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# Compensatory growth response of rainbow trout *Oncorhynchus mykiss* Walbaum following short starvation periods

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**Abstract** This sixty-day study was performed to determine the effects of short-term starvation and re-feeding cycles on growth, feeding performances and body composition of rainbow trout (*Oncorhynchus mykiss*). Three hundred trout fingerlings with an average initial weight of 17.5±0.06 g were randomly distributed in 15 circular fiberglass tanks. The fish were exposed to 5 different feeding regimes; control: continuously fed twice daily to apparent satiation; $T_1$: starved for 1 day and re-fed for 2 days; $T_2$: starved for 1 day and re-fed for 4 days; $T_3$: starved for 3 days and re-fed for 12 days; $T_4$: starved for 4 days and re-fed for 16 days. At the end of the experiment, growth performance, feed utilization, whole body ash and moisture contents were not significantly ($P$>0.05) different among the treatments. However, whole body protein content in T3 was significantly higher than other treatments ($P$<0.05). A significant difference in whole body fat content was observed between T3 and the control group at the end of the experiment ($P$<0.05). In conclusion this experiment suggests that feeding schedules involving starvation (1–4 days) and re-feeding cycles are a promising feed management tool for rainbow trout culture.

**Keyword**: *Oncorhynchus mykiss*; compensatory growth; growth performance; body composition

## 1 INTRODUCTION

Compensatory or catch-up growth is defined as fast growth that usually occurs after a period of reduced growth resulting from restricted food availability or some other unfavorable environmental conditions, apparently in order to reach the weight of continuously fed fish (Jobling, 1994; Mommsen, 1998; Nikki et al., 2004). Food deprivation is not the only way to induce compensatory growth. This phenomenon can also occur by gradual decrease in stocking density (Basiao et al., 1996), hypoxic conditions (Foss and Imsland, 2002), low temperature (Nicieza and Metcalfe, 1997; Maclean and Metcalfe, 2001) or gradual increase in salinity (Damsgård and Arnesen, 1998).

There are differences in compensatory growth response between fish species. For example, Ali et al. (2001) reported different compensatory responses in three-spine stickleback (*Gasterosteus aculeatus*), minnow (*Phoxinus phoxinus*) and gibel carp (*Carassius auratus gibelio*), which had been subjected to single deprivation re-feeding cycles. They suggested that such differences might have resulted from intrinsic interspecific differences in appetite control. In comparison with other species, hybrid tilapia showed a weaker capacity for compensatory growth following 1–4 weeks of starvation (Wang et al., 2000). Wieser et al. (1992) reported a lag in compensatory growth response in chub, *Leuciscus cephalus*, but not in Danube bleak, *Chalcalburnus chalcoides mento* or rudd, *Scardinius erythrophthalmus*. In most studies, compensatory growth was achieved through hyperphagia, an increase in appetite (Miglavs and Jobling, 1989; Jobling et al., 1994; Jobling and Koskela, 1996;

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Hayward et al., 1997). In a few experiments the deprived fish were able to compensate for lost growth by improved growth efficiency (Quinton and Blake, 1990; Boujard et al., 2000; Gaylord and Gatlin, 2001) and also by a combination of hyperphagia and improved growth efficiency (Russell and Wootton, 1992; Jobling et al., 1994; Qian et al., 2000; Morshedi et al., 2013).

Many studies have examined the phenomenon of compensatory growth in cold water fish such as Arctic charr, *Salvelinus alpines* (Miglavs and Jobling, 1989), Atlantic salmon, *Salmo salar* (Nicieza and Metcalfe, 1997), Atlantic cod, *Gadus morhua* (Bélanger et al., 2002) and rainbow trout, *Oncorhynchus mykiss* (Weatherley and Gill, 1981; Dobson and Holmes, 1984; Quinton and Blake, 1990; Jobling and Koskela, 1996; Guzel and Arvas, 2011; Sevgili et al., 2013). However, most of the information on compensatory growth response pertains to longer starvation periods and only a few studies have focused on short-term starvation (1–4 days). In Iranian fish farms, rainbow trout routinely experiences short-term starvation due to stressors, pathogens, turbidity or water quality. Thus, this study was conducted to investigate the compensatory growth response in rainbow trout subjected to short-term starvation and refeeding. This study also aimed to evaluate the effects of feeding strategies on growth, feed utilization and body composition.

## 2 MATERIAL AND METHOD

This sixty-day experiment was carried out in the aquarium facility of the Division of Fisheries, Department of Natural Resources, Isfahan University of Technology. Juvenile trout (*Oncorhynchus mykiss*) were obtained from a commercial local farm, Shahrekord, Iran. Fish were kept in a flow-through system and acclimated to the experimental conditions for 2 weeks before the start of the experiment. During this period, fish were fed *ad libitum* twice a day with a commercial diet (Esfahan Mokammel Co., Isfahan, Iran). Feed used in the experiment (3-mm diameter) had 43% crude protein, 15% crude lipid, 14% moisture and 11% ash. An indoor semi-circulated system with filtered water was used for maintaining fish. During the experiment water temperature was measured twice a day and ranged between 14.2–15.2°C. Oxygen concentration was maintained at 8.2–8.5 mg/L and pH was 7.2–7.5. Fish were kept on 12 L:12 D photoperiod using fluorescent tubes.

After an acclimation period, 300 fish with an average initial weight of 17.24±0.06 g (mean±SE) were distributed randomly among fifteen 100-L polyethylene circular tanks (20 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 deprived groups. Five treatments with three replicates were assigned as follows:

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

$T_1$: fish were deprived for 1 day and then re-fed for 2 days to apparent satiation level (20 cycles throughout the experiment).

$T_2$: fish were deprived for 1 day and then re-fed for 4 days to apparent satiation level (12 cycles throughout the experiment).

$T_3$: fish were deprived for 3 days and then re-fed for 12 d to apparent satiation level (4 cycles throughout the experiment).

$T_4$: fish were deprived for 4 days and then re-fed for 16 days to apparent satiation level (3 cycles throughout the experiment).

During the feeding days, all fish were fed to apparent satiation twice a day. Uneaten feed was siphoned out, air-dried for 5 h and weighed for calculating total amount feed intake of each tank. Fish weight and total length were measured every 15 days under anesthesia (MS-222, 30 mg/L) condition.

The following parameters were calculated according to (Nafisi and Soltani, 2008): specific growth rate (SGR)=100[(ln$W_t$–ln$W_0$)/$t$]; weight gain (WG)=100[($W_t$–$W_0$)/$W_0$], where $W_t$ and $W_0$ are final and initial weight (g) and t is the feeding period (days); feed conversion ratio (FCR)=feed intake (g, dry weight)/wet weight gain (g); feed efficiency ratio (FER)=100[wet weight gain (g)/feed intake (g)]; protein efficiency ratio (PER)=wet weight gain/crude protein intake; condition factor (CF)=weight (g)/total lenght$^3$ (cm)×100; daily feeding intake (DFI)=g feed/day.

At the beginning of the experiment, 10 fish were randomly sampled to determine the initial body composition. At the end of the experiment, after the final measurement, 3 fish from each tank were randomly sampled, all of viscera, head and fin were removed and the carcass was frozen at -20°C. Proximate analysis of whole body and feed was carried out after homogenization of samples (three fish were pooled and analyzed in each replicate). The samples were dried at 105°C for 5 h using an oven to reach the constant weight. Ash content was determined by burning the samples at 450°C for 8 h in a muffle

**Table 1 Growth performance of juvenile rainbow trout *O. mykiss* maintained on different feeding regimes**

| | Control | $T_1$ | $T_2$ | $T_3$ | $T_4$ | *P* value |
|---|---|---|---|---|---|---|
| Initial weight (g) | 17.12±0.79 | 17.32±0.88 | 17.29±0.84 | 17.56±0.91 | 17.30±0.07 | 0.2 |
| Initial length (cm) | 11.94±0.04 | 11.89±0.11 | 11.86±0.14 | 11.77±0.04 | 11.75±0.04 | 0.55 |
| Final weight (g) | 66.23±2.44 | 60.07±3.37 | 59.25±3.14 | 55.68±2.30 | 56.88±1.97 | 0.13 |
| Final length (cm) | 18.20±0.03 | 17.77±0.32 | 17.78±0.34 | 17.18±0.19 | 17.53±0.18 | 0.2 |
| Weight gain (%) | 272.70±10.90 | 242.01±17.49 | 240.17±15.64 | 217.67±10.39 | 228.72±10.79 | 0.12 |
| SGR (% day) | 2.19±0.04 | 2.04±0.08 | 2.03±0.07 | 1.92±0.05 | 1.98±0.05 | 0.13 |
| CF | 1.07±0.00 | 1.06±0.01 | 1.05±0.00 | 1.07±0.01 | 1.05±0.00 | 0.5 |

Values=means±S.E. from three replicates, 10 fish per replicate, $n$=30. SGR (specific growth rate)=100[(ln$W_t$–ln$W_0$)/$t$]; CF (condition factor)=100[$W$/L3]. C: control: fed two times daily to apparent satiation; $T_1$: deprivation for 1 day and then re-fed for 2 days; $T_2$: deprivation for 1 day and then re-fed for 4 days; $T_3$: deprivation for 3 days and then re-fed for 12 days; $T_4$: deprivation for 4 days and then re-fed for 16 days. No significant differences were observed among the treatments.

**Table 2 Feed utilization by juvenile rainbow trout *O. mykiss* reared on different feeding regimes**

| | Control | $T_1$ | $T_2$ | $T_3$ | $T_4$ | *P* value |
|---|---|---|---|---|---|---|
| FCR | 1.19±0.05 | 1.14±0.02 | 1.24±0.01 | 1.27±0.02 | 1.22±0.02 | 0.11 |
| FER (%) | 84.12±4.12 | 87.64±1.58 | 80.59±0.82 | 78.21±1.77 | 81.80±1.49 | 0.14 |
| PER | 2.10±0.10 | 2.19±0.03 | 2.01±0.02 | 1.95±0.04 | 2.04±0.04 | 0.12 |
| DFI (g) | 19.58±0.52 | 24.21±1.51 | 20.65±1.45 | 19.48±0.66 | 20.32±1.42 | 0.09 |

Values=means±S.E. from three replicates, 10 fish per replicate, $n$=30. DFI (daily feeding intake)=g feed /day; FCR (feed conversion ratio)=feed intake (g, dry weight)/wet weight gain (g); FER (feed efficiency ratio)=100[wet weight gain (g)/feed intake (g, dry weight)]; PER (protein efficiency ratio)=wet weight gain/protein consumed. C: control: fed twice daily to apparent satiation; $T_1$: deprivation for 1 day and then re-fed for 2 days; $T_2$: deprivation for 1 day and then re-fed for 4 days; $T_3$: deprivation for 3 days and then re-fed for 12 days; $T_4$: deprivation for 4 days and then re-fed for 16 days. No significant difference was observed among the treatments.

furnace, the protein content of samples was determined using the Kjeldahl method and total lipid using the Soxtec method (AOAC, 1995).

All statistical analyses were performed using Statistical Package for Social Science (SPSS, v.16 for windows). The Kolmogorov-Smirnov test was applied to assess for normality of distributions. The homogeneity of variances was tested using the Levene's $F$ test. The possible differences of the variables among the treatments were tested using one-way ANOVA. Post-hoc comparisons between sample means were made by Tukey's test and $P$<0.05 was taken as the level of significance.

## 3 RESULT

During the experiment, the survival rate was 100% for all treatment. Final weight of fish under different treatments was not significantly different ($P$>0.05). Data in Table 1 showed that specific growth rate and condition factors were also not significantly different among the treatments ($P$>0.05).

Overall, short-term starvation did not affect FCR and FER at the end of the experiment. At the end of the experiment, DFI and PER showed no statistical differences ($P$>0.05) among the treatments.

The whole body moisture and ash contents were not affected by deprivation-re-feeding cycles (Table 3). However, lipid content was significantly lower in $T_3$ fish than the control group ($P$<0.05). Protein content of $T_3$ fish was significantly higher than the other treatments ($P$<0.05, Table 3).

## 4 DISCUSSION

According to some studies, the fish that experienced a period of starvation (fasted for 1 or 7 days) were able to fully catch up in body weight with those fed continuously (Dobson and Holmes, 1984; Quinton and Blake, 1990; Maclean and Metcalfe, 2001; Tian and Qin, 2003; Mattila et al., 2009; Liu et al., 2011; Abolfathi et al., 2012; Morshedi et al., 2013). However, there are several examples reported of only partial compensation, where fish did not fully compensate for the lost growth (Miglavs and Jobling, 1989; Wang et al., 2000; Känkänen and Pirhonen, 2009; Ribeiro and Tsuzuki, 2010; Falahatkar, 2012). In the present study, fish subjected to short-term starvation periods and subsequent feeding were able to catch up with the control fish, as inferred from the comparable final weight and SGR among the treatments. However, growth trajectories of fish in the present experiment suggest that there was no potential in experimental fish to overcompensate if the experiment was continued for more than 60 days, as observed by Hayward et al. (1997) in hybrid sunfish. Hayward and Wang (2001) explained that overcompensation seems to be species-specific or limited to certain life stages. Känkänen and Pirhonen (2009) showed that the whitefish could compensate for growth, without any change in condition factor, which is consistent with the results of the present study.

Daily feed intake amounts of the deprived groups were slightly higher than those of the controls, although not significant. In general a tendency towards hyperphagia was noticed in all deprived groups compared to the control fish. In agreement with the reports of Russell and Wootton (1992), Jobling and Koskela (1996), Wang et al. (2000), Tian and Qin (2003) and Cui et al. (2006), we suggest that hyperphagia during the re-feeding period is one of the main contributing factors for compensatory growth response in juvenile rainbow trout. However, compensatory growth in the present study could not be attributed to an improved feeding efficiency, unlike in other studies reporting positive effects of improved feeding efficiency and feed intake on compensatory growth (Russell and Wootton, 1992; Jobling et al., 1993; Qian et al., 2000)

The results of this study indicate that short-term starvation had no significant effect on ash and moisture contents. In accordance with the results of previous work carried out on rainbow trout, the increase in body lipid reserves corresponded to the increase in body weight (Weatherley and Gill, 1983; Quinton and Blake, 1990). However, lipid content was significantly lower in $T_3$ fish compared to the control fish. This is in accordance with the results obtained in salmonids, where visceral fats and muscle lipid are utilized as an energy source during short-term starvation (Parker and Vanstone, 1966; Smith, 1981; Weatherley and Gill, 1981). Protein content of growing salmonids has been found to be affected by size, but not related to environmental factors, growth rate or diet composition (Shearer, 1994). This seems to be the case in our study, although protein content was significantly higher in T3 fish than in the control group. This is in disagreement with the results obtained in salmonids (Bureau et al., 2006; Quinton et al., 2007). The significant difference in protein content may be attributed to the small number of sampled fish.

**Table 3 Proximate composition of whole body of juvenile rainbow trout *O. mykiss* subjected to five different feeding regimes**

| Treatment | Parameters* | | | |
|---|---|---|---|---|
| | Moisture | Ash | Protein | Lipid |
| Initial body composition | 72.25±0.01 | 2.09±0.29 | 16.25±1.18 | 6.64±0.09 |
| Control | 71.69±0.08 | 1.98±0.24 | 15.32±0.34$^{a}$ | 7.57±0.19$^{b}$ |
| $T_1$ | 72.61±0.30 | 2.13±0.16 | 15.11±0.75$^{a}$ | 7.06±0.49$^{ab}$ |
| $T_2$ | 72.10±0.32 | 2.13±0.25 | 15.51±0.84$^{a}$ | 7.08±0.51$^{ab}$ |
| $T_3$ | 72.11±0.27 | 2.12±0.34 | 16.83±2.09$^{b}$ | 6.89±0.14$^{a}$ |
| $T_4$ | 71.81±0.37 | 2.14±0.16 | 16.03±0.72$^{a}$ | 7.25±0.55$^{ab}$ |
| *P*-value | 0.22 | 0.75 | 0.00 | 0.02 |

Values=means±S.E. from three replicates with two fish per replicate, *n*=6. C: control: fed twice daily to apparent satiation; $T_1$: deprivation for 1 day and then re-fed for 2 days; $T_2$: deprivation for 1 day and then re-fed for 4 days; $T_3$: deprivation for 3 days and then re-fed for 12 days; $T_4$: deprivation for 4 days and then re-fed for 16 days. Mean values in the same column having different superscript letters are significantly different from each other ($P<0.05$). * Concentration of moisture, ash, protein, and lipid expressed in % of wet weight.

In conclusion, the results demonstrate that rainbow trout is well adapted to feeding strategies without significantly affecting growth. Whole body composition of the starved fish was comparable to that of fish fed to satiation (except for $T_3$ fish). The results of the present study indicate that rainbow trout has the ability to achieve full compensatory growth during short-term starvation and re-feeding periods.

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