

Compensatory growth, metabolic responses and economic efficiency in juvenile Persian sturgeon (*Acipenser persicus* Borodin, 1897) under different feeding strategies

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Abstract

This study was undertaken to evaluate compensatory growth, metabolic responses, and economic efficiency in juvenile Persian sturgeon *Acipenser persicus* Borodin, 1897, subjected to different feeding strategies. For this purpose, 120 healthy juvenile Persian sturgeon with an average initial weight of 35.09 ± 0.02 g were randomly divided into twelve fiberglass tanks and were subjected to four feeding strategies: Control group (fed every day), T1 (four periods of two days of feed restriction alternating with eight days of re-feeding), T2 (two periods of four days of feed restriction alternating with a 16-day re-feeding), and T3 (eight days of feed restriction followed by 32 days re-feeding). The results of growth performance showed that there was a significant difference between experimental treatments in weight gain, feed intake, feed conversion ratio, feed efficiency ratio, protein efficiency ratio, specific growth rate, survival rate, hepatosomatic index (HSI) and digestive somatic index (DSI) ($p < 0.05$). There were no significant differences on haematological parameters between treatments. Glucose levels significantly differed between control and feed restriction treatments (T1, T2 and T3) after 40 days trial and T3 had the lowest level ($p < 0.05$). Serum triglycerides markedly declined but total cholesterol increased in feed-restricted fish compared to the control group ($p < 0.05$). Serum total protein in C and T1 were significantly higher compared to other treatments ($p < 0.05$). There was a significant difference in the cost of feed between the full-fed and feed-restricted groups at the end of the experiment and the lowest feed cost was observed in the T3 treatment ($p < 0.05$). Juvenile Persian sturgeons subjected to four consecutive cycles of 2-day feed restriction, followed by 8-day re-feeding (T1) were able to maintain their energy reserves and haemato-physiological variables at levels comparable to the control group throughout the experimental period.

Introduction

Increasing population growth, declining marine resources and fisheries, and rising global demand for farmed aquatic species have highlighted the need to expand sustainable aquaculture production. Accordingly, the farming of high value aquatic species is a promising strategy for reducing pressure on marine resources and providing valuable marine protein. In recent years, sturgeon production has received considerable attention in the aquaculture industry owing to its high-value caviar and meat, broad ecological adaptability, and

potential for coculture with bony fishes (Chebanov *et al.*, 2001; Muller *et al.*, 2018). As a candidate for aquaculture, the Persian sturgeon *Acipenser persicus* Borodin, 1897 is one of the six commercially important sturgeon species inhabiting the Caspian Sea and its surrounding waters.

Feed and nutrition are among the major factors influencing the growth and profitability of sturgeon aquaculture. Feed accounts for about 50-60% of the current aquaculture production costs, thereby contributing substantially to the cost of fish production (Goddard, 2012). Feed efficiency depends not only on feed quality

but also on appropriate feeding management including feeding rate, timing and method (Bascinar *et al.*, 2007; Goddard, 2012; Azodi *et al.*, 2013). Overfeeding results in feed wastage, increased production costs and adversely impact the environmental quality. Underfeeding leads to poor growth and increased mortality (Eroldogan *et al.*, 2006). Appropriate nutritional and feeding management strategies is important for reducing aquaculture production costs (Love, 1970). An appropriate feeding strategy is the use of starvation and refeeding cycles to induce compensatory growth (Azodi *et al.*, 2013). Compensatory growth refers to the accelerated growth following a period of feed restriction or other abnormal conditions such as low temperatures (Dobson, 1984). Compensatory growth following food deprivation or limitation has been reported in various species (Jobling, 1994; Ali *et al.*, 2003; Zhu *et al.*, 2005; Morshedi *et al.*, 2013). However, the degree of compensation occurring after food deprivation is highly variable depending on the species and intensity of the feeding deprivation protocol, including the duration and intensity of deprivation (Ali *et al.*, 2003). Feed restriction may also contribute to the current global demand for environmentally sustainable aquaculture by reducing the discharge of nutrients such as phosphorus and nitrogen as well as organic matter in to the culture environment (Sakyi *et al.*, 2020). Therefore, the use of different starvation/re-feeding protocols have attracted increasing interest in the farming Acipenseridae, specifically Persian sturgeon (*Acipenser persicus* Borodin, 1897). The prolonged culture period and high nutritional costs associated with Persian sturgeon production can adversely affect the economic profitability and investment potential of sturgeon farming. However, Persian sturgeon, like other Acipenserids, can withstand periods of feed restriction both in the wild and captive conditions (Shirvan *et al.*, 2020).

There is a growing body of literature on the effects of cyclic feed restriction and re-feeding on the Acipenseridae family. The morphological and haemato-physiological responses involved in different feed restriction/re-feeding strategies are generally well studied in white sturgeon, *Acipenser transmontanus* (Hung *et al.*, 1997), Adriatic sturgeon, *A. naccarii* (Furue *et al.*, 2008), Persian sturgeon (Yarmohammadi *et al.*, 2015) and great sturgeon, *Huso huso* (Poursaeid and Falahatkar, 2022). However, despite the importance of feeding as a part of the management strategy in aquaculture, there is hardly any research on the economic performance of feed limitation/re-feeding regimes in aquaculture. Previous studies in this field mainly focused on teleost species such as, Nile tilapia, *Oreochromis niloticus* (Limbu and Jumanne, 2014; Elkafrawy, 2020; Klahan *et al.*, 2023) and Asian sea bass, *Lates calcarifer* (Wijayanto *et al.*, 2022). Due to crucial role of feeding in management strategies in aquaculture, the present study was designed to assess the impact of short-term feed restriction and re-feeding on compensatory growth, metabolic response, and economic efficiency in juvenile Persian sturgeon *A. persicus*.

Materials and methods

Fish rearing conditions and experiment design

One hundred and twenty numbers of apparently healthy juvenile Persian sturgeon with an average initial weight of 35.09 ± 05.02 g were obtained from Qarebroun sturgeon culture centre, Mazandaran, Iran. The fish were acclimated in a 1000 l cylindrical fiberglass

tank for 2 weeks and were manually fed at approximating apparent satiation level four times a day using a feed formulated at Qarebroun sturgeon culture centre (Table 1). After the adaptation period, the fish were randomly divided into twelve 300 l fiberglass tanks filled with 200 l @ 10 fish per tank, in a flow-through system (5 l per min) with continuous aeration and a photoperiod of 12 h light and 12 h dark. Water quality was monitored daily and water temperature (18 ± 0.70 °C), pH (7.2 ± 0.40), and dissolved oxygen concentration (7.5 ± 0.50 mg l⁻¹) were maintained at optimum levels during the feeding trial. The tanks were randomly assigned to four experimental treatments each with three replications. Following the experimental design reported by Morshedi *et al.* (2013), fish were subjected to four feeding strategies: Control group (fed every day), T1 (four periods of two days of feed restriction alternating with eight days of re-feeding), T2 (two periods of four days of feed restriction alternating with a 16 day re-feeding) and T3 (eight days of feed restriction followed by 32 of days re-feeding) (Fig. 1). The control and the experimental groups (after each period of feed restriction) were fed four times daily at 7:00, 11:00, 15:00, and 19:00 hrs using the experimental diets at visual satiation level. The formulation and proximate analysis of experimental diets was carried out as per AOAC methods (Jungmin, 2006), and diets were packed and held at -20°C, while daily diets were refrigerated at 4°C (Naghshpour *et al.*, 2021). All experimental protocols were approved by the Faculty of Sciences of the University of Tehran (357; 8 November 2000).

Table 1. Ingredient and proximate composition of the experimental diet

Ingredients	%
Fish meal	54.0
Soybean meal	9.0
Wheat flour	5.0
Fish oil	6.5
Soybean oil	6.5
Filler	4.0
Vitamin premix ¹	3.0
Mineral premix ²	3.0
Lecithin	2.0
Dicalcium phosphate	2.0
Lactic acid	2.5
Methionine	1.0
Lysine	1.0
Antioxidant ³	0.02
Antifungal ⁴	0.48
Total	100
Proximate composition	
Crude protein (%)	45.98
Lipid contents (%)	15.00
Ash (%)	13.50
Moisture (%)	10.0

¹Vitamin premix: Vitamin B - 12 0.1 mg kg⁻¹; Biotin - 2 mg kg⁻¹; Folic acid - 20 mg kg⁻¹; Vitamin K - 20 mg kg⁻¹; Thiamin - 60 mg kg⁻¹; Riboflavin - 60 mg kg⁻¹; Pyridoxine - 100 mg kg⁻¹; Pantothenic acid - 150 mg kg⁻¹; Niacin - 300 mg kg⁻¹; Inositol - 300 mg kg⁻¹; Ascorbic acid - 600 mg kg⁻¹; Vitamin D3 - 2,000 IU kg⁻¹; Choline chloride - 3000 mg kg⁻¹; Vitamin A - 80,000 IU kg⁻¹

²Mineral premix: Se - 20 mg kg⁻¹; Co - 100 mg kg⁻¹; I - 400 mg kg⁻¹; Cu - 600 mg kg⁻¹; Fe - 6,000 mg kg⁻¹; Mn - 5,000 mg kg⁻¹; Zn - 10,000 mg kg⁻¹

³Antioxidant: Butylated hydroxytoluene (BHT).

⁴Anti fungal: Toxiban premix (Component: Aluminosilicate, Ammonium propionate, Bentonate, Zeolite).

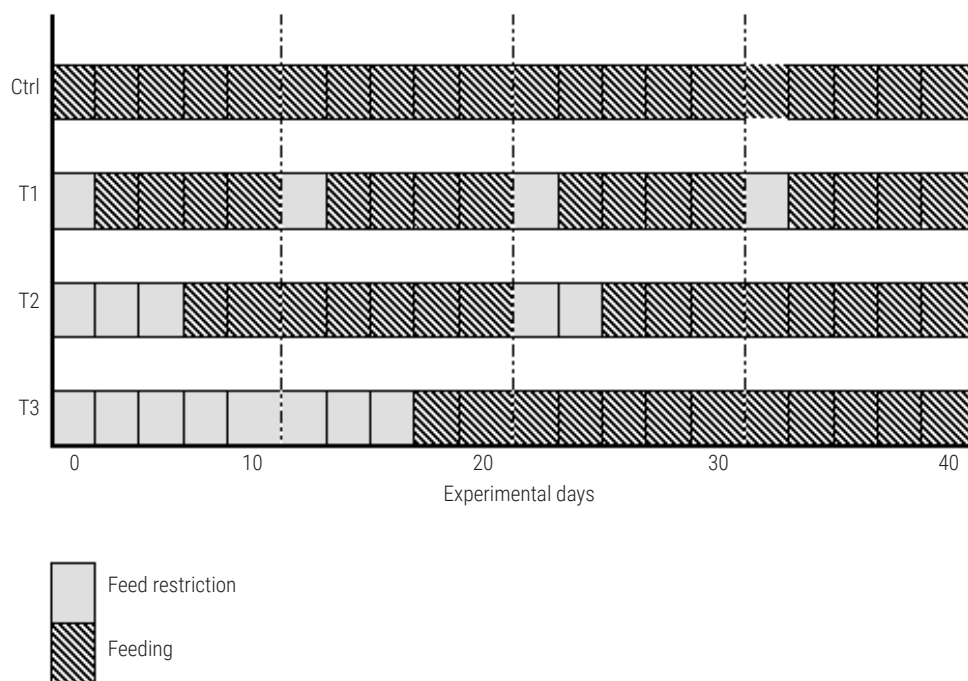


Fig. 1. Flowchart delineating the time schedule of different protocols of feed restriction and re-feeding during the experiment. Control (Ctrl): Fed for 40 days at a satiation level; Treatment1 (T1): Four repetitive cycles of 2-day feed-restriction, and 8-day re-feeding; Treatment (T2): Two repetitive cycles of 4-day feed-restriction, and 16-day re-feeding; Treatment3 (T3): 8-day feed-restriction followed by 32-day re-feeding

Sample collection

At the end of the feeding trial, feeding was stopped for 24 h and all fish in each tank were anaesthetised with MS-222 (125 mg l⁻¹; Sigma-Aldrich) and then weighed individually to the nearest 0.1 g (Ashouri *et al.*, 2020). Three fish from each replicate (9 fish from every treatment) were randomly chosen and anaesthetised with 125 mg l⁻¹ MS-222 (Ashouri *et al.*, 2020). Blood samples were drawn by caudal vein puncture, using a sterile syringe and collected in both heparinised and nonheparinised tubes. Nonheparinised blood was centrifuged (1,500×g for 10 min) to separate serum and stored at -20°C for later analysis. After blood sampling, the fish was immediately euthanised with an overdose of MS-222 (500 mg l⁻¹) and the livers and the entire intestinal tract of the individual examined fish were weighed.

Growth and somatic indices

Growth and somatic indices were calculated using the standard formulae:

Weight gain (WG, g) = Final weight (g) – Initial weight (g)

Specific growth rate (SGR, % day⁻¹) = [ln final weight (g) – ln initial weight (g) / No. of days] × 100

Feed efficiency ratio (FER) = Feed intake (g) / Weight gain (g)

Feed conversion ratio (FCR) = Weight gain (g) / Feed intake (g)

Survival rate (%) = No. of fish in each group remaining on day 40 / Initial no. of fish × 100

Hepatosomatic index (HIS, %) = (Liver weight (g) / Whole body weight (g)) × 100;

Gastrointestinal index (DSI, %) = [Digestive tract weight (g) / Whole body weight (g)] × 100

Haematological parameters

Blood samples were suspended in the diluent (Natt and Herrick, 1952) for determining red blood cells (RBC) and white blood cells (WBC) using a haemocytometer. Hemoglobin concentration (Hb) was calculated using a commercial kit by photometric assay following the cyanmethemoglobin method. Then whole blood was centrifuged in heparinised capillary tubes at 3500 g for 10 min to determine the hematocrit (Hct) value. Mean corpuscular volume (MCV), mean corpuscular haemoglobin concentration (MCHC), and mean corpuscular haemoglobin (MCH) were calculated using standard formulae:

MCV (fl) = (Hct / RBC) × 10

MCHC (%) = (Hb / Hct) × 100; MCH (fl) = (Hb / RBC) × 10.

Serum biochemistry

Total protein, glucose, triglyceride, and cholesterol were determined using commercial kits from Pars Azmoon Co. (Karaj, Iran). Albumin and globulin assays were carried out using standard kits (Biosystem Company, Spain). Serum cortisol was determined using competitive enzyme immunoassay kits (ELISA Micro wells, Diaplus, USA).

Economic efficiency

To analyse the profitability of the various feeding strategies, economic evaluations in terms of the gross profit (GP), net profit value (NPV), investment cost analysis (ICA), and benefit-cost ratio (BCR) of each feed restriction/re-feeding strategy were determined (Wijayanto *et al.*, 2022). using the following formulae:

GP (\$) = Net profit value - Investment cost analysis

NPV (\$) = Total no. of the survived fish (n) × Cost per fish

ICA (\$) = Cost of feeding + Cost of fry stocked

BCR = Total revenue / Total cost of trial

The treatment was considered profitable when the benefit-cost ratio (BCR) was greater than 1.0.

Statistical analyses

All statistical analyses were performed using SPSS statistical software, version 22 for the Windows software package. The Kolmogorov-Smirnov and Leven test was applied to assess the normality of data and homogeneity of variance. One-way ANOVA at a 95% confidence level was used to analyse the variation between treatments. Duncan's multiple-range *post hoc* test was performed to evaluate statistically significant ($p < 0.05$) differences in each group. The results are expressed as Mean ± Standard deviation.

Results

Growth performance and somatic Indices

The results of growth performance and somatic indices are presented in Table 2. There was a significant difference between experimental treatments in weight gain, feed intake, feed conversion ratio, feed efficiency ratio, protein efficiency ratio, specific growth rate, survival rate, hepatosomatic index (HSI) and digestive somatic index (DSI) ($p < 0.05$). Control treatment and Treatment 1 (T1) had the highest weight gain, feed intake, feed efficiency ratio, protein efficiency ratio, specific growth rate, survival rate, hepatosomatic index (HSI) and digestive somatic index (DSI). Lowest feed conversion ratio was recorded in Control treatment and Treatment 1 (T1).

Haematological parameters

The haematological parameters of juvenile Persian sturgeon subjected to different feeding strategies are shown in Table 3. There were no significant differences in haematological parameters including Hb, RBC, WBC, MCH, MCHC, and MCV between treatments ($p > 0.05$).

Serum biochemical parameters

Biochemical parameters of juvenile Persian sturgeon subjected to different feeding strategies are presented in Table 4. Glucose levels significantly differed between control and feed restriction treatments (T1, T2 and T3) after 40 days trial and T3 had the lowest level ($p < 0.05$). Serum triglycerides markedly declined but total cholesterol increased in feed-restricted fish compared to the control group ($p < 0.05$). After 40 days, serum total protein in C and T1 were significantly higher than other treatments ($p < 0.05$). There were no significant differences in albumin and globulin values between treatments ($p > 0.05$). No remarkable difference was seen in cortisol levels between treatments ($p > 0.05$).

Economic efficiency

The outcomes of profitability analysis of the various feeding strategies represented that feed restriction substantially influenced feed cost during the experiment (Fig. 2). There was a significant difference in the cost of feed between the full-fed and feed-restricted groups at the end of the experiment and the lowest feed cost was observed in the T3 treatment ($p < 0.05$). Moreover, the economic efficiency analysis of the experimental feeding strategies in juvenile Persian sturgeons indicated that the highest income was seen in the control group and T1 treatment (103.9 ± 0.22 and 97.08 ± 0.05 USD, respectively), while the lowest income was observed in treatment T3 (67 ± 0.55 USD, $p < 0.05$). The best benefit-cost ratio was also obtained for the T1 treatment and control group (1.14 ± 0.12 and 1.06 ± 0.50), respectively, while the T3 treatment showed a BCR of less than 1.

Discussion

The compensatory growth response differs among fish species and may manifest as excess, complete, or partial compensatory

Table 2. Growth performance and somatic indices of juvenile Persian sturgeon (*A. persicus*) subjected to different feeding regimes

Treatments *	C	T1	T2	T3	SEM	pvalue
Weight gain (g)	110.02 ^a	109.83 ^a	80.05 ^b	65.80 ^c	4.17	0.001
Feed intake (FI)	78.11 ^a	76.88 ^a	64.89 ^b	60.97 ^b	3.42	0.021
Feed conversion ratio (FCR)	0.71 ^c	0.70 ^c	0.81 ^b	0.92 ^a	0.03	0.040
Feed efficiency ratio (FER)	1.41 ^a	1.43 ^a	1.23 ^{ab}	1.08 ^b	0.05	0.001
Protein efficiency ratio (PER)	3.06 ^a	3.10 ^a	2.68 ^b	2.36 ^b	0.13	0.001
Specific growth rate (SGR)	3.47 ^a	3.45 ^a	3.02 ^b	2.75 ^b	0.14	0.033
Survival rate (%)	99.55 ^a	100.00 ^a	90.00 ^b	80.55 ^b	3.05	0.020
Hepatosomatic index (HSI)	4.07 ^a	4.00 ^a	3.50 ^b	3.28 ^b	0.15	0.011
Digestive somatic index (DSI)	13.65 ^a	12.96 ^a	11.33 ^b	11.33 ^b	0.53	0.044
Condition factor	0.40	0.38	0.42	0.49	0.04	0.219

*Control (C): Fed for 40 days at a satiation level; Treatment1 (T1): Four repetitive cycles of 2-day feed-restriction, and 8-day feeding; Treatment (T2): Two repetitive cycles of 4-day feed-restriction, and 16-day feeding; Treatment3 (T3): 8-day feed-restriction followed by 32-day re-feeding. Means within the same row with different superscripts differ significantly ($p < 0.05$)

growth, reflecting species specific responses to feeding strategies (Zhu *et al.*, 2004; Heide *et al.*, 2006; Morshedi *et al.*, 2013). In the present study, Persian sturgeon exposed to 2 days of starvation

Table 3. Haematological indices in juvenile Persian sturgeon (*A. persicus*) subjected to different feeding regimes

Treatments*	C	T1	T2	T3	SEM	p-value
Hb (g dl ⁻¹)	4.28	4.98	4.96	4.33	0.27	0.460
RBC ($\times 10^3$ mm ⁻³)	482.23	485.30	480.15	483.05	11.36	0.892
WBC ($\times 10^3$ mm ⁻³)	24.07	24.16	24.98	24.28	0.75	0.193
MCH (fl)	51.30	49.98	49.94	48.6	0.98	0.062
MCHC (%)	17.28	17.48	17.06	17.00	0.64	0.548
MCV (fl)	290.96	300.2	300.07	300.6	9.26	0.160

*Control (C): Fed for 40 days at a satiation level;

Treatment1 (T1): Four repetitive cycles of 2-day feed-restriction, and 8-day feeding;

Treatment (T2): Two repetitive cycles of 4-day feed-restriction, and 16-day feeding;

Treatment 3 (T3): 8-day feed-restriction followed by 32-day re-feeding.

Table 4. Biochemical indices in juvenile Persian sturgeon (*A. persicus*) subjected to different feeding regimes

Treatments *	Ctrl	T1	T2	T3	SEM	p-value
Glucose (mg dl ⁻¹)	42.50 ^a	41.91 ^a	37.17 ^a	29.25 ^b	0.88	0.011
Cholesterol (mg dl ⁻¹)	36.65 ^b	39.75 ^a	40.55 ^a	40 ^a	0.98	0.010
Triglyceride (mg dl ⁻¹)	205.98 ^a	198.05 ^{ab}	190.71 ^b	186.35 ^b	2.15	0.024
Total protein (g dl ⁻¹)	2.22 ^a	2.22 ^a	1.20 ^b	1.08 ^b	0.12	0.001
Albumin (g dl ⁻¹)	0.52	0.51	0.51	0.50	0.04	0.7493
Globulin (g dl ⁻¹)	2.15	2.05	2.05	1.90	0.19	0.172
Cortisol (μ g dl ⁻¹)	60.31	59.40	59.70	60.70	0.78	0.360

*Control (C): Fed for 40 days at a satiation level; Treatment1 (T1): Four repetitive cycles of 2-day feed-restriction, and 8-day feeding; Treatment (T2): Two repetitive cycles of 4-day feed-restriction, and 16-day feeding; Treatment3 (T3): 8-day feed-restriction followed by 32-day re-feeding.

Means within same row with different superscripts differ significantly ($p < 0.05$)

and 8 days of refeeding (T1) exhibited compensate compensatory growth, with no significant differences in various growth parameters between T1 and the control group. In contrast, fish subjected to 4 and 8 days of starvation followed by 16 and 32 days of refeeding (T2 and T3, respectively) exhibited partial compensatory growth. Significant weight loss was observed in juvenile *A. persicus* in these treatments, and the fish did not attain the body weight of either the control group or T1 group after re-feeding. This weight loss may be associated with the use of body energy reserves for vital physiological processes, such as brain function, respiration, and osmoregulation (Ali *et al.*, 2003; Furne *et al.*, 2012). Similar findings have been reported in beluga subjected to a comparable feeding strategy, where fish exposed to a comparable feeding strategy, where fish exposed to 2 days of starvation followed by 8 days of refeeding attained body weights comparable to those of the control group (Naghshpour *et al.*, 2021). There are also similar reports on complete and partial growth compensation in Chinese sturgeon (Liu *et al.*, 2011), Persian sturgeon (Yarmohammadi *et al.*, 2012), and roach *Rutilus caspicus* (Abolfathi *et al.*, 2012). These results indicate that Persian sturgeon can adapt to periods of feed restriction, with the 2-day starvation treatment followed by 8-days of refeeding resulting in complete compensatory growth, whereas 8 days starvation treatment resulted in lower weight gain than the control, suggesting their partial compensatory growth. These results are contrary to the findings reported by Morshedi *et al.* (2013, 2017) in Siberian sturgeon. The observed differences may reflect the adaptability of fish to different feed restriction regimes. In the present study, complete compensatory growth was observed in Persian sturgeon fry subjected to four repeated cycles of 2 days starvation followed by 8 days of refeeding (T1). In contrast, the relatively short refeeding period in T3 treatment may not have provided sufficient time for the fish to compensate for the weight loss incurred during starvation. Differences in compensatory responses among studies may also be associated with fish species, diet composition, duration and intensity of feed restriction and species-specific adaptation to natural fluctuations

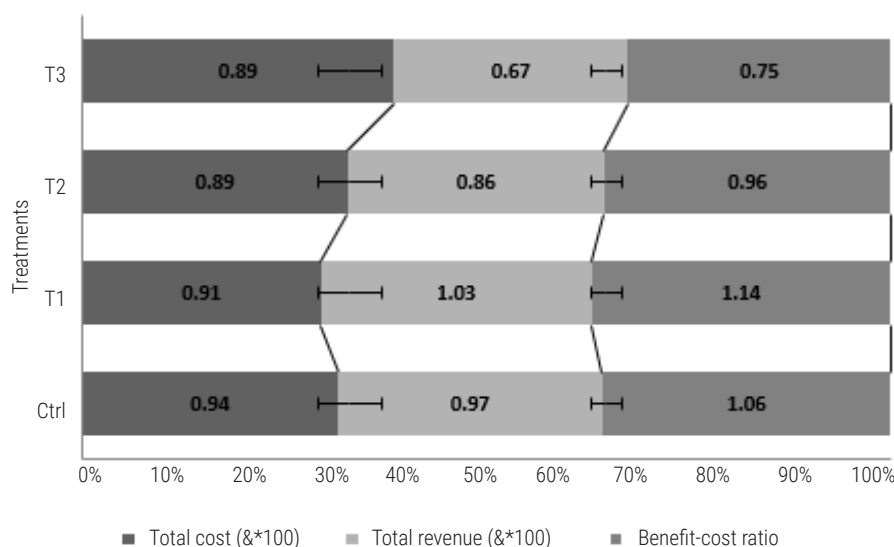


Fig. 2. Economic efficiency analysis for juvenile Persian sturgeon (*A. persicus*) subjected to different feeding regimes. Control (C): Fed for 40 days at a satiation level; Treatment1 (T1): Four repetitive cycles of 2-day feed-restriction, and 8-day feeding; Treatment (T2): Two repetitive cycles of 4-day feedrestriction, and 16-day feeding; Treatment 3 (T3): 8-day feed-restriction followed by 32-day re-feeding

in feed availability (Yong *et al.*, 2019; Naghshpour *et al.*, 2021; Le Francois *et al.*, 2023). The highest feed efficiency was observed in T1 group, despite its lower feed intake compared with the control group. The observed compensatory growth may have resulted from hyperphagia, improved feed efficiency or a combination of both mechanisms (Morshedi *et al.*, 2017; Klahan *et al.*, 2023). According to the results of the present study, it could be proposed that improved feed efficiency serves as the main mechanism involved in the compensatory response in T1 treatment. The lowest survival rate was recorded in T3. In agreement with this study, Naghshpour *et al.* (2021) reported that feed restriction and re-feeding strategies significantly affected the survival rate of great sturgeon, while Jafari *et al.* (2018) reported 100% survival throughout the experimental period in Siberian sturgeon. These results indicate that the fish may restore their metabolic status following a short period of refeeding while continuing compensatory growth. However, the differences in survival rates among studies may be attributable to differences in experimental conditions. It is known that prolonged periods of starvation has adverse effects on survival, as depletion of endogenous energy reserves can ultimately compromise vital physiological functions and reduce survival rate (Perez-Jimenez *et al.*, 2007). Somatic indices are useful indicators of the nutritional status of fish (Morshedi *et al.*, 2017). In the present 10 days study, HSI and DSI, declined significantly in the feed restricted groups. This decline may be attributed to the mobilization of stored nutrients such as glycogen and lipids, to meet metabolic energy requirements during starvation (Ashouri *et al.*, 2020). Similarly, significant reductions in HSI and DSI have been reported in *A. baerii* following 4 and 8 days of starvation (Ashouri *et al.*, 2013). Comparable decreases in these indices have been reported in beluga (Falahatkar, 2012) and white sturgeon (Hung *et al.*, 1997) following 10 days starvation.

The analysis of haematological and biochemical parameters is widely used to assess the physiological condition of fish. The haematological parameters of fish are influenced by various biotic and abiotic factors such as fish age and sex, water temperature, seasonal patterns, and nutritional status (Rehulka and Minarik, 2004). In the present study, no significant differences in the haemoglobin levels were observed between different treatments at the end of the experimental period. These results are consistent with previous reports in different fish species (Abdel-Tawwab *et al.*, 2006; Cho *et al.*, 2006; Caruso *et al.*, 2010, 2012; Falahatkar *et al.*, 2012; Morshedi *et al.*, 2017). Similarly, starvation and refeeding did not significantly affect the RBC count at the end of the experiment, as observed in Nile tilapia (Abdel-Tawwab *et al.*, 2006) and Siberian sturgeon (Morshedi *et al.*, 2017). These findings suggest that the starvation and refeeding strategies did not significantly alter erythrocyte production or circulating RBC levels (Morshedi *et al.*, 2017).

Glucose level is a routinely measured indicator to determine nutritional status and a reliable indicator of secondary stress response in fish (Wanger and Congleton, 2004). In the present study, the glucose level decreased significantly with increasing duration of starvation, and the lowest level was observed in T3. Similarly, a decrease in glucose level was observed in Siberian sturgeon after 3 weeks of starvation and also after 2, 4, and 8 days of starvation (Ashouri *et al.*, 2013, 2020). In our experiment, a significant increase in plasma cholesterol accompanied by a decrease in triglyceride levels suggest enhanced lipid mobilisation from the liver and visceral tissues, the major sites of lipid storage. This response

was consistent with the observed reductions in HSI and DSI. These findings suggests that, lipids serve as an important energy substrates during starvation in Persian sturgeon, with their mobilisation supporting basal energy requirements and gluconeogenesis (Ashouri *et al.*, 2020). Additionally, free fatty acids produced during lipolysis may serve as substrates for cholesterol synthesis, thereby contributing to the observed hypercholesterolemia during starvation (Palmeigiano *et al.*, 1993). Similar metabolic responses have been reported in Siberian sturgeon exposed to different cycles of starvation and refeeding (Morshedi *et al.*, 2017). These findings imply that lipid reserves are preferentially mobilised over protein reserves during feed restriction in Persian sturgeon. Serum protein is described as a relatively stable indicator of nutritional status in fish (Peres *et al.*, 2013), and changes in its concentration may results from amino acid oxidation or environmental proteolysis (Mommensen *et al.*, 1999; Di Marco *et al.*, 2008).

The present study showed that total protein decreased significantly in T2 and T3. Similarly significant reduction in serum protein have been reported in common carp and common dentex (*Dentex dentex*) following starvation for 5 days and 5 weeks, respectively (Blasco *et al.*, 1992; Perez-Jimenez *et al.*, 2012). The decline in protein levels suggests that protein reserves and non-essential amino acids were mobilised to support basal metabolic requirements during starvation. Protein mobilisation may also provide substrates for gluconeogenesis in Persian sturgeon during periods of feed deprivation. Sturgeons are reportedly less sensitive to adverse and stressful environmental conditions (Falahatkar *et al.*, 2009, 2012). In the present study, no significant differences in cortisol levels were observed between treatments, indicating that the starvation regimes did not induce a pronounced cortisol mediated stress response. A similar response was reported in Siberian sturgeon exposed to starvation for 2, 4, and 8 days, indicating a high level of tolerance of these species to starvation (Ashouri *et al.*, 2013). The absence of significant differences in cortisol levels between the treatments in response to starvation may reflect physiological adaptation to prolonged or repeated feed restriction and possible attenuation of the hypothalamic-pituitary-inter-renal (HPI) axis response under chronic nutritional stress. The relatively lower sensitivity of sturgeons to certain stressors compared with many teleosts may also be associated with differences in stressor perception of stressors, differences in inter-renal tissue characteristics and physiological stress responses (Barton, 2002).

The profitability analysis of the various feeding strategies revealed a significant difference in the cost of feed between the full-fed and feed-restricted groups at the end of the experiment. However, the highest income and the best benefit-cost ratio were recorded in T1, which may be attributed to the shorter starvation period and the greater number of starvation and refeeding cycles in T1 treatment. Similar studies in teleosts, Asian seabass and juveniles of Nile tilapia have also demonstrated significant effects of feeding strategies on fish growth performances and benefit-cost ratios (Elkafrawy, 2020; Wijayanto *et al.*, 2022; Klahan *et al.*, 2023). On the contrary, Limbu and Jumanne (2014) reported that prolonged starvation could result in a lower benefit-cost ratio in Nile tilapia under a different feeding protocol.

In the present study, juvenile Persian sturgeons subjected to four repeated cycles of 2-day feed restriction followed by 8 days

of refeeding (T1) maintained energy reserves and haemato-physiological parameters comparable to those of the control group. T1 also demonstrated better FW, FCR, FER and survival rate compared to other experimental groups. Therefore, treatment T1 can be considered the most cost-effective feeding strategy for juvenile Persian sturgeon, in terms of growth performance, physiological condition and economic returns under experimental conditions. These findings provide a basis for investigations on feed restriction/refeeding strategies for improving the economic efficiency of sturgeon farming. However, the study had certain limitations. The short experimental duration may have influenced the assessment of total production costs, growth performance, physiological responses, and attainment of market size. In addition, factors such as water quality management, tank cleaning cost, energy consumption and labour requirements were not incorporated into the benefit-cost analysis and could influence the overall economic returns. Further, long term studies incorporating these operational costs and the production of market sized fish are warranted.

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