs./Ha)	89324.27 ± 6970.47^{d}	39139.77 ± 1866.68^{b}	19802.64 ± 655.14^{a}	62247.48 ± 4209.53^{c}	39534.37 ± 2800.92^{b}
Total Operation Cost (Rs./Ha)	128657.6 ± 7084.29^{d}	78006.43 ± 1826.72^{b}	58669.31 ± 761.41^{a}	101380.81 ± 4096.9^{c}	78467.71 ± 2895.4^{b}
Input interest @ 2.7% per year	3473.76 ± 191.28^{d}	2106.17 ± 49.32^{b}	1584.07 ± 20.56^{a}	2737.28 ± 110.62^{c}	2118.63 ± 78.18^{b}
Total Cost (Rs./Ha)	$132131.36 \pm 7275.57^{d}$	80112.61 ± 1876.04^{b}	60253.38 ± 781.97^{a}	$104118.09 \pm 4207.52^{c}$	80586.33 ± 2973.58^{b}
Sales Revenue (Rs./Ha)	$180253.56 \pm 14066.18^{c}$	121929.6 ± 5815.15^{b}	82181.8 ± 2718.88^{a}	$171320.4 \pm 11585.65^{c}$	$117146.13 \pm 8299.53^{b}$
Net Profit (Rs./Ha)	48122.2 ± 6790.67^{c}	$41816.99 \pm 3960.06^{bc}$	21928.42 ± 1939.15^{a}	67202.31 ± 7378.26^{d}	36559.8 ± 5327.21^{b}
Rate of Return on Operation Cost (%)	36.3 ± 3.23^{a}	52.14 ± 3.79^{b}	36.37 ± 2.74^{a}	64.43 ± 4.4^{c}	45.25 ± 4.91^{b}

Data is expressed as Mean ± SD ($n = 30$). Row wise altered superscript statistically implies significant difference ($P < 0.05$).
[1] TC (daily feeding), T1/1 (1-day feeding/ 1-day starvation), T2/1 (2-days feeding/ 1-day starvation), T2/2 (2-days feeding/ 2-days starvation), and T1/2 (1-day feeding/ 2-days starvation). Currencies are given in Indian National Rupees, INR (1 USD = 79.08 INR as on 1st August, 2022).

Table 7. Pair-wise comparison matrix for assessing relative importance of different growth factors regarding suitability of the different feeding strategies.

	Survival	Weight Gain (g)	Length increment (cm)	Yield (Kg/ha)	SGR	FCR	FCE	PER	Criteria weight (CW)
Survival	1	1	1	1	1	2	2	2	0.154
Weight Gain (g)	1	1	1	1	1	2	2	2	0.154
Length Increment (cm)	1	1	1	1	1	2	2	2	0.154
Yield (Kg/ha)	1	1	1	1	1	2	2	2	0.154
SGR	1	1	1	1	1	2	2	2	0.154
FCR	0.5	0.5	0.5	0.5	0.5	1	1	1	0.077
FCE	0.5	0.5	0.5	0.5	0.5	1	1	1	0.077
PER	0.5	0.5	0.5	0.5	0.5	1	1	1	0.077

$\lambda_{max} = 8$; Consistency Index (CI) = 0.00000; Consistency Ratio (CR) = 0.00000.
Abbreviations: SGR specific growth rate ; FCR feed conversion ratio ; FCE feed conversion efficiency ; PER protein efficiency ratio.

3.6 Expression of hepatic IGF-I mRNA

Periodic starvation and refeeding significantly ($P < 0.05$) affected the mRNA expression of hepatic IGF-1 gene (Fig. 3). The expression of IGF-1 was found to be highest ($P < 0.05$) in T2/1 group, which was found similar ($P > 0.05$) with TC group, followed by T1/1, T2/2 and lowest observed in T1/2 group.

3.7 Production economics

The economics of the pond culture of amur common carp fingerlings under different feeding strategies is summarized in Table 6. Results indicated no significant ($P > 0.05$) difference in fish yield between TC and T2/1. Although there was a positive correlation ($r = 0.945$) between total amount of feed and fish yield, the net return was not parallel to the fish yield. Significantly the highest net return was achieved in T2/1, which was 39.64%, 60.71%, 83.81% and 206.46% higher than TC, T1/1, T2/2 and T1/2 respectively.

3.8 Suitability analysis of feeding strategies

The performance score of different treatments derived from AHP analysis (Tabs. 7 and 8) is displayed in Table 9 and correlation in Table 10. The performance score reflects the suitability of feeding strategies in terms of growth, enzyme/ biochemical assay, and economics. However, the highest performance score was achieved by T2/1 followed by TC, T1/1, T2/2, and T1/2, respectively.

4 Discussion

Growth functions of amur common carp after 120 days showed that maximum body weight gain was accomplished in both TC and T2/1 feeding regimes. Superior growth of fish in TC was apparent because of receiving continuous and maximum amount of diet (Dar et al., 2018a; Gabriel et al., 2018). But the similar weight gain in T2/1 indicated that 1-day food deprivation after 2 consecutive days of feeding

Table 8. Pair-wise comparison matrix for assessing priority among growth, enzyme/biochemical assay, and economics.

	Growth criteria	Economic criteria	Enzyme criteria	Criteria weight (CW)
Growth criteria	1	2	3	**0.538961**
Economic criteria	0.5	1	2	**0.297258**
Enzyme criteria	0.333333	0.5	1	**0.163781**

$\lambda_{max} = 3.0092096$; Consistency Index (CI) = 0.004605; Consistency Ratio (CR) = 0.007.

Table 9. Performance score and ranking of different treatments derived from AHP analysis.

Treatments[1]	Performance score	Rank
T2/1	0.918	1
TC	0.828	2
T1/1	0.739	3
T2/2	0.704	4
T1/2	0.610	5

[1] TC (daily feeding), T1/1 (1-day feeding/ 1-day starvation), T2/1 (2-days feeding/ 1-day starvation), T2/2 (2-days feeding/ 2-days starvation), and T1/2 (1-day feeding/ 2-days starvation).

Table 10. Correlation between weight gain and anti-oxidative enzyme activity of amur common carp fingerlings reared in pond for 120 days.

	Weight gain	SOD	CAT	GPx
Weight gain	1			
SOD	−0.73773	1		
CAT	−0.80353	0.870912	1	
GPx	−0.8978	0.811931	0.825553	1

Abbreviations: SOD, superoxide dismutase; CAT, catalase; GPx, glutathione peroxidase.

(feed deprivation at the rate of 33.33% of the total culture period) had no significant impact upon growth and seemed to be readily compensated by amur common carp fingerlings upon refeeding. Whereas in T1/1, T1/2 and T2/2 poor compensatory growth was found in this study. Pegu (2010) reported complete compensatory growth of *Oreochromis niloticus* when starved for 1 day followed by two days of satiation feeding. Results indicated that feed deprivation up to 33.33% of the total culture period can be compensated, but more than that really have adverse effect on growth. Quite similar result was found by Gabriel et al. (2018) in case of *Oreochromis mossambicus,* where short-term feed deprivation and refeeding cycles
(2-days starvation /2-days refeeding, and 2-days starvation /3-days refeeding) had impact on growth performance and nutrient utilization of *O. mossambicus*, but 2-days starvation /4-days refeeding cycle (feed deprivation at the rate of 33.33% of the total culture period) appeared to be the best among deprived treatment groups. Contrary to our present study, best compensatory growth was found in 1-day deprivation followed by 1-day feeding in *Pangasinodon hypopthalmus* (Rohul Amin et al., 2012). This outcome might be due to lack of such feeding group having more than 1 day of refeeding followed by 1 day of starvation.

Several studies advocated that compensatory growth in fish could be caused by low basal metabolism (Fu et al., 2005) or perfected feed utilization indices like FCR, FCE and PER (Foss et al., 2009; Adakli and Tasbozan, 2015; Anikuttan et al., 2021) after a period of starvation or intermittent feeding. In the present study, along with full growth compensation, lower FCR, higher FCE and higher PER were also reported in T2/1, when compared to control. The improvement in these parameters is attributed to an increase in fish digestive capacity during refeeding as reported by Bolasina et al. (2006) in Japanese flounder, *Paralichthys olivaceus*.

The natural food web had a dominant effect on growth, however the present study demonstrated minimal or no significant differences among the treatment groups. However, the study observed clear differences in growth, suggesting that the commercial feed regime was the primary driver of the results. Moreover, gut content analysis, gill filterable planktons could have added more in depth insights and knowledge about the results of the present study.

The breakdown of large nutrients into small absorbable subunits in the animal's digestive tract is heavily reliant on the availability of enzymes (Haque et al., 2021; Chuphal et al., 2021). It has been found that starvation reduces digestive enzyme activity, which can be restored to a great extent upon refeeding (Krogdahl and Bakke-Mckellep, 2005). Activity of digestive enzymes were markedly higher in T2/1 suggesting the improved digestive capacity of amur common carp in T2/1compared to the other treatments. Elevated protease and amylase activity also suggesting the superior ability to digest protein and carbohydrates, leads to higher compensatory growth in T2/1 group (Yengkokpam et al., 2013).

The final enzyme in the glycolysis pathway is lactate dehydrogenase. By providing NAD^+, LDH aids in the maintenance of the glycolysis cycle. When there is enough oxygen in the tissue, pyruvate enters the Krebs cycle, but when there isn't enough oxygen, pyruvate is transformed to lactate (Talukdar et al., 2021). LDH activity elevates in stress response, such as starvation, reproductive stress (Vijayaraghavan and Rao 1986; Gupta et al., 2021). The T2/1 group had considerably lower LDH activity in the liver than the other deprived groups, which could be attributable to less stress. During stress, elevated energy demand of fishes leads to increased activity of hepatic key enzymes of Krebs cycle such as LDH and MDH for energy production (Jana et al., 2022). Reduced hepatic LDH and MDH activity in the T2/1

group indicated less stress and might aid growth (Dar et al., 2018a).

ALT and AST are both linked to parenchymal cells in the liver. Due to their association with cell necrosis of the liver and skeletal or cardiac muscle, starvation, and vitamin E deficiency, these are commonly measured clinically as markers for liver health (Raghuvaran et al., 2023; Paul et al., 2022). ALT and AST leak into the bloodstream when liver cells are damaged (Bhusare et al., 2023). As a result, they are excellent indictor of acute hepatic damage. In our study, serum ALT and AST levels increased with the severity of starvation, possibly indicating liver damage and starvation stress in experimental groups leading to poor growth and stress of the animal.

SOD plays an anti-oxidative role by detoxifying O_2^- and releasing H_2O_2, while catalase reduces the H_2O_2 generated (Paul et al., 2022; Haque et al., 2023). Glutathione peroxidase (GPx), an intracellular antioxidant enzyme converts H_2O_2 to water enzymatically in order to limit its harmful effects (Gupta et al., 2022). In our study, amur common carp exhibited adoptive response to oxidative stress resulted by periodic starvation, which might be the reason for increased hepatic SOD, catalase, and GPx activity and remained parallel with the intensity of starvation (Yengkokpam et al., 2013). But higher SOD and catalase activity in daily feeding group might be due to environmental stress. However, the growth of amur common carp exhibited a strong negative correlation with the enzyme activity of all three anti-oxidative enzyme.

Glucose is a vital fuel for many tissues and it is especially crucial that glucose levels be maintained during starvation (Mondal et al., 2022). Blood glucose levels may biochemically serve as a reliable predictor of starvation stress (Das et al., 2023). Each species has a different level of glucose homeostasis during starvation. The ability to mobilise tissue reserves has been directly linked to the maintenance of glycaemia during food restriction (Figueiredo-Garutti et al., 2004; Panmei et al., 2023). When the blood glucose level is too low, it means the cells became energy-starved. In this present study, lower blood glucose level was reported in all the starved groups when compared to control, which might refer more energy demand of the fishes subjected to feed depravation. Moreover, decreased blood glucose level in starved groups was also evidenced by Navarro et al. (1992) in case of *Salmo trutta fario*, and Pottinger et al. (2003) in case of *Oncorhynchus mykiss*.

To investigate the terminal regulation of compensatory growth, assessment of the expression levels of IGF-1 is critical (Laron, 2001). IGF-1 mediates the growth-promoting effect of growth hormone, which is synthesised mainly in the liver (Benedet et al., 2005; Anand et al., 2020). In our study, the IGF-1 mRNA expression levels show a significant increase in both restriction feeding and refeeding (T2/1) which is comparable to the control group (TC) with optimum feeding. These results are in agreement with the earlier investigation by who found highest expression of IGF-1 mRNA gene in the restriction feeding group in Persian sturgeon (*Acipenser persicus*) and Dar et al. (2018a) in rohu, *Labeo rohita*. Thus, the upregulated IGF-1 mRNA expression levels during the initial period of refeeding might be one of the reasons behind the compensatory growth in fishes.

Highest net return in T2/1 group was achieved by minimizing feed cost and achieving almost the same yield as daily feeding, TC group. On the other hand, the remaining treatments with different feeding regimes are commercially unfeasible due to very poor yield and limited profit margin.

According to the visual interpretation based on the performance score derived from AHP analysis, it can be observed that cycle of 1-day starvation followed by 2 consecutive days of feeding (T2/1) is the most suitable feeding strategy for pond culture of amur common carp fingerlings in terms of growth, physio-metabolic responses and production performance. Whereas, the cycle of 1-day feeding followed by 2-days starvation (T1/2) is ascertained as the least suitable.

5 Conclusion

Based on growth performance, physio-metabolic responses, antioxidative status, IGF-1 mRNA expression and the economic standpoint, the present study suggests that 2-day feeding followed by 1-day feed restriction (T2/1) as the best feeding strategy for pond culture of amur common carp. The present finding will be helpful for the farmers to have an optimized production with highest net return from the culture practices. However, future research is required to standardize feeding strategy in different growth stages as well as different seasons considering the gill filterable natural food in pond (zooplankton, zoobenthos) and gut content analyses for the proportion of supplementary feed to natural food.

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Conflicts of interest

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

Data availability statement

The corresponding author is responsible to provide supporting data of the findings of this study upon reasonable request.

Author contribution statement

Arka Chowdhury investigated the study, validated data, implemented software programs and prepared the original draft. Tapas Kumar Ghosh conceptualized and supervised the study, reviewed and edited the manuscript. Sanjib Khatua designed methodology, involved in data validation, reviewed and edited the manuscript. Sayani Hore performed data curation, validation and reviewed and edited the manuscript. Prasanta Jana involved in data visualization and validation, reviewed and edited the manuscript. All authors read and approved the final version of manuscript.

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