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FULL PAPER

Metabolic responses to short starvation and re-feeding in rainbow trout (*Oncorhynchus mykiss*)

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Abstract A feeding study was conducted to determine the effect of short-term starvation periods and subsequent re-feeding on some morphological and physiological parameters of rainbow trout (*Oncorhynchus mykiss*) fingerlings. Two hundred and seventy trout fingerlings (mean ± SE, 17.5 ± 0.06 g) were randomly distributed in 15 circular fiberglass tanks. The fish were exposed to five different feeding regimes: control, fed twice daily for 60 days; T1, one day starvation and two days re-feeding (20 cycles); T2, one day starvation and four days re-feeding (12 cycles); T3, three days starvation and 12 days re-feeding (four cycles), T4, four days starvation and 16 days re-feeding (three cycles). Blood samples were taken for biochemical analyses at the end of the experiment. The results indicated that plasma cortisol, glucose, total protein, cholesterol, albumin, low-density lipoprotein, uric acid, creatinine, high-density lipoprotein, alkaline phosphatase, and aspartate aminotransferase levels were not significantly different between the control and starved fish, but plasma triglyceride and glucose levels were significantly higher in the T4 group as compared to the control and other deprived groups. There were no significant differences in perivisceral fat index among the five groups. However, hepatosomatic index significantly decreased in the T3 group in comparison with other groups. The present study demonstrates that rainbow trout could tolerate short-term starvation periods and subsequent feeding without any significant health damage particularly regarding some morphological and physiological parameters.

Keywords Starvation · Re-feeding · Physiological parameters · Morphological parameters · Rainbow trout

Introduction

Many fish species can relatively tolerate periods of starvation without severe consequences, both in their natural environment and in fish farms (Navarro and Gutiérrez 1995; Barcellos et al. 2010). The amount and distribution of food is a factor that has a great effect on the growth of an organism. Food availability can vary during the winter months due to seasonal changes in water temperature (Jobling 1994), reproductive migrations, tidal and long-term ecological changes (Navarro and Gutiérrez 1995; McCue 2010). In aquaculture, rainbow trout (*Oncorhynchus mykiss*) may experience food deprivation in response to several factors such as temperature fluctuation and preharvesting, to reduce the negative effects of stress and mortality due to handling and pathogens (Davis and Gaylord 2011), and to improve management of water quality, reducing feed and labor costs and improving product quality (Gaylord and Gatlin 2000; Caruso et al. 2011).

Organisms such as fish have employed different ways in which they can cope with the limitations of food including a wide range of physiological and behavioral strategies, structural changes, minimizing energy expenditures by decreased locomotion activities, inducing changes in

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mobilization of endogenous reserves (glycogen, lipid or proteins), although the latter help to maintain homeostasis and is dependent on species and duration of the fasting period (McCue 2010).

Many studies on metabolic response to starvation indicate that two principal groups of fish can be distinguished; some fishes such as eel *Anguilla anguilla*, goldfish *Carassius auratus*, rainbow trout and plaice *Pleuronectes platessa* preserve liver glycogen and use protein and lipid as their primary energy sources, whereas other species such as northern pike *Esox lucius*, roach *Rutilus rutilus*, and golden perch *Macquaria ambigua* deplete primarily glycogen stores. However, the reserved lipid in different forms appears to be the primary and earlier source of energy in both situations (Navarro and Gutiérrez 1995; Czesny et al. 2003).

After starvation or food restriction, fish are known to show greater growth rates, when adequate food supplies are restored than the constantly fed fish (Quinton and Blake 1990). The ability of growth compensation is an important adaptation in a fluctuating and unpredictable environment (Maclean and Metcalfe 2001).

Compensatory growth has been studied in various fishes, such as salmonids (e.g., Quinton and Blake 1990; Boujard et al. 2000; Maclean and Metcalfe 2001; Kankanen and Pirhonen 2009), cyprinids (e.g., Abolfathi et al. 2012), channel catfish, *Ictalurus punctatus* (e.g., Gaylord and Gatlin 2000) and sturgeon (e.g. Morshedi et al. 2013), indicating that growth compensation occurs following food deprivation or restricted feeding. However, the degree of compensation is highly variable among fish species (Ali et al. 2003). Although, there are different metabolic responses to re-feeding that depend on many factors including environmental conditions, period of food deprivation, fish species, and the previous feeding history (Navarro and Gutiérrez 1995), in most fish species, metabolites levels are restored to pre-starvation values by re-feeding (Meton et al. 2003).

As reviewed by Navarro and Gutiérrez (1995) and McCue (2010), there are several reported studies on the effects of fasting on metabolic responses in fish. However, many studies have focused on starvation and re-feeding effects on hematological, biochemical and immunological parameters (De Pedro et al. 2003; Pérez-Jiménez et al. 2007; Caruso et al. 2012; Falahatkar 2012; Furné et al. 2012; Perez-Jimenez et al. 2012). Therefore, the aim of present study is to understand the physiological strategies of rainbow trout to short-term starvation and re-feeding. For this objective, we examined some morphological (hepatosomatic index and perivisceral fat index) and physiological parameters (glucose, total protein, triglyceride, cholesterol, cortisol, albumin, low-density lipoprotein, uric acid, urea, creatinine, high-density lipoprotein, alkaline phosphatase and aspartate aminotransferase).

Materials and methods

Fish rearing and feeding regime. All experiments were carried out in the aquarium facility of the Department of Natural Resources, Isfahan University of Technology. Juvenile rainbow trout (*Oncorhynchus mykiss*) were obtained from a commercial local farm from Shahrekord province, Iran. Fish were kept in a water flow system and acclimated to the experimental condition for two weeks before use. During this period, fish were fed ad libitum rations twice a day (especially manufactured pellet for rainbow trout by Esfahan Mokammel Co., Isfahan, Iran). Feed with 3-mm diameter contained 43 % crude protein, 15 % crude lipid, 14 % moisture, and 11 % ash. Proximate analysis of commercial diet was carried out after drying and homogenization of samples. The samples were dried to constant weight at 105 °C. Ash content was determined by burning the samples at 450 °C for 8 h. The protein and total lipid contents of samples were determined using the Kjeldahl method and Soxtec method, respectively (AOAC 2000).

An indoor semi circulated system with filtered water was used for maintaining fish. Water temperature was between 14.2 and 15.2 °C. Oxygen concentration was maintained at 8.5 mg/L and pH was 7.2. Fish were kept on 12 L:12 D photoperiod. After acclimation period, 270 fish with an average initial body weight of 17.5 ± 0.06 g (mean ± SE) were distributed randomly among fifteen 100-L polyethylene circular tanks (18 fish per tank, flow rate of 5 L/min). There were no significant differences in the initial weight and length between the control and the food-deprived groups. In our study, rainbow trout were reared using a fasting and re-feeding protocol described by Eroldogan et al. (2006) and Azodi et al. (2013). Five treatments with three replicates were assigned as follows:

Control: fish were fed to an apparent satiation twice a day throughout the experimental period.

T1: fish were fasted for one day and then re-fed for two days to apparent satiation level (20 cycles throughout the experiment).

T2: fish were fasted for one day and then re-fed for four days to apparent satiation level (12 cycles throughout the experiment).

T3: fish were fasted for three days and then re-fed for 12 days to apparent satiation level (four cycles throughout the experiment).

T4: fish were fasted for four days and then re-fed for 16 days to apparent satiation level (three cycles throughout the experiment).

Sample collection. Three fish per tank (nine per treatment) were randomly sampled at the end of the experiment. Blood samples were rapidly collected from the caudal vein using 2 mL heparinized syringes under anesthesia (MS-222, 30 mg/L) condition. Plasma was immediately

detached after centrifuging blood samples at 3000 rpm for 10 min and then stored at −20 °C for cortisol and metabolites analyses. Six fish per tank were rapidly euthanized, and then whole liver weights and viscera weights were recorded respectively, for determination of hepatosomatic index (HSI) and perivisceral fat index (PFI). HSI and PFI were calculated as [liver weight (g)/total body weight (g)] × 100 and [intraperitoneal fat weight (g)/total body weight (g)] × 100, respectively.

Plasma biochemical parameters were analyzed using an auto-analyzer (Technicon RA-1000, Technicon Instruments, New York, NY, USA), with commercial clinical investigation kits (Pars Azmoon Kit, Tehran, Iran). Plasma cortisol levels were determined by a commercial kit (Immunotech cortisol RIA kit, 1841, Radiova, Czech Republic) using a previously validated cortisol RIA (Pickering et al. 1987). Plasma glucose levels were assayed by a standard enzymatic-colorimetric test, based on the glucose oxidase-peroxidase method using a commercial kit (Pars Azmoon Kit, 110071). Plasma total protein concentration was determined on the basis of Bradford (1976) method with a kit (Bio-Rad Laboratories GmbH, Munich, Germany) and using bovine serum albumin as a standard protein. Plasma albumin was colorimetrically detected according to Rehulka (2000).

Biochemical measurements were analyzed using standard colorimetric tests (Pars Azmoon Kit: 110073, 111509, 111482, 110127, 111491, 111483, 111639, 111562) for uric acid, urea, creatinine, low-density lipoprotein (LDL), high-density lipoprotein (HDL), total cholesterol, triglyceride (TG), alkaline phosphatase (ALP), and aspartate aminotransferase (AST). All the experimental procedures including euthanasia were based on the guidelines provided by International Sturgeon Research Institute (Iran) and European Communities Council directive (86/609/EEC) on the protection of animals used for scientific purpose. Care was taken to use only the minimum possible number of specimens for analytical work and fish were euthanized with an overdose of anesthetic.

Statistical analysis. All statistical analyses were performed by using SPSS, version 16 for Windows. A Kolmogorov–Smirnov test was applied to assess the normality of distributions. The homogeneity of variances was tested using Levene's F test. Differences between various treatments were analyzed using one-way ANOVA. Post hoc comparisons among sample means were tested by Duncan's test and $P < 0.05$ was taken as the level of significance.

Results and discussion

Biochemical and physiological parameters are monitored because the physiological state of fish is the main factor underlying the attainment of the required performance levels. Fluctuations in these parameters may reflect the responses of fish to changes in their environment or exogenous agents (Rehulka 2000). There was no fish mortality during the 60-day feeding trial among the five groups. The plasma cortisol levels were not significantly affected by fasting and re-feeding (Table 1). These results are similar to the results obtained by Sumpter et al. (1991) on rainbow trout (*Oncorhynchus mykiss*), Davis and Gaylord (2011) on sunshine bass (*Morone chrysops* × *Morone saxatilis*), Caruso et al. (2011) on European sea bass (*Dicentrarchus labrax*) and black spot sea bream (*Pagellus bogaraveo*), and Caruso et al. (2012) on red porgy (*Pagrus pagrus*). On the contrary, effects of food deprivation on plasma cortisol levels in fish are variously reported to be reduced by starvation [Barton et al. 1988 (chinook salmon, *Oncorhynchus tshawytscha*); Farbridge and Leatherland 1992 (rainbow trout, *O. mykiss*)], or increased by starvation [Blom et al. 2000 (rainbow trout, *O. mykiss*); Barcellos et al. 2010 (jundia, *Rhamdia quelen*)]. Peterson and Small (2004) observed that the effect of starvation on plasma cortisol levels in channel catfish was dependent on the length of the food deprivation. The present result indicates that these short-term starvations could not induce plasma cortisol, which plays a functional role in mobilizing energy. Nonetheless, it is very difficult to draw a definite conclusion as many contradictory results have been reported on fish.

Proteins are the most important compounds in the serum and have an essential role in physiological and immunological systems (Kumar et al. 2005). Protein catabolism in response to starvation is investigated by the measures of circulating the most commonly measured physiological variables such as tissue enzyme levels, tissue protein content and increased rates of nitrogen excretion (Shimeno et al. 1990). The effects of short-term starvation and re-feeding on rainbow trout biochemical parameters are given in Table 1. The results of the present study showed that feeding strategies had no effects on plasma uric acid, urea, albumin, total protein, alkaline phosphatase (ALP) and aspartate transaminase (AST); in fact no significant differences were observed between the deprived groups and the control group. However, creatinine level was significantly higher in T4 fish than that of T2 and T3 fish ($P < 0.05$, Fig. 1a). At the end of the experiment, plasma creatinine concentration comprised between 0.4 ± 0.04 mg/dl and 0.73 ± 0.13 mg/dl in fasted/re-fed fish. The increases in plasma enzyme activity such as ALT, AST, LDH and ALP in response to exogenous agents are considered to be indicative of liver dysfunction (Rehulka 2000), while urea (Adams et al. 1996) and creatinine (Burtis and Ashwood 1996) were considered as one of the markers of gill or kidney dysfunction. Unfortunately, no

Table 1 Physiological parameters and enzyme activities of rainbow trout juveniles (*Oncorhynchus mykiss*) maintained in five different feeding regimes (mean ± SE)

Parameters	Treatment				
	C	T_1	T_2	T_3	T_4
Cortisol (ng/ml)	22.00 ± 7.02	54.34 ± 9.96	15.00 ± 1.52	24.31 ± 8.83	30.33 ± 7.79
Cholesterol (mg/dl)	306.67 ± 37.65	325.24 ± 19.27	303.00 ± 16.16	316.19 ± 29.17	361.33 ± 25.41
LDL (mg/dl)	66.33 ± 6.35	60.00 ± 4.04	63.32 ± 3.17	62.66 ± 5.23	59.31 ± 3.71
HDL (mg/dl)	174.33 ± 16.83	193.29 ± 8.11	176.00 ± 13.01	187.00 ± 15.56	191.67 ± 14.40
Total protein (g/dl)	5.27 ± 0.18	4.95 ± 0.13	4.98 ± 0.12	5.02 ± 0.18	5.46 ± 0.53
Albumin (g/dl)	1.66 ± 0.03	1.41 ± 0.09	1.50 ± 0.05	1.48 ± 0.07	1.58 ± 0.25
Uric acid (mg/dl)	0.41 ± 0.20	0.25 ± 0.02	0.13 ± 0.03	0.41 ± 0.14	0.59 ± 0.16
Urea (mg/dl)	4.93 ± 0.81	5.30 ± 0.34	4.96 ± 0.40	5.20 ± 0.64	5.43 ± 0.61
AST (U/l)	130.37 ± 35.98	81.03 ± 25.12	69.53 ± 28.26	95.06 ± 17.98	105.60 ± 21.97
ALP (U/l)	1136.73 ± 169.50	1138.03 ± 72.03	971.00 ± 76.70	1176.33 ± 131.36	1272.33 ± 188.54

C control (fed twice a day to apparent satiation); *T1* deprivation for one day and then re-fed for two days; *T2* deprivation for one day and then re-fed for four days; *T3* deprivation for three days and then re-fed for 12 days; *T4* deprivation for four days and then re-fed for 16 days. No significant differences were observed between feeding strategies ($P > 0.05$)

reference is available on the effect of starvation on protein metabolites including changes in plasma uric acid, urea, albumin, and creatinine. Only very little is documented about detecting the response to fasting of total protein, alkaline phosphatase, and aspartate transaminase. Analyzing the result, no clear explanation was found for the increased creatinine, which was supposed to be related to the high inherent variability among the individual fish used in each treatment.

It has been demonstrated in many species of fish that lipids are mobilized during starvation. Statistical analysis of data indicated that there were no significant differences in cholesterol, low-density lipoprotein (LDL), and high-density lipoprotein levels (HDL). However, triglyceride levels were significantly elevated in the deprived fish for four days (T4 fish) than those of control fish and three experimental groups ($P < 0.05$, Fig. 1b). At the end of the experiment, plasma triglyceride varied from 109 ± 5.77 mg/dl to 178 ± 12.52 mg/dl in fasted/re-fed fish. It is known that triglycerides are the most available lipid reserve during the early phases of food deprivation (Navarro and Gutiérrez 1995). Similarly, several studies have reported steady levels of plasma triglyceride during re-feeding after starvation [Pérez-Jiménez et al. 2007 on European sea bass; Furné et al. 2012 on sturgeon (*Acipenser naccarii*) and rainbow trout; Perez-Jimenez et al. 2012 on dentex (*Dentex dentex*)]. In contrast, many studies reported that levels of plasma triglyceride were decreased in response to food deprivation in some fish species (Costas et al. 2011; Falahatkar 2012). It is well known that plasma glucose, total protein, cholesterol, and triglyceride levels fluctuated with protein catabolism (Andenen et al. 1991) and glycogenolysis (Vijayan and Moon 1992). Total triglyceride levels exhibit variable responses; such contradictory results could also result from differences in fish species and their physiology for satisfying their biological needs during the starvation period (Weatherley and Gill 1981). The present results indicated that re-feeding after starvation could cause a release of triglyceride and cholesterol (although not significant) into the blood circulatory system for the longer starvation period (deprivation for four days).

After the 60-day experimental period, plasma glucose ranged from 109 ± 5.77 mg/dl to 178 ± 12.52 mg/dl in fasted/re-fed fish. The findings of the present study showed that plasma glucose levels remained unchanged between the deprived and control groups with the exception of plasma glucose of T4 fish that was significantly lower than those of T2 and T3 fish ($P < 0.05$, Fig. 1c). However, no consistent treatment-related patterns can be discerned. Similarly, Hochachka and Sinclair (1962) on rainbow trout, Barcellos et al. (2010) on adult jundiai, Caruso et al. (2011) on European sea bass and black spot sea bream, and Caruso et al. (2012) on red porgy reported that plasma glucose levels were maintained at a constant level during the different periods of starvation. In contrast, other studies have reported that plasma glucose levels were reduced during starvation period (De Pedro et al. 2003; Pérez-Jiménez et al. 2007; Ceinos et al. 2008). These differences in response to starvation may be related to their interspecies variability, age, past nutritional history, and season (Boujard et al. 2000; Pérez-Jiménez et al. 2007). The common response of fish undergoing starvation is to maintain blood glucose at a constant level by activating processes of glycogenolysis and gluconeogenesis. Moreover, maintaining plasma glucose during food deprivation

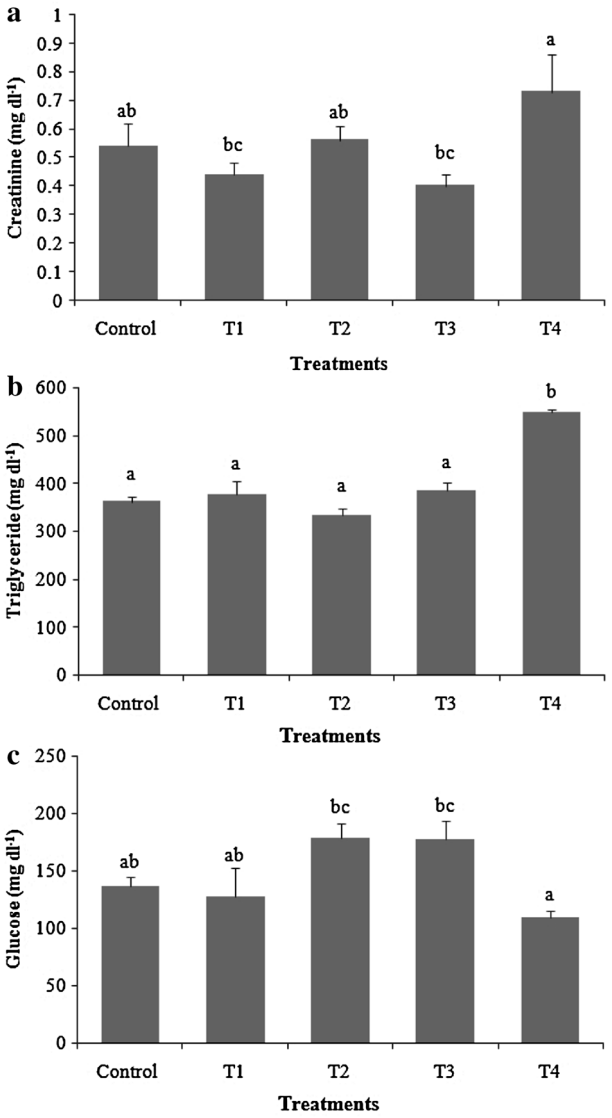

Fig. 1 Plasma creatinine (**a**), triglyceride (**b**) and glucose levels (**c**) of juvenile rainbow trout (*Oncorhynchus mykiss*) maintained in five different feeding regimes (mean ± SE). *C* control (fed twice a day to apparent satiation); *T1* deprivation for one day and then re-fed for two days; *T2* deprivation for one day and then re-fed for four days; *T3* deprivation for three days and then re-fed for 12 days; *T4* deprivation for four days and then re-fed for 16 days. *Different superscripts* on each column indicate significant difference between feeding strategies ($P < 0.05$)

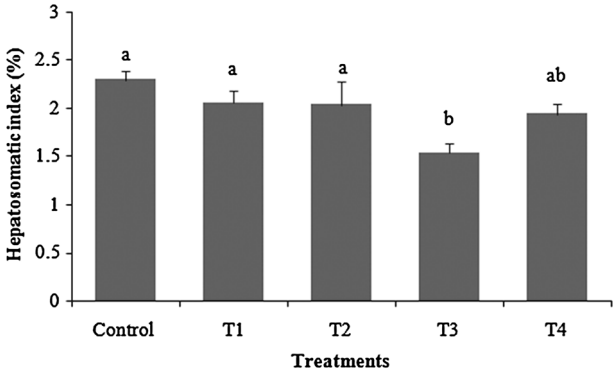

Fig. 2 Changes in hepatosomatic index (HSI) of juvenile rainbow trout (*Oncorhynchus mykiss*) maintained in five different feeding regimes (mean ± SE). *C* control (fed twice a day to apparent satiation); *T1* deprivation for one day and then re-fed for two days; *T2* deprivation for one day and then re-fed for four days; *T3* deprivation for three days and then re-fed for 12 days; *T4* deprivation for four days and then re-fed for 16 days. *Different superscripts* on each column indicate significant difference between feeding strategies ($P < 0.05$)

could be related to lower glucose expenditures (Navarro and Gutiérrez 1995; McCue 2010).

Since, the reduction of hepatic energy reserves due to starvation is reflected in morphological changes of the liver weight, some morphological indices, such as HSI that can also be used as a useful indicator of nutritional status, are commonly estimated (Leatherland and Farbridge 1992). Hepatosomatic index (HSI) was influenced by the fasting periods and re-feeding, as the lowest level was observed in T3 fish (1.54 ± 0.10 %), and the highest in the control fish (2.3 ± 0.09 %). Hepatosomatic index of T1, T2, and control groups was significantly higher than that of the T3 group ($P < 0.05$, Fig. 2). However, no significant difference was found in the perivisceral fat index (PFI) between treatments at the end of the experiment ($P > 0.05$, Fig. 3). Similarly, Hung et al. (1997) reported that several weeks of starvation significantly decreased HSI values in white sturgeon (*Acipenser transmontanus*). Several studies have reported similar results in rainbow trout *O. mykiss* (see Storebakken et al. 1991), tench *Tinca tinca* (see De Pedro et al. 2003), red porgy *P. pagrus* (see Caruso et al. 2012), and beluga *Huso huso* (see Falahatkar, 2012). In the present study, the starvation for a short time did not influence significantly HSI value in experimental groups with the exception of T3 group, supporting the fact that liver function is somehow defended and the liver reserves have a vital role during short-term starvation. In T3 group, it seems that 12 days of re-feeding were not sufficient to recover the possible liver loss caused by the deprivation, but re-feeding in the groups T1, T2, and T4 could cover the possible loss.

Overall, the absence of significant differences in most of the parameters measured between the deprived groups with control group can be attributed to the short length of the starvation periods of the experiment and suggested that rainbow trout exposed to fasting (one to four days) and re-feeding retained plasma metabolites and cortisol hormone at a certain level. The results of the present study show that rainbow trout could tolerate short-term starvation periods and re-feeding without any significant health damages, particularly in some morphological and physiological

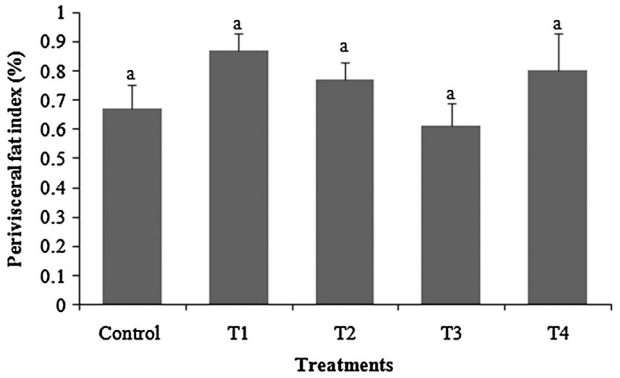

Fig. 3 Changes in perivisceral fat index (PFI) of juvenile rainbow trout (*Oncorhynchus mykiss*) maintained in five different feeding regimes (mean ± SE). *C* control (fed twice a day to apparent satiation); *T1* deprivation for one day and then re-fed for two days; *T2* deprivation for one day and then re-fed for four days; *T3* deprivation for three days and then re-fed for 12 days; *T4* deprivation for four days and then re-fed for 16 days. No significant differences were observed between feeding strategies ($P > 0.05$)

parameters. However, further research on hormonal and immunological responses is needed to completely understand the mechanism during such feeding strategies.

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