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SHORT COMMUNICATION

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Lack of compensatory growth response in longfin yellowtail (*Seriola rivoliana*, Valenciennes, 1833) juveniles related to cyclical fasting and refeeding under rearing conditions

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Compensatory or 'catch-up' growth is a physiological process of unusually fast growth of individuals encountering abundant feed following a period of feed restriction (Jiwyam, 2010). The magnitude of compensatory responses varies largely from over, full, partial or no compensation, according to the biomass attained by the fasted fish comparatively to continuously fed fish (Ali, Nicieza, & Wootton, 2003). This phenomenon could reduce production costs and increase profits for fish farmers without compromising fish welfare (Paz, Pastrana, & Brandão, 2018). Growth compensation is species-specific, being more effective in cyclical feeding when duration and severity of fasting are short (Peres, Santos, & Oliva-Teles, 2011). Mechanisms for compensatory responses in fish are not fully understood, but most probably involves an increased feed intake (hyperphagia, Türkmen et al., 2012) and improved efficiency of feed utilization (Fang, Tian, & Dong, 2017).

Longfin yellowtail (*Seriola rivoliana* Valenciennes, 1833, Pisces: Carangidae) is widely distributed throughout the warm-temperature waters of the world. This species is an excellent aquaculture candidate due to its adaptability to captivity, fast growth rate, flesh quality and high market value (Roo et al., 2014). Based on the results of a previous study (Argüello-Guevara et al., 2018), the current experiment was designed to explore the effect of short- and long-term fasting and subsequent feeding on the compensatory response of longfin yellowtail juveniles.

Juvenile yellowtail individuals (240-day post hatch) were obtained from the Marine Fish Laboratory of CENAIM-ESPOL, Santa Elena, Ecuador, and transported to an indoor system of the Aquaculture Laboratory at Instituto Tecnológico Superior Luis Arboleda Martínez, Manabí, Ecuador. The experiment lasted for 85 days. Fish (n = 120; body weight 261.7 ± 5.6 g) were randomly distributed into six 1,000 L-rectangular and six 1,000 L-circular tanks (10 fish in each tank; approx. 2.6 kg/m^3). Each tank was supplied with running seawater (140% daily water renewal). Fish were hand-fed with a commercial feed as pellets, containing 40% crude protein, 12% crude fat, 2.5% fibre and 12% ash (Skretting-GISIS®, Gye, Ecuador; size 5 and 7 mm) to apparent satiation twice a day (09:00 and 14:00 hr). Captivity and maintenance conditions of fish were approved by Ministerio del Ambiente, Santa Elena, Ecuador (Resolution No. 006-2018-IC-FAU-DPSE-MA).

Dissolved oxygen concentration (08:00 = 6.01 ± 0.31 mg O_2 L^{-1}; 16h00 = 5.87 ± 0.32 mg O_2 L^{-1}) and temperature (08h00 = 25.9 ± 0.1°C; 16h00 = 26.7 ± 0.3°C) were measured using a multiparameter HI 98193 (HANNA® Instruments Inc.). A split plot design was used. Tank shape, as the whole plot, and three feeding regimes were allocated to the split plots. Feeding regimes were conducted in three different treatments and performed in the following manner:

Cont-Feed: continuously fed twice a day (09:00 and 14:00 hr).
Short-F: cyclical short fasting, 3-day fasting and refed twice for 7 days.
Long-F: cyclical long fasting, 7-day fasting and refed twice for 7 days.

Feed supply, feed consumption and uneaten feed estimation were determined according to Argüello-Guevara et al. (2018). Faeces were removed from the tanks using a siphon after the last feeding.

The fish were anaesthetized and sampled as suggested by Argüello-Guevara et al. (2018).

The following indices were calculated:

$$(1)\ \text{Specific Growth Rate (SGR, \% day}^{-1}) = \frac{\ln W_{final} - \ln W_{initial}}{\Delta t} \times 100$$

$$(2)\ \text{Survival } (S, \%) = \frac{\text{Final number of fish}}{\text{Initial number of fish}} \times 100$$

$$(3)\ \text{Condition Factor } (K_F, \text{ g cm}^{-3}) = \frac{W}{SL^3} \times 100$$

where W is the wet weight (g) and SL the standard length (cm) of the juveniles, and Δt is the period of time in days.

$$(4)\ \text{Feed Conversion Rate (FCR)} = \frac{\text{Feed intake (g day}^{-1})}{\text{total weight gain}}$$

$$(5)\ \text{Feed Efficiency (FE)} = \frac{\text{Total weight gain}}{\text{feed intake}}$$

$$(6)\ \text{Hepatosomatic Index (HSI, \%)} = \frac{\text{Liver weight}}{\text{total body weight}} \times 100$$

$$(7)\ \text{Viscerosomatic Index (VSI, \%)} = \frac{\text{Visceral weight}}{\text{total body weight}} \times 100$$

$$(8)\ \text{Economic Conversion Index (ECI, US\\$ kg}^{-1}) = \text{Feed cost(US\\$)} \times \text{FCR}$$

At the end of the feeding trial, two fish from each tank were randomly sampled and euthanized by an overdose of anaesthetic (100 ml/L; Eugenol®, Keystone Ind.) to determine body composition, HSI, VSI and intestinal micromorphology. The muscle was removed, freeze-dried and stored at −20°C until analysis. Protein (Kjeldahl method after acid digestion) and lipid (ether extraction method) content were determined on muscle samples according to AOAC (2016). Samples of the middle intestine were sectioned and preserved in Davidson solution for 24 hr and then transferred to 70% ethanol solution. Once fixed, samples were dehydrated through a graded series of ethanol solution, followed by xylene prior to embedding in paraffin. Microtome sections (4 μm thick) were stained with haematoxylin and eosin (H&E). The slides were examined under a light microscope (OLYMPUS CX 31, Olympus America Inc.) equipped with a camera (LANOPTIK MDX503, Lanoptik Technologies). Fold height, enterocytes height and microvilli height were measured and analysed in different objective magnification lens according to Peng et al. (2013).

The results were expressed as mean ± standard deviation (*SD*). Data were subjected to two-way analysis of variance (ANOVA). Post hoc comparisons between means were tested using Tukey's honestly significant difference test, and differences were considered significant at the p = .05 level. All statistical analyses were performed using XLSTAT® 2016.5 (Addinsoft, Paris, France).

Cyclical fasting and refeeding have been used as an effective management strategy to induce compensatory growth in several fish species (Ali et al., 2003). However, compensatory growth was not evident in this study. Throughout the whole period, the growth of fasted fish was higher than continuously fed fish (Figure 1a), while differences between rectangular and circular tanks were not observed (Figure 1b). Comparable results were reported for *Sparus aurata* juveniles subjected to 1 or 2 weeks feed deprivation and 8 weeks of refeeding (Peres et al., 2011) and in *Orechromis niloticus* after a fasting period of 2–7 days (El-Sayed, Martínez-Llorens, Moñino, Cerdá, & Tomás-Vidal, 2016). Liu et al. (2018) proposed

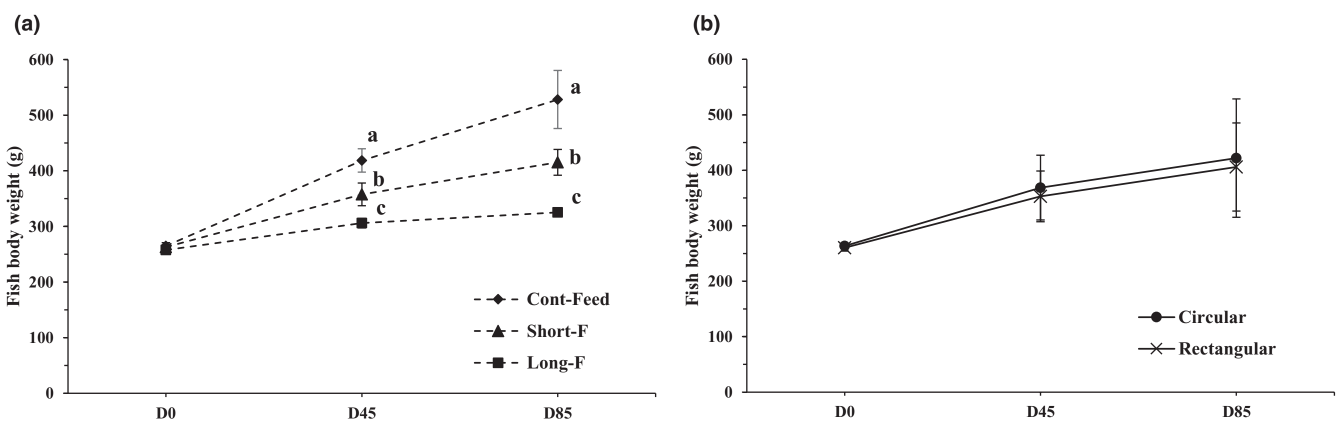

FIGURE 1 Mean growth of juvenile longfin yellowtail fed with different feeding regimes (a) and cultured in two shapes of tanks (b) during 90 days. Values (mean ± *SD*) in the same sampling day with different letters are significantly different (Tukey's test, p < .05)

that after refeeding, fish undergo a compulsory state of craving and increased appetite with subsequent increase in their ingestion rate levels (hyperphagia), as we noted in Short-F, where mean daily feed was significantly higher ($p < .05$) than Cont-Feed (Table 1). Since daily feed intake was similar between Short-F and Long-F treatments, better final weight in Short-F may have resulted from an improved feed efficiency. However, even though Long-F fish became hyperphagic, no compensatory growth was observed. At the end of feeding trial, total feed intake (g/fish) was significantly higher ($p < .05$) in Cont-Feed than Short-F and Long-F. In fasted groups, SGR and FE values were significantly lower than those of continuously fed fish ($p < .05$). Conversely, FCR was significantly higher ($p < .05$) in Long-F treatment. According to Jobling, Meløy, dos Santos, and Christiansen (1994), larger animals may require longer fasting period before any nutritional stress becomes evident to induce a compensatory response. However, in the present study, fasted fish were not able to show partial CG as in our previous study with smaller fish (102.7 ± 5.1 g; Argüello-Guevara et al., 2018). All of the above-mentioned observations may indicate that CG response in longfin yellowtail was mainly influenced by the length of the cyclical fasting period. On the other hand, survival was unaffected by feeding regimes, which is similar to that observed in other studies (Jiwyam, 2010; Türkmen et al., 2012).

Fish have showed species-specific differences in the utilization of energy reserves during periods of feed deprivation. Some fish use muscle protein or lipids as energy source during fasting. In the present study, muscle protein content was not affected in the cyclical fasted treatments. However, lipid content significantly ($p < .05$) decreased in Long-F treatment. Although differences in lipid content between Cont-Feed and Short-F were not detected, lipid content tended to

TABLE 1 Growth performance and feed utilization values of *Seriola rivoliana* juveniles fed at different feeding regimes

	Treatments					Effect of		
Variable	Cont-Feed	Short-F	Long-F	Rectangular	Circular	Feeding regime	Tank shape	Interaction
Initial body weight (g)	264.7 ± 2.5	262.7 ± 8.1	257.8 ± 3.0	260.1 ± 6.0	263.3 ± 5.2	n.s.	n.s.	n.s.
Final body weight (g)	528.1 ± 52.2[a]	415.2 ± 23.1[b]	325.2 ± 6.2[c]	406.0 ± 76.6	421.9 ± 106.6	$p = .008$	n.s.	n.s.
Final standard length (cm)	29.8 ± 0.7[a]	27.7 ± 0.5[b]	26.1 ± 0.1[c]	27.6 ± 1.5	27.7 ± 1.9	$p = .011$	n.s.	n.s.
SGR	0.81 ± 0.11[a]	0.54 ± 0.06[b]	0.27 ± 0.02[c]	0.51 ± 0.22	0.53 ± 0.27	$p = .003$	n.s.	n.s.
FCR	2.64 ± 0.31[b]	3.43 ± 0.40[b]	5.15 ± 0.38[a]	3.95 ± 1.20	3.71 ± 1.19	$p = .004$	n.s.	n.s.
FE	0.38 ± 0.05[a]	0.29 ± 0.03[b]	0.19 ± 0.01[c]	0.27 ± 0.08	0.29 ± 0.10	$p = .013$	n.s.	n.s.
Daily feed intake (g fish^{-1} day^{-1})	8.7 ± 0.6[b]	9.6 ± 0.3[a]	9.1 ± 0.3[ab]	8.9 ± 0.5[b]	9.5 ± 0.3[a]	$p = .036$	$p = .004$	n.s.
Total feed intake (g/fish)	687.7 ± 46.3[a]	517.0 ± 14.3[b]	345.7 ± 10.4[c]	503.2 ± 144.0	499.0 ± 160.9	$p = .001$	n.s.	n.s.
Survival (%)	90.0 ± 10.0	85.0 ± 12.9	95.0 ± 10.0	93.3 ± 8.2	86.0 ± 13.4	n.s.	n.s.	n.s.
ECI (US$ kg^{-1})	2.94 ± 0.34[c]	3.81 ± 0.45[b]	5.72 ± 0.42[a]	4.39 ± 1.33[a]	4.12 ± 1.32[b]	$p = .013$	$p = .022$	n.s.

Note: p-values show the two-way ANOVA effect of feeding regime and shape of tank. Values with a $p > .05$ are marked as n.s.
Values (mean ± *SD*) in the same row (up subdivision line) with different superscript letters are significantly different (Tukey's test, $p < .05$).

TABLE 2 Body composition and welfare indices of *Seriola rivoliana* juveniles fed with different feeding regimes

	Treatments					Effect of		
Variable	Cont-Feed	Short-F	Long-F	Rectangular	Circular	Feeding regime	Tank shape	Interaction
Protein (%)	22.80 ± 0.12	22.60 ± 0.25	21.29 ± 1.29	22.31 ± 1.03	22.02 ± 1.09	n.s.	n.s.	n.s.
Lipid (%)	4.10 ± 1.05[a]	3.24 ± 0.59[ab]	1.69 ± 1.03[b]	3.08 ± 1.25	2.71 ± 1.48	$p = .029$	n.s.	n.s.
VSI (%)	6.13 ± 0.38	6.39 ± 0.94	5.06 ± 1.03	5.92 ± 1.18	5.73 ± 0.86	n.s.	n.s.	n.s.
HSI (%)	0.97 ± 0.22	1.07 ± 0.39	0.55 ± 0.18	0.87 ± 0.37	0.83 ± 0.37	n.s.	n.s.	n.s.
K_F (g/cm^3)	2.00 ± 0.05[a]	1.96 ± 0.06[a]	1.84 ± 0.02[b]	1.92 ± 0.08	1.95 ± 0.09	$p = .011$	n.s.	n.s.

Note: p-values show the two-way ANOVA effect of feeding regime and shape of tank. Values with a $p > .05$ are marked as n.s.
Values (mean ± *SD*) in the same row (up subdivision line) with different superscript letters are significantly different (Tukey's test, $p < .05$).

TABLE 3 Micromorphology of the midgut of juvenile longfin yellowtail fed with different feeding regimes

Variable	Treatments					Effect of		
	Cont-Feed	Short-F	Long-F	Rectangular	Circular	Feeding regime	Tank shape	Interaction
Enterocyte height (μm)	17.99 ± 2.66	15.81 ± 1.15	16.96 ± 0.98	16.10 ± 0.93	17.69 ± 2.12	n.s.	n.s.	n.s.
Fold height (μm)	964.10 ± 25.39	886.26 ± 04.09	860.34 ± 63.54	906.29 ± 53.11	888.20 ± 105.23	n.s.	n.s.	n.s.
Microvillus height (μm)	4.31 ± 0.25	4.21 ± 0.38	4.40 ± 0.64	4.50 ± 0.44	4.08 ± 0.33	n.s.	n.s.	n.s.

Note: p-values show the two-way ANOVA effect of feeding regime and shape of tank. Values with a $p > .05$ are marked as n.s.
Values (mean ± *SD*) in the same row (up subdivision line) with different superscript letters are significantly different (Tukey's test, $p < .05$).

decrease in feed deprivation treatments (Table 2). In addition, cyclical fasting and refeeding did not affect VSI and HSI (Table 2). According to Morshedi et al. (2017), HSI can be used as indicator of nutritional status of fish. In this case, unaffected liver weight by fasting periods could be the results of a better catabolic rate from muscle lipids than liver or visceral tissues. After repeated cycles of fasting and refeeding, longfin yellowtail seemed to use muscle lipids as an energy source. Similar finding was reported for *Pampus argenteus* after 2 and 6 days of fasting (Liao et al., 2017) and *Labeo rohita* experiencing cycles of feed deprivation and refeeding (Yengkokpam et al., 2013). On the contrary, *Acipenser baerii* preferentially mobilized muscle protein reserves as energy source (Morshedi et al., 2017). The condition factor (K_F) is a valuable index to describe the nutritional condition of farmed fish (Mozanzadeh et al., 2017). In this study, the condition factor was significantly lower ($p < .05$) in Long-F. Similar findings were reported in *Oreochromis niloticus* (Gao, Wang, Hur, & Lee, 2015) and *Mugil cephalus* (Akbary & Jahanbakhshi, 2016). Microscopical observations of midgut showed that fold height, enterocyte height and microvillus height were not affected by any treatments proven in this study (Table 3). Unexpectedly, fasted fish showed the same micromorphology of the midgut as Cont-Feed, which has no clear explanation in light of our findings. However, Fang et al. (2017) demonstrated that the morphology of intestine in *Cynoglossus semilaevis* was disturbed when the refeeding time extend was not enough. Our results suggest that refeeding with 7 days, the morphology of midgut could be recovered. More physiological studies are needed in order to elucidate these implications. The higher ECI of Long-F and Short-F (Table 1) shows that fasted group did not utilize the feed efficiently. Similar results were reported in *Dicentrarchus labrax* (Adaki & Taşbozan, 2015).

In conclusion, our cyclical fasting and refeeding regimes were shorter compared with other studies. Despite this, Longfin yellowtail juveniles do not adapt well to sub-optimum feeding levels due to fasting beyond 2 days of rearing. Therefore, a maximum fasting period of 2 days could induce a compensatory response on growth without affecting fish welfare in this species.

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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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