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

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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 (BWi) 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 (BWf) 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 BWf 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.

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.

Materials and Methods

Experimental design

The present study was conducted in the Marine Fish Research Station of the South Iranian Aquaculture Research Center (SIARC), Sarbandar, Iran. 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^{-1}). 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^{-1}, 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 $tank^{-1}$) and 900 *A. latus* juveniles (0.8 ± 0.01 g) were distributed into 15 tanks (60 fish $tank^{-1}$). Both species were propagated at SIARC facilities and kept in 5,000L polyethylene tanks; thus, juvenile 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^{-1} crude protein, 180 g kg^{-1} crude fat, 107 g kg^{-1} ash and 40 g kg^{-1} fiber) twice daily (0800 and 1300 h) according to the RL for 30 days. At the end of the RRP, fish from each tank were individually weighted and their and length were measured at accuracy of 1 mm.

At the end of the RRP, all fish from each group (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 second part of the trial, the one corresponding to the NRP. During this experimental period, 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. 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, the biomass of each tank was bulk weighted and then, the number of fish was counted for determining the mean BW of fish in each tank. 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., 2017c). Standard formulae were used to determine growth performance, feed utilization and somatic indices: SGR: specific growth rate (%) = ((ln BW_f − ln BW_i) / t) × 100, where t is experimental period = 30 days; WG: weight gain (%) = ((BW_f - BW_i)/BW_i) × 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) / BWf (g)) × 100; VSI: viscerosomatic index (%) = (visceral weight (g) / BWf (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.

Statistics

Data were analyzed by means of SPSS ver. 20 (Chicago, Illinois, USA). 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 ($P < 0.05$), 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 product moment correlation test was used to determine any correlation among parameters, and in all cases, $P < 0.05$ was considered as significant.

Results

Restricted feeding ration

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 $SGR = -0.0186RL2 + 0.504RL + 0.8987$ (R2 = .8959); meanwhile in A. latus (Figure 1b), it was described as $SGR = -0.173 RL2 + 0.5257RL + 0.2508$ (R2 = .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.

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 $FER = 0.0037RL2 - 0.1031RL + 1.4221$ (Figure 2).

Normal feeding ration period

At the start of the NRP, the BWi 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, BWf of S. hasta fed at 10% RL was higher than the other treatments, but there were not any differences in

BWf 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 BWf 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 BWf compared with those fed at 10% RL, but fish fed at 4% RL had lower BWf 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).

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 BWf 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, BWf 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

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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, HIS 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.

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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). A different superscript in the same row denotes statistically significant differences ($P < 0.05$).

Parameters	Ration level (% body weight day^{-1})				
	2	4	6	8	10
Restricted-ration phase					
BW$_f$ (g)[a]	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})[b]	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 (%)[c]	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 (%)[d]	95.0 ± 0.6	93.8 ± 0.6	97.3 ± 2.7	94.0 ± 2.6	97.0 ± 0.6
FI (g fish^{-1})[e]	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[f]	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 (%)[g]	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 (%)[h]	9.7 ± 2.3	9.6 ± 0.4	9.4 ± 0.8	10.6 ± 1.6	9.4 ± 0.3
K (%)[i]	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^{-1})	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^{-1})	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

[a] BW$_f$: final body weight

[b] SGR: specific growth rate (%) = ((ln BW$_f$ – ln BW$_i$) / t) × 100, where t is experimental period = 30 days.

[c] WG: weight gain (%) = ((BW$_f$ - BW$_i$)/BW$_i$) × 100

[d] SUR: survival (%) = number of fish in each group remaining on day 30/initial number of fish) × 100

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

[f] FER: feed efficiency ratio = (weight gain (g) / feed intake (g))

[g] HSI: hepatosomatic index (%) = (liver weight (g) / BW$_f$ (g)) × 100

[h] VSI: viscerosomatic index (%) = (visceral weight (g) / BW$_f$ (g)) × 100

[i] K: Fulton's condition factor = (BW$_f$ (g)/ standard length (cm)^3) × 100

[j] RFI: relative feed intake = (feed consumption per tank (g)/ initial biomass of fish in tank (g)) × 100

Table 2. 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).A different superscript in the same row denotes statistically significant differences (P < 0.05).

Parameters	Ration level (% body weight day^{-1})				
	2	4	6	8	10
Restricted-ration phase					
BW$_f$ (g)[a]	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})[b]	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 (%)[c]	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 (%)[d]	100 ± 0.0	97.5 ± 1.4	92.5 ± 0.5	100 ± 0.0	95.0 ± 0.0
FI (g fish^{-1})[e]	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[f]	0.8 ± 0.0	0.8 ± 0.1	0.7 ± 0.0	0.8 ± 0.0	0.8 ± 0.0
HSI (%)[g]	2.2 ± 0.2	1.6 ± 0.3	2.0 ± 0.1	2.3 ± 0.3	1.8 ± 0.2
VSI (%)[h]	7.9 ± 0.8	9.0 ± 0.7	9.9 ± 0.4	8.2 ± 0.4	8.9 ± 1.1
K (%)[i]	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^{-1})	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^{-1})	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

[a] BW$_f$: final body weight

[b] SGR: specific growth rate (%) = ((ln BW$_f$ − ln BW$_i$) / t) × 100, where t is experimental period = 30 days.

[c] WG: weight gain (%) = ((BW$_f$ - BW$_i$)/BW$_i$) × 100

[d] SUR: survival (%) = number of fish in each group remaining on day 30/initial number of fish) × 100

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

[f] FER: feed efficiency ratio = (weight gain (g) / feed intake (g))

[g] HSI: hepatosomatic index (%) = (liver weight (g) / BW$_f$ (g)) × 100

[h] VSI: viscerosomatic index (%) = (visceral weight (g) / BW$_f$ (g)) × 100

[i] K: Fulton's condition factor = (BW$_f$ (g)/ standard length (cm)^3) × 100

[j] RFI: relative feed intake = (feed consumption per tank (g)/ initial biomass of fish in tank (g)) × 100
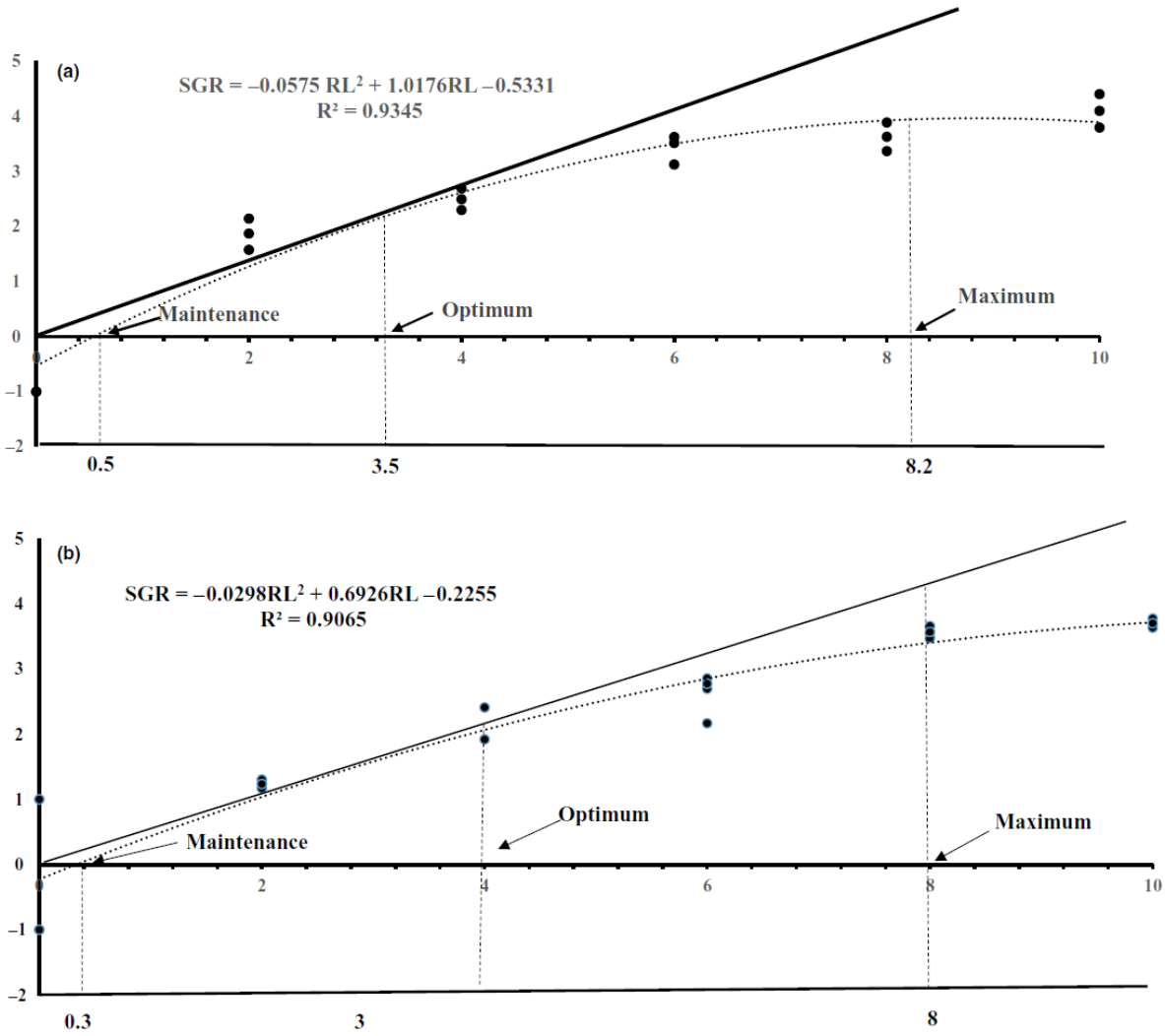
Fig 1. Second-degree polynomial relationship between specific growth rate (SGR) and feed ration level in *S. hasta* (a) and *A. latus* (b) during nursery phase.

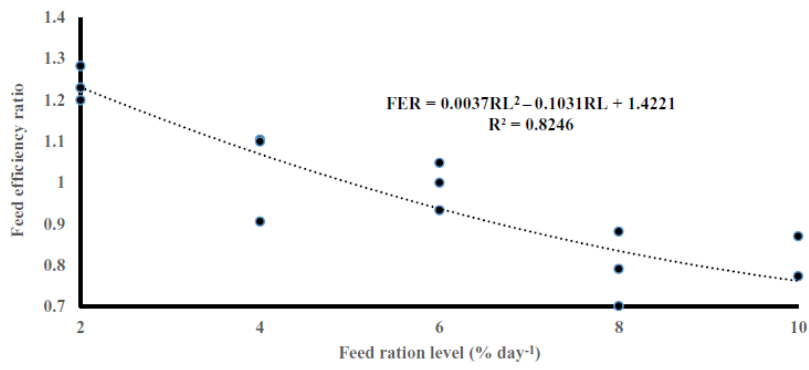**Fig 2.** Second-degree polynomial relationship between feed efficiency ratio and ration level (RL) for *S. hasta* during nursery phase