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Compensatory growth, plasma hormones and metabolites in juvenile Siberian sturgeon (*Acipenser baerii*, Brandt 1869) subjected to fasting and re-feeding

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Abstract

A 7-week study was conducted to investigate the effect of different fasting and re-feeding regimes on compensatory growth and some physiological parameters of juvenile Siberian sturgeon (*Acipenser baerii*). Fish (46.5 ± 0.5 g) were fed on a diet (containing 450 g/kg crude protein and 20 MJ/kg digestible energy) according to four feeding regimes in triplicate including: control group (C, fed everyday), W1 (2 weeks of feeding followed by 1 week of fasting and 4 weeks of re-feeding), W2 (1 week of feeding followed by 2 weeks of fasting and 4 weeks of re-feeding) and W3 (3 weeks of fasting followed by 4 weeks of re-feeding). The fasted groups including W1 (119.6 ± 2.1 g), W2 (118.0 ± 1.7 g) and W3 (108.5 ± 4.8) significantly lost their weights during fasting phase and did not attain the final weight of the C (137.3 ± 1.7 g) after re-feeding phase. The re-feeding phase increased the specific growth rate in the fasted groups compared to the C ($p < .05$). After the fasting phase, concentrations of T_3, T_4, glucose, total protein and triglyceride in plasma of fasted groups were decreased, but levels of total cholesterol, aspartate aminotransferase, alkaline phosphatase and lactate dehydrogenase increased compared to the C. After re-feeding phase, except for glucose level, all mentioned metabolites were restored in the plasma of W1 group, but total protein level and aspartate aminotransferase concentrations in plasma were not restored in W2 and W3 groups. Overall, our finding demonstrated 4 weeks of re-feeding was too short to induce full compensatory growth in *A. baerii* juveniles.

KEYWORDS
Acipenser baerii, fasting, plasma metabolites, re-feeding, thyroid hormones

1 | INTRODUCTION

Siberian sturgeon (*Acipenser baerii*) is the most commonly used species in aquaculture to produce caviar and sturgeon meat throughout the world due to its fast growth rate and caviar production, sexual maturity in a short time and amenability to a wide range of diets and culture conditions (Abdolahnejad, Pourkazemi, khoshkholgh, & Yarmohammadi, 2015; Bronzi, Rosenthal, & Gessner, 2011). During recent years, several studies have been done regarding the farming-related biology (Williot, Nonnotte, & Chebanov, 2018) and nutritional requirements (Babaei, Kenari, Hedayati, & Yazdani-Sadati, 2017; Babaei, Kenari, Hedayati, Yazdani-Sadati, & Metón, 2016; Furné et al., 2008) aimed at developing aquaculture programmes and reducing native sturgeons overfishing. Starvation or fasting is

one of the common factor challenging fish health in the natural environment because of food limitation, spawning migration or temperature (Falahatkar, 2012). In aquaculture, a short-term fasting might be applied to reduce stress (e.g., prior to shipping, quarantine periods or medical treatments), controlling the mortality due to disease outbreaks and water quality management (e.g., turbidity or minimizing the nitrogen and organic wastes; Davis & Gaylord, 2011). Furthermore, feed withdrawal periods can also be used for production purposes such as gut evacuation, increasing fillet quality (Grigorakis & Alexis, 2005), reducing feed and labour costs as well as inducing compensatory growth (CG) (Gaylord & Gatlin, 2001). Like other vertebrates during fasting, fish adjust their metabolism through mobilizing their endogenous energy reserves for maintaining vital processes and homoeostasis (Navarro & Gutiérrez, 1995) through endocrine system and hormonal regulation including cortisol (Mommsen, Vijayan, & Moon, 1999) and thyroid hormones (Power, Melo, & Santos, 2000). It has been suggested that sturgeons reduce their energy consumption during starvation and mobilize their energy reserves for maintaining the basal metabolic rate (Furné et al., 2012). Furthermore, tolerance to fasting and degree of compensation are highly variable depending on the fish species, age (size), energy reserves availability, postnutritional history and feeding protocols (length of food-deprivation period) (Ali, Nicieza, & Wootton, 2003; Pérez-Jiménez, Guedes, Morales, & Oliva-Teles, 2007). Falahatkar, Poursaeid, Shakoorian, and Barton (2009) showed that *Huso huso* (197 g) could partially compensate growth rate after the fasting period if ad libitum feeding was subsequently provided. In addition, fasting periods may drastically affect liver function, which could consequently alternate the metabolism of energy and nutrients in fish (Pérez-Jiménez et al., 2007). As a result, plasma metabolite (e.g., protein, glucose, cholesterol and triglycerides) concentrations (Morshedi et al., 2017; Yarmohammadi, Shabani, Pourkazemi, Soltanloo, & Imanpour, 2012) and liver nonspecific enzyme activities (e.g., alanine aminotransferase, aspartate aminotransferase, alkaline phosphatase and lactate dehydrogenase; Peres, Santos, & Oliva-Teles, 2013; Pérez-Jiménez et al., 2012) may also pronouncedly change during fasting periods. Thus, in this study, different periods of fasting and re-feeding regimes were tested to explore the CG potential and some physiological responses in *A. baerii* juvenile for optimizing its aquaculture production.

2 | MATERIALS AND METHODS

2.1 | Fish maintenance and experimental design

One hundred and twenty *A. baerii* juveniles (Initial body weight [BW_I] = 46.5 ± 0.5, mean ± standard deviation, n = 120) were obtained from a fish farm (Shahid Beheshti Sturgeon Propagation Complex, Rasht, Guilan, Iran; 49°36′N, 37°18′E). Fish were acclimated in a 1,000-L cylindrical fibreglass tank for 10 days and were fed with artificial feed manufactured by the feed laboratory of International Sturgeon Research Institute (Rasht, Guilan, Iran). The composition of the feed was 450 g/kg crude protein, 180 g/kg crude fat, 100 g/kg ash, 12 g/kg fibre and 20 MJ/kg digestible energy, 2 mm (Table 1). After adaptation, fish were randomly stocked into twelve 300-L fibreglass tanks filled with 200 L (10 fish in each tank) of sand-filtered freshwater (supplied from Sefidrood River) in a flow-through system (5 L/min) with continuous aeration. Water quality parameters were monitored daily using 340i Multimeter (WTW) to ensure fish welfare. The water temperature (17.2 ± 1.5°C), DO (7.8 ± 0.2), pH (7.2 ± 0.2) and total ammonia nitrogen (TAN <0.1 mg/L) were maintained in all tanks during the experiment. Natural photoperiod (49°36′N, 37°18′E) was adopted during the feeding trial. Following the same experimental design described by Montserrat, Gabillard, Capilla, Navarro, and Gutierrez (2007), fish were subjected to four feeding regimes in triplicates: control group (fed everyday), W1 (2 weeks feeding followed by 1 week fasting and 4 weeks re-feeding), W2 (1 week feeding followed by 2 weeks fasting and 4 weeks re-feeding) and W3 (3 weeks fasting followed by 4 weeks re-feeding) (Figure 1). Fish were fed up to visual satiation four times daily at 08:00, 12:00, 17:00 and 22:00 hr during the trial. As illustrated in the Figure 1, the timing of fasting phase was such that all groups finished their fasting period at the same time and were re-fed simultaneously during the final 4 weeks.

2.2 | Sample collection

All fish from the four experimental groups were weighed individually to the nearest 0.1 g at the start (initial body weight, BW_I), after third (body weight after fasting, BW_F) and after seventh week (body

TABLE 1 Formulation of the experimental diet

Formulation (g/kg)	
White fish meal[a]	530
Wheat flour	180
Wheat gluten	50
Soybean meal[b]	70
Fish oil	18
Soybean oil[b]	13
Molasses	30
Yeast	50
Vitamin premix[c]	20
Mineral premix[d]	13
Cellulose	26

[a]Pars Kilka Corporation.
[b]Khorak-dam Abzian Corporation.
[c]Vitamin mixture contained the following vitamins per kilogram of feed: A, 1,400,000 IU; D3, 400,000 IU; E, 40 mg/kg; K3, 2 mg/kg; B1, 6 mg/kg; B2, 8 mg/kg; B3, 12 mg/kg; B5, 40 mg/kg; B6, 4 mg/kg; B9, 2 mg/kg; B12, 8 mg/kg; biotin 0.24 mg/kg; iInositol, 20 mg/kg; B.H.T, 20 mg/kg; carrier up to 1 kg.
[d]Mineral mixture contained the following minerals per kilogram of feed: Fe, 2,600 mg/kg; Zn, 1,250 mg/kg; Se, 200 mg/kg; Co, 48 mg/kg; Cu 420 mg/kg; Mn, 158 mg/kg; I, 100 mg/kg; choline chloride, 12,000 mg/kg; career up to 1 kg.

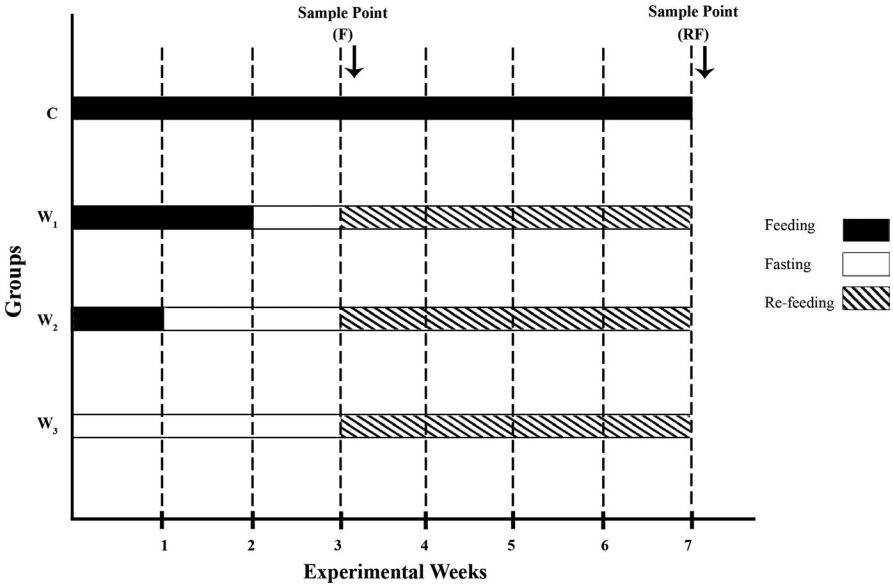

FIGURE 1 Flow chart delineating feeding schedule to test different scenarios of fasting and re-feeding. The control was fed along the 7 weeks, while W1 received 2 weeks feeding, 1 week fasting (sampling point F) and 4 weeks re-feeding (sampling point RF); W2: 1 week feeding, 2 weeks fasting (sampling point F) and 4 weeks re-feeding (sampling point RF); W3: 3 weeks fasting (sampling point F) and 4 weeks re-feeding (sampling point RF)

weight after re-feeding, BW_{RF}). Control group was sampled simultaneously with the other groups at the end of third- and seventh-week sampling points as showed in Figure 1. At the end of the seventh week, fish in all groups were fasted for 24 hr (in RF sample point) before being anaesthetized (MS-222 at 125 mg/L; Sigma-Aldrich Chemicals Ltd.). Blood samples were rapidly collected from the caudal vein in three fish (n = 3 fish per replicate, n = 9 fish per treatment) using heparinized syringes. Plasma was immediately separated after centrifugation (1500 *g*, 10 min, at room temperature) and stored at −20°C. Then the same fish was rapidly euthanized with an overdose of MS-222 (500 mg/L), after which liver, viscera and digestive tract weights were recorded for the determination of hepatosomatic index (HSI), viscerosomatic index (VSI) and digestive somatic index (DSI), respectively.

2.3 | Whole-body proximate composition, plasma hormones and biochemical analyses

The proximate composition of fish whole body was measured according to standard methods (AOAC, 2005). The concentration of plasma cortisol was measured by radioimmunoassay (RIA) as described by Ellis, James, Stewart, and Scott (2004), using a commercial kit (#IM1841, Beckman Coulter, Immunotech). Plasma thyroid hormones levels were measured using established double-antibody T_3 and T_4 RIA kit from Immunotech (#IM1447-IM3286 for T_4 and #IM1699-IM3287 for T_3; Leiner, Han, & MacKenzie, 2000). Plasma glucose, total protein, cholesterol, triglycerides, alanine aminotransferase (ALT), aspartate aminotransferase (AST), alkaline phosphatase (ALP) and lactate dehydrogenase (LDH) were measured by means of an autoanalyser (Technicon RA-1000, Technicon Instruments) using commercial clinical investigation kits (Pars Azmoon Kit; www.parsazmun.com) as described by Jafari, Falahatkar, and Sajjadi (2018).

2.4 | Indexes and calculations

The standard formulae were used to assess growth and somatic indices: BW_i = initial body weight, BW_f = final body weight, Specific growth rate (% day^{-1}): $SGR = ((\ln BW_f\ (g) - \ln BW_i\ (g))/t) \times 100$, where t is experimental period (day); weight gain (%): $WG = ((BW_f\ (g) - BW_i\ (g))/BW_i\ (g)) \times 100$; Survival (%): S = (number of fish in each group remaining on day 49/initial number of fish) × 100; Hepatosomatic index (%): HSI = (liver weight (g)/whole body weight (g)) × 100; Viscerosomatic index (%): VSI = (visceral weight (g)/whole body weight (g)); Digestive somatic index (%): DSI = (digestive tract weight (g)/whole body weight (g)) × 100. Growth compensation in the fasted groups during experimental periods was calculated by the compensation coefficient (CC), which was calculated as $CC = \Delta T/\Delta C$, where ΔT was the average weight gain (g) in the treated groups divided by the number of feeding days and ΔC was the average weight gain (g) in the group C divided by the number of feeding days. Thus, values of CC >1.0 would indicate a compensatory process for the weight gain (Mattila, Koskela, & Pirhonen, 2009). The feeding days for the C, W1, W2 and W3 groups were 49, 42, 35 and 28 days, respectively.

2.5 | Statistical analysis

Data were analysed using SPSS ver.16.0. All the data are presented as means ± standard error of the mean calculated from three replicates. Arcsine transformations were conducted on all data expressed as percentages to achieve homogeneity of variance before statistical analysis. One way ANOVA was performed at a significance level of 0.05 following confirmation of normality (One-Sample Kolmogorov-Smirnov Test) and homogeneity of variance (Levene's test). Duncan's procedure was used for multiple comparisons.

TABLE 2 Growth performance in *Acipenser baerii* subjected to different fasting (F) and re-feeding regimes (RF)

Sample point	Group	BW_f (g)	SGR (% BW/day)	WG (%)	HSI (%)	VSI (%)	DSI (%)
F	C	71.0 ± 2.6^a	2.0 ± 0.1^a	52.3 ± 4.3^a	2.9 ± 0.1^a	17.1 ± 1.7^a	11.9 ± 1.4^a
	W_1	45.8 ± 0.4^b	−0.1 ± 0.0^b	−1.3 ± 0.6^b	2.1 ± 0.5^b	11.5 ± 1.2^b	6.9 ± 0.8^b
	W_2	40.5 ± 1.0^c	−0.6 ± 0.0^c	−12.2 ± 0.3^c	1.9 ± 0.1^b	10.5 ± 0.9^b	6.7 ± 1.0^b
	W_3	38.7 ± 0.8^c	−0.8 ± 0.1^c	−16.2 ± 1.1^c	1.7 ± 0.1^b	10.0 ± 1.1^b	6.0 ± 1.0^b
RF	C	137.3 ± 1.7^a	2.4 ± 0.1^c	93.7 ± 4.6^c	3.4 ± 0.1^a	13.4 ± 0.3^a	8.1 ± 0.1^a
	W_1	119.6 ± 2.1^b	3.4 ± 0.0^b	161.1 ± 2.6^b	3.4 ± 0.2^a	13.8 ± 0.8^a	8.3 ± 0.6^a
	W_2	118.0 ± 1.7^b	3.8 ± 0.0^a	191.8 ± 3.1^a	3.7 ± 0.2^a	13.9 ± 1.2^a	8.1 ± 0.6^a
	W_3	108.5 ± 4.8^c	3.7 ± 0.3^a	179.9 ± 6.6^a	3.5 ± 0.3^a	15.2 ± 1.1^a	9.7 ± 0.8^a

Note: Values are mean ± *SEM* (n = 3 of mean). Different superscript letters in each column represent significant differences among groups (Duncan's test, $p < .05$) in each sample point.

Abbreviations: BW_f, final body weight; C, control group (fed everyday); DSI, digestive somatic index; HSI, hepatosomatic index; SGR, specific growth rate; VSI, vicerosomatic index; W1, 2 weeks of feeding followed by 1 week of fasting and 4 weeks of re-feeding; W2, 1 week of feeding followed by 2 weeks of fasting and 4 weeks of re-feeding; W3, 3 weeks of fasting followed by 4 weeks of re-feeding; WG, weight gein.

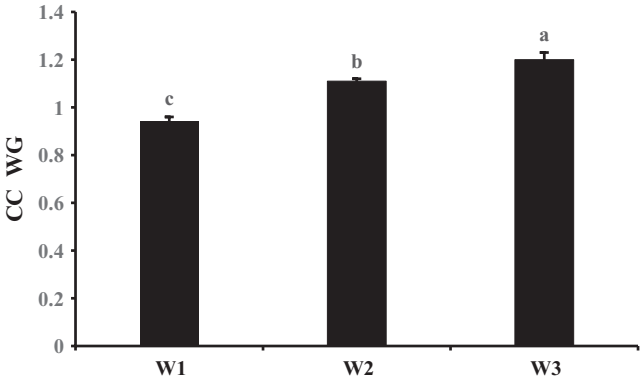

FIGURE 2 Compensation coefficients (CC) for weight gain in *Acipenser baerii* fed according to different feeding regimes for 7 weeks. CC >1 indicates compensation. Each bar represents the treatment average of three replicates (mean ± *SEM*). Fish fasted for 1 (W1), 2 (W2) or 3 (W3) weeks and then 4 weeks of re-feeding period. Different letters in each column represent significant differences among groups (Duncan's test, $p < .05$)

3 | RESULTS

3.1 | Growth performance and somatic indices

Fish survival rate was 100% in all treatments. After the fasting phase, fish that were subjected to the three different feed-deprivation regimes significantly lost their weights compared to the C (Table 2). After the re-feeding phase, none of the fasted groups attained the final weight of the C ($p < .05$). Moreover, after fasting phase, specific growth rate (SGR) and weight gain (WG) were significantly higher in the C group compared to those observed in the other treatments. However, after re-feeding phase, SGR and WG in fasted fish were significantly higher than in the C, indicating CG response in feed-restricted groups ($p < .05$). In addition, W3 and W1 groups had the highest and the lowest CC for WG (1.2 vs. 0.9), respectively, while W2 showed intermediate values (Figure 2). Furthermore, after fasting phase somatic indices including HSI, VSI and DSI were reduced in fasted groups compared to the C. After re-feeding phase, all somatic indices were restored in the fasted groups same as the C ($p > .05$).

3.2 | Proximate composition

After fasting phase, fish in W3 and C showed the greatest and the least whole-body moisture content, meanwhile after re-feeding phase all treatments had the same whole-body moisture content (Table 3). After fasting phase, fish in W3 had the lowest whole-body lipid content, whereas their whole-body lipid content restored after re-feeding phase. After fasting phase, fish in W3 showed the lowest protein level, whereas after re-feeding period, whole-body protein content in C group was higher than the fasted treatments. Whole-body ash level did not change among groups after fasting and re-feeding phases. Whole-body nitrogen-free extract in fasted groups was lower than C group after fasting phase, but it was completely compensated after re-feeding phase.

3.3 | Plasma hormones and biochemical parameters

The different fasting treatments did not affect plasma cortisol levels after fasting and re-feeding periods ($p > .05$, Figure 3a). On the contrary, after fasting phase, T_3 level in the plasma was significantly lower in the fasted groups than the C ($p < .05$, Figure 3b). After re-feeding phase, W1 and W3 groups had the highest and the lowest plasma T_3 (1.1 vs. 0.7 ng/ml) levels, respectively. Meanwhile, the other groups showed intermediate values ($p < .05$). Plasma T_4 level in the C and W1 groups was higher than the other treatments. In addition, after the re-feeding phase, fish in W3 group showed the lowest T_4 level ($p < .05$, Figure 3c). After fasting period, plasma glucose significantly decreased in the fasted groups compared to the C ($p < .05$, Table 4). After re-feeding phase, plasma glucose levels in the fasted groups increased, but it was significantly lower than C. After the fasting phase, plasma total protein in C and W1 groups were significantly higher than other treatments, meanwhile after re-feeding phase, plasma total protein in

TABLE 3 Whole-body proximate composition (g/kg) of *Acipenser baerii* subjected to different fasting (F) and re-feeding regimes (RF)

Sample point	Group	Moisture	Lipid	Protein	Ash	NFE
F	C	705 ± 3^{c}	37 ± 3^{a}	153 ± 5^{a}	36 ± 1^{a}	69 ± 6^{a}
	W_1	727 ± 5^{b}	36 ± 2^{a}	148 ± 4^{a}	34 ± 2^{a}	55 ± 5^{b}
	W_2	734 ± 4^{b}	33 ± 1^{a}	143 ± 2^{a}	37 ± 1^{a}	53 ± 4^{b}
	W_3	759 ± 2^{a}	22 ± 2^{b}	125 ± 1^{b}	39 ± 3^{a}	55 ± 2^{b}
RF	C	696 ± 7^{a}	59 ± 1^{a}	160 ± 2^{a}	26 ± 1^{a}	59 ± 9^{a}
	W_1	703 ± 6^{a}	66 ± 03^{a}	148 ± 1^{b}	27 ± 1^{a}	56 ± 6^{a}
	W_2	701 ± 7^{a}	62 ± 3^{a}	145 ± 4^{b}	29 ± 2^{a}	63 ± 8^{a}
	W_3	706 ± 9^{a}	56 ± 4^{a}	149 ± 3^{b}	25 ± 1^{a}	64 ± 8^{a}

Note: Values are mean ± *SEM* ($n = 6$; number of fish sampled in each sampling point). Different superscript letters in each column represent significant differences among groups (Duncan's test, $p < .05$) in each sample point. Amounts of moisture, lipid, protein and ash are expressed as g/kg of wet body mass. Nitrogen-free extracts (NFE) = 1,000 − (moisture + protein + lipid + ash).
Abbreviations: C, control group (fed everyday); W1, 2 weeks of feeding followed by 1 week of fasting and 4 weeks of re-feeding; W2, 1 week of feeding followed by 2 weeks of fasting and 4 weeks of re-feeding; W3, 3 weeks of fasting followed by 4 weeks of re-feeding.

W1 was higher than in W2 and W3 groups and C showed intermediate value ($p < .05$). After fasting phase, plasma triglycerides were significantly decreased, but total cholesterol increased in feed-restricted fish compared to the group C; however, following re-feeding phase, the plasma triglycerides and total cholesterol concentrations were not significantly different among groups ($p > .05$).

The study of plasma non-specific enzymes revealed that, ALT concentration was not affected by different fasting and re-feeding regimes ($p > .05$, Table 5). However, fish in W3 group had the highest plasma AST, ALP and LDH concentrations after fasting phase ($p < .05$). Fish in W2 group had higher plasma AST than those in the W1 group following 4 weeks of re-feeding ($p < .05$). Plasma ALT, ALP and LDH did not show any significant differences among treatments after re-feeding phase ($p > .05$, Table 4).

4 | DISCUSSIONS

The results of the present study showed that fasting for 1, 2 or 3 weeks resulted in significant weight loss in the *A. baerii* juveniles. This weight loss has been attributed to mobilization of body energy reserves for vital physiological processes such as brain function, respiration and osmoregulation (Ali et al., 2003; Furné et al., 2012). Moreover, the present study showed trajectory growth as indicated by higher WG and SGR in feed-restricted groups. However, their BW_{RF} were lower than the C, indicating partial CG. It has been suggested that hyperphagia (Ali et al., 2003), recovering of energy reserves and metabolic profile (Alvarez & Nicieza, 2005), protein synthesis (Quinton & Blake, 1990), adjustment of endocrine system to regulate the altered nutritional condition (Davis & Gaylord, 2011) and reducing basal metabolic rate may induce CG in fish during re-feeding phase. In agreement with the present findings, long-term fasting periods over 2 weeks prior to re-feeding had significant negative impacts on growth performance and metabolite indices of Chinese sturgeon (*A. sinensis*: Liu et al., 2011), Persian sturgeon (*A. persicus*: Yarmohammadi et al., 2012; Yarmohammadi et al., 2015) and beluga (*H. huso*: Falahatkar, 2012) with mean weights of 75, 180 and 197 g, respectively. In contrast, cyclical short-term fasting periods for 2, 4 or 8 days followed by 8, 16 or 32 days of re-feeding in 40 days (Morshedi et al., 2013) or 80 days (Morshedi et al., 2017) in sub-yearling *A. baerii*, as well as 3 or 7 days fasting and then re-feeding to 70 days in *A. sinensis* (Liu et al., 2011), provoked full CG. Furthermore, in the current study increasing fasting periods led to an increase in the CC for WG suggesting adaptability of *A. baerii* juveniles to feed-deprivation conditions as also reported in whitefish (*Coregonus lavaretus*: Känkänen & Pirhonen, 2009) and pikeperch (*Sander lucioperca*: Mattila et al., 2009).

The results of the present study revealed that somatic indexes including HSI, VSI and DSI significantly decreased in feed-restricted groups as a consequence of depletion and mobilization of stored nutrients (e.g., glycogen and fat) for supplying metabolic energy during fasting period. In this context, remarkable reduction of HSI, VSI and DSI has been previously reported in *A. baerii* after 4 and 8 days of fasting (Ashouri et al., 2013). Significant decrease in HSI values of *H. huso* (Falahatkar, 2012) as well as DSI values in white sturgeon after 10 weeks of fasting (*A. transmontanus*: Hung, Liu, Li, Storebakken, & Cui, 1997) and in Adriatic sturgeon after 72 days of fasting (*A. naccarii*: Furné et al., 2012) has been previously reported. Moreover, significant reduction in liver, digestive tract and visceral mass was observed, indicating them as the most rapidly mobilized depot of nutrients as well as suggesting the phenotypic size flexibility responses of these organs in *A. baerii*. Furthermore, in the present study upon re-feeding for 4 weeks, all somatic indexes restored to the control levels, confirming the results in *A. persicus* (Yarmohammadi et al., 2012) and sub-yearling *A. baerii* (Morshedi et al., 2017). In this sense, it has been suggested that restoring the tissue reserves during re-feeding phase can occur through hyperphagia by prompting some metabolic pathways to recover the energy reserves (Furné et al., 2012). The results of our study suggest that the

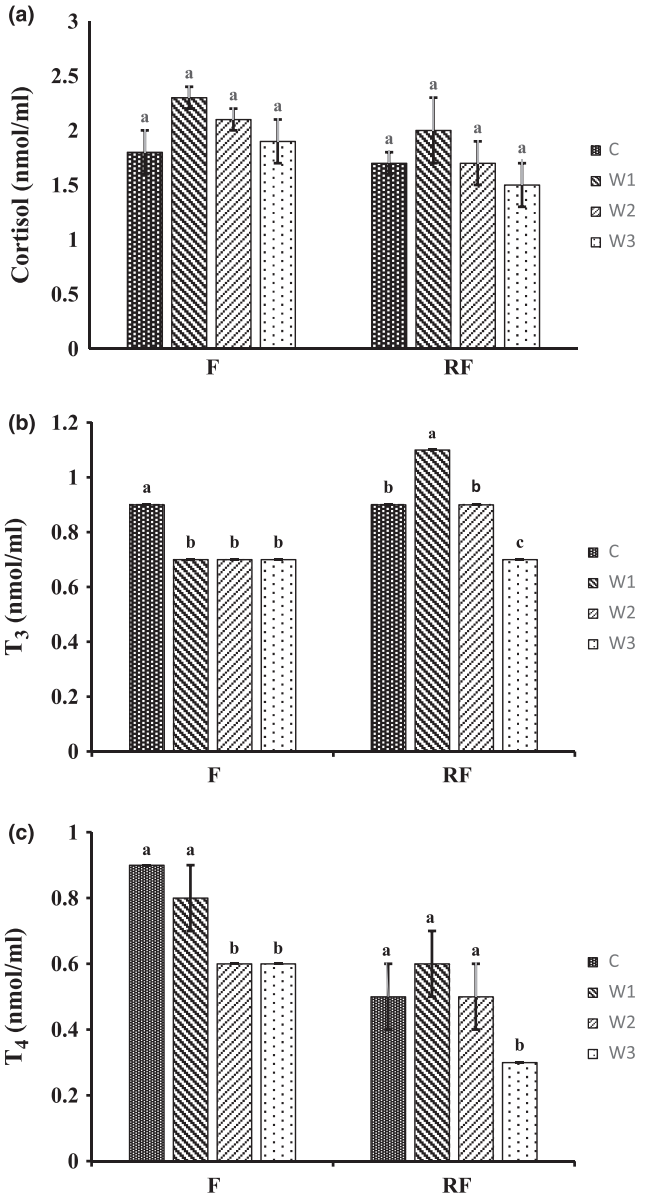

FIGURE 3 Plasma hormone levels including cortisol (a), T_3 (b) and T_4 (c) in *Acipenser baerii* juveniles subjected to different fasting (F) and re-feeding strategies (RF). Control (C) and fish fasted for 1 (W1), 2 (W2) or 3 (W3) weeks and then 4 weeks of re-feeding period. Values are mean ± *SEM* (n = 9; number of fish sampled per sample point). Different letters in each column represent significant differences among groups (Duncan's test, $p < .05$) in each sample point. Refer to the Methods section and Figure 1 for details of the feeding regimes of the treatment groups

juvenile of *A. baerii* metabolize body energy sources, mainly lipids, proteins and carbohydrates (NFE), possibly to sustain gluconeogenesis during starvation period as previously described by McCue (2010) in different species. In addition, *A. baerii* could retrieve whole-body lipid and carbohydrate stores during re-feeding phase, but it could not compensate protein deposition during 4 weeks of re-feeding. It seems that this species needs more time for restoring the structural energy sources such as proteins. In this regard, Morshedi et al. (2017) described a significant reduction in whole-body protein level of *A. baerii* juveniles fasted for 8 days, meanwhile the fish starved for 2 or 4 days did not show any change in the whole-body biochemical composition. We postulated that *A. baerii* catabolized muscle protein as the main energy source with extending the fasting period, which was in line with the findings of our study. Similarly, it has been reported that in *A. transmontanus* subjected to short-term fasting, muscular protein reserves were preferentially mobilized to supply energy (Kiessling, Hung, & Storebakken, 1993).

A previous study also demonstrated that sturgeons have a lower susceptibility to husbandry stressors (e.g., high stocking density, handling, sever confinement and transportation) and show lower magnitude corticosteroid response compared to teleost (Falahatkar, Akhavan, Efatpanah, & Meknatkhah, 2012; Falahatkar et al., 2009). In the present study, the plasma cortisol concentration was not affected by different fasting and re-feeding regimes and was almost similar to that previously reported for *A. baerii* starved for 2, 4 and 8 days (Ashouri et al., 2014), indicating high tolerance of this species to fasting. The lack of significant differences in plasma cortisol concentrations in response to different fasting periods may be due to resistance and adaptation or downregulation of the inter-renal axis by the chronic stress over time of *A. baerii* juveniles. As a matter of fact, studies in aquaculture conditions demonstrated a lower susceptibility to stressors in sturgeons when compared to teleosts, probably due to the differences in sensory perception of the stressors, anatomical differences in inter-renal tissue and its sensitivity, as well as differences in the physiological response capacity (Barton, 2002). In literature, data about the effects of food deprivation on plasma cortisol in fish drastically varies depending on species, feeding programme, experimental condition, health status and fish feeding history (Falahatkar, 2012). Notwithstanding the contradictory results, the precise metabolic role of cortisol in fish during starvation is not comprehensively known (Ashouri et al., 2014).

It has been suggested that the fasting periods in fish also downregulate the hypothalamo-hypophyseal-thyroidal axis, reduce thyroid tissue sensitivity to thyroid-stimulating hormone (TSH), cause a reduction in 5′-monodeiodinase and eliminate the plasma thyroid hormone daily patterns that result in the suppression of the plasma T_4 and T_3 levels (Hornick, Van Eenaeme, Gérard, Dufrasne, & Istasse, 2000; Power et al., 2000). In the present study, weight loss in feed-restricted groups was associated with a decrease in plasma circulating thyroid hormone levels, which suggests the adoption of a homoeostatic mechanism to promote fish survival through reducing the anabolic activity and preserving nutritional reserves during fasting periods. However, after re-feeding phase, fish in W3 had the lowest plasma T_3 and T_4 levels, suggesting that lower basal metabolic rate may result in higher CC in WG in this group with respect to the others. Similar to our result, De Pedro, Delgado, Gancedo, and Alonso-Bedate (2003) reported that plasma thyroid hormone concentrations significantly decreased following 1-week fasting in *Tinca tinca*, and the levels of these hormones were partially restored after 2 days of re-feeding. Several studies have also proved that fasting induces downregulation of the hypothalamus-pituitary-thyroid axis and reduces thyroid-stimulating hormone secretion in

TABLE 4 Plasma metabolites in *Acipenser baerii* subjected to different fasting (F) and re-feeding regimes (RF)

Sample point	Group	Glucose (mmol/L)	Total protein (g/L)	Triglyceride (mmol/L)	Cholesterol (mmol/L)
F	C	3.89 ± 0.08^{a}	3.00 ± 0.30^{a}	10.57 ± 0.24^{a}	4.31 ± 0.26^{b}
	W_1	3.19 ± 0.19^{b}	3.00 ± 0.10^{a}	8.39 ± 0.56^{b}	5.73 ± 0.57^{ab}
	W_2	2.90 ± 0.13^{bc}	2.50 ± 2.50^{b}	8.08 ± 0.21^{b}	6.05 ± 0.23^{a}
	W_3	2.51 ± 0.09^{c}	2.40 ± 0.10^{b}	7.52 ± 0.48^{c}	6.08 ± 0.57^{a}
RF	C	4.23 ± 0.24^{a}	2.60 ± 0.10^{ab}	7.97 ± 0.60^{a}	2.71 ± 0.17^{a}
	W_1	3.37 ± 0.16^{b}	2.80 ± 0.10^{a}	9.23 ± 0.30^{a}	3.44 ± 0.22^{a}
	W_2	3.79 ± 0.16^{b}	2.30 ± 0.10^{b}	7.95 ± 0.59^{a}	3.09 ± 0.26^{a}
	W_3	3.40 ± 0.21^{b}	2.30 ± 0.10^{b}	7.27 ± 0.75^{a}	2.94 ± 0.16^{a}

Note: Values are mean ± *SEM* (n = 9; number of fish sampled in each sampling point). Different superscript letters in each column represent significant differences among groups (Duncan's test, $p < .05$) in each sample point.
Abbreviations: C, control group (fed everyday); W1, 2 weeks of feeding followed by 1 week of fasting and 4 weeks of re-feeding; W2, 1 week of feeding followed by 2 weeks of fasting and 4 weeks of re-feeding; W3, 3 weeks of fasting followed by 4 weeks of re-feeding.

TABLE 5 Plasma non-specific enzyme activities (U/L) in *Acipenser baerii* subjected to different fasting (F) and re-feeding regimes (RF)

Sample point	Group	ALT	AST	ALP	LDH
F	C	1.3 ± 0.2^{a}	107.2 ± 15.7^{b}	549.8 ± 28.2^{c}	535.8 ± 45.2^{b}
	W_1	1.5 ± 0.2^{a}	116.3 ± 15.3^{b}	606.0 ± 28.7^{c}	557.3 ± 37.3^{ab}
	W_2	1.3 ± 0.2^{a}	124.0 ± 5.0^{ab}	954.8 ± 31.0^{b}	624.0 ± 45.8^{ab}
	W_3	1.2 ± 0.2^{a}	171.2 ± 10.7^{a}	1,098.2 ± 8.1^{a}	703.2 ± 39.5^{a}
RF	C	2.0 ± 0.4^{a}	156.0 ± 9.5^{ab}	464.3 ± 41.6^{a}	538.8 ± 48.2^{a}
	W_1	1.7 ± 0.2^{a}	117.3 ± 7.3^{b}	411.0 ± 33.0^{a}	436.5 ± 30.0^{a}
	W_2	1.8 ± 0.3^{a}	159.5 ± 12.6^{a}	417.2 ± 32.0^{a}	489.3 ± 39.6^{a}
	W_3	2.2 ± 0.3^{a}	148.0 ± 11.4^{ab}	471.7 ± 28.4^{a}	563.8 ± 45.5^{a}

Note: Values are mean ± *SEM* (n = 9; number of fish sampled in each sampling point). Different superscript letters in each column represent significant differences among groups (Duncan's test, $p < .05$) in each sample point.
Abbreviations: ALP, alkaline phosphatase, ALT, alanine aminotransferase, AST, aspartate aminotransferase; C, control group (fed everyday), LDH, lactate dehydrogenase; W1, 2 weeks of feeding followed by 1 week of fasting and 4 weeks of re-feeding; W2, 1 week of feeding followed by 2 weeks of fasting and 4 weeks of re-feeding; W3, 3 weeks of fasting followed by 4 weeks of re-feeding.

different teleost species (Deng, Zhang, Lin, & Cheng, 2004; Leiner et al., 2000; Power et al., 2000; Raine, Cameron, Vijayan, Mackenzie, & Leatherland, 2005). In contrast, Ashouri et al. (2013) reported that plasma T_3 and T_4 levels did not change after short-term fasting periods (2, 4 and 8 days) in *A. baerii*, suggesting a species-specific response to fasting duration.

The plasma glucose level is a routine index for determining nutritional condition and is also regarded as a reliable indicator of secondary stress response in fish (Wagner & Congleton, 2004). In the current study, the glucose plasma levels in *A. baerii* significantly decreased over the 3 weeks of feed deprivation and were not completely restored after re-feeding. Similarly, plasma glucose significantly decreased after short-term fasting (2, 4 and 8 days) in *A. baerii* (Ashouri et al., 2013) or after long-term fasting in *A. transmontanus* (Hung et al., 1997) and *A. naccarii* (Furné et al., 2012). In contrast, some studies reported that the plasma glucose levels remained stable during fasting periods in different sturgeon species such as lake sturgeon (*A. fulvescens*: Gillis & Ballantyne, 1996) and *A. persicus* (Yarmohammadi et al., 2012).

Plasma protein level is described as a very stable plasma nutritional index in fish (Peres et al., 2013), and its alternations often occur as a consequence of amino acid oxidation or peripheral proteolysis (Di Marco et al., 2008; Mommsen et al., 1999). The results of the present experiment showed that plasma protein level in W2 and W3 groups was decreased significantly during fasting phase and that it was not restored after re-feeding to the levels found in C and W1 groups. In this context, it has also been reported that plasma protein significantly decreased in common carp (*Cyprinus carpio*: Blasco, Fermtndez, & Gutierrez, 1992) and common dentex (*Dentex dentex*: Pérez-Jiménez et al., 2012) after 5 days or 5 weeks of fasting, respectively. The results obtained in the present study suggest that protein and non-essential amino acids are readily available nutrient reserves to maintain basal metabolism following 2 weeks of fasting in *A. baerii* juvenile. Interestingly, the fact that protein reduction in

plasma was associated with an increase in plasma AST and ALP levels during fasting phase suggests protein mobilization as substrate for gluconeogenesis in *A. baerii* during feed deprivation. In contrast, plasma protein in *A. baerii* juveniles significantly increased after 8 days of fasting (Ashouri et al., 2013).

In the present experiment, a marked increase in plasma cholesterol and decrease of triglycerides during the fasting phase suggested high lipid mobilization from liver and visceral tissues as was also indicated by a drastic reduction in HSI, VSI and DSI indices, which are the main sites for lipid deposition. These results suggested that the lipids are the preferred energy substrates for gluconeogenesis during lipolytic processes for supplying basal energy during *A. baerri* fasting periods. Furthermore, free fatty acids produced during lipolysis might be used as substrate for cholesterol synthesis and thus lead to hypercholesterolaemia during fasting phase (Palmegiano et al., 1993). In this sense, Hung et al. (1997) reported that viscerosomatic index was drastically reduced compared to carcass index in *Acipenser naccarii* starved for 10 weeks, suggesting that lipid was stored as preferred nutrient over protein for mobilization in this species. Similar results were previously reported in Adriatic sturgeon (*A. naccarii*: Furné et al., 2012) and in sub-yearling Siberian sturgeon (*A. baerii*: Morshedi et al., 2017) subjected to different cycles of fasting and re-feeding periods.

The results of our study showed that fish in the feed-restricted groups had higher plasma AST, ALP and LDH levels than the control group, suggesting higher gluconeogenesis from non-carbohydrate substrates such as amino acids and lactate during fasting phase in *A. baerri* juveniles. It is reported that AST, ALP and LDH are responsible for gluconeogenesis and increase in a stressful status (Furné et al., 2012; Pérez-Jiménez et al., 2012). In addition, in the present study except for plasma AST level, the plasma ALP and LDH values were recovered after the re-feeding phase in the feed-restricted groups. Similar to our results, Yarmohammadi et al. (2015) reported that plasma AST and ALP significantly increased in *A. persicus* during 4 weeks of fasting and their values recovered after re-feeding phase. Moreover, the use of lactate as energy substrate for gluconeogenesis led to an increase in LDH activity in gilthead seabream (*Sparus aurata*: Polakof et al., 2006). In contrast, Furné et al. (2012) reported that ALT and LDH activities decreased, but AST activity increased during 72 days of fasting in white muscle of *A. naccarii*, confirming a species-specific metabolism process in all these species.

The results of the present study indicated long-term fasting (more than 1 week) have a negative influence on growth and 4 weeks of re-feeding was too short to induce full compensatory growth in *A. baerii* juveniles. In addition, fat stores in the liver and visceral cavity are more mobilized compared to muscular nutrients during fasting for supplying energy metabolism. Our results suggest that this species could adapt to short-terms fasting by reducing the rate of metabolism as well as mobilization of nutrient reserves, especially lipids, in the feed-restricted groups through a decrease in thyroid activity and increase in gluconeogenesis pathway. Finally, plasma metabolites showed considerable alternations after fasting and re-feeding phases, which may suggest them as useful indices for monitoring nutritional and health status in this species. Our results demonstrated that fasting periods over 1 week have negative effects on growth performance, thyroid hormones, as well as plasma biochemical health indices in *A. baerii* juveniles. In addition, this study has proven that with optimal period of fasting and re-feeding strategy, *A. baerii* juveniles are able to recover plasma thyroid hormones and metabolites. Further studies on transcriptomics and proteomics will provide a more holistic approach to confirm our findings.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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