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ORIGINAL ARTICLE

Compensatory growth, antioxidant capacity and digestive enzyme activities of Sobaity (*Sparidentex hasta*) and yellowfin seabreams (*Acanthopagrus latus*) subjected to ration restriction

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Abstract

The compensatory growth response (CGR) and some selected physiological parameters were evaluated in sobaity (*Sparidentex hasta*, 10 g) and yellowfin seabreams (*Acanthopagrus latus*, 4.3 g) juveniles subjected to a 2-week restricted feeding. Fish were first fed at 0%, 25%, 50% and 75% of the satiation level for a 2-week period, and then, they were refed for 6 weeks at the visual satiation level. The control group was fed to the satiation everyday for 8 weeks. Three hundred sobaty seabream juveniles were stocked into 15 tanks (20 fish $tank^{-1}$), and 450 yellowfin seabream juveniles were allocated into 15 tanks (30 fish $tank^{-1}$) and were fed on a commercial feed (500 g kg^{-1} crude protein and 150 g kg^{-1} crude fat). Survival rate was decreased in R0% group in *S. hasta* because of the cannibalism, which was triggered by feed restriction. After the 2 weeks of feed restriction, the control and R0% treatments in *S. hasta* (16.0 vs. 9.3 g) and *A. latus* (3.9 vs. 6.2 g) had the highest and lowest body weight, respectively. After the 6 weeks of refeeding trial, all the ration-restricted groups showed a full CGR in *S. hasta*. Regarding *A. latus* juveniles, except for R0%, the other groups showed a full CGR. Feed conversion ratio was improved in *S. hasta* that subjected to the 2-week feed restriction, but this parameter did not change in *A. latus*. Antioxidant enzyme activities in the liver of *S. hasta* juveniles, including glutathione-S-transferase, glutathione peroxidase, superoxide dismutase and catalase along with liver enzymes including alkaline aminotransferase, aspartate amino transferase, lactate dehydrogenase and alkaline phosphatase gradually were decreased with reducing the severity of the feed restriction. Regarding *A. latus*, all mentioned antioxidant and the liver enzymes in the feed-restricted groups were higher than the control. R75% and control groups in *S. hasta* had the greatest and the least trypsin and alkaline phosphatase activities. In *A. latus*, R25%, R50% and R75% groups had higher trypsin, chymotrypsin and lipase activities compared with the other groups ($p < .05$). By considering all the selected physiological responses in both species, it can be concluded that increasing the feed restriction severity can trigger oxidative stress that may compromise health condition.

KEYWORDS
feeding regime, growth metrics, hepatic antioxidant system, pancreatic digestive enzymes, Sparidae, starvation and refeeding

1 | INTRODUCTION

Aquatic animals tolerate short or long periods of starvation in their niches because of seasonal changes in food supply, reproductive cycle and migration (Ali et al., 2003). A short-term feed restriction may also be used in aquaculture for different purposes such as reducing the handling stress (e.g. before shipping or medical treatments), controlling the mortality as a result of infectious diseases, increasing water quality (e.g. minimizing the excretion of nitrogenous metabolites and organic matter wastes), optimizing the final product quality (e.g. by gut evacuation or prevention of excessive lipid deposition in the fillet) and enhancing economical profits (e.g. by reducing feeding and labour costs as well as avoiding errors in the estimation of feeding rate) (Davis & Gaylord, 2011; Grigorakis & Alexis, 2005; Krogdahl & Bakke-McKellep, 2005; Turchini et al., 2007). Furthermore, it has been proved that an application of appropriate fasting and refeeding strategy provokes compensatory growth response (CGR) in fish (Ali et al., 2003). Compensatory growth response in fish is a distinct stage of fast growth that happens after refeeding phase following different disturbing factors (e.g. high stocking density and low temperature) mainly by feed deprivation period (Ali et al., 2003). There are some mechanisms that proposed underlying CGR including hyperphagia, reduction in metabolic expenditures and elevation of feed efficiency (Ali et al., 2003). Recently, it has been reported that compensatory mechanism in fish can be controlled and stimulated by some appetite genes (npy and pyy) and the growth hormones, and the degree of the compensation is also affected by the severity of starvation (Wu et al., 2020). Different CGR have been described in fish including negligible CGR, partial CGR, full CGR and over CGR, and these responses are species-specific and mainly depend on type, length and the feed restriction severity (Ali et al., 2003). Other biotic and abiotic factors may also affect CGR such as fish age, health, feed quality, feeding programme, gender, sexual maturation and developmental stages as well as feeding history of fish (Ali et al., 2003). In addition, comprehension of CGR pattern of a fish species can be applied for designing a feeding programme that not only reduces production expenditures but also helps to manage water quality by reducing wastes (e.g. organic matter and nitrogen metabolites) that ultimately promote fish growth rate and welfare (Ali et al., 2003; Kankanen & Pirhonen, 2009). When fish underwent feed restriction and refeeding schedules, the monitoring of its physiological responses should be considered. For example, previous studies demonstrated that feed deprivation provoked oxidative stress by overproduction of reactive oxygen species (ROS) (Bar, 2014; Morales et al., 2004). Moreover, feed deprivation may deplete antioxidant reserves in tissues that will, in turn, exacerbate the overproduction ROS, particularly in the liver (Bayir et al., 2011; Furné et al., 2009; Morales et al., 2004; Pascual et al., 2003; Pérez-Jiménez et al., 2007). The liver has vital in degradation of the metabolic products and detoxification of ROS (Lee et al., 2015). Thus, feed deprivation may adversely affect the liver function that increases the gluconeogenic enzyme activities (Ashouri et al., 2020; Peres et al., 2013; Pérez-Jiménez et al., 2012). Furthermore, it has been confirmed that digestive enzyme activities greatly were suppressed in fish during feed deprivation (Gisbert et al., 2011; Zeng et al., 2012), but interestingly, their activities were recovered after the refeeding period (Cara et al., 2007; Fang et al., 2017; Gisbert et al., 2011).

During two past decades, a plethora of studies has been conducted to evaluate the influences of fasting and refeeding strategies in marine fish species (Pérez-Jiménez et al., 2007; Zheng et al., 2016; Ziheng et al., 2007), especially in various sparids (Peres et al., 2011; Yilmaz & Eroldoğan, 2011; Pérez-Jiménez et al., 2012; Oh et al., 2013; Xiao et al., 2013; Mohapatra et al., 2017). Among the different sparid species, yellowfin (*Acanthopagrus latus*) and sobaity seabream (*Sparidentex hasta*) are considered as favourable candidates for extending marine cage culture programmes in Iran (Mozanzadeh, Marammazi, Yaghoubi, Agh, et al., 2017). Since 2014, the production of these two native species decreased mainly due to the introduction of two exotic aquaculture species in the Persian Gulf and Oman sea regions namely Asian seabass (*Lates calcalifer*) and gilthead seabream (*Sparus aurata*) (FAO, 2016). In recent years, *S. hasta* and *A. latus* have been regularly propagated in some private hatchery centres and also in the Marine Fish Research Station of the South Iran Aquaculture Research Center (Sarbandar, Iran). Juveniles have regularly been released into the Persian Gulf for increasing their stocks and transferred to earthen ponds or sea cages for culture.

During recent years, many research carried out to evaluate the effects of fasting and refeeding strategies in the both species. In this context, Mozanzadeh, Marammazi, Yaghoubi, Yavari, et al. (2017) reported complete CGR in *S. hasta* juveniles were fasted for 1 day and refed for 2 days during 60 days. In addition, Tamadoni et al. (2020) found complete CGR in *A. latus* juveniles were fasted for 4 days and refed for 16 days. In the current study, it was aimed to assess the feed restriction severity effects for 2 weeks and subsequently 6 weeks of refeeding on CGR and some physiological responses in *A. latus* and *S. hasta* juveniles.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The current research was carried out in a private marine fish hatchery centre (Sarbandar, Khuzestan, Iran; 30°32′N, 49°20′E). The research design was carried out according to the study by Tian and Qin (2004). In this regard, five different feeding regimes were designed including the control (CO) in which fish were fed to apparent satiation thrice (09:00; 12:00 and 16:00 h) for 8 weeks. The other groups were subjected to a 2-week feed restriction in which fish fed at 0%, 25%, 50% and 75% of the satiation ration; then, they were refed to satiation level three times a day for 6 weeks. The husbandry system consisted of thirty 300-L tanks filled with filtered and disinfected running seawater (1 L min^{-1}). The mean (mean ± standard deviation) values of water salinity, temperature, pH and dissolved oxygen were 48.0 ± 0.5‰, 29.2 ± 0.5°C, 7.7 ± 0.3 and 6.5 ± 0.8 mg L^{-1},

respectively. Three hundred sobaty seabream juveniles were distributed into 15 tanks (20 fish tank^{-1}), and 450 yellowfin seabreams juvenile were allocated into 15 tanks (30 fish tank^{-1}). Each treatment had three replicates for each species, and each tank held only for one of the species. The satiation level was determined based on apparent visual satiety for each species. In this regard, a week before the beginning of the experimental trial, fish were fed three meals to satiation each day and the amounts of feed eaten by the fish in each tank being recorded. Then, fish that had already been allocated to their test tanks then weighed to obtain information about tank biomass immediately before the start of the husbandry trial with the feed rations. The initial weight (BW_i) for *S. hasta* and *A. latus* was 10 ± 0.1 g (mean ± standard error) and 4.3 ± 0.0 g, respectively. The experiment was carried out for both species simultaneously. Fish were fed on a commercial feed (500 g kg^{-1} crude protein, 150 g kg^{-1} crude fat, 107 g kg^{-1} ash and 40 g kg^{-1} fibre, Beyza Feed Mill 21; the information about the nutrient composition of the feed provided by the manufacturer) and ensure that no feed was left uneaten. Two different sizes of feeds were used, including 1 and 2 mm for *A. latus* and *S. hasta*, respectively. Mortality was recorded daily for each tank during the experiment, and the survival rate was estimated throughout the experiment.

2.2 | Sampling

Weight of fish including body, liver and viscera of was individually measured to the nearest 0.1 g every 2 weeks, and their body length measured to the nearest 1 mm. The calculation of viscerosomatic index (VSI) made with inclusion of the weight of the liver. At the end of the 8-week feeding trial, fish were being anaesthetized (2-phenoxyethanol, 0.3 ml L^{-1}) and their weight and length were determined at accuracy of 0.1 g and 1 mm, respectively. Six fish of each tank were sacrificed with overdose of 2-phenoxyethanol (0.5 ml L^{-1}) to measure the liver and viscera weight. In addition, the liver and the whole gut (i.e. pyloric caeca, foregut, midgut and hindgut) of the sacrificed fish were dissected on ice and snap-frozen with liquid nitrogen, then were kept in a freezer (−80°C).

2.3 | Antioxidant and liver enzymes activities

The frozen livers were homogenized in ice-cold physiological buffer saline (1:10, w/v; NaCl 0.9%, pH 7.0) then centrifuged (2900 *g*, 15 min, 4°C), and the supernatants were separated, aliquoted (10 aliquots and each contained 1000 μl) and kept in −80°C (Jaroli & Sharma, 2005).

Glutathione S-transferase was determined by using a reagent contained 30 mM 1-chloro-2,4 dinitrobenzene and, 100 mM glutathione in phosphate buffer (110 mM, pH 6.5) and 50 μl homogenate (Habig et al., 1974) The absorbance was measured at 340 nm ($\varepsilon = 9.6$ mM^{-1} cm^{-1}). Glutathione peroxidase activity was measured using the method described by Noguchi et al. (1973). Glutathione peroxidase neutralize hydrogen peroxide in the presence of reduced glutathione (GSH).

Activities of superoxide dismutase (SOD) (McCord & Fridovich, 1969), catalase (CAT) (Aebi, 1984) and lipid peroxidation level (thiobarbituric acid reactive substances, TBARs) (Buege & Aust, 1978) were measured by using standard methods.

Liver enzymes including alanine aminotransferase (ALT), aspartate aminotransferase (AST), alkaline phosphatase (ALP) and lactate dehydrogenase (LDH) were analysed utilizing an auto-analyser (Technicon RA-1000; Technicon Instruments) using diagnostic kits (Pars Azmoon Kit, Iran). Soluble protein content of the homogenates was measured by the Bradford method (Bradford, 1976).

2.4 | Digestive enzyme activities

The whole gut (i.e. pyloric caeca, foregut, midgut and hindgut) samples were homogenized in ice-cold mannitol-Tris buffer (1:30, w/v) contained 50 mM Mannitol and 2 mM Tris-HCl (pH 7.0) for 30 s (Gisbert et al., 2016). Ultimately, the supernatants were separated, aliquoted (10 aliquots and each contained 1000 μl) and kept at −80°C. Trypsin activity was measured with N-α-benzoyl-dlarginine-pnitroanilide (BAPNA) as substrate at 25°C, and absorbance was recorded at 410 nm (Erlanger et al., 1961). Chymotrypsin activity was quantified at 25°C using BTEE as substrate in 80 mM Tris-HCl, 100 mM $CaCl_2$ buffer (pH 7.2). Chymotrypsin activity (U) corresponded to the μmol BTEE hydrolysed min^{-1} ml^{-1} of extract at 256 nm (Worthington, 1991). The alkaline phosphatase activity was measured according to the method described by Gisbert et al. (2018). The activities of α-amylase and bile-salt dependent lipase were measured according to Worthington (1991) and Gawlicka et al. (2000), respectively.

2.5 | Statistics

SPSS ver. 20 was used for data analyses. Data are presented as means ± standard error of the mean. Kolmogorov–Smirnov was used to evaluate the normality of data, and a Levene's test was applied for determining the homogeneity of variances. Significant differences among groups were evaluated by one-way ANOVA ($p < .05$), and the Tukey's post hoc test was used for multiple comparisons.

3 | RESULTS

3.1 | Growth performance

Weekly changes in body weight of *S. hasta* and *A. latus* were reported in Figure 1a,b. After the 2 weeks of feed restriction, body weight gradually increased by elevation of ration level. Thus, fish in the control group had the highest weight, while R0% group had the lowest body weight in both fish species. Regarding *S. hasta*,

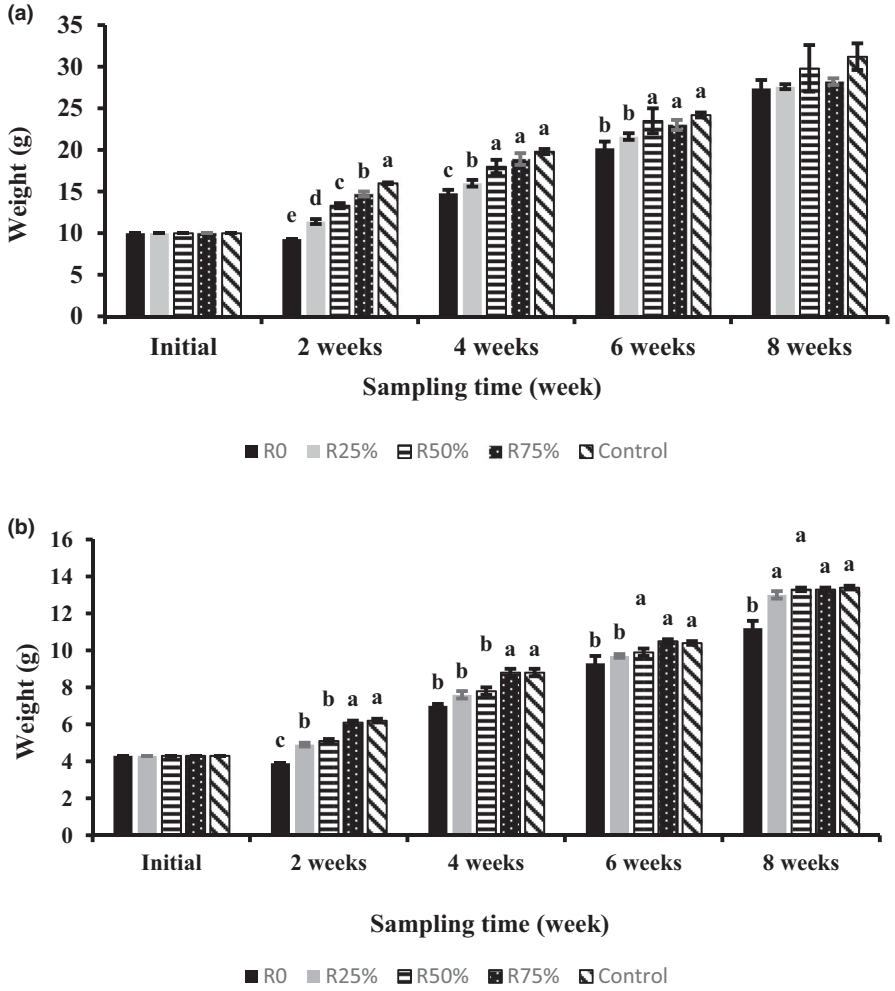

FIGURE 1 Biweekly change in weight (g) of *S. hasta* (a) and *A. latus* (b) juveniles fed according to different feeding regimes for 8 weeks. (R0) fish fed at 0% satiation; (R25%) fish fed at 25% satiation; (R50%) fish fed at 50% satiation; and (R75%) fish fed at 75% of satiation for 2 weeks then they were fed to satiation level for 6 weeks. A different superscript on each set of bars (sampling time) denotes statistically significant differences ($p < .05$)

at the end of the 6-week refeeding episode, fish reared at all the ration-restricted treatments showed complete CG (Figure 1a). With regard to *A. latus*, except for R0%, fish in R25%, R50% and R75% demonstrated full CG (Figure 1b). The lowest survival rate in *S. hasta* was observed in R0% group mainly due to the cannibalistic behaviour (Table 1). Regarding *A. latus* juveniles, the survival rate did not change. At the end of the 6-week refeeding, R0 group in *S. hasta* showed higher specific growth rate (SGR) compared with the other groups. Regarding *A. latus*, SGR values in R0%, R25% and R50% were higher than the other groups. In *A. latus*, by considering the results of body weight and SGR, R0 group was demonstrated partial CG. At the end of the husbandry trial, weight gain (WG) in *S. hasta* juveniles subjected to the feed restriction reached to the control after 6 weeks of refeeding; however, in *A. latus*, R0 had lower WG compared with other groups. In *S. hasta*, R75% and control groups had higher feed intake (FI) compared with the other treatments, but in *A. latus*, control group had higher FI than R0% and R25%. In *S. hasta*, R50% and control groups had the lowest and the highest feed conversion ratio (FCR) values, respectively; meanwhile, the FCR was not affected by feeding regimes in *A. latus*.

Hepatosomatic index (HSI) did not affect by feeding schedule, but VSI value was remarkably increased in *S. hasta* subjected to R50% treatment compared with the control and R25% groups. Regarding *A. latus*, control group had higher HSI and VSI values compared with the restricted-ration groups. In *S. hasta*, *K* value did not affect by the feed schedules but in *A. latus* the Fulton's condition factor (*K*) value in R0% was lower than R25%, R75% and control groups; meanwhile, R50% had intermediate value (Table 1, $p < .05$).

3.2 | Antioxidant activity

The highest levels of GST, SOD and GPx activates in the liver of *S. hasta* juveniles were found in R0% and R25% groups, and the control had the lowest values ($p < .05$, Table 2). In *A. latus*, control group had the lowest GST, SOD and GPx compared with the feed-restricted groups. In *S. hasta*, fish in R0% group had higher CAT activity in the liver compared with the other groups, but in *A. latus*, catalase activity in the control was relatively lower than the other experimental groups ($p < .05$). The level of TBARs remarkably enhanced in the liver of both fish species subjected to R0% and R25% treatments, but fish in R75% and the control group had the lowest values.

TABLE 1 Growth performance and survival rate in *S. hasta* and *A. latus* at the end of the husbandry trial subjected to the following feeding regimes: (control) fish fed to satiation for 8 weeks; (0) fish fed at 0% satiation; (R25%) fish fed at 25% satiation; (R50%) fish fed at 50% satiation; and (R75%) fish fed at 75% satiation for 2 weeks then they were fed to satiation level for 6 weeks. A different superscript in the same row denotes statistically significant differences ($p < .05$)

	R0	R25%	R50%	R75%	Control
S. hasta					
SGR[1] (% BW_i day^{-1})	2.2 ± 0.0^{a}	1.8 ± 0.1^{b}	1.8 ± 0.2^{b}	1.4 ± 0.1^{b}	1.8 ± 0.1^{b}
WG[2] (%)	175.5 ± 22.6	177.9 ± 5.9	198.3 ± 29.8	180.8 ± 3.4	215.9 ± 1.9
Total FI[3] (g $fish^{-1}$)	24.1 ± 0.3^{c}	24.5 ± 0.0^{c}	25.5 ± 0.5^{c}	28.3 ± 0.1^{b}	34.9 ± 0.8^{a}
FCR[4]	1.2 ± 0.1^{b}	1.2 ± 0.0^{b}	1.0 ± 0.1^{a}	1.3 ± 0.0^{bc}	1.4 ± 0.0^{c}
HSI[5] (%)	1.5 ± 0.3	1.5 ± 0.2	1.7 ± 0.1	1.4 ± 0.0	1.4 ± 0.1
VSI[6] (%)	9.0 ± 0.3^{ab}	8.2 ± 0.2^{b}	10.0 ± 0.4^{a}	8.8 ± 0.8^{ab}	7.9 ± 0.8^{b}
K[7] (%)	1.0 ± 0.0	1.3 ± 0.1	1.1 ± 0.1	1.1 ± 0.0	1.2 ± 0.2
Survival[8] (%)	83.3 ± 4.5^{b}	96.1 ± 1.6^{a}	93.9 ± 4.8^{a}	91.7 ± 4.8^{a}	93.3 ± 5.6^{a}
A. latus					
SGR (% BW_i day^{-1})	2.0 ± 0.0^{a}	2.1 ± 0.0^{a}	2.2 ± 0.1^{a}	1.7 ± 0.0^{b}	1.8 ± 0.4^{b}
WG (%)	158.3 ± 10.8^{b}	201.9 ± 4.9^{a}	210.3 ± 3.2^{a}	208.5 ± 5.5^{a}	212.0 ± 2.3^{a}
Total FI (g $fish^{-1}$)	13.1 ± 0.7^{ab}	12.3 ± 0.0^{b}	13.1 ± 0.5^{ab}	13.2 ± 0.2^{ab}	14.3 ± 0.5^{a}
FCR	1.5 ± 0.1	1.4 ± 0.0	1.5 ± 0.1	1.5 ± 0.0	1.6 ± 0.0
HSI (%)	2.6 ± 0.4^{b}	2.3 ± 0.1^{b}	2.2 ± 0.1^{b}	2.5 ± 0.1^{b}	3.7 ± 0.6^{a}
VSI (%)	14.0 ± 0.8^{b}	13.3 ± 0.6^{b}	13.8 ± 0.6^{b}	14.1 ± 0.7^{b}	15.2 ± 0.6^{a}
K (%)	1.1 ± 0.0^{b}	1.4 ± 0.0^{a}	1.2 ± 0.1^{ab}	1.4 ± 0.1^{a}	1.3 ± 0.0^{a}
Survival (%)	93.3 ± 0.0	96.7 ± 0.0	96.7 ± 0.0	100 ± 0.0	96.7 ± 0.0

Note: BW_i and BW_f are initial body weight and final body weight, respectively, and t is the experimental period = 56 days.

[1]SGR: specific growth rate (%) = $((\ln BW_f - \ln BW_i)/t) \times 100$.

[2]WG: weight gain (%) = $((BW_f - BW_i)/BW_i) \times 100$.

[3]Feed intake = total feed intake per tank (g)/number of fish.

[4]FCR: feed conversion ratio = (feed intake (g)/weight gain (g)).

[5]HSI: hepatosomatic index (%) = (liver weight (g)/BW_f (g)) × 100.

[6]VSI: viscerosomatic index (%) = (visceral weight (g)/BW_f (g)) × 100.

[7]K: Fulton's condition factor = (BW_f (g)/standard length $(cm)^3$) × 100.

[8]Survival (%) = number of fish in each group remaining on day 56/initial number of fish) × 100.

3.3 | Liver enzymes

Regarding liver enzymes, the greatest levels of ALT, AST, LDH and ALP were in the liver of *S. hasta* subjected to R0% and R25% treatments, but the lowest values were in the control (Table 3). In *A. latus* juveniles, the control group had the lowest levels of ALT, AST and ALP compared with the ration-restricted treatments. In addition, fish in R25%, R50% and R75% groups had higher LDH activity in the liver compared with R0% and the control.

3.4 | Digestive enzyme activities

The effects of feeding regimes on digestive enzymes activities were reported in Table 4. In *S. hasta*, R75% and control had the highest, and the lowest trypsin and ALP activities, respectively ($p < .05$). The activities of chymotrypsin, α-amylase and lipase were not affected by different treatments in *S. hasta* ($p > .05$). In *A. latus*, R25%, R50% and R75% had higher trypsin, chymotrypsin and lipase activities compared with the other groups ($p < .05$). The activity of ALP and α-amylase was lower in the control compared with the ration-restricted groups ($p < .05$).

4 | DISCUSSION

After 2 weeks of feed-restricted phase, both fish species lost weight, mainly due to mobilization of energy storages in the body for maintaining vital physiological processes (Ali et al., 2003). In addition, after restricted-ration phase, fish showed species-specific CGR. For example, in *S. hasta*, the CGR of fish during 6 weeks of satiation feeding was attributed to remarkable increase in SGR and improvement of FCR as previously reported by Mozanzadeh, Marammazi, Yaghoubi, Yavari, et al. (2017), Mozanzadeh et al. (2020). However, in *A. latus* juveniles, the CGR only associated with the accelerated SGR in this species as reported previously in this species (Mozanzadeh et al., 2020; Tamadoni et al., 2020). It should be mention that in this study, *S. hasta* fed at 50% and 75% of dietary ration levels for 2 weeks

	Ration level (% body weight day^{-1})				
	R0	R25%	R50%	R75%	Control
S. hasta					
GST	1.8 ± 0.1^{a}	1.7 ± 0.2^{a}	1.6 ± 0.2^{ab}	1.5 ± 0.1^{ab}	1.3 ± 0.0^{b}
GPx	1.8 ± 0.1^{a}	1.6 ± 0.2^{a}	1.5 ± 0.2^{ab}	1.4 ± 0.1^{ab}	1.3 ± 0.0^{b}
SOD	1.9 ± 0.0^{a}	1.9 ± 0.3^{a}	1.5 ± 0.1^{ab}	1.4 ± 0.0^{ab}	1.2 ± 0.0^{b}
CAT	1.1 ± 0.1^{a}	0.9 ± 0.1^{b}	0.8 ± 0.2^{b}	0.9 ± 0.0^{b}	0.8 ± 0.0^{b}
TBARs	2.7 ± 0.1^{a}	2.6 ± 0.2^{a}	2.5 ± 0.4^{ab}	2.2 ± 0.2^{b}	2.3 ± 0.0^{b}
A. latus					
GST	1.6 ± 0.0^{a}	1.7 ± 0.1^{a}	1.7 ± 0.1^{a}	1.7 ± 0.2^{a}	1.1 ± 0.0^{b}
GPx	1.3 ± 0.0^{a}	1.2 ± 0.1^{a}	1.1 ± 0.2^{a}	1.2 ± 0.2^{a}	0.5 ± 0.0^{b}
SOD	1.1 ± 0.0^{a}	1.2 ± 0.2^{a}	1.2 ± 0.1^{a}	1.3 ± 0.0^{a}	0.8 ± 0.0^{b}
CAT	0.9 ± 0.05^{ab}	1.1 ± 0.1^{a}	1.0 ± 0.0^{a}	1.1 ± 0.1^{a}	0.7 ± 0.0^{b}
TBARs	2.0 ± 0.1^{a}	2.1 ± 0.2^{a}	1.9 ± 0.2^{ab}	1.6 ± 0.0^{b}	1.5 ± 0.0^{b}

TABLE 2 Antioxidant enzymes (U mg protein^{-1}) and lipid peroxidation index (TBARs, nmol g^{-1} tissue) in *S. hasta* and *A. latus* at the end of the husbandry trial subjected to the following feeding regimes: (control) fish fed to satiation for 8 weeks; (0) fish fed at 0% satiation; (R25%) fish fed at 25% satiation; (R50%) fish fed at 50% satiation; and (R75%) fish fed at 75% satiation for 2 weeks then they were fed to satiation level for 6 weeks. A different superscript in the same row denotes statistically significant differences ($p < .05$)

Abbreviations: CAT, catalase; GPx, glutathione peroxidase; GST, glutathione-S-transferase; SOD, superoxide dismutase; TBARs, thiobarbituric acid.

	Ration level (% body weight day^{-1})				
	R0	R25%	R50%	R75%	Control
S. hasta					
ALT	1.6 ± 0.3^{a}	1.3 ± 0.3^{a}	1.0 ± 0.2^{b}	1.0 ± 0.0^{b}	0.7 ± 0.0^{c}
AST	1.4 ± 0.1^{a}	1.2 ± 0.1^{a}	1.1 ± 0.1^{ab}	1.0 ± 0.0^{ab}	0.9 ± 0.0^{b}
LDH	1.4 ± 0.1^{a}	1.5 ± 0.2^{a}	1.3 ± 0.2^{ab}	1.1 ± 0.0^{ab}	1.0 ± 0.0^{b}
ALP	2.7 ± 0.3^{a}	2.3 ± 0.4^{a}	1.9 ± 0.2^{b}	1.8 ± 0.0^{b}	1.5 ± 0.0^{c}
A. latus					
ALT	1.8 ± 0.0^{a}	1.3 ± 0.1^{a}	1.5 ± 0.1^{a}	1.5 ± 0.2^{a}	0.8 ± 0.0^{b}
AST	1.4 ± 0.1^{a}	1.1 ± 0.1^{a}	1.1 ± 0.1^{a}	1.1 ± 0.0^{a}	0.8 ± 0.0^{b}
LDH	1.2 ± 0.1^{b}	1.7 ± 0.1^{a}	1.7 ± 0.2^{a}	1.8 ± 0.2^{a}	1.2 ± 0.0^{b}
ALP	1.4 ± 0.1^{a}	1.5 ± 0.1^{a}	1.4 ± 0.0^{a}	1.5 ± 0.1^{a}	0.6 ± 0.0^{b}

TABLE 3 Liver enzymes (U mg protein^{-1}) in *S. hasta* and *A. latus* at the end of the husbandry trial subjected to the following feeding regimes: (control) fish fed to satiation for 8 weeks; (R0) fish fed at 0% satiation; (R25%) fish fed at 25% satiation; (R50%) fish fed at 50% satiation; and (R75%) fish fed at 75% of satiation for 2 weeks then they were fed to satiation level for 6 weeks. A different superscript in the same row denotes statistically significant differences ($p < .05$)

Abbreviations: ALP, alkaline phosphatase; ALT, alanine aminotransferase; AST, aspartate aminotransferase; LDH, lactate dehydrogenase.

reached to the body weight of the control only after 2 weeks of satiation ration; meanwhile, R0% and R25% groups caught up with the control in weight after 6 weeks of satiation ration. In addition, the survival rate in fish that fasted for 2 weeks (R0) significantly was reduced as a consequence of cannibalism, suggesting prolonged starvation provoked cannibalistic behaviour in *S. hasta*. It has been reported that the hunger restricts recognition capability of fish to discriminate siblings, thus adjusting feeding regimes have vital role in the reduction in the cannibalism rate in fish (Liu et al., 2017). In this context, Liu et al. (2017) reported that feed deprivation for 24 h was almost doubled the rate of intercohort cannibalism in Asian seabass (*Lates calcarifer*). Regarding yellowfin seabream, fish in R75% group caught up the body weight of the control over the course of a 2-week satiation ration, whereas R25% and R50% groups caught up with the control in weight after 6 weeks of satiation feeding, but R0 group did not catch up the control in weight after 6 weeks of satiation ration. Full CGR also reported in other sparid species subjected to different starvation and refeeding strategies such as red seabream (*Pagrus pagrus*, Rueda et al., 1998), gilthead seabream, (*Sparus aurata*, Bavcevic et al., 2010), blackhead seabream, (*Acanthopagrus schlegelii schlegelii*, Oh et al., 2013), sobaity seabream (Mozanzadeh, Marammazi, Yaghoubi, Yavari, et al., 2017; Mozanzadeh et al., 2020) and yellowfin seabream (Mozanzadeh et al., 2020; Tamadoni et al., 2020). Partial CGR also reported in gilthead seabream experienced various patterns of feed restriction such as one-day fasting followed by two days of refeeding during 60 days (Eroldoğan et al., 2006) and feeding at 50% of satiation level for two days followed by two days of feeding at apparent satiation over the course of 48 days (Eroldoğan et al., 2008). Different mechanisms were suggested to related to CGR in fish such as hyperphagia (Ali et al., 2003), optimizing metabolic rate (Alvarez & Nicieza, 2005), biosynthesis of protein (Quinton & Blake, 1990), acclimation of endocrine system to restricted-feeding periods (Davis & Gaylord, 2011), decrease in basal metabolic rate and improvement of FCR (Mozanzadeh et al., 2020).

TABLE 4 Digestive enzymes (U mg protein^{-1}) in *S. hasta* and *A. latus* at the end of the husbandry trial subjected to the following feeding regimes: (control) fish fed to satiation for 8 weeks; (0) fish fed at 0% satiation; (R25%) fish fed at 25% satiation; (R50%) fish fed at 50% satiation; and (R75%) fish fed at 75% satiation for 2 weeks then they were fed to satiation level for 6 weeks. A different superscript in the same row denotes statistically significant differences ($p < .05$)

	Ration level (% body weight day^{-1})				
	R0	R25%	R50%	R75%	Control
S. hasta					
Trypsin	1.4 ± 0.0^{ab}	1.4 ± 0.1^{ab}	1.4 ± 0.2^{ab}	1.6 ± 0.0^{a}	1.2 ± 0.0^{b}
Chymotrypsin	1.5 ± 0.0	1.5 ± 0.1	1.6 ± 0.2	1.7 ± 0.0	1.4 ± 0.0
Alkaline phosphatase	1.5 ± 0.1^{b}	1.6 ± 0.2^{b}	1.5 ± 0.2^{b}	2.2 ± 0.0^{a}	1.2 ± 0.0^{c}
α-Amylase	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
Lipase	1.1 ± 0.0	1.1 ± 0.1	1.3 ± 0.2	1.3 ± 0.0	1.0 ± 0.0
A. latus					
Trypsin	1.3 ± 0.3^{b}	1.6 ± 0.1^{a}	1.6 ± 0.2^{a}	1.6 ± 0.1^{a}	1.1 ± 0.2^{b}
Chymotrypsin	1.5 ± 0.0^{b}	1.8 ± 0.1^{a}	1.7 ± 0.2^{a}	1.8 ± 0.0^{a}	1.4 ± 0.2^{b}
Alkaline phosphatase	1.5 ± 0.0^{a}	1.0 ± 0.1^{a}	1.3 ± 0.0^{a}	1.1 ± 0.0^{a}	0.6 ± 0.1^{b}
α-Amylase	1.4 ± 0.0^{a}	0.6 ± 0.0^{b}	0.9 ± 0.0^{b}	0.7 ± 0.1^{b}	0.4 ± 0.0^{c}
Lipase	1.1 ± 0.4^{b}	1.5 ± 0.2^{a}	1.5 ± 0.1^{a}	1.5 ± 0.1^{a}	1.0 ± 0.0^{b}

In the present study, FCR was improved in *S. hasta* subjected to feed restriction that might be partially associated with the elevation of digestive enzyme activities and improvement in nutrients absorption as also reported in other studies (Furne et al., 2008; Krogdahl & Bakke-McKellep, 2005).

The reduction in somatic indices (HSI, VSI and K) in fish during feed restriction could be due to utilization of energy storages (e.g. glycogen and lipid) in body for supporting vital physiological processes. The findings of current research showed that the values of HSI and K in feed-restricted groups caught up to the control after 6 weeks of refeeding in *S. hasta* juveniles. However, in *A. latus*, the values of HSI and VSI pronouncedly were decreased in fish subjected to the restricted-feeding period. Also, reduction in HSI value also reported in different sparids due to feed restriction such as gilthead sea bream (Grigorakis & Alexis, 2005), red porgy (Mohapatra et al., 2017), black seabream (Xiao et al., 2013) and sobaity seabream (Mozanzadeh, Marammazi, Yaghoubi, Yavari, et al., 2017). In addition, the value of *K* in R0 group in *A. latus* was lower than the other treatments as previously reported in other sparids such as red porgy (Caruso et al., 2012) and common dentex (*Dentex dentex*, Pérez-Jiménez et al., 2012). It has been reported that starvation not only induces oxidative stress in fish but also could deplete the nutrients and antioxidant storages such as sulphur amino acids (e.g. methionine, cysteine and taurine) and glutathione in body, which consequently negatively affect the activity of glutathione-dependent antioxidant enzymes (e.g. GST, GPx, and GR) (Morales et al., 2004; Pascual et al., 2003). In our study, both sparid species may resist oxidative stress caused by feed restriction mainly through increasing different antioxidant enzymes in the liver. In addition, the elevation of the antioxidant enzyme activities in both sparids may be related to the increased hydrogen peroxides produced by the neutralization of ROS generated through lipid peroxidation during restricted-ration period (Najafi et al., 2014). In this regard, Dar et al. (2019) reported that starvation boosted up the activities of SOD and CAT in Indian major carp (*Labeo rohita*). Similar to these results, Tamadoni et al. (2020) also reported that increasing fasting duration elevated CAT and GST activities in the liver and resulted in oxidative stress in *A. latus* juveniles. In addition, the results of the current research clearly demonstrated that increasing the severity of the feed restriction, especially in R0% and R25% groups, pronouncedly enhanced lipid peroxidation index (TBARs value) in the liver in both species. These results indicating the antioxidant defences were overcome by oxidative stress, and ROS were not adequately diminished in these groups. Similar to the results of the present study, partial food deprivation increased lipid oxidation index in the liver of rainbow trout (*Oncorhynchus mykiss*, Hidalgo et al., 2002) and gilthead seabream (Pascual et al., 2003).

Increment of energy turnover in the liver through processing energy substrates over the course of fasting and refeeding episodes may elevate the activity of hepatic enzymes (e.g. ALP, AST, AST and LDH) that eventually increase the leakage of these enzymes into the blood (Furné et al., 2012; Pérez-Jiménez et al., 2012; Ashouri et al., 2020). For instance, it has been found that ALP increased during refeeding episode to elevate trans-membrane transportation of ions and water in fish (Congleton and Wagner, 2006). Furthermore, ALT, AST and LDH have main role in gluconeogenesis in different fish species during fasting period (Furné et al., 2012; Pérez-Jiménez et al., 2012; Ashouri et al., 2020). The results of the current study revealed that the levels of the liver enzymes were gradually decreased with the reduction in the severity of feed restriction in *S. hasta*. Thus, the values of the liver enzymes in R50% and R75% were caught up to the values of the control after the refeeding phase in *S. hasta*, but the values of these enzymes did not recover in R0% and R25% groups. Regarding *A. latus* juveniles, the levels of hepatic enzymes in the liver of fish experienced feed restriction were higher than the control, suggesting higher gluconeogenesis from non-carbohydrate substrates such as amino acids and lactate during restricted-feeding period in this species. Also, Ashouri et al. (2020) reported that after the

fasting phase, the levels of plasma AST, ALP and LDH were increased in juvenile Siberian sturgeon (*Acipenserbaerii*, Brandt 1869) starved for 1, 2 or 3 weeks compared with the fish that were fed throughout the husbandry trial. Dar et al. (2019) also reported that the serum AST and ALT levels were increased during starvation in *Labeo rohita*, but they were recovered to the values of the control group during refeeding phase. In contrast, Azodi et al. (2015) reported that plasma alkaline phosphatase and aspartate aminotransferase did not affect by cyclical fasting and refeeding periods in rainbow trout (*Oncorhynchus mykiss*).

It has been reported that during feed restriction, fish tend to adjust their digestive capacity by boosting up digestive enzyme activities to hydrolyse feed in order to extract more nutrients which ultimately improve FCR (Eroldogan et al., 2004; Silva et al., 2007). In the present study, the activity of trypsin was overcompensated in R75% group compared with the control; however, the activities of chymotrypsin, lipase and α-amylase did not affect by fasting suggesting that these enzymes did not exert substantial regulatory effect on CGR in *S. hasta*. Regarding *A. latus*, the activities of trypsin, chymotrypsin and lipase in R25%, R50% and R75% groups were higher than the control and R0 groups suggesting the overcompensation of these digestive enzymes during refeeding period. Enhancement of digestive enzyme activities may be enabled *A. latus* to efficiently digest protein and lipid that consequently resulted in the full CGR in R25, R50% and R75%. Other studies also reported the elevation and recovery of proteases and lipase activity after refeeding period in different fish species such as rainbow trout and sturgeon (*Acipenser naccarii*) (Furné et al., 2005; Furne et al., 2008), *Megalobrama Pellegrini* (Zheng et al., 2015), and Nile tilapia (*Oreochromis niloticus*, Sakyi et al., 2020). Alkaline phosphatase is mainly distributed in the brush border of the enterocytes, and its role is associated with the hydrolysis of inorganic phosphates for energy production and nutrients absorption in the intestine (Gisbert et al., 2018). In the current study, in both sparid species, the feed restriction increased ALP activity suggesting an improvement in luminal digestive capacity that may lead to better nutrients absorption during refeeding period. Also, the activity of ALP was increased in *A. latus* juvenile that were fasted for 4 and 8 days, and then were refed for 16 and 32 days, respectively compared with the control (Tamadoni et al., 2020). Moreover, in *A. latus*, the activity of α-amylase elevated in fish experienced the feed restriction especially in R0 that may be enabled fish to elevate glucose mobilization capacity from liver glycogen reserves as previously reported in other sparid species (Eroldoğan et al., 2008; Sangiao-Alvarellos et al., 2005; Tamadoni et al., 2020). These results suggested that the impacts of the feed restriction and refeeding on the digestive system are enormous, and CGR in both species is closely related to the activity of digestive enzymes.

5 | CONCLUSION

In summary, the results of our research showed that the CGR in sparid species is species-specific. In *S. hasta* juveniles, all the ration-restricted groups showed full CGR, but survival rate in R0 was decreased due to cannibalism. The full CGR in *S. hasta* was associated with hyperphagia, improvement in FCR as well as increase in activity of proteases including trypsin and ALP. Regarding *A. latus* juveniles, except for R0, fish subjected to feeding restriction showed full CGR that mainly attributed to overcompensation of digestive enzymes in these groups. In *S. hasta*, the antioxidant enzyme activities and liver enzymes were gradually decreased with alleviation of the feed restriction severity. Regarding *A. latus*, all antioxidant and liver enzymes in feed-restricted groups were higher than the control. In addition, with increasing the severity of the feed restriction especially in R0% and R25% groups, the lipid peroxidation index (TBARs value) pronouncedly enhanced in the liver in both fish species, indicating the antioxidant defences could not compensate oxidative stress in these groups. By considering all selected physiological responses in both sparid species, it can be concluded that prolonged fasting can induce cannibalism, oxidative stress condition and may increase metabolic burden on the liver that eventually may lead to the liver malfunction.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

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

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