Received: 12 March 2020 | Revised: 23 August 2020 | Accepted: 16 November 2020
DOI: 10.1111/anu.13199

ORIGINAL ARTICLE

Aquaculture Nutrition WILEY

Compensatory growth of Sobaity (*Sparidentex hasta*) and yellowfin seabreams (*Acanthopagrus latus*) relative to feeding rate during nursery phase

Mansour Torfi Mozanzadeh[1] | Mojtaba Zabayeh Najafabadi[1] | Mohammad Torfi[2] | Omid Safari[3] | Rahim Oosooli[1] | Shapour Mehrjooyan[1] | Esmaeil Pagheh[4] | Seyed Javad Hoseini[1] | Hamid Saghavi[1] | Javad Monem[1] | Enric Gisbert[5]

[1]South Iran Aquaculture Research Centre, Iranian Fisheries Science Institute (IFSRI), Agricultural Research Education and Extension organization (AREEO), Ahwaz, Iran

[2]Khuzestan Department of Environment, Iranian Department of Environment, Khuzestan, Iran

[3]Department of Fisheries, Faculty of Natural Resources and Environment, Ferdowsi University of Mashhad, Khorasan Razavi, Iran

[4]Inland Waters Aquatic Stocks Research Center, Iranian Fisheries Science Research Institute (IFSRI), Agricultural Research, Education and Extension Organization (AREEO), Gorgan, Iran

[5]Centre de Sant Carles de la Rápita (IRTA-SCR), IRTA, Sant Carles de la Rápita, Spain

Correspondence
Mansour Torfi Mozanzadeh, South Iran Aquaculture Research Centre, Iranian Fisheries Science Institute (IFSRI), Agricultural Research Education and Extension organization (AREEO), Ahwaz, Iran.
Emails: M.torfi@areeo.ac.ir; Mansour.torfi@gmail.com

Funding information
South Iran Aquaculture Research Centre, Iranian Fisheries Science Institute (IFSRI); Agricultural Research Education and Extension organization (AREEO)

Abstract

A 60-day study was conducted to investigate the compensatory growth (CG) responses of sobaity (*Sparidentex hasta*) and yellowfin (*Acanthopagrus latus*) seabreams to restricted feeding ration and normal feeding ration phases during the nursery period. Fry stage of *S. hasta* and *A. latus* with initial weight (BW_i) of 1 and 0.8 g, respectively, were fed a commercial diet at five ration levels (RL) including 2%, 4%, 6%, 8% and 10% of their BWi over a period of 30 days (restricted-ration phase) and then re-fed up to visual satiation for another 30 days (normal-ration period). According to the second-degree polynomial relationship between specific growth rate and RL, the maintenance, optimum and maximum feeding rates for SGR in *S. hasta* were estimated to be 0.5%, 3.5% and 8.2%; meanwhile in *A. latus*, they were 0.3%, 4% and 8%, respectively. At the end of the normal-ration phase, final body weight (BW_f) of *S. hasta* fed at 10% RL was higher than the other treatments. In addition, *A. latus* fed at 6% and 8% RL showed full CG regarding BW_f compared with fish fed at 10% RL. The findings of this study confirmed partial CG in *S. hasta* and full CG in *A. latus* after re-feeding period.

KEYWORDS

fasting, feed efficiency, growth performance, re-feeding, Sparidae, trajectory growth

1 | INTRODUCTION

Sobaity (*Sparidentex hasta*) and yellowfin (*Acanthopagrus latus*) seabreams are commercially important carnivorous fish species in the Persian Gulf and Oman sea regions. These sparids are considered as potential candidates for developing marine aquaculture due to their high economic value, great adaptability to culture conditions and domestication and easy propagation in captivity (Mozanzadeh, Marammazi, Yaghoubi, Agh, Pagheh, et al., 2017). As a matter of fact, the commercial success in aquaculture operation of any candidate aquatic species will partially depend on the determination of its optimum feed formulation and feeding schedules. Therefore, economic profitability and production viability of any aquatic species drastically depend on the appropriate feeding programme during the grow-out phase (Dias et al., 2010). As feed costs represent the greatest operating expenses in aquaculture (Henry et al., 2015), identifying the optimal ration level (RL) not only ensures fish farmers to produce healthy fish with maximal growth rates and high feed efficiency, but also minimizes size heterogeneity, feed wastage and deterioration of water quality (Rondan et al., 2004; Schnaittacher et al., 2005). On the other hand, optimal RL is species-specific and depends on the developmental stages, water temperatures, stocking densities, rearing systems and feeding strategies, among others (Ng et al., 2000). Inappropriate RL such as underfeeding or overfeeding results in unsuitable conditions that enhance production costs and induce stress and may compromise fish welfare (López-Olmeda et al., 2012). Regarding Sparids, the optimum RL has been estimated at 2% body weight (BW)/day in red porgy juveniles (*Pagrus pagrus*, Mihelakakis et al., 2001), 2.3% BW/day in gilthead seabream juveniles (*Sparus aurate*, Mihelakakis et al., 2002), 4.4% BW/day in blackspot seabream juveniles, (*Pagellus bogaraveo*, Otavio et al., 2009) and 7% BW/day in yellow seabream juveniles (*Acanthopagrus arabicus*, Ahmad et al., 2018).

Along with determination of optimal RL, inducing compensatory growth (CG) in cultured fish species by applying feed restriction and re-feeding strategies has received great attention in feeding management (Ali et al., 2003; Gaylord & Gatlin, 2001; Jobling, 2010; Känkänen & Pirhonen, 2009). Compensatory growth is a direct response to hyperphagia that is generally stimulated by a restricted-ration phase; meanwhile, during the re-feeding phase, trajectory growth is stimulated by either a decrease in metabolic costs, an increase in feed consumption or an enhancement in feed utilization due to better digestibility and absorption of nutrients (Ali et al., 2003). In addition, CG manipulations may reduce feeding and labour expenditures, as well as avoiding any errors in feed estimation, which may enhance the economical profit of fish farming (Krogdahl & Bakke-McKellep, 2005). Furthermore, understanding CG pattern of a fish species may help in defining a feeding schedule, which could lead to improvement in growth performance and feed efficiency (Hayward et al., 1997; Wang et al., 2000). Similar to RL, growth compensatory response is species-specific and depends on type, duration and severity of feed restriction before re-feeding (Hayward et al., 1997). Regarding sparids, the CG responses varied from negligible (Mozanzadeh, Marammazi, Yaghoubi, Yavari, et al., 2017; Peres et al., 2011) or partial CG (Eroldogan et al., 2006, 2008; Yilmaz & Eroldogan, 2011) to complete CG (Bavcevic et al., 2010; Oh et al., 2013; Rueda et al., 1998; Tamadoni et al., 2020). Such differences are due to feeding strategies, water temperatures and culture conditions. Studies on compensatory growth at young ages are really relevant since fish growth is very fast during their initial larval and juvenile phases, when a deviation in feed administration may result in food restriction; thus, negatively impacting on growth performance. In this sense, these stages of fast growth are even more sensitive that at older stages, when specific growth rate reduces and may compromise fish performance in other stages (Jiwyam, 2010). In addition, it is important to provide tools for improving rearing management practices and evaluating how feeding ratios can be optimized, since from a sustainable and environmental point of view adjusting and improving feeding practices are critical for improving the rearing process, especially when feeding costs represent 50%–60% of total production costs. Thus, the aim of the current research was to determine the CG response of Sobaity and yellowfin seabreams relative to restricted feeding rate in nursery phase.

2 | MATERIALS AND METHODS

2.1 | Experimental design

The present study was conducted in the Marine Fish Research Station of the South Iran Aquaculture Research Center (SIARC), Sarbandar, Iran. The research design was carried out according to Jiwyam (2010) with minor modifications. The feeding trial lasted for 60 days, and it was divided into two phases including a 30-day restricted-ration period (RRP) and a 30-day normal-ration period (NRP). Each experimental condition was tested by triplicate. The husbandry system consisted of 30 cylindrical polyethylene tanks with volume of 300 L, which were filled with 250 L of sand-filtered and disinfected running seawater (1 L/min). The average water quality values (mean ± standard deviation) for salinity, temperature, pH and dissolved oxygen were 47.0 ± 0.5‰, 27.2 ± 0.8°C, 7.5 ± 0.2 and 6.5 ± 0.8 mg/L, respectively.

For the RRP, 750 *S. hasta* juveniles (body weight, BW = 1.0 ± 0.01 g, mean ± standard error) were stocked into 15 tanks (50 fish/tank) and 900 *A. latus* juveniles (0.8 ± 0.01 g) were distributed into 15 tanks (60 fish/tank). Both species were propagated at SIARC facilities and kept in 5000 L polyethylene tanks; thus, fry fishes were acclimatized to the experimental condition prior to the beginnings of the research trial. The total biomass of fish in each tank was recorded and considered for calculating the amount of feed according to the RL. During the RRP, fish were hand-fed at five different ration levels (RL = 2%, 4%, 6%, 8% and 10% of the initial fish biomass). The amount of feed for each RL was not changed during this period. Fish were fed on a commercial feed (Biomar, France; particle size: 800 μm, 560 g/kg crude protein, 180 g/kg crude fat, 107 g/kg ash and 40 g/kg fibre) twice daily (0800 and 1300 h) according to the RL for 30 days, making sure that no feed was left uneaten. At the end of the RRP, fish from each tank were individually weighted and their and length was measured at accuracy of 1 mm.

At the end of the RRP, all fish from each treatment (RL = 2%, 4%, 6%, 8% and 10% of the initial fish biomass) were grouped and 120 *S. hasta* and 150 *A. latus* juveniles were selected for the NRP. During the NRP, fish were hand-fed on the same commercial feed that was offered during the RRP (particle size: 1 mm) to visual satiation two times a day (0800 and 1300 h) for 30 days, making sure that no feed was left uneaten. As feed was provided by hand at visual satiation, feeding rate was adjusted to fish growth. Each experimental condition was tested by triplicate (n = 40 and n = 50 juveniles of *S. hasta* and *A. latus*, respectively). Fish biomass in each tank was adjusted according to their final BW at the end of the RRP. At the end of the NRP, fish from each tank were individually weighted and their length were measured at accuracy of 1 mm. At the end of each phase, five fish per tank were sacrificed for evaluating the somatic indices. In this regard, at the end of each phase, five fish per tank were sacrificed with an overdose of anaesthetic (2-phenoxyethanol); then, viscera (with liver) and liver were dissected and weighted (Mozanzadeh et al., 2017). Standard formulae were used to determine growth performance, feed utilization and somatic indices: SGR: specific growth rate (%) = $((\ln BW_f - \ln BW_i) / t) \times 100$, where t is experimental period = 30 days; WG: weight gain (%) = $((BW_f - BW_i)/BW_i) \times 100$; SUR: survival (%) = number of fish in each group remaining on day 30/initial number of fish) × 100; feed intake = total feed intake per tank (g) / number of fish; FER: feed efficiency ratio = (weight gain (g) / feed intake (g)); HSI: hepatosomatic index (%) = (liver weight (g) / BW_f (g)) × 100; VSI: viscerosomatic index (%) = (visceral weight (g) / BW_f (g)) × 100; K: Fulton's condition factor = (BW_f (g)/ standard length (cm)^3) × 100; RFI: relative feed intake = (feed consumption per tank (g)/ initial biomass of fish in tank (g)) × 100 in which BW_i and BW_f are initial body weight and final body weight, respectively. The methodology described by in Eroldogan et al. (2004) based on the relationship between feeding rates and SGR values was used to determined maintenance, optimum and maximum feeding rates in both sparid species.

2.2 | Statistics

Data were analysed by means of SPSS ver. 20. Data are presented as means ± standard error of the mean. Normality of data was tested with the Kolmogorov–Smirnov test, and homogeneity of variance evaluated with the Levene's test. One-way ANOVA was used for evaluating whether significant differences existed among group ($p < .05$), the Tukey's post hoc test was used for multiple comparisons. For determining the relationships between specific growth ratio, feed efficiency ratio and feeding rate percentage a second-degree polynomial regression was conducted. The Pearson

TABLE 1 Effects of feeding ratio on growth performance of *S. hasta* during restricted-ration (30-day) and normal-ration (30-day) phases (mean ± *SEM*, *n* = 3)

	Ration level (% body weight/day)				
Parameters	**2**	**4**	**6**	**8**	**10**
Restricted-ration phase					
BW_i (g)	1.0 ± 0.01	1.0 ± 0.01	1.0 ± 0.01	1.0 ± 0.01	1.0 ± 0.01
BW_f (g)	1.7 ± 0.1^d	2.0 ± 0.1^{cd}	2.6 ± 0.2^b	2.8 ± 0.2^b	3.2 ± 0.2^a
SGR (% BW_i/day)	1.9 ± 0.2^d	2.5 ± 0.1^c	3.4 ± 0.2^b	3.6 ± 0.2^b	4.1 ± 0.2^a
WG (%)	69.0 ± 7.7^d	101.5 ± 6.4^c	161.4 ± 10.9^b	177.3 ± 11.7^b	216.8 ± 15.6^a
Survival (%)	95.0 ± 0.6	93.8 ± 0.6	97.3 ± 2.7	94.0 ± 2.6	97.0 ± 0.6
FI (g/fish)	0.6 ± 0.0^e	1.2 ± 0.0^d	1.7 ± 0.1^c	2.5 ± 0.1^b	2.9 ± 0.0^a
FER	1.23 ± 0.1^a	0.96 ± 0.1^b	0.9 ± 0.1^b	0.78 ± 0.1^b	0.76 ± 0.1^b
HSI (%)	2.0 ± 0.1^c	2.5 ± 0.2^b	2.8 ± 0.2^{ab}	2.8 ± 0.0^{ab}	3.2 ± 0.8^a
VSI (%)	9.7 ± 2.3	9.6 ± 0.4	9.4 ± 0.8	10.6 ± 1.6	9.4 ± 0.3
K (%)	1.7 ± 0.1	2.0 ± 0.1	1.9 ± 0.0	1.9 ± 0.1	1.8 ± 0.1
Normal-ration phase					
BW_i (g)	1.7 ± 0.1^d	2.0 ± 0.1^{cd}	2.6 ± 0.2^b	2.8 ± 0.2^b	3.2 ± 0.2^a
BW_f (g)	8.5 ± 0.3^b	8.8 ± 0.3^b	9.6 ± 0.2^b	8.6 ± 0.0^b	11.1 ± 0.4^a
SGR (% BW_i/day)	4.8 ± 0.1^a	4.3 ± 0.0^b	3.7 ± 0.1^c	3.5 ± 0.2^c	3.7 ± 0.0^c
WG (%)	418.4 ± 22.2^a	335.6 ± 21.3^b	269.2 ± 11.4^c	211.2 ± 13.5^{cd}	251.7 ± 4.8^c
Survival (%)	92.5 ± 4.3	93.8 ± 0.8	95.0 ± 1.2	96.3 ± 0.7	96.3 ± 2.2
FI (g/fish)	8.4 ± 0.2^b	8.4 ± 0.0^b	9.8 ± 0.0^a	7.5 ± 0.4^b	9.5 ± 0.2^a
RFI (%)^j	14.8 ± 0.5^a	12.3 ± 0.5^b	9.5 ± 0.4^c	8.1 ± 0.4^c	9.1 ± 0.1^c
FER	0.8 ± 0.0	0.8 ± 0.0	0.8 ± 0.1	0.8 ± 0.0	0.8 ± 0.0
HSI (%)	1.8 ± 0.1	1.8 ± 0.1	2.0 ± 0.0	1.9 ± 0.4	1.5 ± 0.0
VSI (%)	8.5 ± 0.8^a	8.0 ± 0.7^a	7.7 ± 0.2^a	8.2 ± 0.3^a	6.4 ± 0.4^b
K (%)	1.6 ± 0.1	1.6 ± 0.1	1.7 ± 0.0	1.6 ± 0.0	1.6 ± 0.0

Note: A different superscript in the same row denotes statistically significant differences ($p < .05$).

Abbreviations: BW_f, final body weight; BW_i, initial body weight; FER, feed efficiency ratio; FI, feed intake; HSI, hepatosomatic index; K, Fulton's condition factor; RFI, relative feed intake; SGR, specific growth rate; SUR, survival; VSI, viscerosomatic index; WG, weight gain.

product-moment correlation test was used to determine any correlation among parameters, and in all cases, $p < .05$ was considered as significant.

3 | RESULTS

3.1 | Restricted feeding ration period

There were not statistically significant differences in survival rates at either the end of the RR and NR periods in both sparid species (Tables 1 and 2, $p > .05$). During the RRP, growth rate of both species increased with increasing RL. There was a significant and positive correlation between RL and final body weight values in *S. hasta* ($r = .949$; $p = .001$) and *A. latus* ($r = .980$; $p = .001$) juveniles. Regarding *S. hasta*, SGR and WG values for fish fed at 2% RL were 1.9% and 69.0%, respectively, whereas these parameters increased to 4.1% and 216.8% in fish fed at 10% RL ($p < .05$, Table 1). In *A. latus*, growth rate increased with an increase of the RL from 2% to 8% ($p < .05$), but there were not any differences in growth performance of fish fed at 8% or 10% RL ($p > .05$). Values of SGR and WG in *A. latus* juveniles fed at 2% RL during the RRP were 1.2% and 45%, respectively and these parameters increased to 3.7% and 204.1% in fish fed at a feeding ration of 10% ($p < .05$). In *S. hasta*, FER in fish fed at 2% RL was higher than other treatments; meanwhile in *A. latus*, there were not any differences in FER of fish fed at different RL ($p < .05$, Table 2). Hepatosomatic index (HSI) in *S. hasta* increased with enhancing RL from 2% in fish fed at 2% RL to 3.2% in fish fed at 10% RL ($p < .05$), whereas in *A. latus* HSI was not affected by RL ($p > .05$). Other somatic indices including VSI and K were not influenced by RL in both fish species ($p > .05$). Second-degree polynomial relationship between SGR and RL in *S. hasta* (Figure 1a) was described as $SGR = -0.0186RL^2 + 0.504RL + 0.8987$ ($R^2 = .8959$); meanwhile in *A. latus* (Figure 1b), it was described as $SGR = -0.173\ RL^2 + 0.5257RL + 0.2508$ ($R^2 = .9264$). The maintenance, optimum and maximum feeding rates for SGR in *S. hasta* were estimated to be 0.5%, 3.5% and 8.2%; meanwhile in *A. latus*, they were 0.3%, 4% and 8%, respectively.

TABLE 2 Effects of feeding ratio on growth performance of *A. latus* during restricted-ration (30-day) and normal-ration (30-day) phases (mean ± *SEM*, *n* = 3)

	Ration level (% body weight/day)				
Parameters	2	4	6	8	10
Restricted-ration phase					
BW_i (g)	0.8 ± 0.01	0.8 ± 0.01	0.8 ± 0.01	0.8 ± 0.01	0.8 ± 0.01
BW_f (g)	1.2 ± 0.0[c]	1.6 ± 0.1[bc]	1.9 ± 0.0[b]	2.4 ± 0.0[a]	2.5 ± 0.0[a]
SGR (% BW_i/day)	1.2 ± 0.1[d]	2.2 ± 0.0[c]	2.8 ± 0.1[b]	3.6 ± 0.1[a]	3.7 ± 0.0[a]
WG (%)	45.0 ± 1.7[d]	92.2 ± 14.2[c]	130.2 ± 3.7[b]	192.0 ± 4.6[a]	204.1 ± 3.6[a]
Survival (%)	100 ± 0.0	97.5 ± 1.4	92.5 ± 0.5	100 ± 0.0	95.0 ± 0.0
FI (g/fish)	0.5 ± 0.0[e]	1.0 ± 0.0[d]	1.6 ± 0.0[c]	2.0 ± 0.0[b]	2.6 ± 0.0[a]
FER	0.8 ± 0.0	0.8 ± 0.1	0.7 ± 0.0	0.8 ± 0.0	0.8 ± 0.0
HSI (%)	2.2 ± 0.2	1.6 ± 0.3	2.0 ± 0.1	2.3 ± 0.3	1.8 ± 0.2
VSI (%)	7.9 ± 0.8	9.0 ± 0.7	9.9 ± 0.4	8.2 ± 0.4	8.9 ± 1.1
K (%)	2.4 ± 0.1	2.5 ± 0.2	2.4 ± 0.2	2.5 ± 0.2	2.5 ± 0.2
Normal-ration phase					
BW_i (g)	1.2 ± 0.0[d]	1.6 ± 0.1[c]	1.9 ± 0.0[b]	2.4 ± 0.0[a]	2.5 ± 0.0[a]
BW_f (g)	3.9 ± 0.1[c]	4.5 ± 0.0[b]	5.0 ± 0.1[ab]	5.1 ± 0.1[ab]	5.6 ± 0.3[a]
SGR (% BW_i/day)	3.9 ± 0.1[a]	3.5 ± 0.2[b]	3.2 ± 0.0[c]	2.5 ± 0.0[d]	2.6 ± 0.1[d]
WG (%)	226.1 ± 7.9[a]	182.7 ± 9.5[b]	162.7 ± 10.1[c]	111.2 ± 2.8[d]	119.5 ± 8.2[d]
Survival (%)	95.0 ± 0.6	98.7 ± 1.3	92.0 ± 3.5	100 ± 0.0	96.7 ± 3.3
FI (g/fish)	4.3 ± 0.1	4.2 ± 0.2	4.3 ± 0.2	3.7 ± 0.0	4.1 ± 0.1
RFI (%)[j]	11.0 ± 0.2[a]	8.5 ± 0.1[b]	6.7 ± 0.2[c]	4.9 ± 0.1[d]	5.3 ± 0.1[d]
FER	0.6 ± 0.0	0.6 ± 0.0	0.6 ± 0.0	0.6 ± 0.0	0.6 ± 0.1
HSI (%)	1.3 ± 0.2	1.5 ± 0.3	1.6 ± 0.3	1.7 ± 0.2	2.2 ± 0.3
VSI (%)	7.5 ± 0.7	8.8 ± 0.6	10.3 ± 2.2	8.6 ± 0.6	10.5 ± 0.3
K (%)	1.8 ± 0.0	1.8 ± 0.0	1.8 ± 0.1	1.8 ± 0.0	1.8 ± 0.1

Note: A different superscript in the same row denotes statistically significant differences ($p < .05$).

Abbreviations: BW_f, final body weight; BW_i, initial body weight; FER, feed efficiency ratio; FI, feed intake; HSI, hepatosomatic index; K, Fulton's condition factor; RFI, relative feed intake; SGR, specific growth rate; SUR, survival; VSI, viscerosomatic index; WG, weight gain.

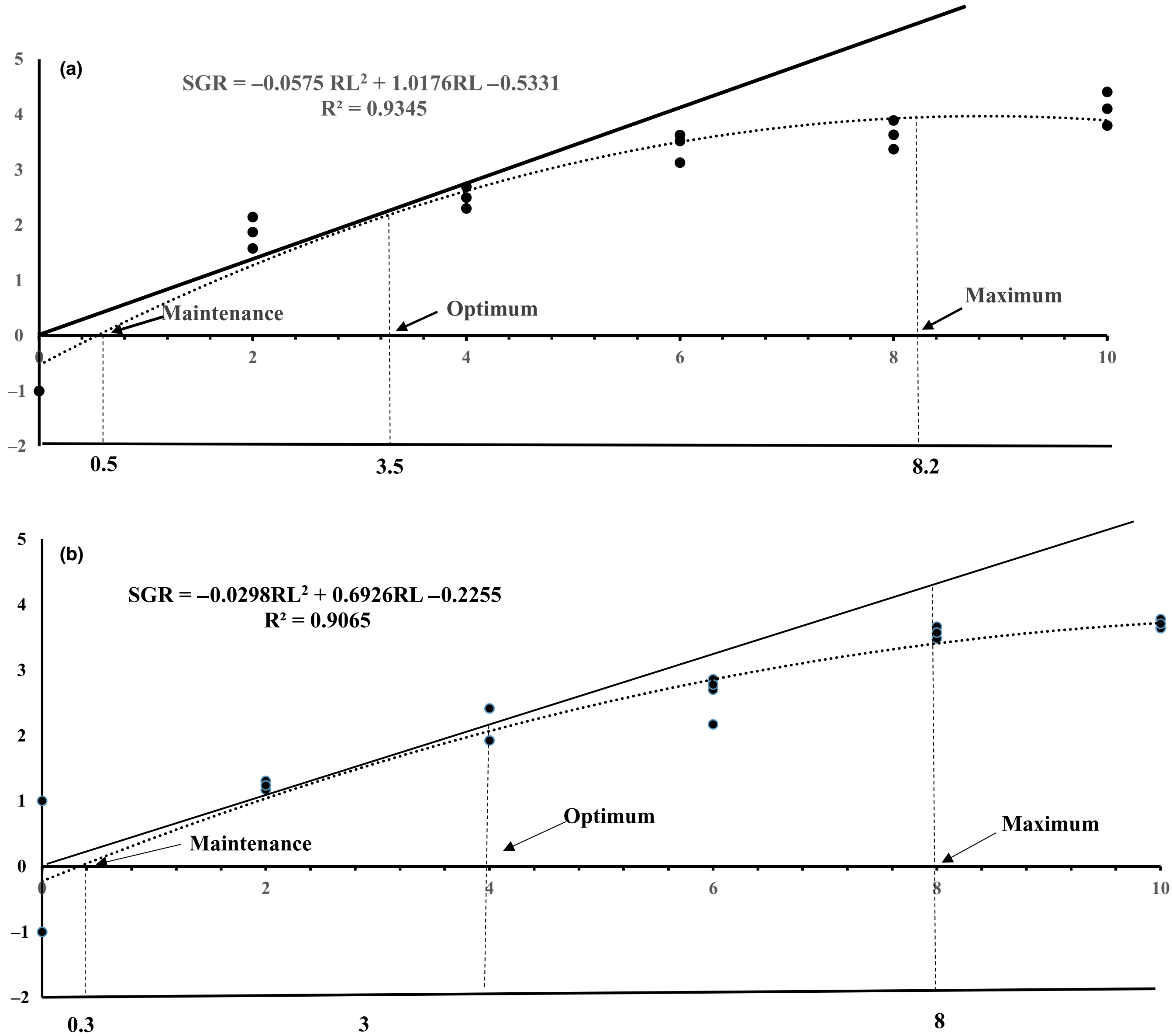

FIGURE 1 Second-degree polynomial relationship between specific growth rate (SGR) and feed ration level in *S. hasta* (a) and *A. latus* (b) during nursery phase. Dashed line, running from the origin, strikes the curve at a tangent indicating the point of feeding rate

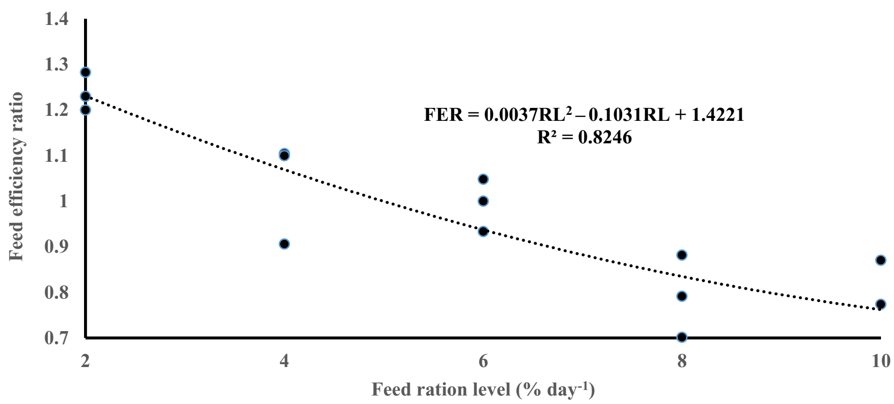

FIGURE 2 Second-degree polynomial relationship between feed efficiency ratio and ration level (RL) for *S. hasta* during nursery phase

There was not a clear relationship between FER and RL in *A. latus*, but regarding *S. hasta* a second-degree polynomial relationship between FER and RL was described as $FER = 0.0037RL^2 - 0.1031RL + 1.4221$ (Figure 2).

3.2 | Normal feeding ration period

At the start of the NRP, the BW_i of fish was significantly different in both species because they were fed on the different RL during the RRP (Tables 1 and 2). At the end of the NRP, BW_f of *S. hasta* fed at 10% RL was higher than the other treatments, but there were not any differences in BW_f of fish fed at 2% RL up to 8% RL in this period ($p > .05$, Table 1). Regarding *A. latus*, fish fed at 2% RL had lower BW_f values than the other groups in the NRP ($p < .05$, Table 2). In addition, *A. latus* fed at 6% and 8% RL showed full CG regarding BW_f compared with those fed at 10% RL, but fish fed at 4% RL had lower BW_f values compared with fish fed at 10% RL at the end of the NRP. In both fish species, fish fed at 2% RL had the highest SGR, WG and RFI values during the NRP and these parameters gradually decreased with increasing RL. In the NRP, FER did not change among different treatments in both species ($p > .05$, Tables 1 and 2). In *S. hasta*, fish fed at 10% RL had lower VSI than the other groups ($p < .05$), but other somatic parameters were not affected in the NRP (Table 1). Regarding *A. latus*, at the end of NRP all somatic indices were similar among different groups (Table 2).

4 | DISCUSSION

Any feeding rate between maintenance and maximum RL results in weight gain, but the maximum weight gain per unit of added ration is achieved before the maximum RL, which considered as optimum RL (Brett & Grove, 1979). In the present study, fish were not subjected to prolonged fasting; thus, their overall performance was not negatively affected during the compensatory growth phase. In the present study, both fish species showed a curvilinear growth- feeding ration relationship; thus, according to Eroldogan et al. (2004) the best feeding regimes would be those feeding fish at a sub-maximum level, because FER values at the maximum RL were declined or remained stagnant in juveniles of *S. hasta* and *A. latus*, respectively (Figure 2). Similar to our results, a sub-maximum ration levels were also recommended for juvenile cobia (*Rachycentron canadum*, Sun et al., 2006) and Basa catfish (*Pangasius bocourti*, Jiwyam, 2010) for promoting a rapid growth rate and high FER values. In addition, the maintenance, optimum and maximum RL in *S. hasta* were higher than those in *A. latus* that may be correlated with the higher growth rate of *S. hasta* compared with *A. latus*.

At the end of NRP, the BW_f of *S. hasta* fed at 10% RL was higher than the other groups suggesting partial CG was occurred in fish fed at 2%, 4%, 6% and 8% RL during the RRP. Furthermore, during NRP, those groups that were under severe restricted ration especially those fed at 2% and 4% RL showed high SGR, WG and hyperphagia indicating these groups could be able to compensate their growth delay if the NRP was extended over 30 days. Similarly, partial CG was achieved in gilthead seabream with 50% restricted feeding ratio for 2 days followed by 2 days feeding to apparent satiation for 48 days (Eroldogan et al., 2008) or 1-day fasting followed by 5 days re-feeding for 60 days (Yilmaz & Eroldogan, 2011).

In *A. latus*, BW_f of fish fed at 6% and 8% RL was not different from fish fed at 10% RL during the NRP indicating a complete CG. In this context, it has been proved that growth efficiency enhances during CG as cumulative maintenance costs are lower for fish that stay small initially and then grow rapidly compared with those grow steadily (Skalski et al., 2005). In addition, it has been confirmed that fish receiving a low RL has higher feed assimilation and/or conversion that associates with lower mass-specific maintenance costs during RRP (Skalski et al., 2005). In this sense, Tamadoni et al. (2020) reported that *A. latus* juveniles showed full CG when fish subjected to 2, 4 and 8 days of feed deprivation followed by 8, 16 or 32 days of re-feeding for 80 days. Furthermore, Oh et al. (2013) found complete compensation in blackhead seabream (*Acanthopagrus schlegelii schlegelii*), with 1 day fasting followed by 5 or 6 days re-feeding for 16 weeks. Xiao et al. (2013) reported fasting for 1 and 2 days per week in juvenile black sea bream (*Acanthopagrus schlegelii schlegelii*) could achieve over and full compensation, respectively. However, in the current study fish fed at 2% and 4% RL showed partial CG as these groups showed hyperphagic response and higher SGR compared with fish fed at 10% RL but they did not reach the same final weight suggesting these groups might be required more time to compensate their growth retardation during restricted-ration phase.

Hyperphagia and increase in feed intake are the main mechanisms involved in CG response, which mainly depend on the severity and duration of feed deprivation (Ali et al., 2003). In the present study, relative feed intake [feed consumption per tank (g)/ initial biomass of fish in tank (g) × 100] pronouncedly increased in both fish species during the NRP relative, especially in those groups that were fed at 2% and 4% RL during the RRP, indicating the GC response in both species was accompanied by an increase in FI. Similarly, the CG response in fish with an increase of feed intake has also been reported in other fish species such as hybrid tilapia (*Oreochromis mossambicus* × *O. niloticus*, Wang et al., 2000), gibel carp (*Carassius auratus gibelio*, Xie et al., 2001), rainbow trout, (*Oncorhynchus mykiss*, Nikki et al., 2004), Asian seabass (*Lates calcarifer*, Tian & Qin, 2004), black rockfish (*Sebastes schlegeli*, Oh et al., 2008) and black seabream (Xiao et al., 2013).

In *S. hasta* during the RRP, values of FER decreased with increasing RL as it has also been reported in Nile tilapia (*Oreochromis niloticus*, Xie et al., 1997), bagrid catfish (*Mystus nemurus*, Ng et al., 2000), juvenile cobia (Sun et al., 2006), grass carp (*Ctenopharyngodon idella*, Zhen-Yu et al., 2006), common carp (*Cyprinus carpio*, Desai & Singh, 2009) and Basa catfish (*Pangasius bocourti*, Jiwyam, 2010). In this sense, it has been suggested that the digestion efficiency decreases in carnivorous fish when the feeding level moves towards the maximum daily consumption and it can restrict the energy supply dedicated for growth (Brett &

Grove, 1979). If nutrient intake exceeds the requirements for maximum intrinsic growth rate of the fish, surplus resources will be lost via increased faecal losses or stored as glycogen or neutral lipid deposits (Jobling, 1994). On the other hand, at low feeding rate, fishes tend to optimize their digestion through high digestive enzyme activities to extract more nutrients that result in better FER as also reported in European seabass (*Dicentrarchus labrax*, Eroldogan et al., 2004) and tambaqui (*Colossoma macropomum*, Silva et al., 2007).

It has been speculated that the switch from RRP to NRP would influence the patterns of energy deposition in fish. It has been speculated that the relative size of the liver is correlated with the nutritional condition of fish and HSI could be a valuable index to reflect CG in fish (Caruso et al., 2010; Metona et al., 2003). In the present study, HSI in *S. hasta* increased gradually with increasing RL, indicating that energy could be stored as glycogen or lipid deposits in the liver. It has been demonstrated feed restriction reduced HSI in different sparids such as red porgy (Mohapatra et al., 2017; Rueda et al., 1998), gilthead sea bream (Grigorakis & Alexis, 2005), black seabream (Xiao et al., 2013) and sobaity seabream (Mozanzadeh, Marammazi, Yaghoubi, Yavari, et al., 2017). At the end of the NRF, HSI in *S. hasta* that were under different restricted RL reached the same value as those fed at 10% RL, which might be due to restoration of liver energy reserves in re-feeding period as also described in gilthead seabream (Eroldogan et al., 2008). Furthermore, after NRP, *S. hasta* juveniles fed at 10% RL had lower VSI than other treatments, suggesting this species tend to compensate growth by depositing extra energy as lipid in visceral cavity. In accordance with our results, Mozanzadeh, Marammazi, Yaghoubi, Yavari, et al. (2017) reported that cyclic fasting (1 day) and re-feeding (2 days) for 60 days induced lipid deposition in the visceral cavity of sobaity seabream. Similarly, in brook trout (Skalski et al., 2005) (*Salvelinus fontinalis*) lipid increased in fish displaying CG (Francois et al., 1999). In contrast, HSI was not affected by RL restriction in *A. latus* as also previously described in common dentex during prolonged starvation (*Dentex dentex*, Perez-Jimenez et al., 2012). In this context, in contrast, Tamadoni et al. (2020) reported that *A. latus* juveniles that were under 4 days of fasting and 16 days re-feeding periods showed higher HSI compared with the control. It seems that difference in starvation and re-feeding strategies, the severity of feed deprivation, experimental condition and feed composition may resulted in such discrepancies among results.

Our findings demonstrated that *S. hasta* showed partial CG, but *A. latus* showed full CG after 30 days. It seems that both species could compensate their growth retardation during RRP if the NRP was extended for 60 days. In addition, both fish species showed curvilinear growth-ration relationship; thus, the best feeding regimes would be to feed them at a sub-maximum level, because FER at the maximum RL were declined or remained stagnant. According to the second-degree polynomial relationship between SGR and RL, the maintenance, optimum and maximum feeding rates for SGR in *S. hasta* were estimated to be 0.5%, 3.5% and 8.2%; meanwhile in *A. latus*, they were 0.3%, 4% and 8%, respectively.

ACKNOWLEDGEMENTS

This study was financed by South Iran Aquaculture Research Centre, Iranian Fisheries Science Institute (IFSRI), Agricultural Research Education and Extension organization (AREEO), Ahwaz, Iran. Authors are thankful to Majid Moghadasi Zadeh and Cheraghali Pajand for their kind help during husbandry.

DATA AVAILABILITY STATEMENT

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

ORCID

Mansour Torfi Mozanzadeh https://orcid.org/0000-0002-2011-799X
Omid Safari https://orcid.org/0000-0001-8378-8291
Enric Gisbert https://orcid.org/0000-0002-7457-8468

REFERENCES

Ahmad, N., Siddiqui, P. J. A., Khan, K. M., Akbar, N. U., Rashid, M., & Masroor, R. (2018). THE Growth performance of juvenile yellowfin seabream (*Acanthopagrus arabicus*) fed at different feeding rates while reared in flouting net cages. *Journal of Animal and Plant Sciences*, *28*, 1014–1020.

Ali, M., Nicieza, A., & Wootton, R. J. (2003). Compensatory growth in fishes: A response to growth depression. *Fish and Fisheries*, *4*, 147–190. https://doi.org/10.1046/j.1467-2979.2003.00120.x

Bavcevic, L., Klanjscek, T., Karamarko, V., Anicic, I., & Legovic, T. (2010). Compensatory growth in gilthead sea bream (*Sparus aurata*) compensates weight, but not length. *Aquaculture*, *301*, 57–63. https://doi.org/10.1016/j.aquaculture.2010.01.009

Brett, J. R., & Grove, T. D. D. (1979). Physiological energetics. In W. S. Hoar, D. J. Randall, & J. R. Brett (Eds.), *Fish Physiology. Bioenergetics and Growth*, *vol. VIII* (pp. 279–352). : Academic Press.

Caruso, G., Maricchiolo, G., Micale, V., Genovese, L., Caruso, R., & Denaro, M. (2010). Physiological responses to starvation in the European eel (*Anguilla anguilla*): Effects on haematological biochemical, non-specific immune parameters and skin structures. *Fish Physiology and Biochemistry*, *36*, 71–83.

Desai, A. S., & Singh, R. K. (2009). The effects of water temperature and ration size on growth and body composition of fry of common carp, *Cyprinus carpio*. *Journal of Thermal Biology*, *34*, 276–280. https://doi.org/10.1016/j.jtherbio.2009.03.005

Dias, J., Yúfera, M., Valente, L. M. P., & Rema, P. (2010). Feed transit and apparent protein, phosphorus and energy digestibility of practical feed ingredients by Senegalese sole (*Solea senegalensis*). *Aquaculture*, *302*, 94–99. https://doi.org/10.1016/j.aquaculture.2010.02.013

Eroldogan, O. T., Kumlu, M., & Aktas, M. (2004). Optimum feeding rates for European sea bass *Dicentrarchus labrax* L. reared in seawater and freshwater. *Aquaculture*, *231*, 501–515.

Eroldogan, O. T., Kumlu, M., Kiris, G. A., & Sezer, B. (2006). Compensatory growth response of *Sparus aurata* following different starvation and refeeding protocols. *Aquaculture Nutrition*, *12*, 203–210. https://doi.org/10.1111/j.1365-2095.2006.00402.x

Eroldogan, O. T., Tasbozan, O., & Tabakoglu, S. (2008). Effects of restricted feeding egimes on growth and feed utilization of juvenile gilthead sea bream, *Sparus aurata*. *Journal of the World Aquaculture Society*, *39*, 267–274.

Gaylord, T. G., & Gatlin, D. M. (2001). Dietary protein and energy modifications to maximize compensatory growth of channel catfish (*Ictalurus punctatus*). *Aquaculture*, *194*, 337–348. https://doi.org/10.1016/S0044-8486(00)00523-8

Grigorakis, K., & Alexis, M. N. (2005). Effects of fasting on meat quality and fat deposition of commercial-size farmed gilthead sea bream (*Sparus aurata*, L) fed different dietary regimes. *Aquaculture Nutrition*, *11*, 341–344.

Hayward, R. S., Noltie, D. B., & Wang, N. (1997). Use of compensatory growth to double hybrid sunfish growth rates. *Transactions of the American Fisheries Society*, *126*, 316–322. https://doi.org/10.1577/1548-8659(1997)126<0316:NUOCGT>2.3.CO;2

Henry, M., Gasco, L., Piccolo, G., & Fountoulaki, E. (2015). Review on the use of insects in the diet of farmed fish: Past and future. *Animal Feed Science and Technology*, *203*, 1–22. https://doi.org/10.1016/j.anifeedsci.2015.03.001

Jiwyam, W. (2010). Growth and compensatory growth of juvenile *Pangasius bocourti* Sauvage, 1880 relative to ration. *Aquaculture*, *306*, 393–397. https://doi.org/10.1016/j.aquaculture.2010.05.005

Jobling, M. (1994). *Fish bioenergetics*. Chapman and Hall.

Jobling, M. (2010). Are compensatory growth and catch-up growth two sides of the same coin? *Aquaculture International*, *18*, 501–510. https://doi.org/10.1007/s10499-009-9260-8

Känkänen, M., & Pirhonen, J. (2009). The effect of intermittent feeding on feed intake and compensatory growth of whitefish *Coregonus lavaretus* L. *Aquaculture*, *288*, 92–97. https://doi.org/10.1016/j.aquaculture.2008.11.029

Krogdahl, A., & Bakke-McKellep, A. M. (2005). Fasting and re-feeding cause rapid changes in intestinal tissue mass and digestive enzyme capacities of Atlantic salmon (*Salmo salar* L.). *Comparative Biochemistry and Physiology*, *141A*, 450–460.

Le Francois, N. R., Blier, P. U., Adambounou, L. T., & Lacroix, M. (1999). Exposures to low-level ionizing radiation: Effects on biochemical and whole-body indices of growth in juvenile brook charr (*Salvelinus fontinalis*). *Journal of Experimental Zoology*, *283*, 315–325.

López-Olmeda, J. F., Noble, C., & Sánchez-Vázquez, F. J. (2012). Does feeding time affect fish welfare? *Fish Physiology and Biochemistry*, *38*, 143–152.

Metona, I., Fernandez, F., & Baanante, I. V. (2003). Short- and long-term effects of re-feeding on key enzyme activities in glycolysis–gluconeogenesis in the liver of gilthead seabream (*Sparus aurata*). *Aquaculture*, *225*, 99–107.

Mihelakakis, A., Tsolkas, C., & Yoshimatsu, T. (2002). Optimization of feeding rate of hatchery-produced juvenile gilthead sea bream *Sparus aurata*. *Journal of World Aquaculture Society*, *33*, 169–175.

Mihelakakis, A., Yoshimatsu, T., & Tsolkas, C. (2001). Effects of feeding rate on growth, feed utilization and body composition of red porgy fingerlings: Preliminary results. *Aquaculture International*, *9*, 237–245.

Mohapatra, S., Chakraborty, T., Reza, A. M. N., Shimizu, S., Matsubara, T., & Ohta, K. (2017). Short-term starvation and realimentation helps stave off Edwardsiella tarda infection in red sea bream (Pagrus major). *Comparative Biochemistry and Physiology*, *206B*, 42–53.

Mozanzadeh, M. T., Marammazi, J. G., Yaghoubi, M., Agh, N., Pagheh, E., & Gisbert, E. (2017). Macronutrient requirements of silvery black porgy (*Sparidentex hasta*): A comparison with other farmed sparid species. *Fishes*, *2*, 5.

Mozanzadeh, M., Marammazi, J., Yaghoubi, M., Yavari, V., Agh, N., & Gisbert, E. (2017). Somatic and physiological responses to cyclic fasting and re-feeding periods in sobaity sea bream (*Sparidentex hasta*, Valenciennes 1830). *Aquaculture Nutrition*, *23*, 181–191.

Mozanzadeh, M. T., Yavari, V., Marammazi, J. G., Agh, N., & Gisbert, E. (2017). Optimal dietary carbohydrate-to-lipid ratios for silvery-black porgy (*Sparidentex hasta*) juveniles. *Aquaculture Nutrition*, *23*, 470–483.

Ng, W. K., Lu, K. S., Hashim, R., & Ali, A. (2000). Effects of feeding rate on growth, feed utilization and body composition of tropical bagrid catfish. *Aquaculture International*, *8*, 19–29.

Nikki, J., Pirhonen, J., Jobling, M., & Karjalainen, J. (2004). Compensatory growth in juvenile rainbow trout, *Oncorhynchus mykiss* (Walbaum), held individually. *Aquaculture*, *235*, 285–296. https://doi.org/10.1016/j.aquaculture.2003.10.017

Oh, S. Y., Kim, M. S., Kwon, J. Y., & Venmathi Maran, B. A. (2013). Effects of feed restriction to enhance the profitable farming of blackhead seabream (*Acanthopagrus schlegelii schlegelii*) sea cages. *Ocean Science Journal*, *48*, 263–268.

Oh, S. Y., Noh, C. H., Kang, R. S., Kim, C. K., Cho, S. H., & Jo, J. Y. (2008). Compensatory growth and body composition of juvenile black rockfish *Sebastes schlegeli* following feed deprivation. *Fisheries Science*, *74*, 846–852.

Otavio, P., Ozorio, A., Andrade, C., Timoteo, V. M. F. A., Conceicao, L. E. C., & Valente, L. M. P. (2009). Effects of feeding levels on growth response, body composition, and energy expenditure in blackspot Seabream, *Pagellus bogaraveo*, Juveniles. *Journal of World Aquaculture Society*, *40*, 95–103.

Peres, H., Santos, S., & Oliva-Teles, A. (2011). Lack of compensatory growth response in gilthead seabream (*Sparus aurata*) juveniles following starvation and subsequent re-feeding. *Aquaculture*, *318*, 384–388. https://doi.org/10.1016/j.aquaculture.2011.06.010

Perez-Jimenez, A., Cardenete, G., Hidalgo, M. C., Garcıa-Alcazar, A., Abellan, E., & Morales, A. E. (2012). Metabolic adjustments of *Dentex dentex* to prolonged starvation and refeeding. *Fish Physiology and Biochemistry*, *38*, 1145–1157. https://doi.org/10.1007/s10695-011-9600-2

Rondan, M., Hernandez, M. D., Egea, M. A., Garcia, B., Rueda, F. M., & Martinez, F. J. (2004). Effect of feeding rate on fatty acid composition of sharpsnout seabream (*Diplodus puntazzo*). *Aquaculture Nutrition*, *10*, 301–307. https://doi.org/10.1111/j.1365-2095.2004.00304.x

Rueda, F. M., Martinez, F. J., Zamora, S., Kentouri, M., & Divanach, P. (1998). Effect of fasting and refeeding on growth and body composition of red porgy (*Pagrus pagrus* L.). *Aquaculture Research*, *29*, 447–452.

Schnaittacher, G., King, W., & Berlinsky, D. L. (2005). The effects of feeding frequency on growth of juvenile Atlantic halibut, *Hippoglossus hippoglossus* L. *Aquaculture International*, *36*, 370–377. https://doi.org/10.1111/j.1365-2109.2005.01218.x

Silva, C. R., Gomes, L. C., & Brandao, F. R. (2007). Effect of feeding rate and frequency on tambaqui (*Colossoma macropomum*) growth, production and feeding costs during the first growth phase in cages. *Aquaculture*, *264*, 135–139. https://doi.org/10.1016/j.aquaculture.2006.12.007

Skalski, G. I., Picha, M. E., Gilliam, J. F., & Borski, R. J. (2005). Variable intake, compensatory growth, and increased growth efficiency in fish: Models and mechanisms. *Ecology*, *86*, 1452–1462. https://doi.org/10.1890/04-0896

Sun, L., Chen, H., Huang, L., Wang, Z., & Yan, Y. (2006). Growth and energy budget of juvenile cobia (*Rachycentron canadum*) relative to ration. *Aquaculture*, *257*, 214–220. https://doi.org/10.1016/j.aquaculture.2006.02.074

Tamadoni, R., Nafisi Bahabadi, M., Morshedi, V., Bagheri, D., & Mozanzadeh, M. T. (2020). Effect of short term fasting and refeeding on growth, digestive enzyme activities and antioxidant defense in yellowfin seabream, *Acanthopagrus latus* (Houttuyn, 1782). *Aquaculture Research*, *51*, 1437–1445. https://doi.org/10.1111/are.14489

Tian, X. L., & Qin, J. G. (2004). Effects of previous ration restriction on compensatory growth in barramundi (*Lates calcarifer*). *Aquaculture*, *235*, 273–283. https://doi.org/10.1016/j.aquaculture.2003.09.055

Wang, Y., Cui, Y., Yang, Y., & Cai, F. (2000). Compensatory growth in hybrid tilapia, *Oreochromis mossambicus* × *O. niloticus*, reared in seawater. *Aquaculture*, *189*, 101–108. https://doi.org/10.1016/S0044-8486(00)00353-7

Xiao, J.-X., Zhou, F., Yin, N., Zhou, J., Gao, S., Li, H., Shao, Q.-J., & Xu, J. (2013). Compensatory growth of juvenile black sea bream, *Acanthopagrus schlegelii*, with cyclical feed deprivation and refeeding. *Aquaculture Research*, *44*, 1045–1057.

Xie, S., Cui, J., Yang, Y., & Liu, J. (1997). Energy budget of Nile tilapia (*Oreochromis niloticus*) in relation to ration size. *Aquaculture*, *154*, 57–68. https://doi.org/10.1016/S0044-8486(97)00039-2

Xie, S., Zhu, X., Cui, Y., Wootton, R. J., Lei, W., & Yang, Y. (2001). Compensatory growth in the gibel carp following feed deprivation: Temporal patterns in growth, nutrient deposition, feed intake and body composition. *Journal of Fish Biology*, *58*, 999–1009. https://doi.org/10.1111/j.1095-8649.2001.tb00550.x

Yilmaz, H. A., & Eroldogan, O. T. (2011). Combined effects of cycled starvation and feeding frequency on growth and oxygen consumption of gilthead sea bream, *Sparus aurata*. *Journal of the World Aquaculture Society*, *42*, 522–529. https://doi.org/10.1111/j.1749-7345.2011.00494.x

Zhen-Yu, D., Yong-Jian, L., Li-Xia, T., Jian-Guo, H., Jun-Ming, C., & Gui-Ying, L. (2006). The influence of feeding rate on growth, feed efficiency and body composition of juvenile grass carp (Ctenopharyngodon idella). *Aquaculture International*, *14*, 247–257. https://doi.org/10.1007/s10499-005-9029-7

How to cite this article: Torfi Mozanzadeh M, Zabayeh Najafabadi M, Torfi M, et al. Compensatory growth of Sobaity (*Sparidentex hasta*) and yellowfin seabreams (*Acanthopagrus latus*) relative to feeding rate during nursery phase. *Aquacult Nutr*. 2020;00:1–9. https://doi.org/10.1111/anu.13199