Received: 19 May 2018 | Revised: 3 August 2018 | Accepted: 11 August 2018

DOI: 10.1111/are.13825

ORIGINAL ARTICLE

WILEY Aquaculture Research

# Effects of intermittent feeding on water quality, skin parasites, feed consumption, and growth performance of juvenile longfin yellowtail *Seriola rivoliana* (Valenciennes, 1833)

Wilfrido Argüello-Guevara[1] | Wilson Apolinario[2] | Milton Bohórquez-Cruz[1] | Samira Reinoso[1] | Sandra Rodríguez[1] | Stanislaus Sonnenholzner[1]

[1]Escuela Superior Politécnica del Litoral, ESPOL, CENAIM, ESPOL Polytechnic University, Guayaquil, Ecuador

[2]Facultad de Ciencias del Mar, Universidad Estatal Península de Santa Elena, La Libertad, Ecuador

**Correspondence**
Wilfrido Argüello-Guevara, Centro Nacional de Acuicultura e Investigaciones Marinas CENAIM-ESPOL, Guayaquil, Ecuador.
Email: warguell@espol.edu.ec

**Funding information**
Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT) of Ecuador, Grant/Award Number: PIC-14-CENAIM-002

## Abstract

This study investigated the effect of intermittent feeding on the water quality, occurrence of skin parasites, feed consumption, and growth performance of juveniles (102.7 ± 5.1 g) longfin yellowtail, *Seriola rivoliana*. Fish were exposed for 89 days to six different feeding regimes: continuous daily feeding fed one or twice a day (treatment 24R1 and 24R2); 2-day fasting and refed once or twice a day for 1 day (treatment 48R1 and 48R2); and 3-day fasting and refed once or twice a day for 1 day (treatment 96R1 and 96R2). Water quality was not affected by feeding strategies. Likewise, condition factor was not affected by fasting up 48 hr. On the other hand, lowest survival in 96R1 was not related with abundance of skin parasites (*Neobenedenia girellae*). Specific growth rate, feed intake, feed efficiency, and morphological indices were not statistically different ($p > 0.05$) between 2 days fasted fish and continuously fed fish. Partial compensatory growth in 48R2 could be attributed to a hyperphagic consumption (8.2 ± 1.1 g day$^{-1}$ fish$^{-1}$) and feed conversion efficiency (0.61 ± 0.03). A feeding strategy based on cyclical 48 hr of starvation followed by 1 day of refeeding twice may be used for on-growing juvenile longfin yellowtail without reduction in growth or welfare of fish.

KEYWORDS
feeding regimes, hyperphagia, *Neobenedenia girellae*, starvation

## 1 | INTRODUCTION

The successful growth of fish in aquaculture depends on a number of factors including abiotic conditions (water temperature, salinity; Huang, Ma, Wang, & Lei, 2014), feed management (Hanssen et al., 2012), diet composition (Kissinger, García-Ortega, & Trushenski, 2016), rearing conditions (Salas-Leiton, Anguis, Manchado, & Cañavate, 2008) among others. Determination of growth relationship for different production and management systems is essential for the economic evaluation of feeding protocols (Jiwyam, 2010). Strategies of feed deprivation in aquaculture has been practised to establish feeding schedules that enhance growth rates and feed conversion efficiency, thus reducing labour costs and water quality problems (Morshedi et al., 2017; Mozanzadeh et al., 2017). However, restricted feeding impairs fish health due to increased stress condition (Shah, Hussain, Ali, & Salam, 2017) and fostering disease susceptibility (Li, Tian, Zhang, Jiang, & Liu, 2014). Conversely, overfeeding enhances water quality deterioration, also affecting fish growth (Okorie et al., 2013). In addition, several opportunistic parasites begin to appear, especially in stressed fish during periods of

adverse growth conditions (Paperna, 1991). Diseases caused by monogeneans (e.g., *Neobenedenia* sp.) have been reported as the main cause of broodstock mortality in *Seriola rivoliana* (Roo et al., 2014), while many other pathogens in finfish sea-cage aquaculture. Heavily infected fish display irritability, loss of appetite, anorexia, and reduced growth (Ernst, Whittington, Corneillie, & Talbot, 2002).

In the wild, many fish species may undergo natural starvation periods due to feed shortage, spawning, or seasonal migration and therefore developed an impressive ability to withstand fasting periods (Yengkokpam et al., 2013). On the other hand, when fish are deprived of feed, they utilize stored body nutrients to maintain life triggering behavioural and physical changes causing stress and affecting its growth (Kojima et al., 2015; Yengkokpam et al., 2013).

Longfin yellowtail (*S. rivoliana*, Valenciennes 1833) belonging to the Carangidae family of fish are widely distributed throughout the warm-temperature waters of the world. It has been identified as an excellent candidate species for intensive marine aquaculture due to its adaptability to captivity, fast growth rate, high flesh quality, and high market value (Kissinger et al., 2016; Quiñones-Arreola et al., 2015; Roo et al., 2014). First farming attempts to develop longfin yellowtail culture techniques were carried out in Ecuador during the 1990s by Benetti, Acosta, and Ayala (1995). Commercial production of *S. rivoliana* has been developed in Hawaii (USA) reaching 500 tonnes per year and marketed as a sashimi-grade product (Sims, 2013). Countries, such as México (Benitez-Hernández et al., 2017) and Spain (Roo et al., 2014), have started commercial cultures of this species in the past decade. However, the aquaculture development of *S. rivoliana* has been limited due to unreliable spawning success particularly in temperate regions, low hatchery survival, and parasite-related diseases (Fernández-Palacios, Schuchardt, Roo, Hernández-Cruz, & Izquierdo, 2015; Roo et al., 2014). In addition, information on feeding regimes is scarce or not available. Previous observations in our laboratory showed an increased water turbidity after feeding and presence of skin parasites in juveniles reared in outdoor tanks.

The aim of this study was to evaluate the effect of feeding regimes with short-term feed deprivation on water quality, skin parasites occurrence, and growth performance of *S. rivoliana* juveniles.

## 2 | MATERIALS AND METHODS

### 2.1 | Source of fish

Full siblings (130-day post-hatch juveniles) of longfin yellowtail were obtained from the National Center of Aquaculture and Marine Biology of ESPOL Polytechnic University of Ecuador (CENAIM-ESPOL). A total of 250 fish were initially selected and anaesthetized in 15 mg/L Eugenol® (Keystone Ind., Gibbstown, NJ, USA), individually weighed, and tagged with Trovan® passive transponders ID-100A tags (Trovan Ltd., Douglas, UK). Fish were maintained in two 6,000-L conditioning tanks and fed constantly for 30 days. After this acclimation period, 180 fish within one standard deviation of the mean weight were selected for the experiment (102.7 ± 5.1 g).

### 2.2 | Experimental procedure and feeding

Selected fish were randomly distributed among eighteen 1,000-L rearing tank (10 fish in each tank; 1 kg/m) 3 days prior to the start of the experiment and fed ad libitum twice daily. Each tank was supplied with running seawater (200% water renewal), water temperature approximately 26°C, and natural photoperiod (12 hr light:12 hr darkness). Additionally, air was supplied to each tank through airlines with air-stones. The experiment lasted 89 days. The experiment consisted of six treatments explained as follow:

- 24R1: fish fed once daily everyday.
- 24R2: fish fed twice daily everyday.
- 48R1: 2-day fasting and refed once a day for 1 day.
- 48R2: 2-day fasting and refed twice a day for 1 day.
- 96R1: 3-day fasting and refed once a day for 1 day.
- 96R2: 3-day fasting and refed twice a day for 1 day.

All treatment had three replicates. Fish were handfed with commercial pellets containing 40% crude protein, 12% crude fat, 2.5% fibre, and 12% crude ash (Skretting-GISIS®, Gye, Ecuador; size: 4 and 7 mm). The feed was administrated to apparent satiation. Uneaten pellets were collected within 15 min. Likewise, uneaten pellets (if present) were collected after 1 hr (considered as regurgitated pellets). According to feeding schedules, the feed provided was weighed and uneaten pellets were counted. The total mass of uneaten feed was estimated by multiplying the number of uneaten pellets with the mean weight of a sample of 500 pellets. The feed consumption in each tank was calculated by subtracting the weight of uneaten feed from the amount of feed presented (Thorarensen et al., 2010). Faeces were removed twice a day (after feeding) from the tanks using a siphon.

### 2.3 | Measurements and sampling collection

Measurements of temperature and dissolved oxygen were taken twice daily (8:00 and 16:30 hr) with the aid of a multiparameter YSI550A (YSI Incorporated, Yellow Springs, OH, USA).

On days 32 (D30), 61 (D60), and 89 (D90), all tagged fish were anaesthetized (Eugenol® 15 ml/L) and individually sampled for standard body length ($L_s$) and weighed ($W$) to the nearest 1 g. Fish were not fed on sampling days to minimize handling stress, but sampling was performed a day after all fish were fed according to feeding schedule. After weighing, each fish was dipped in a 10-L bucket filled with dechlorinated freshwater for 45–60 s to dislodged skin parasites. Freshwater was mesh-filtered (100 μm) in order to identify and quantify the numbers of parasites in each fish. All tanks were cleaned and fish were stocked in a new clean tank after measurements. At 75 days, all culture tanks were treated with 100 mg/L formalin dissolved in seawater for 30 min due to an increased rubbing behaviour of fish associated with skin parasites infections.

Water samples were obtained from each rearing tank at days D60 and D90. Total ammonia nitrogen (TAN), pH, nitrite ($N\text{-}NO_2^-$),

total suspended solids (TSS), and total dissolved solids (TDS) were determined according to American Public Health Association (APHA) American Water Works Association (AWWA) and Water Environment Federation (WEF) (1998).

At the end of experiment (D90), two fishes were sampled at random from each tank and anaesthetized with Eugenol® 15 ml/L. Blood was withdrawn from the caudal vein by puncture, and immediately transferred to a heparin-coated capillary tube. Right after extraction, haematocrit (HCT) condition was determined by centrifuging the blood in a capillary tube at 2,380 *g* for 5 min (Centrifuge Sorvall ST 8/R; Thermo Fisher Scientific®, Waltham, MA, USA) and expressed as total volume percentage. The fish were then dissected to remove visceral content and flesh. Each part was weighed to determine the hepatosomatic index (HSI) and viscerosomatic index (VSI), as well as flesh yield.

## 2.4 | Molecular identification of parasites

Collected parasites were preserved in 90% ethanol for DNA extraction. Total genomic DNA was extracted from parasites individually into 1.5-ml Eppendorf tubes. Organisms were lysed by incubation at 55°C for 1 hr in 200 µl of STE-buffer solution (5 mM tris-HCl, 2 mM EDTA, and 60 mM NaCl, pH 8), continuing with purification, adding an equal volume of phenol–chloroform–isoamylalcohol (25:24:1) followed by extraction of chloroform–isoamyl alcohol (24:1). DNA was recovered with ethanol (70%) followed by centrifugation at 16,060 *g* for 10 min. The pellet was washed with 70% ethanol, dried, and resuspended in 50 µl of ultrapure water (pH 7.0). DNA was preserved at −20°C for further use. DNA concentration and purity were estimated with a Varioskan™ LUX multimode microplate reader (Thermo Fisher Scientific®). The mitochondrial gene cytochrome *c* oxidase subunit 1 (COI) and 28S ribosomal DNA fragments were amplified using primers suggested by Sepúlveda and González (2014). COI DNA was amplified by polymerase chain reaction (PCR) using the forward primer JB3 (5′-TTTTTTGGGCATCCTGAGGTTTAT-3′) and reverse primer COX (5′-AATCATGATGCAAAAGGTA-3′). The 28S LSU rDNA was amplified with the forward primer C1 (5′-ACCCGCTGAATT TAAGCAT-3′) and the reverse primer D2 (5′-TGGTCCGTGTTTCAAGAC-3′). PCR was performed in a 30 µl reaction mixture containing 1× buffer $NH_4$ (Bioline®, Sydney, New South Wales, Australia), 1.8 mM $MgCl_2$ (Invitrogen®, Carlsbad, CA, USA), 2 mM of each dNTP, 0.3 µM of each primer, 0.5 units of Taq DNA polymerase, and 2 µl of DNA. PCR cycling conditions were: cycle 1 was 95°C for 5 min, 45°C for 2 min, and 72°C for 90 s. This was followed by 25 cycles of 95°C for 40 s, 54°C for 50 s, and 72°C for 90 s; and a last cycle of 10 min at 72°C to complete the elongation. Amplicons were separated by 1.5% agarose (1.5% wt/vol) gel electrophoresis, stained with SYBR® Safe DNA gel stain (Thermo Fisher Scientific®), and illuminated under UV light. Images were captured with an E-Gel® Imager System (Thermo Fisher Scientific®). PCR products were purified and dissolved in 30 µl of ultrapure water for direct sequencing (Macrogen Inc®, Seoul, Korea). A BigDye Terminator Cycle sequencing kit (Perkin Elmer®, Madrid, Spain) was used for sequencing. The sequencing products were analysed with the ABI 3000 sequencer (Applied Biosystems®, Foster City, CA, USA). Sequencing of the PCR products was performed by Macrogen Inc®.

A phylogenetic analysis was carried out with the concatenated sequences from the parasites, together with different sequences obtained from GenBank. The sequence alignments were generated with ClustalW (Thompson, Gibson, & Higgins, 2003) and the specific regions were identified using Bioedit 7.0.0 (Hall, 2004). Values of amino acid substitutions per site for the gene were calculated with the program Molecular Evolutionary Genetics Analysis MEGA 6.0 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013).

## 2.5 | Calculation and data analysis

Fish mortality was recorded every day. At the end of experiment, all fish were counted and final survival was calculated as S % = 100 × ($N_f/N_i$), where $N_f$ is the number of juveniles survived at D90 and $N_i$ is the number at the beginning of the experiment (D0).

All indices were calculated as follows:

Specific growth rate SGR (% $day^{-1}$) = 100 × ($\ln W_2 - \ln W_1$)/*t*, where $W_2$ and $W_1$ are the final and initial wet weights (g), and *t* is the interval (days) between weighing. While absolute growth was calculated as $\Delta G = W_2 - W_1$, or individual growth by day ($\Delta G/t$).

Feed conversion ratio (FCR) and feed efficiency (FE) were calculated as follow for each tank: FCR = F/$\Delta G$ and FE = $\Delta G/F$, where *F* is feed supplied to tank (g/day).

Condition factor (*K*) was calculated from the wet weight and standard length relationship, $K = 100 \times (W/L_s^3)$.

Hepatosomatic and viscerosomatic indices were calculated as HIS = 100 × ($W_L/W_B$) and VSI = 100 × ($W_V/W_B$), where $W_L$ and $W_V$ are wet liver and viscera weights, respectively, and $W_B$ is total wet body weight in grams.

All data were subjected to the Bartlett's test to verify homogeneity of variances. If non-homogeneity of variances were detected (e.g., ΔG and FCR), data were ln-transformed to comply with parametric test assumptions. A Dixon's *Q* test for atypical data was run for the number of parasites in D30 and D60. One-way ANOVA at a significance level of 0.05% was used to compare the effects of short-term feed deprivation. When a significant effect was found, a post hoc Tukey's honestly significant difference test was performed. All statistical analyses were conducted using XLSTAT®2016.5 (Addinsoft, Paris, France).

# 3 | RESULTS

## 3.1 | Water quality and longfin yellowtail juvenile welfare

There was no statistical distinction in TAN (D60 = 0.09 ± 0.02–0.22 ± 0.04 mg/L; D90 = 0.03 ± 0.02–0.27 ± 0.11 mg/L), $NO_2^-$ (D60 = 0.03 ± 0.01 mg/L; D90 = 0.03 ± 0.01–0.04 ± 0.01 mg/L), TSS (D60 = 18.90 ± 15.10–54.13 ± 19.42 mg/L; D90 = 6.90 ± 0.56–7.93 ± 0.21

mg/L), and TDS (D60 = 41.67 ± 4.04–53.00 ± 9.85 mg/L; D90 = 50.67 ± 16.50–73.33 ± 15.95 mg/L) values among treatments ($p > 0.05$). In 24 and 48 hr deprived feed treatments, pH was slightly lower compared to 96 hr treatments (pH ranged between 7.71 ± 0.09 and 8.04 ± 0.01). Dissolved oxygen in treatment 24R2 (5.36 ± 0.09 at 8:00 hr and 4.93 ± 0.15 at 16:30 hr) was significantly lower ($p < 0.05$) than all treatments, except for treatments 24R1 and 48R2.

Final survival in all treatments was similar except for treatment 96R1 that recorded the lowest survival ($p < 0.05$; Table 1), severely reduced (from 86.7% to 30.0%) between D30 and D60 period. Some mortality was accounted for trapped fish in the mesh-lid that covered culture tank (one fish in 24R2 at D60 and two fish in 96R2 at D30) and after fresh water dip (4 fish in 24R2). A complete replicate in 48R1 (D60) was lost due to malfunction of the standpipe.

The lowest condition factor was registered in the longer starvation treatments ($p < 0.05$). No significant differences in HSI, VSI, and HCT among the feeding groups were found ($p > 0.05$; Table 1). The obvious difference in flesh yield (%) was observed between treatment groups 24R2 and 96R1 that presented the highest and lowest values, respectively.

Skin parasites were identified as *Neobenedenia girellae* by molecular analyses. Although skin parasites were present in all treatments, its abundance was variable and inconsistent among replicates (ranging from 20 to 193 parasites per fish; Figure 1). Only one statistical difference was observed in treatment 96R1 (224 ± 32 parasites per fish) during the 30- to 60-day period. In the last period (60–90 interval), skin parasites were negligible.

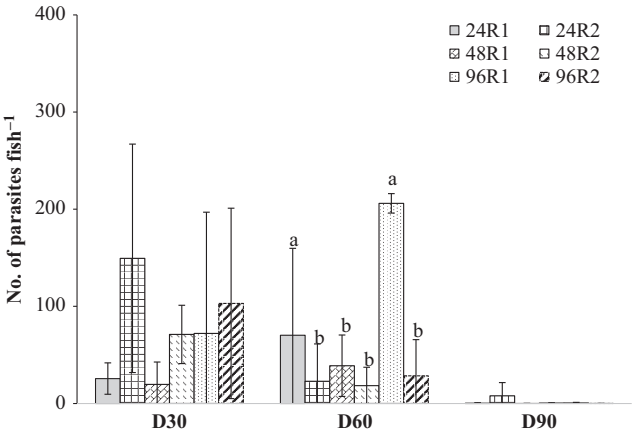


**FIGURE 1** Number of parasites *Neobenedenia girellae* per fish over a 30-day test period (mean and *SD* of three replications). Significant differences are indicated with superscripted letters (Tukey's test, $p < 0.05$) within each time period

## 3.2 | Growth performance and feed utilization of longfin yellowtail

At the start of experiment, there were no significant differences in fish weight among treatment groups. Treatments 24R1 and 24R2 gained significantly ($p < 0.05$) more weight as compared to the other feeding regimes at the end of experiment (380.77 ± 11.67 g and 423.45 ± 59.37 g, respectively). Growth performance and feed consumption of longfin yellowtail under different feeding regimes are shown in (Table 2). The relationship between standard length (cm) and total weight (g) for longfin yellowtail juvenile showed a high correlation ($r^2 = 0.97$; $N = 652$; Figure 2) when all observations were pooled, and it is represented by the equation $W = 7.6503\ e^{0.147Ls}$.

Feeding regimes affected fish growth. For the entire culture period (overall), mean SGR was significantly greater ($p < 0.05$) in treatment 24R2 but similar to treatment 24R1 (Figure 3). When SGR was analysed at 30-day intervals, the period between 60 and 90 days showed the lowest value (0.64% ± 0.45% per day). Otherwise, 48R1 showed similar SGR value in all periods (0.87% ± 0.04% per day). We detected significant lowest SGR in 96R1 and 96R2 in all periods. A negative growth was even denoted in treatment 96R1 between the 30–60 days periods in all replicates (Figure 3).

Mean daily feed intake (g fish$^{-1}$ day$^{-1}$) in treatment 48R2 was significantly higher ($p < 0,05$) only comparable to treatment 24R2 (Table 2). Feed efficiency was higher in 24 hr and 48 hr feed treatments throughout the 89 culture days ($p < 0.05$; Figure 4). A negative FE was also observed for treatment group 96R1 during the 30–60-day time period. Average FE was lower during the last ~30-day intervals (0.35 ± 0.23) for all treatments.

## 4 | DISCUSSION

Water quality parameters were kept within the safety levels for fish farming in our study (Tucker, 1998). Even though, dissolved oxygen was significantly lower in treatments 24R1, 24R2, and 48R2 critical

**TABLE 1** Survival and welfare indices of the juvenile longfin yellowtail fed at different feeding regimes. Values (mean ± *SD* of three replications) in the same row with different superscript letters are significantly different (Tukey's test, $p < 0.05$)

| Treatments | 24R1 | 24R2 | 48R1 | 48R2 | 96R1 | 96R2 |
|---|---|---|---|---|---|---|
| Viscerosomatic index (VSI, %) | 5.38 ± 0.51 | 4.76 ± 0.40 | 5.49 ± 2.46 | 4.41 ± 1.31 | 5.82 ± 0.48 | 5.40 ± 0.51 |
| Hepatosomatic index (HSI, %) | 1.53 ± 0.33 | 1.49 ± 0.12 | 1.77 ± 0.21 | 1.32 ± 0.31 | 1.15 ± 0.17 | 1.25 ± 0.24 |
| Flesh yield (%) | 49.89 ± 4.45$^{ab}$ | 54.10 ± 3.50$^{a}$ | 43.85 ± 6.95$^{ab}$ | 48.05 ± 2.13$^{ab}$ | 38.76 ± 6.59$^{b}$ | 44.36 ± 2.57$^{ab}$ |
| Hematocrit (%) | 38.33 ± 4.16 | 38.83 ± 4.86 | 34.25 ± 11.67 | 35.33 ± 8.75 | 29.83 ± 10.68 | 40.33 ± 2.47 |
| Condition factor (g/cm$^3$) | 2.03 ± 0.04$^{a}$ | 2.09 ± 0.08$^{a}$ | 1.98 ± 0.09$^{ab}$ | 2.04 ± 0.04$^{a}$ | 1.63 ± 0.11$^{c}$ | 1.77 ± 0.05$^{bc}$ |
| Survival (%) | 90.00 ± 10.00$^{a}$ | 80.00 ± 26.46$^{a}$ | 90.00 ± 14.14$^{a}$ | 96.67 ± 5.77$^{a}$ | 23.33 ± 15.28$^{b}$ | 90.00 ± 10.00$^{a}$ |

**TABLE 2** Growth performance and feed utilization values of the juvenile longfin yellowtail fed at different feeding regimes. Values (mean ± *SD* of three replications) in the same row with different superscript letters are significantly different (Tukey's test, $p < 0.05$)

| Treatments | 24R1 | 24R2 | 48R1 | 48R2 | 96R1 | 96R2 |
|---|---|---|---|---|---|---|
| Initial body weight (g) | 107.27 ± 6.88$^{a}$ | 97.48 ± 6.52$^{a}$ | 96.41 ± 5.57$^{a}$ | 104.85 ± 5.84$^{a}$ | 101.32 ± 5.21$^{a}$ | 108.87 ± 7.54$^{a}$ |
| Final body weight (g) | 380.77 ± 11.67$^{ab}$ | 423.45 ± 59.37$^{a}$ | 218.32 ± 36.21$^{cd}$ | 322.78 ± 45.55$^{bc}$ | 128.93 ± 8.91$^{d}$ | 140.36 ± 7.02$^{d}$ |
| Final standard length (cm) | 26.59 ± 0.43$^{a}$ | 27.24 ± 1.30$^{a}$ | 22.25 ± 1.56$^{bc}$ | 25.05 ± 1.02$^{ab}$ | 19.95 ± 0.90$^{c}$ | 19.92 ± 0.40$^{c}$ |
| Absolute growth (g/fish) | 275.12 ± 14.68$^{a}$ | 324.29 ± 61.80$^{a}$ | 120.32 ± 26.15$^{b}$ | 218.94 ± 43.79$^{a}$ | 13.98 ± 1.49$^{d}$ | 31.86 ± 4.46$^{c}$ |
| Individual fish growth (g/day) | 3.09 ± 0.20$^{a}$ | 3.64 ± 0.70$^{a}$ | 1.35 ± 0.30$^{b}$ | 2.46 ± 0.50$^{a}$ | 0.16 ± 0.00$^{d}$ | 0.36 ± 0.10$^{c}$ |
| Feed conversion ratio (FCR) | 1.60 ± 0.05$^{b}$ | 1.63 ± 0.14$^{b}$ | 1.84 ± 0.11$^{b}$ | 1.63 ± 0.08$^{b}$ | 3.39 ± 0.32$^{a}$ | 3.67 ± 0.85$^{a}$ |
| Daily feed intake (g fish$^{-1}$ day$^{-1}$) | 5.35 ± 0.39$^{bc}$ | 6.42 ± 0.61$^{ab}$ | 4.92 ± 0.77$^{bc}$ | 8.21 ± 1.15$^{a}$ | 3.96 ± 0.21$^{c}$ | 5.14 ± 0.50$^{bc}$ |

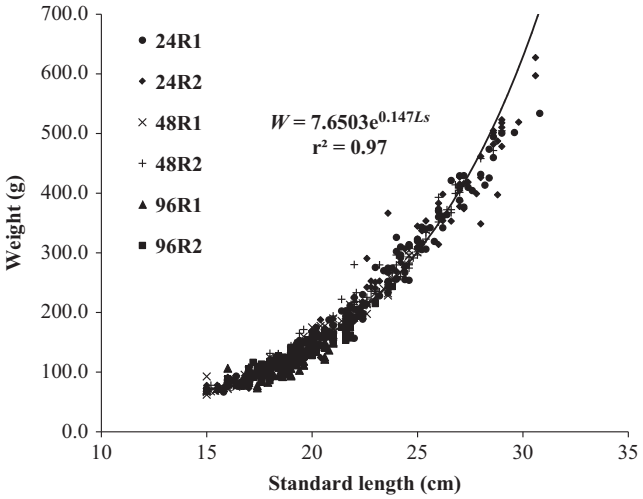


**FIGURE 2** Weight-at-length nonlinear relationship of *Seriola rivoliana* fed at six different feeding regimes. Solid line indicates pooled data ($n$ = 18 tanks)

dissolved oxygen levels below 4 mg$O_2$/L were not detected. In farms, fish are routinely fed on a daily basis producing water quality problems due to uneaten feed, nutrient leaching and waste products from fish. Deterioration of water quality promotes helminth infection of fish (Zargar et al., 2012) and growth reduction (Okorie et al., 2013). There was no evidence of *N. girellae* infection related to the water quality in our study. However, the number of parasites per fish varied considerably among replicates and culture periods. A relative high mortality was registered in treatment group 96R1 between period D30 and D60, most likely related to the fish starving condition, despite high *N. girellae* infestation also observed during this period.

Morphological indices, such as HSI or VSI, and haematological analysis (e.g., HCT counts) are considered useful indicators of the nutritional and physiological condition of fishes (De Pedro, Guijarro, López-Patiño, Martínez-Álvarez, & Delgado, 2005). Feeding regimes evaluated here did not show any significant differences in HSI and VSI among treatments. These results are in accordance with results

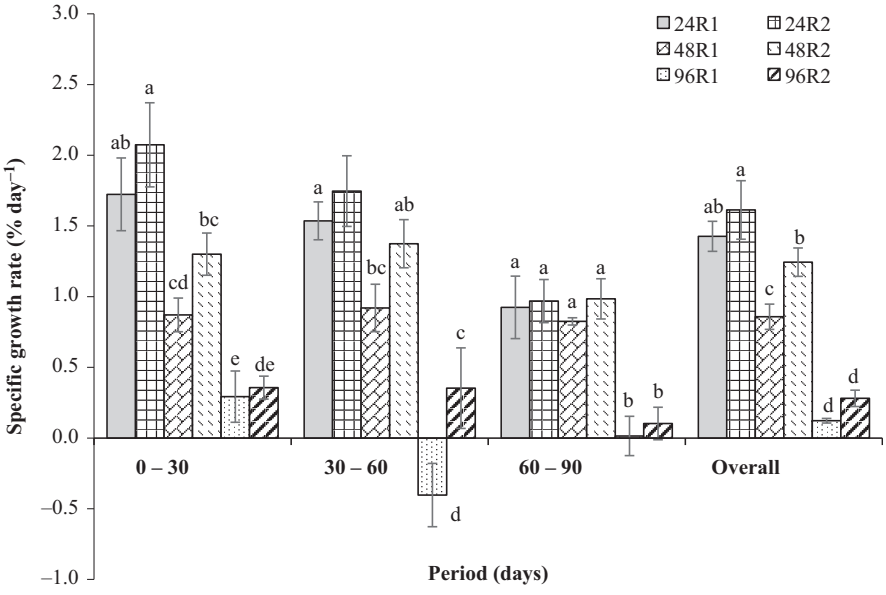


**FIGURE 3** Mean specific growth rates (SGR) of fish reared at different feeding regimes during the experimental period (mean and *SD* of three replications). Significant differences are indicated with superscripted letters (Tukey's test, $p < 0.05$) within each time period

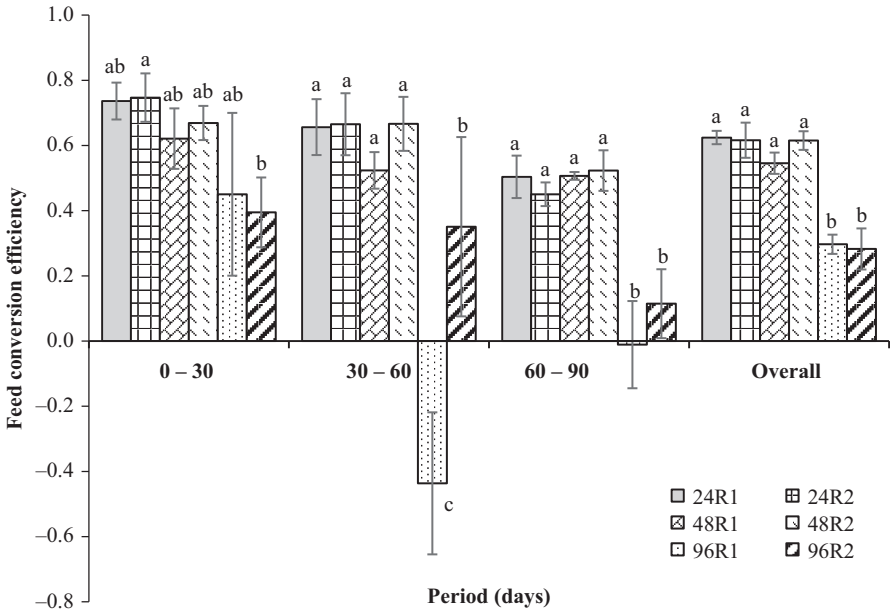


**FIGURE 4** Feed efficiency (FE) of juvenile longfin yellowtail reared at different feeding regimes during the experimental period (mean and *SD* of three replications). Significant differences are indicated with superscripted letters (Tukey's test, $p < 0.05$) within each time period

reported for *Oreochromis mossambicus* (Gabriel, Omoregie, Martin, Kukuri, & Shilombwelwa, 2018) and *Acipenser baerii* (Morshedi et al., 2017). As Thongprajukaew and Rodjaroen (2017) hypothesized, not having differences in HSI probably indicates that there was no malnutrition. Our morphological results suggest the absence of malnutrition in longfin yellowtail despite feed restriction. Similarly, HCT counts did not differ among starved and continuously fed treatments groups in our study. These results agree with HCT counts reported for *A. baerii* (Morshedi et al., 2017) despite presenting slightly lower percentages (17%–23%) when compared to our study. The percentage of HCT found in our study corresponds to healthy fish proposed by Del Rio-Zaragoza, Fajer-Ávila, Almazán-Rueda, and Abdo de la Parra (2011), falling within the range of 33%–71%. However, Benitez-Hernández et al. (2017) found higher levels (53%–61%) in longfin yellowtail fed with marine by-products. Our work differs from the study of De Pedro et al. (2005) who asserts that starvation reduces the percentage of HCT in fishes. Nevertheless, further research is needed to assess the effects of starvation in fish HCT levels. Although differences in flesh yield were not found among treatments, starved fish recorded lower values as compared to continuously fed fish. The condition factor (*K*) is commonly used as a valuable index to describe the nutritional condition of farmed fish (Mozanzadeh et al., 2017). In our study, the condition factor was significantly lower in fish under 96 hr of restricted feed. The 2-day fasting and 1-day refed fish was not affected. Likewise, no differences in condition factor during intermittent feeding with 48 hr of starvation in *Coregonus lavaretus* and *O. mossambicus* were observed, suggesting that compensatory mechanisms had taken place (Gabriel et al., 2018; Känkänen & Pirhonen, 2009).

Reduction in fish production costs could be attained through feeding strategies that derive from compensatory growth (Eroldoğan, Kumlu, & Sezer, 2006). The occurrence of compensatory growth in a restricted number of fish taxa used in aquaculture has been compiled by Ali, Nicieza, and Wootton (2003). They listed several taxonomic distribution studies on teleost fish species that presented full, partial, over-compensation or the absence of compensatory growth. Furthermore, starvation appears to be well tolerate by many fish species. In our findings, 48R2 fish achieved partial compensation. According to the definition given by Ali et al. (2003), in partial compensation, the deprived animals fail to achieve the same size at the same age as non-restricted contemporaries, but do show relatively rapid growth rates, and may have better feed conversion ratios during the re-feeding period. Similar results were achieved in gilthead seabream, (*Sparus aurata*) with 1-day feed deprivation and 2-days refeeding at satiation (Eroldoğan et al., 2006); juvenile tilapia, (*O. mossambicus*) subjected to 2 days deprivation and 4 days refeeding (Gabriel et al., 2018); and juvenile yellow mystus (*Hemibagrus nemurus*) fasted by 1, 2, and 4 days per week and fed ad libitum on the remaining days. However, in the same study, yellow mystus fasted for 3 days achieved fully compensatory growth (Thongprajukaew & Rodjaroen, 2017). On the other hand, no compensatory growths were reported for *Scophthalmus maximus*, at just 1 day of starvation per week (Blanquet & Oliva-Teles, 2010), *S. aurata* after 1 and 2 weeks of starvation followed by subsequent refeeding (Peres, Santos, & Oliva-Teles, 2011), and *O. niloticus* with restricted feeding between 2 and 7 days (Gao, Wang, Hur, & Lee, 2015).

Partial compensation achieved in 48R2 could be explained due to the greater feed consumption (hyperphagia) and feed efficiency registered in this treatment group as suggested by Fang, Tian, and Dong (2017). According to our overall FE, fish exerted daily feed intake efficiently when they were fasted for short period up 48 hr. Similar findings on increased daily feed intake on deprived Siberian sturgeon, *A. baerii* were observed by Morshedi et al. (2017). Interestingly, the inverse seems to occur in juvenile gilthead seabream

studies, where no increase in feed intake or feed efficiency was observed following feed restriction (Peres et al., 2011). During short periods of feed deprivation followed by ample feed supply, hyperphagic response may avert measurable growth depression, thereby, growth patterns between continuously fed and temporarily deprived fish might not be distinguishable (Ali et al., 2003; Eroldoğan et al., 2006; Thongprajukaew & Rodjaroen, 2017). This could be the reason for not accounting statistical significant differences in final biomass, individual fish growth, FE and FCR between the treatment group 48R2 and every single day fed fish group (24R1 and 24R2) in our study. Growth performance of fish fed once after 48 hr of starvation (48R1) exerted intermediate values. Statistical significant differences were only observed in fish growth in the treatment group 48R1 in contrast with the aforementioned treatments. This result could be explained in part, because fish were able to consume a larger amount of feed during peak appetite before the start stomach evacuation, as reported for juvenile *Pagrus auratus* under different feeding frequencies regimes (Booth, Tucker, Allan, & Fielder, 2008). In 96 hr treatments, all growth parameters were significantly lower in comparison to the other treatment groups. Probably, the refeeding time (1 day) was not sufficient to trigger a compensatory response after 4 days of starvation. Fang et al. (2017) stated that the degree of compensatory growth in *Cynoglossus semilaevis* juveniles depends on both, the length of feed deprivation and refeeding period. Likewise, stress conditions exerted from continuous starvation could lead into delayed growth and immune depression (Morshedi et al., 2017; Shah et al., 2017). Although the overall SGR in 48R2 was lower than in 24R2, it seems to be a result of acclimation to the cyclical starvation and subsequent feeding, because statistical significant differences were only observed in the 30-day period. As it is observed in length–weight relationship in our study, standard length also increased along with fish weight, but negatively related to fasting time. Up to date, mechanisms for compensatory responses are poorly understood in fish. However, previous studies suggested that compensatory growth in fish could be a result of improved digestive enzymes activity during starvation/refeeding cycling (Yengkokpam et al., 2013); intermittent feeding schedule (Känkänen & Pirhonen, 2009; Thongprajukaew & Rodjaroen, 2017); the promotion of feed efficiency and digestibility coefficiency (Fang et al., 2017; Morshedi et al., 2017); and hyperphagia (Gao et al., 2015; Türkmen et al., 2012).

Our research showed that juvenile longfin yellowtail was able to achieve partial compensatory growth under restricted feeding up 48 hr followed by refeeding twice a day. The 2-day fasting period was compensated in part by an increased feed intake and feed efficiency during the 1-day refed period without compromising fish welfare and water quality. Nevertheless, compensatory growth appears to be a specie-specific response, as several studies have shown variable and contradictory results on this subject. These results represent a promising alternative to improve feeding schedule of this species. Nonetheless, more studies need to be conducted to explore economic benefits of increased fasting and refeeding periods.

## ACKNOWLEDGEMENTS

The authors thank Leda Restrepo for molecular identification of parasites and Yessenia Pozo for water quality analysis. Furthermore, we acknowledge Jefferson Borbor for his assistance with experiments, measurements and culture's cleaning. This work was supported by Secretaría Nacional de Educación Superior, Ciencia, Tecnología e Innovación (SENESCYT) of Ecuador (grant number PIC-14-CENAIM-002).

## ORCID

*Wilfrido Argüello-Guevara* http://orcid.org/0000-0003-1522-152X

## REFERENCES

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

American Public Health Association (APHA), American Water Works Association (AWWA), & Water Environment Federation (WEF). (1998). *Standard methods for the examination of water and wastewater* (20th ed.). Washington, DC: American Water Works Association, and Water Environment Federation.

Benetti, D. D., Acosta, A., & Ayala, J. C. (1995). Cage and pond aquaculture of marine finfish aquaculture in Ecuador. *World Aquaculture*, *26*, 7–13.

Benitez-Hernández, A., Jiménez-Bárcenas, S. P. L., Sánchez-Gutiérrez, E. Y., Pérez-Urbiola, J. C., Tovar-Ramírez, D., Palacios, E., & Civera-Cerecedo, R. (2017). Use of marine by-product meals in diets for juvenile longfin yellowtail *Seriola rivoliana*. *Aquaculture Nutrition*, *24*(1), 562–570. https://doi.org/10.1111/anu.12588

Blanquet, I., & Oliva-Teles, A. (2010). Effect of feed restriction on the growth performance of turbot (*Scophthalmus maximus* L.) juveniles under commercial rearing conditions. *Aquaculture Research*, *41*, 1255–1260. https://doi.org/10.1111/j.1365-2109.2009.02416.x

Booth, M. A., Tucker, B. J., Allan, G. L., & Fielder, D. S. (2008). Effect of feeding regime and fish size on weight gain, feed intake and gastric evacuation in juvenile Australian snapper *Pagrus auratus*. *Aquaculture*, *282*, 104–110. https://doi.org/10.1016/j.aquaculture.2008.06.027

De Pedro, N., Guijarro, A. I., López-Patiño, M. A., Martínez-Álvarez, R., & Delgado, M. J. (2005). Daily and seasonal variations in haematological and blood biochemical parameters in the tench, *Tinca tinca* Linnaeus, 1758. *Aquaculture Research*, *36*, 1185–1196. https://doi.org/10.1111/j.1365-2109.2005.01338.x

Del Rio-Zaragoza, O. B., Fajer-Ávila, E. J., Almazán-Rueda, P., & Abdo de la Parra, M. I. (2011). Hematological characteristics of the spotted rose snapper *Lutjanus guttatus* (Steindachner, 1869) healthy and naturally infected by dactylogyrid monogeneans. *Tissue & Cell*, *43*, 137–142. https://doi.org/10.1016/j.tice.2011.01.002

Ernst, I., Whittington, I. D., Corneillie, S., & Talbot, C. (2002). Monogenean parasites in sea-cage aquaculture. *Austasia Aquaculture*, *16*, 46–48.

Eroldoğan, O. T., Kumlu, M., & Sezer, B. (2006). Effects of starvation and re-alimentation periods on growth performance and hyperphagic response of *Sparus aurata*. *Aquaculture Research*, *37*, 535–537. https://doi.org/10.1111/j.1365-2109.2006.01445.x

Fang, Z., Tian, X., & Dong, S. (2017). Effects of starving and re-feeding strategies on the growth performance and physiological characteristics of the juvenile tongue sole (*Cynoglossus semilaevis*). *Journal of*

*Ocean University of China*, *16*, 517–524. https://doi.org/10.1007/s11802-017-3198-7

Fernández-Palacios, H., Schuchardt, D., Roo, J., Hernández-Cruz, C., & Izquierdo, M. (2015). Spawn quality and GnRHa induction efficiency in longfin yellowtail (*Seriola rivoliana*) broodstock kept in captivity. *Aquaculture*, *435*, 167–172. https://doi.org/10.1016/j.aquaculture.2014.09.021

Gabriel, N. N., Omoregie, E., Martin, T., Kukuri, L., & Shilombwelwa, L. (2018). Compensatory growth responses in *Oreochromis mossambicus* submitted to short-term cycles of feed deprivation and refeeding. *Turkish Journal of Fisheries and Aquatic Sciences*, *18*, 161–166. https://doi.org/10.4194/1303-2712-v18_1_18

Gao, Y., Wang, Z., Hur, J. W., & Lee, J. Y. (2015). Body composition and compensatory growth in Nile tilapia *Oreochromis niloticus* under different feeding intervals. *Chinese Journal of Oceanology and Limnology*, *33*, 945–956. https://doi.org/10.1007/s00343-015-4246-z

Hall, T. (2004). *Bioedit 7.0.0*. Raleigh, NC: North Carolina State University.

Hanssen, H., Imsland, A. K., Foss, A., Vikingstad, E., BjØrnevik, M., Solberg, C., … Powell, M. D. (2012). Effect of different feeding regimes on growth in juvenile Atlantic cod, *Gadus morhua* L. *Aquaculture*, *364–365*, 298–304. https://doi.org/10.1016/j.aquaculture.2012.08.027

Huang, Z. H., Ma, A. J., Wang, X. A., & Lei, J. L. (2014). The interaction of temperature, salinity and body weight on growth rate and feed conversion rate in turbot (*Scophthalmus maximus*). *Aquaculture*, *432*, 237–242. https://doi.org/10.1016/j.aquaculture.2014.04.013

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

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

Kissinger, K. R., García-Ortega, A., & Trushenski, J. T. (2016). Partial fish meal replacement by soy protein concentrate, squid and algal meals in low fish-oil diets containing *Schizochytrium limacinum* for longfin yellowtail *Seriola rivoliana*. *Aquaculture*, *452*, 37–44. https://doi.org/10.1016/j.aquaculture.2015.10.022

Kojima, J. T., Leitão, N. J., Menossi, O. C. C., Freitas, T. M., Silva, M.-D.-P., & Portella, M. C. (2015). Short periods of food restriction do not affect growth, survival or muscle development on pacu larvae. *Aquaculture*, *436*, 137–142. https://doi.org/10.1016/j.aquaculture.2014.11.004

Li, X. F., Tian, H. Y., Zhang, D. D., Jiang, G. Z., & Liu, W. B. (2014). Feeding frequency affects stress, innate immunity and disease resistance of juvenile blunt snout bream *Megalobrama amblycephala*. *Fish & Shellfish Immunology*, *38*, 80–87. https://doi.org/10.1016/j.fsi.2014.03.005

Morshedi, V., Kochanian, P., Bahmani, M., Yazdani, M. A., Pourali, H. R., Ashouri, G. h., & Pasha-Zanoosi, H. (2017). Cyclical short-term starvation and refeeding provokes compensatory growth in sub-yearling Siberian sturgeon, *Acipenser baerii* Brandt, 1869. *Animal Feed Science and Technology*, *232*, 207–214. https://doi.org/10.1016/j.anifeedsci.2016.10.005

Mozanzadeh, M. T., Marammazi, J. G., 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. https://doi.org/10.1111/anu.12379

Okorie, O. E., Bae, J. Y., Kim, K. W., Son, M. H., Kim, J. W., & Bai, S. C. (2013). Optimum feeding rates in juvenile olive flounder, *Paralichthys olivaceus*, at the optimum rearing temperature. *Aquaculture Nutrition*, *19*, 267–277. https://doi.org/10.1111/j.1365-2095.2012.00956.x

Paperna, I. (1991). Diseases caused by parasites in the aquaculture of warm water fish. *Annual Review of Fish Diseases*, *1*, 155–194. https://doi.org/10.1016/0959-8030(91)90028-i

Peres, H., Santos, S., & Oliva-Teles, A. (2011). Lack of compensatory growth response in gilthead seabream (*Sparus aurata*) juveniles following starvation and subsequent refeeding. *Aquaculture*, *318*, 384–388. https://doi.org/10.1016/j.aquaculture.2011.06010

Quiñones-Arreola, M. F., Arcos-Ortega, F. G., Gracia-López, V., Casillas-Hernández, R., Weirich, C., Morris, T., … Ibarra-Gámez, C. (2015). Reproductive broodstock performance and egg quality of wild-caught and first-generation domesticated *Seriola rivoliana* reared under same culture conditions. *Latin American Journal of Aquatic Research*, *43*, 953–962. https://doi.org/10.3856/vol43-issue5-fulltext-15

Roo, J., Fernández-Palacios, H., Hernández-Cruz, C. M., Mesa-Rodríguez, A., Schuchardt, D., & Izquierdo, M. (2014). First results of spawning and larval rearing of longfin yellowtail *Seriola rivoliana* as a fast-growing candidate for European marine finfish aquaculture diversification. *Aquaculture Research*, *45*, 689–700. https://doi.org/10.1111/are.12007

Salas-Leiton, E., Anguis, V., Manchado, M., & Cañavate, J. P. (2008). Growth, feeding and oxygen consumption of Senegalese sole (*Solea senegalensis*) juveniles stocked at different densities. *Aquaculture*, *285*, 84–89. https://doi.org/10.1016/j.aquaculture.2008.08.001

Sepúlveda, F. A., & González, M. T. (2014). Molecular and morphological analyses reveal that the pathogen *Benedenia seriolae* (Monogenea: Capsalidae) is a complex species: Implications for yellowtail *Seriola* spp. aquaculture. *Aquaculture*, *418–419*, 94–100. https://doi.org/10.1016/j.aquaculture.2013.10.012

Shah, S. Q. A., Hussain, M. Z., Ali, M., & Salam, A. (2017). Effect of stress conditions on body composition parameters of farmed rohu (*Labeo rohita*). *Turkish Journal of Fisheries and Aquatic Sciece*, *17*, 471–476. https://doi.org/10.4194/1303-2712-v17_3_03

Sims, N. A. (2013). Kona Blue Water Farms case study: permitting, operations, marketing, environmental impacts, and impediments to expansion of global open ocean mariculture. In A. Lovatelli, J. Aguilar-Manjarrez, & D. Soto (Eds.), *Expanding mariculture farther offshore: Technical, environmental, spatial and governance challenges* (pp. 263–296). FAO Fisheries and Aquaculture Proceedings 24, Rome.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, *30*, 2725–2729. https://doi.org/10.1093/molbev/mst197

Thompson, J. D., Gibson, T. J., & Higgins, D. G. (2003). Multiple sequence alignment using ClustalW and ClustalX. *Current Protocols in Bioinformatics*, *1*, 2.3.1–2.3.22. https://doi.org/10.1002/0471250953.bi0203s00

Thongprajukaew, K., & Rodjaroen, S. (2017). Intermittent feeding induces compensatory growth of juvenile yellow mystus (*Hemibagrus nemurus*). *Aquatic Living Resources*, *30*, 9 pp. https://doi.org/10.1051/alr/2017001

Thorarensen, H., Gústavsson, A., Mallya, Y., Gunnarsson, S., Árnason, J., Arnarson, I., … Imsland, A. K. (2010). The effect of oxygen saturation on the growth and feed conversion of Atlantic halibut (*Hippoglossus hippoglossus* L.). *Aquaculture*, *309*, 96–102. https://doi.org/10.1016/j.aquaculture.2010.08.019

Tucker, J. W. (1998). *Marine fish culture*. Harbor Branch Oceanographic Institution and Florida Institute of Technology. Kluwer Academic Publishers. https://doi.org/10.1007/978-1-4615-4911-6

Türkmen, S., Eroldoğan, O. T., Yilma, H. A., Ölçülü, A., Kiris, G. A., Erçen, Z., & Tekelioğlu, N. (2012). Compensatory growth response of European sea bass (*Dicentrarchus labrax* L.) under cycled starvation and

restricted feeding rate. *Aquaculture Research*, *43*, 1643–1650. https://doi.org/10.1111/j.1365-2109.2011.02970.x

Yengkokpam, S., Debnath, D., Pal, A. K., Sahu, N. P., Jain, K. K., Norouzi-tallab, P., & Baruah, K. (2013). Short-term periodic feed deprivation in *Labeo rohita* fingerlings: Effect on the activities of digestive, metabolic and anti-oxidative enzymes. *Aquaculture*, *412–413*, 186–192. https://doi.org/10.1016/j.aquaculture.2013.07.025

Zargar, U. R., Yousuf, A. R., Chishti, M. Z., Ahmed, F., Bashir, H., & Ahmed, F. (2012). Effects of water quality and trophic status on helminth infections in the cyprinid fish, *Schizothorax niger* Heckel, 1838 from three lakes in the Kashmir Himalayas. *Journal of Helminthology*, *86*, 70–76. https://doi.org/10.1017/S0022149X11000071

**How to cite this article:** Argüello-Guevara W, Apolinario W, Bohórquez-Cruz M, Reinoso S, Rodríguez S, Sonnenholzner S. Effects of intermittent feeding on water quality, skin parasites, feed consumption, and growth performance of juvenile longfin yellowtail *Seriola rivoliana* (Valenciennes, 1833). *Aquac Res*. 2018;49:3586–3594. https://doi.org/10.1111/are.13825