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Effects of Different Durations of Fasting/Re-feeding Bouts on Growth, Biochemical and Histological Changes in the Digestive Tract of Gansu Golden Trout (*Oncorhynchus mykiss*)

*Xia Liu[1], Ibrahim Magdy Mohamed Hegab[2, 3], Junhu Su[3], Xiaohua Du[4], Xiping Fan[4], Qiong Zhang[1], Yuan Gao[1], Haifang Wang[1]**

[1]*College of Life Science and Technology, Gansu Agricultural University, Lanzhou, P.R. China*

[2]*Department of Hygiene, Zoonosis and Animal Behaviour and Management, Faculty of Veterinary Medicine, Suez Canal University, Ismailia, Egypt*

[3]*College of Grassland, Gansu Agricultural University, Lanzhou, P.R. China*

[4]*Faculty of Veterinary Medicine, Gansu Agricultural University, Lanzhou, P.R. China*

**Corresponding author: w35126799@qq.com*

ABSTRACT

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This study was conducted to explore the outcomes of starvation/re-feeding techniques on growth performance, liver antioxidant activities, and histological changes of the gastrointestinal organs of Gansu golden trout. A total of 225 juveniles were divided into 5 treatment groups; the control group (N_0) was routinely fed every day while the other groups (N_7, N_{14}, N_{21}, and N_{28}) were starved for 7, 14, 21, and 28 days, respectively and after the starvation session, each group was re-fed for 28 days. Compensatory growth was statistically recorded in N_{14}. Weight gain rate and feeding ratio were the highest in the N_{14} group, while specific growth rate and feeding conversion ratio showed significant increases in the fish groups exposed to longer starvation periods. Liver antioxidant activities showed a significant increase and decrease in malondialdehyde and superoxide dismutase levels in N_{21} and N_{28}, respectively, which returned to normal levels after re-feeding. Stomach, intestine, and liver showed histological alterations in all groups and the severity was correlated with the fasting periods. Those changes were restored to a certain degree after feeding was resumed. The compensation by group N_{14} presents potential for economic usefulness of the fasting/re-feeding strategy in Gansu golden trout.

Keywords: biochemistry; food deprivation; phenotypic changes; histology; productive traits

Starvation is a potential risk to the well-being of organisms and occurs in nature due to various ecological or anthropogenic changes. Aquatic organisms undergo bouts of feeding restriction either in the wild population or frequently in farmed fish. Wild fish experience cycles of limited food

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availability due to forage shortages or inclement weather conditions and during certain stages of their reproduction events (Gingerich et al. 2010). Likewise, cultured fish may suffer periods of hunger for the same reasons, but may also encounter periods of feeding restriction or deprivation deliberately induced during farming. For example, food restriction may be one of the solution strategies to combat certain farming problems such as the negative effects of disease outbreaks (Davis and Gaylord 2011).

The role of aquaculture in guaranteeing a steady supply of aquatic species for human consumption cannot be ignored; however, feed cost is notably the greatest variable cost at aquaculture facilities (Ali et al. 2016) and, therefore, the balance between benefit and cost should be thoroughly considered. Food restriction/re-feeding practices have been proven to be efficient in improving aquafarming in diverse ways. In order to increase productivity, different studies have been conducted to introduce suitable feeding regimes based on starvation/re-feeding cycles that might equalise the feed-related costs and the profits from gain in body weight (Mukherjee and Maitra 2015). Moreover, withholding food decreases the production costs by reducing the amount of food supplied to the fish and enhancing the water characteristics (e.g., minimising excretion of ammonia), and so resulting in less pollution during fasting periods. Finally, food suspension is a common welfare practice during the 24 to 48 h prior to transportation and harvest, and appears to improve gut evacuation, reduce metabolic rate and physical activity, and abolish social hierarchy, which subsequently increases the tolerance of the fish to the transportation stress (Rob 2008).

The phenomenon of compensatory growth that may occur as a reaction to food deprivation and re-feeding has been documented across various species including birds, mammals, and fish (Hornick et al. 2000). Compensatory growth highlights the physiological mechanisms in which animals display phases of improved growth and weight gain following periods of slowed development that are usually associated with reduced feed intake (Thongprajukaew and Rodjaroen 2017). In fish, different results have been obtained, which range from no compensatory growth at all to hypergrowth of fish when rounds of food deprivation and re-feeding have been applied (Hayward et al. 1997). Although this technique has been found to induce various compensatory growth levels in fish, some growth parameters (e.g. feed conversion efficiency) varied among studies, such as a previous study on rainbow trout, *Oncorhynchus mykiss*, which showed that the feed conversion efficiency did not vary among fish subjected to different starvation/re-feeding cycles (Nikki et al. 2004), while improved feed utilization has been reported in pacu (*Piaractus mesopotamicus*) during food satiation sessions after food deprivation (Souza et al. 2000). However, this discrepancy across literature deserves further investigation.

Fish also showed various biochemical and structural changes in response to adaptations to starvation stress. Starvation and nutrient deprivation are known to provoke significant alterations in the physiology of fish, predominantly in their patterns of reactive oxygen species (ROS), with a massive release of ROS that may bond with the polyunsaturated fatty acids to stimulate the production of toxic aldehyde metabolites, such as malondialdehyde (MDA), which is one of the end products of the lipid peroxidation (Tsikas 2017). The massive production of ROS is controlled by various defense-related enzymes such as superoxide dismutase (SOD) and total antioxidant capacity (T-AOC). Nonetheless, if this defense system fails to control the elevated levels of ROS, oxidative stress occurs that leads to injuries of internal organs by causing damage to mucosal membranes, or cellular injury of membrane lipids, proteins and nucleic acids (Bhattacharyya et al. 2014). In the same vein, the histological outcomes of food deprivation were mainly obvious in various regions of the digestive tract (Ostaszewska et al. 2006). A study on laboratory-reared miiuy croaker (*Miichthys miiuy*) demonstrated degeneration of cells in digestive organs, seen in the shrinkage and separation of cells and the loss of intercellular substances in the liver, pancreas, intestine and stomach following starvation (Shan et al. 2016), which became more aggravated with longer durations of starvation. In addition, the loss of the histological structures of the digestive tracts of the starved larvae and juveniles of miiuy croaker partly recovered after re-feeding, showing that food deprivation may greatly damage the structures of digestive system (Zeng et al. 2012).

Gansu golden trout (*Oncorhynchus mykis*) is an important freshwater species, which has been farmed for more than thirty years in Gansu Prov-

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ince, China. The different environmental conditions and feeding tactics, faster growth rates, higher palatability among consumers, and the various breeding goals make this species a main point of concern for research studies. Gansu golden trout is a cold-water species, suitable for breeding and raising in cold climatic areas, a quality particularly desirable when dealing with new species, and which might give an excellent example of the growth, biochemical and structural responses of other cold-water fishes to different durations of starvation/re-feeding cycles, providing data that could establish new understanding to set up appropriate rearing and management protocols and establishing the justification for the present study.

MATERIAL AND METHODS

Fish rearing and management conditions. A total of 225 healthy juvenile Gansu golden trout (*Oncorhynchus mykiss*), 54 ± 0.51 g in mean weight were used. The fish were obtained from a rainbow trout breeding centre, in Yongdeng County, Gansu Province, China. The procedures were conducted in an outdoor concrete pond (6 × 6 × 1.6 m) and the water flow was 1 l/s. Within the pond, several smaller wire-mesh cages (0.80 × 0.60 × 0.60 m) were arranged that contained the experimental groups. The tops of the cages were covered with wire mesh (size 20) to prevent fish escaping. The water pH was 8.5, dissolved oxygen was 7.00–14.00 mg/l, and temperature was 7–8°C. During the re-feeding period, the fish were fed the same artificial diet supplied before the starvation period (Ningbo Tianbang Co., Ltd, China). Fish had been accustomed to the diet for two weeks before the start of the experiment.

Experimental design. The tested individuals were randomly allocated into 5 groups (in triplicates, each containing 15 fish), so each group included 45 fish in total. Fish were subjected to five different treatment groups: N_0 (fish were fed normally every day), N_7 (fish were starved for 7 days), N_{14} (fish were starved for 14 days), N_{21} (fish were starved for 21 days), and N_{28} (fish were starved for 28 days). After the end of starvation session, re-feeding was continued for 28 days for each group. The fish were fed once a day at 8.00 h.

Growth parameters. Growth indices including initial weight (W_0), weight after starvation (W_1), and final weight after re-feeding (W_2) were recorded. Weight gain rate (WGR), specific growth rate (SGR), feed conversion ratio (FCR), and feeding ratio (FR) were calculated according to the formulae below:

$$WGR\ (\%) = 100 \times (W_2 - W_1)/W_1$$

$$SGR\ (\%/day) = 100 \times (\ln W_2 - \ln W_1)/t$$

$$FCR\ (\%/day) = 100 \times [(W_2 - W_1)/C]$$

$$FR\ (\%/day) = 100 \times C/[t \times (W_1 + W_2)/2]$$

where:
ln = natural logarithm
t = number of re-feeding days
C = total amount of food consumed (g)

Sampling procedures. To collect the biological samples, three fish per singlicate (9 per treatment) were randomly sampled after starvation and re-feeding sessions. The fish were quickly dissected, and livers were excised and immediately homogenized on an ice bath. Later, the homogenates were centrifuged at 3000 rpm for 20 min and supernatants were collected and stored for further analysis. All samples were analyzed within 24 h. At the end of the fasting and re-feeding periods for each group, different organs were collected (stomach, intestine, and liver) for histological examination and divided into two separate samples. Tissue samples were washed in saline and then fixed in 10% formalin, embedded in paraffin, sectioned using a Leica microtome RM 2145 (Leica, Germany) and stained with haematoxylin-eosin (H&E), then viewed and photographed with an Olympus cx31 imaging system (Olympus, Japan).

Biochemical parameters. SOD activity, MDA content, and T-AOC in liver tissue were measured by spectrophotometer (model 722S; Shanghai Precision Science Instrument Co., Ltd, China) using commercial kits (Nanjing Jiancheng, China). T-AOC was assessed by the Fe^{3+} reduction method, MDA was measured by thiobarbituric acid (TBA) method to determine free MDA, and SOD was determined by the xanthine oxidase inhibition method. Each sample was quantified in triplicate according to the manufacturer's instructions for each kit. Absorbance was measured at 532 nm using a visible spectrophotometer PharmaSpec 1700 (Shimadzu, Japan).

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Statistical analysis. For data processing and statistical analysis we used the SPSS 20.00 and MS Excel 2016 software. One-way ANOVA was used between treatment groups followed by Duncan multiple comparisons post-hoc tests. The level of significance at which the null hypothesis was rejected was $\alpha = 0.05$. Data values are presented as means ± SE.

RESULTS

Body weight changes and growth indices after starvation and re-feeding sessions in Gansu golden trout. The results in Figure 1A showed that means of fish initial weight (W_0) did not significantly differ between treatment groups at the start of the experiment ($P > 0.05$). The mean body weight of juveniles was significantly influenced by the duration of food deprivation (Figure 1). Mean body weights of the N_{21} and N_{28} groups were significantly lower than those of N_0, N_7, and N_{14} ($P < 0.05$). After re-feeding for four weeks, the N_7 and N_{14} groups showed a significant degree of body weight recovery ($P < 0.05$) compared to the N_{21} and N_{28} groups (Figure 1). Growth indices in Figure 1B showed that after continued re-feeding for 28 days, the treatment groups displayed significantly varying degrees of WGR% ($P < 0.05$) with the highest mean found in the N_{14} group. Similarly, the four starvation groups showed a steady, significant increase in SGR% ($P < 0.05$) and FCR% ($P < 0.05$) across longer durations of starvation sessions (Figure 2).

Biochemical changes after starvation and re-feeding sessions in Gansu golden trout. At the end of the starvation period (Figure 2A), the contents of MDA in the liver tissue of Gansu golden trout showed significant increases ($P < 0.01$) in both the N_{21} and N_{28} groups compared with the control

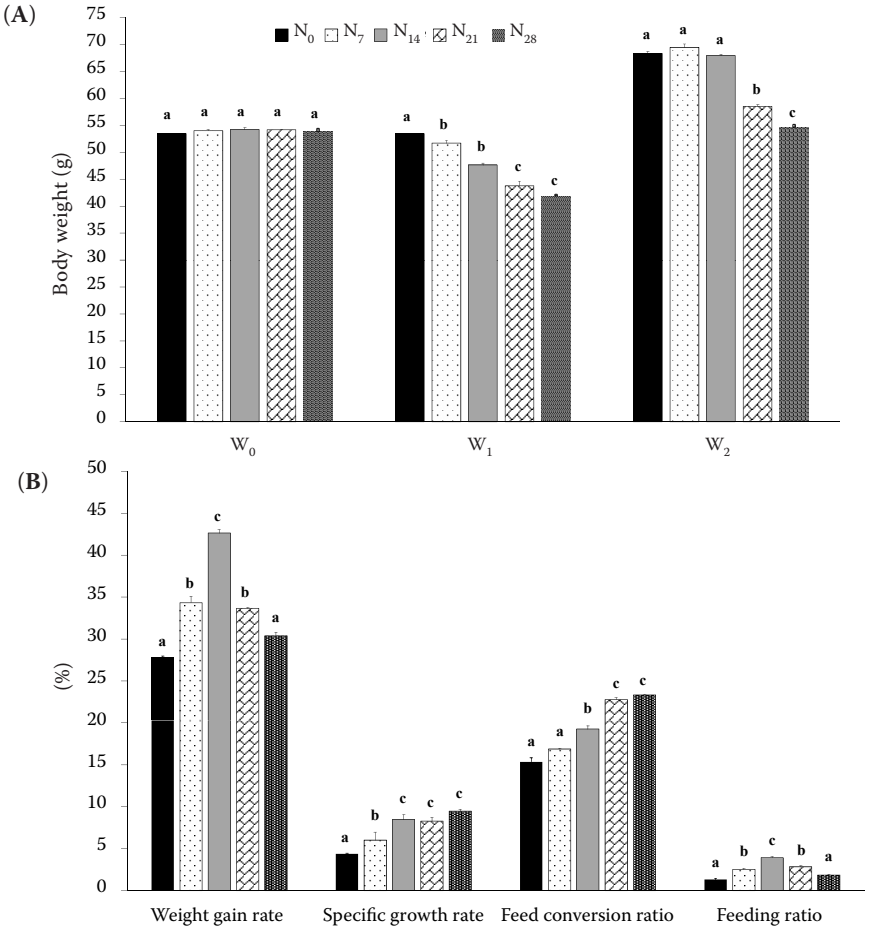

Figure 1. Initial body weight (W_0), body weights after starvation (W_1) and re-feeding sessions (W_2) (**A**) and growth indices (**B**) in Gansu golden trout after re-feeding sessions for different treatment groups

[a–c]columns with different superscripts are statistically different at $P < 0.05$

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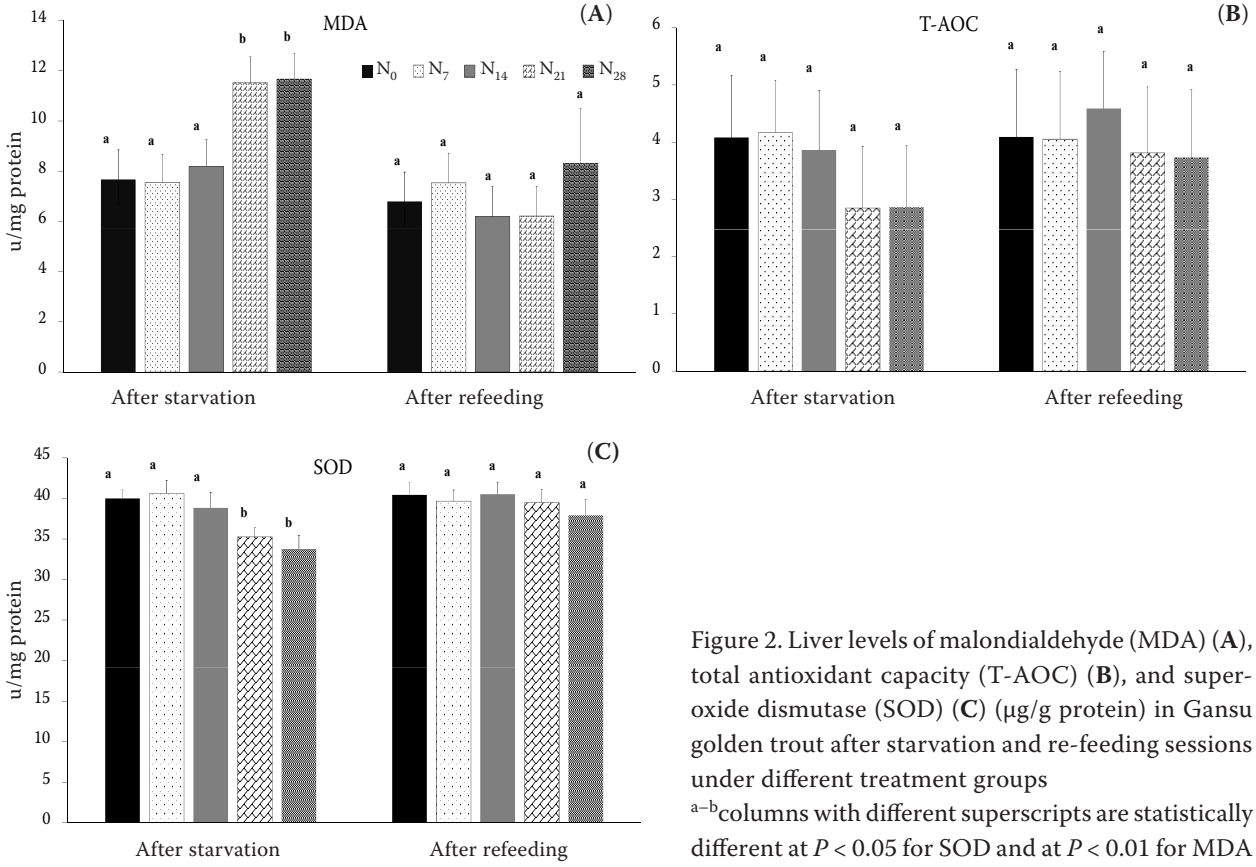

Figure 2. Liver levels of malondialdehyde (MDA) (**A**), total antioxidant capacity (T-AOC) (**B**), and superoxide dismutase (SOD) (**C**) (μg/g protein) in Gansu golden trout after starvation and re-feeding sessions under different treatment groups

[a–b]columns with different superscripts are statistically different at $P < 0.05$ for SOD and at $P < 0.01$ for MDA

groups N_7 and N_{14}. However, after re-feeding, there were no significant differences ($P > 0.05$) in liver MDA levels between treatment groups, and the previous significant higher levels of MDA in groups N_3 and N_4 returned to non-significant levels compared with other treatment groups. Results of T-AOC from Figure 2B revealed that liver levels of T-AOC showed no significant changes between treatment groups, neither after starvation ($P > 0.05$) nor after re-feeding ($P > 0.05$), although levels in the N_{21} and N_{28} groups were lower than in other treatment groups after starvation session. Finally, during the starvation session (Figure 2C), SOD levels in the liver tissue of Gansu golden trout showed a tendency to decrease significantly ($P < 0.05$) in the N_{21} and N_{28} groups compared with other treatment groups. At the end of the re-feeding session, the activity of SOD in the liver of the starved treatment group was basically restored compared with the control group ($P > 0.05$).

Histopathological alterations of digestive organs of Gansu golden trout after starvation and re-feeding sessions

Changes in stomach tissue structures. At the beginning of the experiment, Gansu golden trout juveniles showed thick muscular layers of the stomach, with well-developed mucosal folds (Figure 3A); gastric epithelium was a single layer of columnar cells arranged in regular, clear boundaries between the cells, the nucleus was nearly round, with stomach cells containing eosinophilic secretory particles (Figure 3B). By the end of starvation session, changes in thickness of the muscular layer and the height of the columnar epithelium were not obvious in the N_7 group compared with the control group (Figure 3C,D). With the prolongation of hunger, the thickness of the muscular layer in N_{14}, N_{21}, and N_{28} groups was reduced by different degrees (Figure 3E–G) and the height of the columnar epithelial cells was also significantly reduced with the cell boundaries becoming unclear (Figure 3H–J). Moreover, stomach glands clutter and the glandular cavity turned into a thin seam, gastric cell volume was significantly reduced, and the secretory particles became smaller (Figure 3K–M). After re-feeding was restored by the end of the trial, the above-mentioned changes were restored to the same levels as those of the control group, but the thickness of the gastric muscle and the gastric gland was still small (Figure 3N, O).

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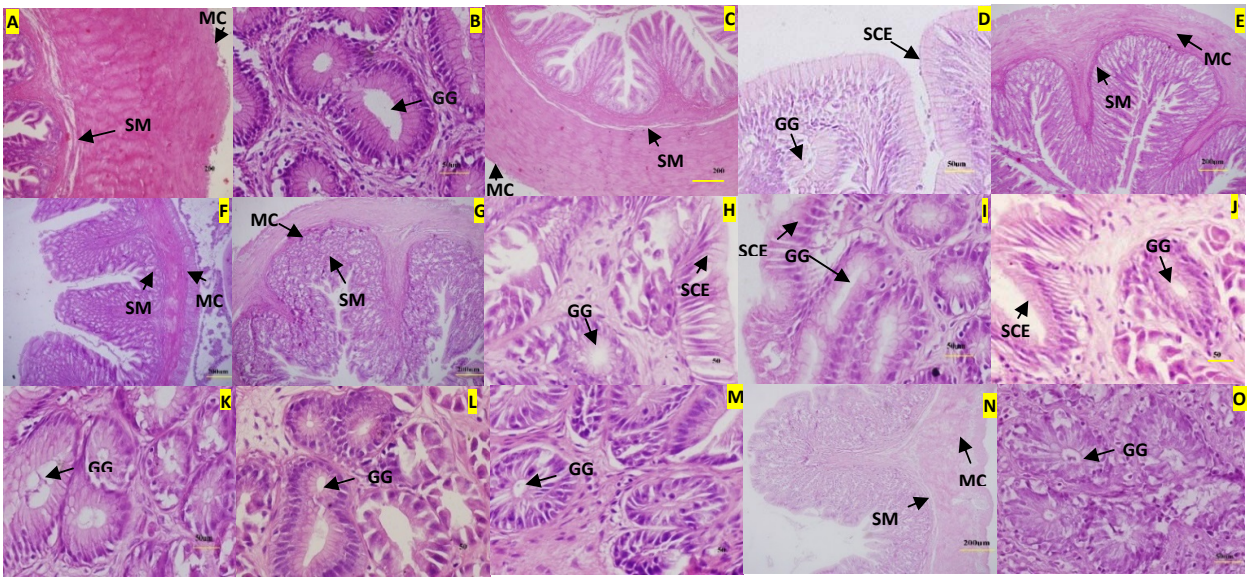

Figure 3. Changes in stomach tissue structures in Gansu golden trout at the beginning of experiment in control group muscular layers of stomach (**A**), gastric epithelium (**B**); changes at the end of starvation session in N_7 group muscular layer (**C**) and columnar epithelium (**D**), in N_{14}, N_{21}, and N_{28} muscular layer (**E**, **F**, **G**, respectively), in columnar epithelial tissue (**H**, **I**, **J**, respectively), and glandular tissue (**K**, **L**, **M**, respectively); changes after re-feeding session in N_{28} gastric mucosa (**N**) and gastric glands (**O**)
GG = gastric glands, MC = muscular coat, SCE = simple columnar epithelium, SM = submucosa

Changes of intestinal wall tissue structures. At the beginning of the experiment, the intestinal epithelial cells of Gansu golden trout juvenile fish were a single layer of columnar cells and the free end surface had a neatly striated edge, with the epithelial cells mixed with a certain number of goblet cells (Figure 4A). At the end of the starvation session, there was no significant change in the structure of the fish intestine in the N_7 group (Figure 4B). However, in the N_{14} group, the diameter of the intestine was decreased, the thickness of the intestinal muscular layer and the height of columnar epithelium were decreased, all significantly different from those of the control group

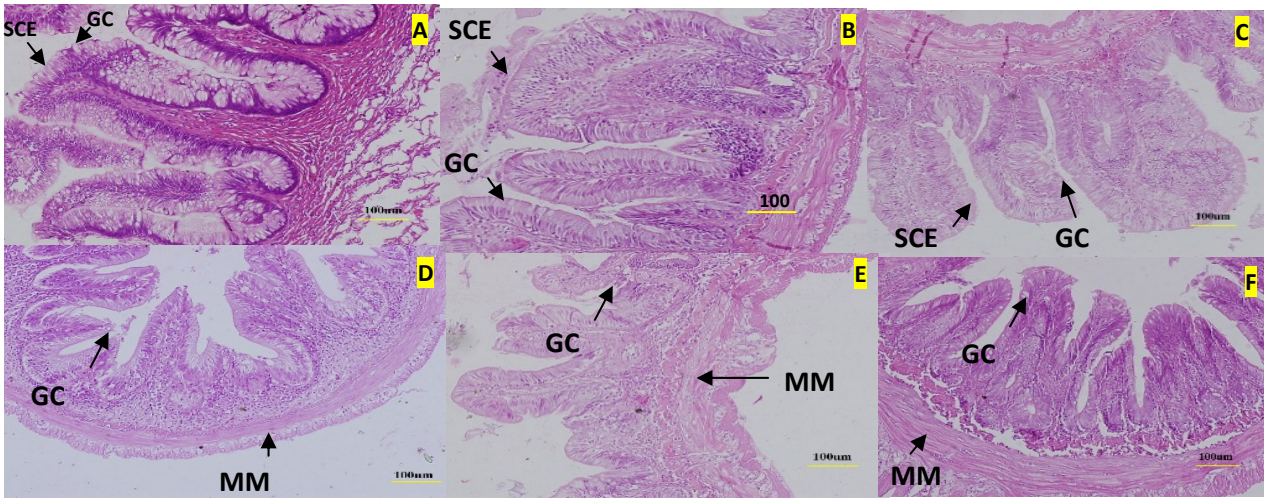

Figure 4. Changes in structures of intestinal wall in Gansu golden trout at the beginning of experiment (**A**), at the end of starvation session in N_7 (**B**), N_{14} (**C**), N_{21} (**D**), and N_{28} (**E**) groups and after re-feeding session in N_{28} group (**F**)
SCE = simple columnar epithelium, GC = goblet cell, MM = muscularis mucosa

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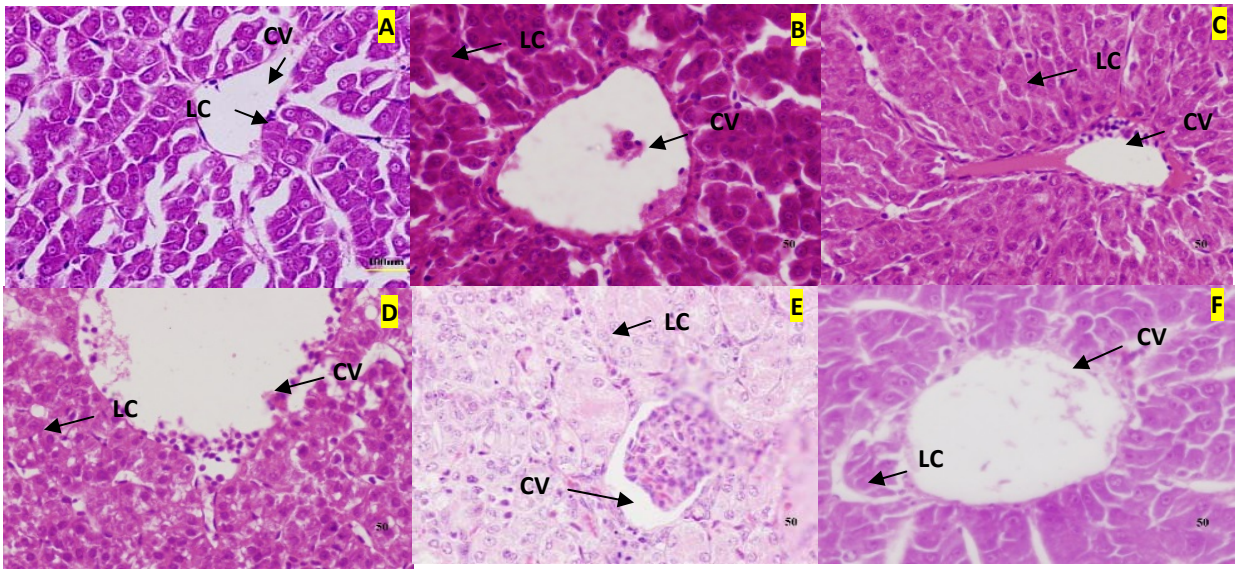

Figure 5. Changes in liver tissue structure in Gansu golden trout at the beginning of experiment (**A**), at the end of starvation session in N_7 (**B**) and in N_{14}, N_{21}, and N_{28} groups (**C**, **D**, **E**, respectively), and after re-feeding session in N_{28} group (**F**)
CV = central vein, LC = liver cell

(Figure 4C). These changes were aggravated in the N_{21} and N_{28} groups in that the tissue structure of the fish intestine was further severely reduced, the striatum had also shed away, and the goblet cells were reduced by varying degrees, showing corresponding degrees of damage (Figure 4D, E). After re-feeding, the fish in the N_7 and N_{14} groups were all restored compared with the control group, and the N_{21} group was close to the control group. However, in the N_{28} group, although re-feeding continued, the height of the intestinal epithelial cells and the clarity of the striatum were restored with various degrees of change compared with the control group (Figure 4F).

Changes in liver tissue structures. At the beginning of the experiment, the boundaries between the liver cells of Gansu golden trout were clear, filled with large volumes of lipid vacuoles and the nuclei were deviated to one side (Figure 5A). However, at the end of starvation session, there was no significant change in fish liver cells in the N_7 group (Figure 5B, C), whereas the N_{14}, N_{21}, and N_{28} groups showed swelling and disarrangement of the hepatocytes to different degrees: the cell volume had shrunk; the lipid vacuoles were reduced in volume and number, and there was depletion of the secretory granules (Figure 5D, E) compared with the control group. However, after re-feeding, the liver cell boundaries became clearer, the cell volume was restored, and the number of lipid droplets increased significantly in the N_{28} group (Figure 5F).

DISCUSSION

In our study, all groups subjected to starvation, regardless of the duration of food restriction, showed a significant decrease in their body weight compared with control groups at the end of starvation session, and the degree of weight loss correlated (Wang et al. 2014) to the length of food restriction (Figure 1A). Animals under conditions of food restriction and hunger will show a decline in their body weight, and the severity of the weight loss depends mainly on the duration of the starvation session. Results from Figure 1B showed that the weight gain rate and feeding rate percentage were significantly higher in the N_{14} group than in the other treatment groups (Wang et al. 2014). Furthermore, the direct comparisons of SGR and FCR between control and starved fish in the present study revealed that the magnitude of growth and feed conversion enhancement appear to be lower in the control group, and this enhancement seems to be higher in starved fish,

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especially in the N_{14} group (Figure 1B). Different theories have been adopted to illustrate the phenomenon of compensatory growth in fish after various durations of food restriction. When fish were subjected to starvation, they started to slow down their basal metabolic rates and activity levels in a defensive reaction to conserve energy and to avoid mobilization of body fat and nutrients (Gingerich et al. 2010). However, when feeding was resumed, the low basal metabolic rate and activities were maintained for some time and the surplus energy was diverted toward improving food conversion and growth rates, which ultimately leads to the compensatory growth (Prabhakar et al. 2008). Although this theory may sound plausible, the nature of Gansu golden trout (*Oncorhynchus mykiss*) may contradict it with the metabolic cold adaptation (MCA) syndrome, which hypothesises that fish living in colder environments have relatively high metabolic rates (White et al. 2012), but perhaps under exceptional circumstances, such as hunger and starvation, fish may modulate their basal metabolic rates to lower levels in order to survive, at the expense of thermoregulation. This assumption needs more investigation in Gansu golden trout. An alternative theory has been described to explain the compensatory growth: that, immediately after re-feeding, fish will undergo a compulsory state of craving and increased appetite and subsequently increase their feeding levels, which results in the increase in body weight. When tilapia (O*reochromis niloticus* × *o.aureus*) were subjected to starvation stress, they showed an increase in appetite, feeding ratio, and final body weight after resuming their feeding (Wang 2001). Finally, the phenomenon of compensatory growth could also be the result of an interplay between an increase in appetite and food intake on one hand, and an increase in the feed conversion efficiency that took place as a means to compensate weight loss in the recovery stages on the other (Bilton and Robins 1973). Our results strongly support the third assumption that the compensatory increase of body weights in the N_{14} group might result from increased feed conversion rates and feed intake compared with other treatment groups (Figure 1B). From these findings, we hypothesise that fish may employ different approaches and mechanisms to restore their body weights, and that the hyper-growth that took place in the N_{14} group is similar to that in the study of Hayward et al. (1997), who reported that starved fish during certain starvation/re-feeding cycles substantially outgrew (by a factor of 1.4 to 2) the control group.

Our results showed that liver MDA enzyme levels in the N_{21} and N_{28} groups were significantly elevated following starvation and were restored to normal levels compared with the control group (Figure 2A). Starvation is a potent stressor on fish and, therefore, fish utilise different biochemical reactions in order to tackle and lessen the severity of starvation stress (El-Khaldi 2010). Exposing fish to starvation stress generates excessive free radicals and ROS, which are considered major threats to cellular stability and homeostasis (Scherz-Shouval and Elazar 2009). These free radicals and ROS are highly reactive and enhance the process of lipid peroxidation which, in turn, generates other metabolites that further harm the cellular structures. MDA is the most-used biomarker affording an indication of the severity of lipid peroxidation (Ho et al. 2013); therefore, the elevated liver levels of MDA are a clear marker of the severity of the starvation stress in the N_{21} and N_{28} groups, in contrast to other treatment groups. To control and neutralise the adverse effect of ROS, the production and buildup of antioxidants took place; these are active substances that, even at low concentrations compared with ROS, significantly interrupt or stop oxidation of that substrate (Chokshi et al. 2017). However, our results showed that the T-AOC did not show a significant difference between treatment groups, although the levels were lower in N_{21} and N_{28} (Figure 2B) than in the other groups. Although the results of T-AOC did not reveal any significant differences, our results conform to those of Brock et al. (2004), in which non-significant local levels of T-AOC were found, but the plasma T-AOC revealed significant differences between control and stressed subjects. Our study was conducted on liver tissues, which might match the previous results, but, unfortunately, we did not measure serum levels of T-AOC. This point should be considered in future research. Finally, the levels of SOD (Figure 2C) were significantly lower in the N_{21} and N_{28} groups and returned to normal after feeding was resumed. SOD is considered a powerful antioxidant and contributes to the antioxidant capability of the fish to nullify the adverse effects of the starvation stress. Our explanation agreed with that reported by Bennett et al. (2014).

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The structural components of the gastrointestinal (GI) tract and related organs differ in response to starvation. Moreover, we have found that these structural and histological changes differ according to the length of the food restriction phase, and, after re-feeding, restoration of these changes took place except in cases of prolonged exposure to hunger. In our study, the histological examination of the GI tract and related organs revealed that starvation had a powerful effect on the structures of the stomach, intestine, and liver, which ultimately led to absorption and transport dysfunctions. At the end of starvation sessions, changes were observed in the thickness of the muscular layer, height of the columnar epithelial cells, and glandular tissue of the stomach (Segner and Moller 1984) (Figure 3). The intestinal structures also showed some changes, manifested in a diminution in the thickness of the intestinal muscular layer, the height of columnar epithelium, and the number of goblet cells (Hall and Bellwood 1995) (Figure 4). Similar changes were also observed in the liver (Segner and Moller 1984) (Figure 5), and all the previous changes were restored to a certain degree when feeding was resumed. Similar results were also observed by Zeng et al. (2012). We assume that fish showed a significant structural decrease in the GI tract and accompanying organs equal to the purposeful down-regulation during food deprivation (Wang et al. 2006); this is because the GI tract and other linked organs constitute about 40% of the total animal weight and hence, as a means of energy conservation during starvation, fishes tend to downregulate the structure of their organs (Cant et al. 1996).

CONCLUSION

In conclusion, starvation led to significant weight loss, changes in antioxidant activity levels, and histological differences between starved and control fish. When feeding was resumed, a compensatory growth and restoration of antioxidant levels took place alongside with various degrees of restoration of the histological structures of the GI tract. Our findings show that the compensatory growth responses that took place in various groups – especially the hypergrowth response, the non-significant change in antioxidant levels, and fewer histological GI tract changes in group N_{14} – can be utilised as a managerial tactic in some fish species to make them significantly exceed the growth of their conspecifics that are fed every day without limitations in size.

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REFERENCES

Ali T.E.S., Martinez-Llorens S., Monino A.V., Cerda M.J., Tomas-Vidal A. (2016): Effects of weekly feeding frequency and previous ration restriction on the compensatory growth and body composition of Nile tilapia fingerlings. The Egyptian Journal of Aquatic Research, 42, 357–363.

Bennett K.A., MacMillan I.S., Hammill M., Currie S. (2014): HSP70 abundance and antioxidant capacity in feeding and fasting gray seal pups: suckling is associated with higher levels of key cellular defenses. Physiological and Biochemical Zoology, 87, 663–676.

Bhattacharyya A., Chattopadhyay R., Mitra S., Crowe S.E. (2014): Oxidative stress: An essential factor in the pathogenesis of gastrointestinal mucosal diseases. Physiological Reviews, 94, 329–354.

Bilton H.T., Robins G.L. (1973): The effects of starvation and subsequent feeding on survival and growth of Fulton Channel sockeye salmon fry (Oncorhynchus nerka). Journal of the Fisheries Research Board of Canada, 30, 1–5.

Brock G.R., Butterworth C.J., Matthews J.B., Chapple I.L. (2004): Local and systemic total antioxidant capacity in periodontitis and health. Journal of Clinical Periodontology, 31, 515–521.

Cant J.P., McBride B.W., Croom Jr. W.J. (1996): The regulation of intestinal metabolism and its impact on whole animal energetics. Journal of Animal Science, 74, 2541–2553.

Chokshi K., Pancha I., Ghosh A., Mishra S. (2017): Nitrogen starvation-induced cellular crosstalk of ROS-scavenging antioxidants and phytohormone enhanced the biofuel potential of green microalga Acutodesmus dimorphus. Biotechnology for Biofuels, 10: 60.

Davis K.B., Gaylord T.G. (2011): Effect of fasting on body composition and responses to stress in sunshine bass. Comparative Biochemistry and Physiology – Part A: Molecular and Integrative Physiology, 158, 30–36.

https://doi.org/10.17221/107/2017-CJAS

El-Khaldi A.T. (2010): Effect of different stress factors on some physiological parameters of Nile tilapia (Oreochromis niloticus). Saudi Journal of Biological Sciences, 17, 241–246.

Gingerich A.J., Philipp D.P., Suski C.D. (2010): Effects of nutritional status on metabolic rate, exercise and recovery in a freshwater fish. Journal of Comparative Physiology – Part B: Biochemical, Systemic, and Environmental Physiology, 180, 371–384.

Hall K.C., Bellwood D.R. (1995): Histological effects of cyanide, stress and starvation on the intestinal mucosa of Pomacentrus coelestis, a marine aquarium fish species. Journal of Fish Biology, 47, 438–454.

Hayward R.S., Noltie D.B., Wang N. (1997): Use of compensatory growth to double hybrid sunfish growth rates. Transactions of American Fisheries Society, 126, 316–322.

Ho E., Karimi Galougahi K., Liu C.C., Bhindi R., Figtree G.A. (2013): Biological markers of oxidative stress: Applications to cardiovascular research and practice. Redox Biology, 1, 483–491.

Hornick J.L., Van Eenaeme C., Gerard O., Dufrasne I., Istasse L. (2000): Mechanisms of reduced and compensatory growth. Domestic Animal Endocrinology, 19, 121–132.

Mukherjee S., Maitra S.K. (2015): Effects of starvation, re-feeding and timing of food supply on daily rhythm features of gut melatonin in carp (Catla catla). Chronobiology International, 32, 1264–1277.

Nikki J., Pirhonen J., Jobling M., Karjalainen J. (2004): Compensatory growth in juvenile rainbow trout, Oncorhynchus mykiss (Walbaum), held individually. Aquaculture, 235, 285–296.

Ostaszewska T., Korwin-Kossakowski M., Wolnicki J. (2006): Morphological changes of digestive structures in starved Ictalurus punctatus (L.) juveniles. Aquaculture International, 14, 113–126.

Prabhakar S.K., Sardar P., Das R.C. (2008): Effect of starvation with subsequent realimentation with respect to compensatory growth of Indian Major Carp, Rohu (Labeo rohita H.). Animal Nutrition and Feed Technology, 8, 89–96.

Robb D.H. (2008): Welfare of fish at harvest. In: Branson E.J. (ed.): Fish Welfare. Blackwell Publishing Ltd, Oxford, UK.

Scherz-Shouval R., Elazar Z. (2009): Monitoring starvation-induced reactive oxygen species formation. Methods in Enzymology, 452, 119–130.

Segner H., Moller H. (1984): Electron microscopical investigations on starvation induced liver pathology in flounders Platichthys flesus. Marine Ecology Progress Series, 19, 193–196.

Shan X., Quan H., Dou S. (2016): Morphological and histological changes in digestive tract development during starvation in the miiuy croaker. Fish Physiology and Biochemistry, 42, 529–546.

Souza V.L., Sipaubatavares L.H., Urbinati E.C. (2000): Types of feeding for pacu fish (Piaractus mesopotamicus), and optimum duration of residence in ponds. Ciência Animal Brasileira, 1, 115–121.

Thongprajukaew K., Rodjaroen S. (2017): Intermittent feeding induces compensatory growth of juvenile yellow mystus (Hemibagrus nemurus). Aquatic Living, 30: 6.

Tsikas D. (2017): Assessment of lipid peroxidation by measuring malondialdehyde (MDA) and relatives in biological samples: Analytical and biological challenges. Analytical Biochemistry, 524, 13–30.

Wang Y. (2001): Bioenergetics of hybrid tilapia (Oreochromis niloticus × O. aureus) reared in seawater, in relation to compensatory growth. Oceanologia et Limnologia Sinica, 3, 115–119.

Wang T., Hung C.C.Y., Randall D.J. (2006): The comparative physiology of food deprivation: From feast to famine. Annual Review of Physiology, 68, 223–251.

Wang H.F., Liu X., Xu Y.J. (2014): Effect of starvation and refeeding on growth and muscle composition of "Gansu golden trout" larvals. Journal of Gansu Agricultural University, 49, 37–42.

White C.R., Alton L.A., Frappell P.B. (2012): Metabolic cold adaptation in fishes occurs at the level of whole animal, mitochondria and enzyme. Proceedings of the Royal Society B –Biological Sciences, 279, 1740–1747.

Zeng L.Q., Li F.J., Li X.M., Cao Z.D., Fu S.J., Zhang Y.G. (2012): The effects of starvation on digestive tract function and structure in juvenile southern catfish (Silurus meridionalis Chen). Comparative Biochemistry and Physiology – Part A: Molecular and Integrative Physiology, 162, 200–211.

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