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Research Article

Biochemical and physiological adaptations of Pacific fat sleeper (*Dormitator latifrons*) exposed to starvation and refeeding periods

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ABSTRACT. Starvation is a common process in many fishes, which rely on their energy reserves to cope. The Pacific fat sleeper (*Dormitator latifrons*) is an amphidromous fish distributed in the Eastern Pacific, found in marine and freshwater environments, and can tolerate wide ranges of temperatures and low oxygen levels. The present research studied the biochemical and physiological effects of different starvation and refeeding periods on fat sleeper juveniles and focused on understanding the use of energy reserves and health status. During starvation, the fat sleeper uses lipid reserves in the liver and mesentery fat as the primary energy source, but by the fourth week, an increase in serum protein and glucose levels suggests the use of muscle protein and initiation of mesentery fat as the primary energy source, using muscle protein and initiation of gluconeogenesis to maintain a glucose balance, indicating a metabolic shift towards long-term starvation. Intestinal morphology indices were affected by four starvation weeks; however, they showed a clear recovery by the end of the refeeding period. Albumin concentration was reduced after starvation, and globulin concentration increased, compromising fish health; nevertheless, normal levels at the end of the refeeding period were registered, while white blood cells did not recover normal values after four weeks of refeeding. Despite the partial compensatory growth observed, *D. latifrons* still prefer to use lipid sources during the initial three weeks of starvation without compromising their health. However, after four weeks, there is a switch to protein muscular use to cope with long-term starvation, which may compromise its health. Hence, *D. latifrons* show a high capacity to maintain homeostasis and restore their biochemical and physiological status.

Keywords: *Dormitator latifrons*; blood chemistry; gluconeogenesis; health; hematology; metabolism; energy reserves

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INTRODUCTION

In nature, many species undergo starvation periods (Wu et al. 2021) related to reproduction, development, hibernation, estivation, migration, infrequent feeding habits, competition, unequal spatial distribution of food, seasonal variations, and ecological instability (McCue 2010, Secor & Carey 2016, Gou et al. 2023). Hence, several fish species have developed the ability to withstand starvation by adopting physiological, biochemical, cellular, and molecular strategies to reduce metabolic rates and energy consumption to maintain homeostasis, using energy reserves acquired during food abundance periods (Land & Bernier 1995, Secor & Carey 2016).

Starvation challenges the body condition of any fish. Nutritional deficiencies can intensify infections caused by opportunistic agents because of the direct relationship between disease resistance and a good nutritional status. (Secor & Carey 2016). During starvation, organisms can use the glycogen or lipids stored in their muscle or liver to obtain the energy needed for basic metabolic functions and maintenance (Gaylord & Gatlin 2000, Zhu et al. 2001). Under this physiological challenge, lipids are the main energy source, while proteins are mobilized only when necessary (McCue 2010, Secor & Carey 2016). However, in some fishes, such as the spotted rose snapper (*Lutjanus guttatus*) (Hernández et al. 2019) and the red porgy (*Pargus pargus*) (Rueda et al. 1998), zebrafish (*Danio rerio*) and hybrid striped bass (*Morone saxatilis* × *M. chrysops*) (Jia et al. 2017), in which a preferential use of protein is reported as the first energy source.

Therefore, tools are needed to infer the adaptative mechanisms of energy reserve mobilization, such as changes in biochemical body composition, morphological indices, blood chemistry, and hematological parameters to determine the nutritional and health status of fish in response to food deprivation stress and refeeding, since the metabolic mechanisms used to face starvation may vary from specie to specie as well to age, physical condition and starvation period (Gaylord & Gatlin 2000, McCue 2010, Furné et al. 2012, Fazio 2018, Dai et al. 2022).

The Pacific fat sleeper (*Dormitator latifrons*) is an amphidromous fish that occupies a demersal habitat with omnivorous behavior by feeding primarily on detritus. It is found in coastal lagoons, rivers, and streams of the Pacific slope, from California (USA) to Ecuador, with reports in southern California, Costa Rica, Panama, Galapagos Island and widely distributed along the Mexican Pacific coast, including Baja California Sur with economic and social importance in the states of Guerrero and Oaxaca due to its high consumption in coastal communities by fisheries (De la Cruz Agüero et al. 1997, Ruiz-Campos 2010, Nordlie 2012, Vega-Villasante et al. 2021).

This species is characterized by tolerating a wide range of salinity and temperature, surviving under anoxic conditions (up to 1 mg mL^{-1} of oxygen), being capable of breathing air, and showing higher gas exchange capacity than other fishes in low oxygen environments (Todd 1973, Chang 1984, Nordlie 2012, Santana-Piñeros et al. 2023). The previous characteristics generate high interest in the aquaculture development of the species, where Ecuador is the only country with aquaculture production of this species, with production volumes ranging between 800 and 1,000 t per year (Gonzalez-Martinez et al. 2020, Santana-Piñeros et al. 2023). Although this species has been proposed for aquaculture, the few published studies on its physiology and the lack of larvae and juvenile technological production currently limit the production potential of this species (Vega-Villasante et al. 2021).

In aquaculture, the use of starvation and refeeding strategies can reduce feeding time and production costs, leading to higher yields than continuous feeding (Fang et al. 2017), however, there is still a lack of understanding about the physiological response and health state of the Pacific fat sleeper exposed to starvation and its capacity to restore homeostasis after refeeding. Hence, it is hypothesized that the Pacific fat sleeper will be able to restore biochemical and physiological equilibrium when exposed to the same refeeding period as it was exposed to starvation because this species has shown a mechanism of upregulating metabolism under stress. Therefore, the present study aimed to evaluate the changes in somatic indices, body bromatological composition, blood chemistry, and hematological parameters of the Pacific fat sleeper (*D. latifrons*) exposed to different starvation and refeeding periods as a tool to understand biochemical and physiological adaptations of the species.

MATERIALS AND METHODS

Fish

Pacific fat sleeper (*D. latifrons*) juveniles were obtained from the Aguadulce-Ermitaño lagoon-estuarine system in Jalisco, Mexico. Capture was performed by artisanal fishing, using a 5×2 m trawl net with a 1 mm mesh grid. The organisms were trans-

ported to the Water Quality and Experimental Aquaculture Laboratory (LACUIC-CUCosta, by its Spanish acronym, University of Guadalajara) and placed in a 1,500 L tank connected to a recirculation system. The organisms (8.07 ± 0.79 cm and 11.44 ± 0.55 g) were subjected to a preventive chemical treatment (oxytetracycline 500 mg 500 L^{-1}) for 7 days to eliminate any pathogen that could compromise the health of the animals. After preventive treatment, the organisms were acclimatized for 30 days and were fed once a day (17:00 h) to satiety with commercial feed (30% protein and 8% lipids, Purina®). Dissolved oxygen and temperature were evaluated daily using a YSI 2030 multiparameter to maintain optimum ranges for the species. Water quality parameters were monitored weekly: average temperature 28.7 ± 1.4°C; salinity 1.0 ± 0.3; dissolved oxygen > 5.2 mg L^{-1}; and pH 7.8 ± 0.3.

Experimental design

Four treatments were established to evaluate the effects of starvation and refeeding on the nutritional condition and health status of *D. latifrons*: treatment 1 was used as control group (0W) with daily feeding throughout the experiment; in treatment 2 (2W), juveniles were exposed to starvation for two weeks, followed by two weeks of refeeding; in treatment 3 (3W), juveniles were exposed to starvation for 3 weeks, followed by 3 weeks of refeeding and, treatment 4 (4W), where juveniles were exposed for 4 weeks to starvation, followed by four weeks of refeeding (Fig. 1). All treatments began starvation at the same time. However, Figure 1 shows that the treatments are arranged according to the final day of starvation and the beginning of refeeding. A total of 360 juveniles (30.74 ± 1.13 g) were randomly distributed in 12 experimental tanks (30 juveniles per tank) with a 600 L water reservoir connected to aeration pumps. During starvation, 30% of the water in each tank was replaced daily. During refeeding, organisms were fed once a day (17:00 h) to apparent satiety. The previously mentioned commercial feed tanks were siphoned daily, and 30% of the water in each tank was replaced.

During the experiment, 5 organisms were sampled from each experimental unit: at the end of the starvation period (ESP), after one week of refeeding (1WR), and at the end of the refeeding period (ERP) to obtain biometric data tissues and blood samples. Fish management and sacrifice were carried out under the protocols established in the Official Mexican Standard "NOM-062-ZOO-1999, Technical specifications for producing, caring and using laboratory animals". Clove oil (200 µL L^{-1}) was used for sampling, as Aréchiga-Palomera et al. (2023) reported. The anesthetized fish were used to extract blood samples from the caudal vein with a 3 mL syringe without anticoagulant. Half of the sample (500 µL) was placed in a tube with EDTA-K2 as an anticoagulant and the other half in Eppendorf® vials without anticoagulant for further analysis. Then, the same organisms were returned to clove oil solution until death, and then, fish were dissected to obtain the weight of viscera, intestine, liver, mesenteric fat, and length of intestine, data used to calculate somatic indexes. Finally, muscle and liver samples were freeze-dried (SCIENTZ-10N) and stored at -20°C for subsequent bromatological analysis.

Somatic indexes

The somatic indexes were calculated as follows: condition factor (K): $(Wf / Lt^3) \times 100$; hepatosomatic index (HSI) = [liver weight (g) / Wf (g)] × 100; mesenteric fat index (MFI) = [mesenteric fat weight (g) / Wf (g)] × 100; viscerosomatic index (VSI) = [visceral weight (g) / Wf (g)] × 100; relative intestine length (RIL) = [Li (cm) / Lt (cm)] × 100; and Zihler index (ZI) = Li (mm) × [10 × (body mass (g) 1/3)]$^{-1}$; where Wf was the weight at the end of refeeding period (ERP); Lt is the total fish length and Li is the total intestine length at the ERP.

Bromatological analysis

AOAC (2015) methods were followed to determine the bromatological composition of muscle and liver; the moisture content was determined by drying in an oven at 105°C for 24 h and calculating the gravimetric difference. All analyses were performed and are reported on a dry weight basis. Total nitrogen was determined by the micro Kjeldahl method using an automatic distillation system VAPODEST 10s, Gerhardt, and an automatic titration system (TitroLine® 5000, SI Analytics). For protein quantification, the N factor = 6.25 was considered. The Soxhlet method was performed for lipid content, using petroleum ether as the extracting solution. Ash was determined by calcination of a sample in a muffle at 600°C for 6 h. The determination of the nitrogen-free extract (NFE) was calculated by the dry matter difference using the formula NFE = 100 - (% crude protein + % total lipids + % ash).

Blood chemistry and hematological parameters

Samples were collected without anticoagulant and centrifuged for 10 min at 2,000 *g* to evaluate blood chemistry. The supernatant was separated for albumin

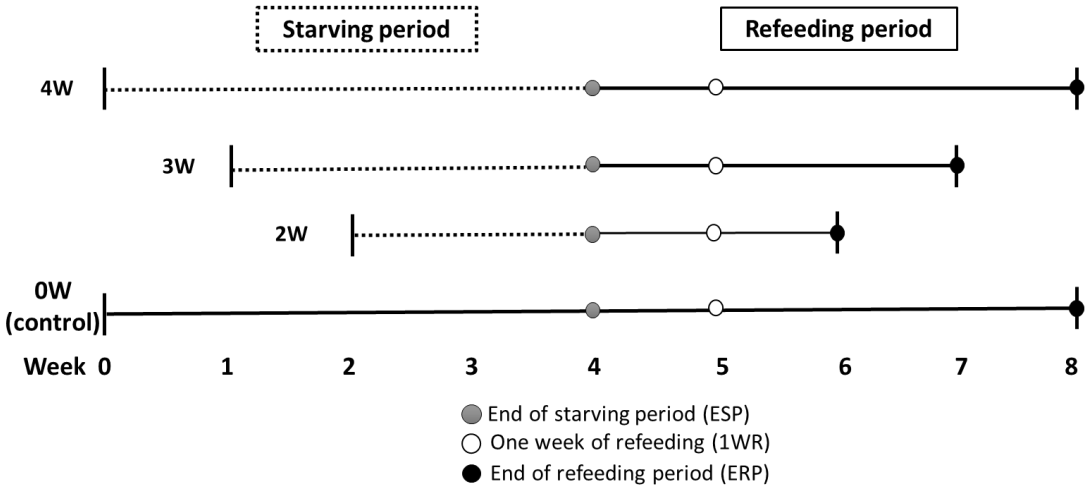

Figure 1. Experimental design of the starvation and refeeding trial in fat sleeper (*Dormitator latifrons*) juveniles. 0W: control group, juveniles with daily feeding throughout the experiment; 2W: juveniles exposed to starvation for 2 weeks, followed by 2 weeks of refeeding; 3W: juveniles exposed to starvation for 3 weeks, followed by 3 weeks of refeeding; and 4W: juveniles exposed to 4 weeks of starvation, followed by 4 weeks of refeeding.

quantification using the MexLab® kits (BCG, 620 nm), total protein (BIURET, 540 nm), glucose (God-Pad, 505 nm), total cholesterol (CHOD-PAP Valtek, 505 nm) and triglycerides (GPO-PAP Valtek, 510 nm). Globulin was calculated by the difference between total protein and albumin, and the albumin/globulin ratio (A/G) was also determined.

Hematological parameters were evaluated according to the method described by Ruíz-González et al. (2020). Samples for hematocrit (HCT), red blood cell count (RBC), white blood cell count (WBC), mean corpuscular volume (MCV), and respiratory burst were distributed in tubes with EDTA-K2 as an anticoagulant. For the HCT analysis, in glass capillaries, 60 µL of each sample was centrifuged at 4,000 *g* for 10 min (Scilogex DM1424c). The percentage of HCT was determined using a circular hematocrit reader. For RBC and WBC quantification, 20 µL of the sample was mixed with 4 mL of the Natt-Herrick solution, from which 5 µL of the solution was taken and placed in a Neubauer chamber. The analysis was performed by observation under a professional binocular microscope (Quasar Qm20 Binocular 2500x). MCV was calculated with the formula: MCV = (HCT × 10) / number of erythrocytes (million mm^3). For the respiratory burst, 100 µL of the sample was placed in 100 µL of a 0.2% nitro-blue tetrazolium (NBT) solution and incubated for 30 min at room temperature. Subsequently, 50 µL of the mixture was mixed with 1 mL of N,N-dimethylformamide, and centrifuged for 5 min at 2,000 *g*. The supernatant was recovered and analyzed by spectrophotometry (Velab, model VE- 5000V) at 620 nm (Ibrahem et al. 2010).

Growth and survival

At the ERP, during the final sampling process for each treatment, all remaining fish were sampled to record weight (g) and size (cm) using a digital scale (Ohaus® PR2201) and an ichthyometer, respectively. Weight gain was calculated using the total days of the experiment depending on the treatment (56 days for 0W and 4W treatments, 28 days for 2W treatment, and 42 days for 3W treatment). Weight gain was calculated as follows: WG (%) = [(Wf - Wi) / Wi] × 100. The specific growth rate was calculated using only the days corresponding to the feeding period of each treatment (56 days for 0W, 14 days for 2W treatment, 21 days for 3W treatment, and 28 days for 4W treatment) and with the following formula: SGR (% d^{-1}) = [(Ln Wf - Ln Wi) / t] × 100. The survival rate was calculated as SR (%) = (Nt / No) × 100. Ln means natural logarithm, Wf, and Wi were the weight at the ERP and initial fish weight, respectively; Nt was the initial number of fishes, and No was the final number of fishes at ERP; t was the duration of the experimental in days.

Statistical analysis

For somatic index, hematological parameters, blood chemistry, and bromatological data were subjected to normality (Shapiro-Wilk test) and homoscedasticity (Levine test) before conducting two-way ANOVA comparing the factor treatment (0W, 2W, 3W, and 4W) and factor period (ESP, 1WR, and ERP), and when differences were found a *post-hoc* Tukey test was applied ($P < 0.05$). Growth, SGR, and survival data

were also subjected to normality and homoscedasticity before conducting one-way ANOVA to determine the existence of differences between treatments ($P < 0.05$), where survival (%) was arcsin ($x^{1/2}$)-transformed before one-way ANOVA analysis. A *post-hoc* Tukey test was applied to identify the differences between treatments when necessary. All statistical analyses were performed using the Sigma Plot 12.0.

RESULTS

Somatic indexes

Somatic indexes of *D. latifrons* juveniles exposed to different starvation and refeeding periods are reported in Table 1. Differences among treatments in each period and differences among each treatment in different periods were not found in K and ZI values ($P > 0.05$). Also, no interaction between periods and treatments was found in K ($P = 0.126$) or ZI ($P = 0.088$).

Within periods at the ESP, the HSI showed no differences ($P > 0.05$). However, at 1WR and at the ERP, HSI was lower among treatments compared to the control (0W) ($P < 0.05$). Among the different periods, the treatments showed no differences ($P > 0.05$), and no interaction between periods and treatments was found ($P = 0.811$).

At the ESP, MFI values among treatments were significantly different ($P < 0.05$) with the lowest value in the 2W group. However, at 1WR, no differences were found between treatments ($P > 0.05$), and at ERP, the highest MFI value was found with the 2W treatment and the lowest values in the 3W and 4W treatments ($P < 0.05$). Among periods, MFI in the 2W treatment showed the highest value at ERP and the lowest value at ESP ($P < 0.05$). The 3W treatment showed the highest values at ESP and the lowest value at ERP ($P < 0.05$). The 0W and 4W treatments did not show differences at different periods ($P > 0.05$). However, an interaction between periods and treatments was found ($P = 0.002$).

The highest VSI values at the ESP were found with the 0W treatment ($P < 0.05$). Nevertheless, at 1WR, no differences were found between treatments ($P > 0.05$). Meanwhile, at ERP, the highest VSI value was found with the 0W treatment and the lowest with the 2W and 3W treatments ($P < 0.05$). At different periods, no differences were found between the treatments ($P > 0.05$), neither an interaction between periods nor treatments ($P = 0.275$).

RIL did not show differences among the treatments in each period. However, among periods, the highest RIL value was found with the 4W treatment at ERP and the lowest value in ESP ($P < 0.05$), and no interaction was found between periods and treatments ($P = 0.173$).

Bromatological analysis

Bromatological analysis of muscle and liver of *D. latifrons* juveniles exposed to different starvation and refeeding periods are shown in Figure 2. At the ESP, the lowest values of total protein in muscle were registered with the 0W and 4W treatments, and the highest values were found with the 2W and 3W treatments ($P < 0.05$). At 1WR, the lowest value was found with the 0W treatment and the highest value with the 2W treatment ($P < 0.05$), and at the ERP, the lowest value was found with the 0W treatment ($P < 0.05$). Among periods, muscle protein in the 0W treatment showed the highest values at ESP and ERP, and the lowest value in the 1WR treatment ($P < 0.05$). The 2W treatment showed the highest values at ESP and 1WR and the lowest value in ERP ($P < 0.05$), and the 3W treatment showed the highest value at ESP and the lowest values at 1WR and ERP ($P < 0.05$). The 4W treatment showed the highest values at ERP and the lowest value at 1WR ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$) (Fig. 2a).

Total lipids in muscle are shown in Figure 2b. At the ESP and 1WR, the lowest total lipid values were found in the 2W treatment ($P < 0.05$). However, the lowest value was observed at the ERP in the 0W treatment ($P < 0.05$). Among the periods, muscle lipids in the 0W treatment were higher at 1WR and lower at ESP and ERP ($P < 0.05$). The 2W treatment produced the highest values at ERP and the lowest value at ESP and 1WR ($P < 0.05$). In the 3W treatment, the highest value was found at ERP and the lowest value at ESP ($P < 0.05$). The 4W treatment showed the highest values at ESP and ERP, while the lowest was at 1WR ($P < 0.05$). An interaction between periods and treatments was found ($P < 0.001$).

At the ESP, the highest value was found with the 0W treatment ($P < 0.05$). At 1WR and ERP, the highest value was registered for 0W treatments and the lowest values for 2W and 3W treatments ($P < 0.05$). NFE did not show differences within treatments among periods ($P > 0.05$), and interaction between periods and treatments was not found ($P = 0.148$) (Fig. 2c).

Total ash content is shown (Fig. 2d). At the ESP, the highest significant value was found with the 3W treatment ($P < 0.05$). At 1WR, the lowest value was registered with the 2W treatments ($P < 0.05$), and at the

Table 1. Somatic indexes of Pacific fat sleeper (*Dormitator latifrons*) juveniles exposed to different starvation and refeeding. ESP: end of starvation period; 1WR: 1 week of refeeding; ERP: end of refeeding period. K: condition factor; HSI: hepatic somatic index; MFI: mesenteric fat index; VSI: viscerosomatic index; RIL: relative intestine length; and ZI: Zihler index. Lower-case letters show differences between treatments in the same period; upper-case letters show differences in the same treatment at different periods. The results are presented as mean ± standard deviation. n = 5. 0W: control group, juveniles with daily feeding throughout the experiment; 2W: juveniles exposed to starvation for 2 weeks, followed by 2 weeks of refeeding; 3W: juveniles exposed to starvation for 3 weeks, followed by 3 weeks of refeeding; and 4W: juveniles exposed to 4 weeks of starvation, followed by 4 weeks of refeeding.

	Treatment	K	HSI	MFI	VSI	RIL	ZI
ESP	0W	1.45 ± 0.03	3.48 ± 0.86^{a}	1.75 ± 0.39^{a}	9.30 ± 1.35^{a}	1.95 ± 0.30	7.84 ± 0.74
	2W	1.44 ± 0.04	2.50 ± 0.47^{b}	0.75 ± 0.42^{b,B}	7.06 ± 0.60^{b}	1.88 ± 0.27	7.96 ± 3.46
	3W	1.29 ± 0.13	2.64 ± 0.18^{b}	1.59 ± 0.39^{a,A}	6.85 ± 0.49^{b}	1.59 ± 0.10	7.80 ± 1.20
	4W	1.30 ± 0.04	3.06 ±0.64^{ab}	1.45 ± 0.30^{ab}	7.32 ± 0.35^{b}	1.50 ± 0.13^{B}	5.33 ± 0.97
1WR	0W	1.46 ± 0.01	3.28 ± 0.15^{a}	1.48 ± 0.25	8.79 ± 0.64	1.60 ± 0.17	7.39 ± 1.39
	2W	1.36 ± 0.09	2.90 ± 0.38^{b}	1.24 ± 0.49^{AB}	7.55 ± 1.02	1.50 ± 0.11	5.85 ± 0.65
	3W	1.29 ± 0.13	2.86 ± 0.57^{b}	1.19 ± 0.16^{AB}	8.28 ± 0.59	1.66 ± 0.11	6.20 ± 1.13
	4W	1.28 ± 0.10	2.63 ± 0.55^{b}	1.05 ± 0.27	7.65 ± 1.12	1.72 ± 0.18^{AB}	7.60 ± 0.51
ERP	0W	1.51 ± 0.05	3.83 ± 0.90^{a}	1.47 ± 0.47^{a}b	10.73 ± 0.58^{a}	2.27 ± 0.53	11.08 ± 2.13
	2W	1.30 ± 0.08	2.71 ± 0.38^{b}	1.40 ± 0.16^{a,A}	8.39 ± 0.93^{b}	1.58 ± 0.35	6.00 ± 1.51
	3W	1.36 ± 0.02	2.94 ± 0.51^{b}	0.77 ± 0.11^{b,B}	8.48 ± 0.35^{b}	1.81 ± 0.25	7.48 ± 0.66
	4W	1.46 ± 0.08	2.83 ± 0.41^{b}	0.93 ± 0.10^{ab}	9.74 ± 0.50^{ab}	2.04 ± 0.44^{A}	9.23 ± 1.70

ERP, the 3W treatment produced the highest value ($P < 0.05$). Among periods, total ash in the 0W treatment showed the highest values at 1WR ($P < 0.05$). The 2W treatment did not show differences among periods ($P > 0.05$), the 3W treatment produced the highest value at ESP ($P < 0.05$), and, with the 4W treatment, the highest values at 1WR ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

At the ESP, the highest value in the 4W treatment ($P < 0.05$). At 1WR, the highest values were registered for 2W and 4W treatments ($P < 0.05$). The highest value was found at ERP with 2W treatment ($P < 0.05$). Among periods, total hepatic lipids with the 0W treatment showed the highest values at ESP ($P < 0.05$). The 2W treatment showed the highest values at 1WR and the lowest value at ESP ($P < 0.05$). The 3W and 4W treatments showed the highest value at ESP and the lowest value at ERP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$) (Fig. 2e).

Blood chemistry

Blood chemistry parameters of *D. latifrons* juveniles exposed to different starvation and refeeding periods are shown (Fig. 3). Serum protein at the ESP showed the highest values with the 4W treatment ($P < 0.05$). At 1WR, the highest value was registered with the 3W treatment ($P < 0.05$). At ERP, no differences were found between treatments ($P > 0.05$). Among periods, the 0W treatment showed the highest values at 1WR and the lowest value at ESP ($P < 0.05$). The 2W treatment did not show differences among the different periods ($P > 0.05$), and the 3W treatment showed the highest value at 1WR ($P < 0.05$). The 4W treatment showed the highest values at ESP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

Triglycerides are shown (Fig. 3b). At the ESP, triglycerides did not show differences between treatments ($P > 0.05$). At 1WR, the highest values were found with the 0W treatment and the lowest in the 2W treatment ($P < 0.05$). At ERP, the highest values were found with the 3W treatment and the lowest value in the 2W treatment ($P < 0.05$). Among periods, the 0W treatment showed the highest values at 1WR and the lowest value at ESP ($P < 0.05$). The 2W treatment did not show differences among the periods ($P > 0.05$). The 3W and 4W treatments showed the highest values at ERP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

Glucose is shown (Fig. 3d), where at the ESP, the highest value was found with the 4W treatment and the

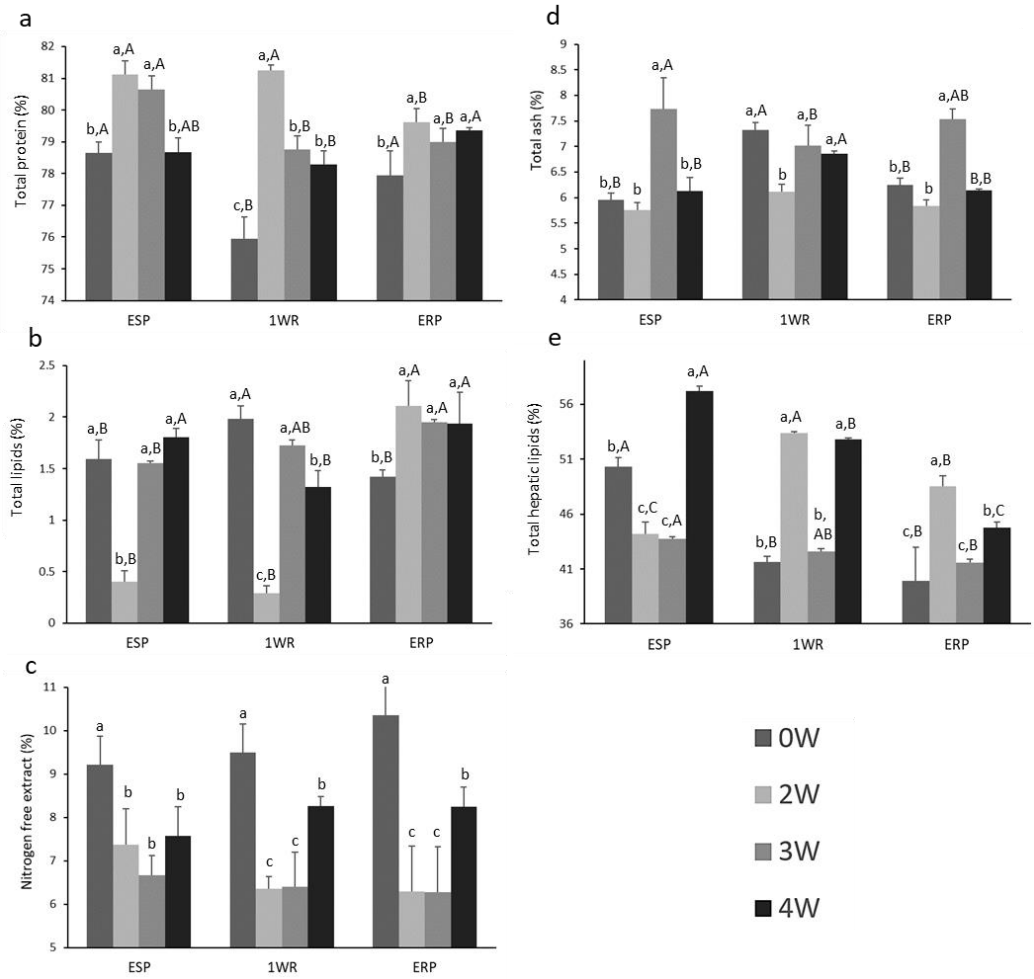

Figure 2. Bromatological analysis of muscle a) protein, b) lipids, c) nitrogen free extracts, d) ash and e) lipids in liver of Pacific fat sleeper (*Dormitator latifrons*) juveniles exposed to different starvation and refeeding periods. ESP: end of starvation period; 1WR: 1 week of refeeding; ERP: end of refeeding period. Lower-case letters show differences between treatments in the same period; upper-case letters show differences in the same treatment at different periods ($P < 0.05$). Values are shown as mean ± standard deviation. n = 3. 0W: control group, juveniles with daily feeding throughout the experiment; 2W: juveniles exposed to starvation for 2 weeks, followed by 2 weeks of refeeding; 3W: juveniles exposed to starvation for 3 weeks, followed by 3 weeks of refeeding; and 4W: juveniles exposed to 4 weeks of starvation, followed by 4 weeks of refeeding.

lowest value with the 2W and 3W treatments ($P < 0.05$). At 1WR, the lowest value with the 2W treatment ($P < 0.05$). At ERP, the highest value was registered with the 0W treatment, and the lowest values were registered with the 3W and 4W treatment ($P < 0.05$). Among periods, the 0W and 2W treatments showed the highest values at the ERP ($P < 0.05$). The lowest value was found with the 3W treatment at ESP ($P < 0.05$). Nonetheless, the 4W treatment showed the highest value at ESP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$). Cholesterol and albumin are shown (Figs. 3c,e), where no differences were found between treatments at the different periods ($P > 0.05$).

Globulins are shown (Fig. 3f). At the ESP, the highest value was found with the 4W treatment and the lowest with 2W ($P < 0.05$). However, at 1WR, the highest values were recorded with the 3W treatment ($P < 0.05$). At ERP, no differences were found between treatments ($P > 0.05$). Among periods, 0W and 2W treatments did not show differences ($P > 0.05$). However, the 3W treatment showed the highest value at 1WR ($P < 0.05$), and the 4W treatment showed the highest value at ESP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

The A/G ratio is shown (Fig. 3g). At the ESP, the highest values were found with the 2W and 3W treat-

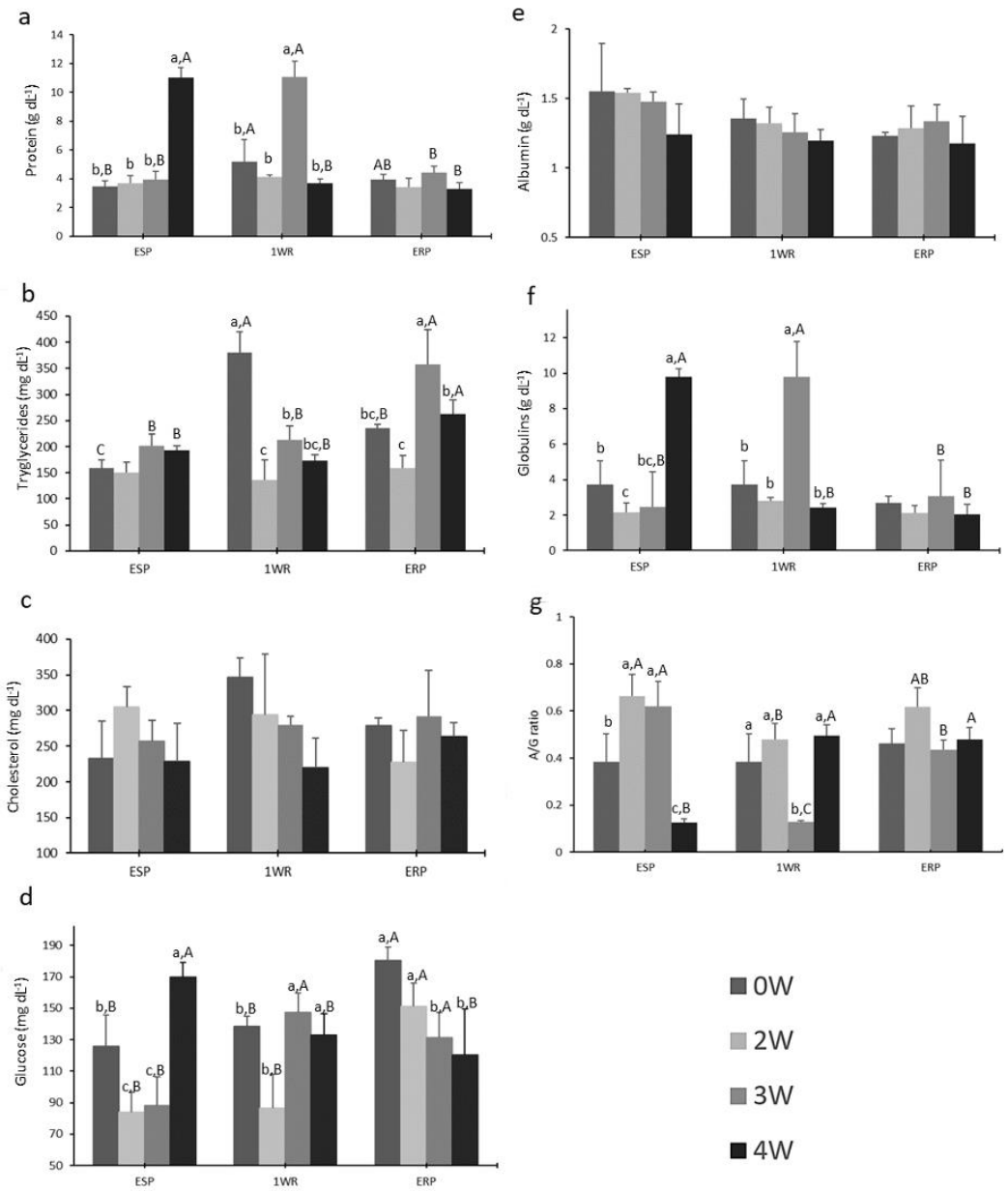

Figure 3. Blood chemistry of Pacific fat sleeper (*Dormitator latifrons*) juvenile exposed to different starvation and refeeding periods; a) protein, b) cholesterol, c) triglycerides, d) glucose, e) albumin, f) globulins and g) albumin/globulins (A/G) ratio. ESP: end of starvation period; 1WR: 1 week of refeeding; ERP: end of refeeding period. Lower-case letters show differences between treatments in the same period; upper-case letters show differences in the same treatment at different periods ($P < 0.05$). Values are shown as mean ± standard deviation. n = 5. 0W: control group, juveniles with daily feeding throughout the experiment; 2W: juveniles exposed to starvation for 2 weeks, followed by 2 weeks of refeeding; 3W: juveniles exposed to starvation for 3 weeks, followed by 3 weeks of refeeding; and 4W: juveniles exposed to 4 weeks of starvation, followed by 4 weeks of refeeding.

ments and the lowest value with the 4W treatment ($P < 0.05$). At 1WR, the lowest value with the 3W treatment ($P < 0.05$). However, at ERP, no differences were found between treatments ($P > 0.05$). Among the periods, the 0W treatment did not show differences ($P > 0.05$). The 2W and 3W treatments showed the highest values at ESP and the lowest values with the 1WR treatment ($P < 0.05$). The 4W treatment showed the lowest value at ESP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

Table 2. Hematological parameters of Pacific fat sleeper (*Dormitator latifrons*) juveniles exposed to different starvation and refeeding periods. ESP: end of starvation period; 1WR: 1 week of refeeding; ERP: end of refeeding period. RBC: red blood cell; WBC: white blood cell; MCV: mean corpuscular volume; NBT: nitro-blue tetrazolium. Lower-case letters show differences between treatments in the same period; upper-case letters show differences in the same treatment at different periods. The results are presented as mean ± standard deviation. n = 5. 0W: control group, juveniles with daily feeding throughout the experiment; 2W: juveniles exposed to starvation for 2 weeks, followed by 2 weeks of refeeding; 3W: juveniles exposed to starvation for 3 weeks, followed by 3 weeks of refeeding; and 4W: juveniles exposed to 4 weeks of starvation, followed by 4 weeks of refeeding.

Treatment		Hematocrit (%)	RBC × 10^6 (cells mm^{-3})	WBC × 10^3 (cells mm^{-3})	MCV (fL)	NBT
ESP	0W	$30.33 \pm 2.52^{ab,B}$	$3.41 \pm 0.25^{a,B}$	13.8 ± 0.25^{b}	88.11 ± 6.86^{b}	$0.31 \pm 0.03^{a,AB}$
	2W	$27.00 \pm 2.00^{b,B}$	$2.26 \pm 0.26^{b,B}$	$30.5 \pm 9.5^{a,A}$	$77.81 \pm 17.71^{b,B}$	$0.18 \pm 0.57^{bc,B}$
	3W	34.00 ± 1.00^{a}	$3.04 \pm 0.34^{ab,B}$	11.3 ± 0.2^{b}	86.94 ± 7.8^{b}	$0.15 \pm 0.03^{c,B}$
	4W	$28.00 \pm 0.0^{b,C}$	$2.80 \pm 0.04^{ab,C}$	$14.5 \pm 2.00^{b,A}$	$108.9 \pm 72.1^{a,A}$	0.30 ± 0.04^{ab}
1WR	0W	$43.67 \pm 3.79^{a,A}$	$4.67 \pm 0.14^{ab,A}$	8.30 ± 1.20^{b}	87.37 ± 0.13^{a}	$0.4 \pm 0.10^{a,A}$
	2W	$31.11 \pm 1.17^{c,B}$	$5.17 \pm 0.035^{a,A}$	$8.50 \pm 1.30^{b,C}$	$69.12 \pm 9.45^{b,B}$	$0.19 \pm 0.03^{b,B}$
	3W	37.00 ± 1.00^{b}	$4.47 \pm 0.5^{ab,A}$	15.00 ± 2.00^{ab}	83.90 ± 0.18^{ab}	$0.35 \pm 0.08^{a,B}$
	4W	$33.17 \pm 0.76^{bc,B}$	$4.26 \pm 1.18^{b,B}$	$15.50 \pm 0^{a,A}$	$78 \pm 5.03^{b,B}$	0.30 ± 0.01^{a}
ERP	0W	34.33 ± 1.53^{B}	5.02 ± 0.60^{A}	10.00 ± 1.00^{b}	73.97 ± 3.66^{b}	$0.19 \pm 0.05^{b,B}$
	2W	38.33 ± 2.31^{A}	4.62 ± 0.62^{A}	$20.50 \pm 2.00^{a,B}$	$95.98 \pm 3.48^{a,A}$	$0.35 \pm 0.86^{a,A}$
	3W	36.00 ± 2.00	4.93 ± 0.51^{A}	10.50 ± 1.50^{b}	85.77 ± 1.79^{ab}	$0.34 \pm 0.04^{a,A}$
	4W	38.33 ± 2.87^{A}	5.24 ± 0.14^{A}	$4.50 \pm 0.50^{b,B}$	$68.30 \pm 6.22^{b,B}$	0.21 ± 0.04^{b}

Hematological parameters

Hematological parameters of *D. latifrons* juveniles exposed to different periods and treatments are reported (Table 2). At the ESP, HCT showed the highest value with the 3W treatment and the lowest with the 2W and 4W treatments ($P < 0.05$). At 1WR, the highest value was registered with the 0W treatment, and the lowest was with the 2W treatment ($P < 0.05$). At ERP, no differences were found between treatments ($P > 0.05$). Among periods, the 0W treatment showed the highest value at 1WR ($P < 0.05$). The 2W treatment showed the highest value at ERP ($P < 0.05$). The 3W treatment did not show differences ($P > 0.05$), while the 4W treatment showed the highest values at ERP and the lowest values at ESP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

At the ESP, RBC was higher in the 0W treatment and lower in the 2W treatment ($P < 0.05$). At 1WR, the highest value was registered with the 2W treatment and the lowest with the 4W treatment ($P < 0.05$). At ERP, no differences were found between treatments ($P > 0.05$). Among the periods, the 4W treatment showed the lowest value at ESP ($P < 0.05$). The 4W treatment showed the highest values at ERP and the lowest value at ESP ($P < 0.05$), finding an interaction between periods and treatments ($P = 0.003$).

The highest WBC value was observed with the 2W treatment ($P < 0.05$) at the ESP. However, at 1WR, the highest value was registered with the 4W treatment and the lowest values with the 0W and 2W treatments ($P < 0.05$). At ERP, the highest value was registered for the 2W treatment ($P < 0.05$). Among periods, 0W and 3W treatments did not show differences ($P > 0.05$). The 2W treatment showed the highest value at ESP and the lowest values with 1WR ($P < 0.05$), while the 4W treatment showed the lowest values at ERP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

After the ESP, the MCV showed the highest value with the 4W treatment ($P < 0.05$). At 1WR, the highest value was registered for the 0W treatment and the lowest values with 2W and 4W treatment ($P < 0.05$), while at ERP, the highest value was found for the 2W treatment and the lowest values with 0W and 4W treatments ($P < 0.05$). Among periods, 0W and 3W treatments did not show differences ($P > 0.05$). The 2W treatment showed the highest value at ERP ($P < 0.05$), while the 4W treatment showed the highest values at

Table 3. Growth performance and survival of Pacific fat sleeper (*Dormitator latifrons*) juveniles at the end of the refeeding period. Letters in the same column show differences between treatments ($P < 0.05$). The results are presented as mean ± standard deviation. n = 3. WG: weight gain, SGR: specific growth rate. *WG calculated using the trial period according to each treatment. **SGR calculated using the total days of refeeding, according to each treatment. 0W: control group, juveniles with daily feeding throughout the experiment; 2W: juveniles exposed to starvation for 2 weeks, followed by 2 weeks of refeeding; 3W: juveniles exposed to starvation for 3 weeks, followed by 3 weeks of refeeding; and 4W: juveniles exposed to 4 weeks of starvation, followed by 4 weeks of refeeding.

Treatment	*WG (%)	**SGR (% d^{-1})	Survival (%)
0W	7.60 ± 1.47^{a}	0.44 ± 0.02^{a}	100.00 ± 0.00
2W	-4.96 ± 0.69^{d}	-0.18 ± 0.31^{b}	98.89 ± 1.92
3W	5.92 ± 0.35^{c}	0.34 ± 0.11^{ab}	97.78 ± 1.92
4W	16.84 ± 2.05^{b}	0.40 ± 0.27^{ab}	95.56 ± 7.70

ESP ($P < 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

At the ESP, NBT showed the highest value at 0W and the lowest with the 3W treatment ($P < 0.05$). At 1WR, the lowest value was observed with the 2W treatment ($P < 0.05$), while at ERP, the highest values were found with 2W and 3W treatments and the lowest values with 0W and 4W treatment ($P < 0.05$). Among periods, the 0W treatment showed the highest value at 1WR and the lowest value at ERP ($P < 0.05$). The 2W and 3W treatments showed the highest values at ERP ($P < 0.05$), while the 4W treatment did not show differences ($P > 0.05$), finding an interaction between periods and treatments ($P < 0.001$).

Growth and survival

WG was different in all treatments ($P < 0.05$). The 0W treatment (control) showed the highest WG value, while the 2W treatment showed the lowest value. SGR did not show differences between 0W, 3W, and 4W, with the 2W treatment having the lowest SGR value ($P < 0.05$). Survival did not show differences among treatments ($P > 0.05$) (Table 3).

DISCUSSION

The liver is a source of energy reserves, storing glycogen and lipids. Therefore, a liver reduction indicates depletion of reserves because of the mobilization of energy resources for metabolism maintenance during a short starvation period (Cassidy et al. 2018). In the present study, 2 starving weeks generated the lowest values of HSI and MFI in *D. latifrons*. In channel catfish subjected to 4 weeks of fasting, the somatic indices were lower than those of the control (Bosworth & Wolters 2005). Hence, *D. latifrons* facing short-term starvation compensate for the lack of energy through the catabolism of mesenteric fat and fat liver reserves. In the same period, the 3W and 4W treatments showed higher values compared to the 2W treatment. We could suggest that the total weight decreases with longer starvation periods, where the first energy source comes from the liver and the mesenteric fat during the first 2 weeks of starvation in *D. latifrons*. Hence, higher levels of HSI and MFI in 3W and 4W correspond to the relative proportion of energy storage distribution at different starvation periods, as reported in yellowcheek (*Elopichthys bambusa*) (Xie et al. 2023). The starvation period determines the metabolic machinery that is active in the liver (Metón et al. 2003, Li et al. 2018a). Transcriptomic studies in yellowcheek show that 8 days of starvation generate the downregulation of genes associated with glycolysis/gluconeogenesis, citrate cycle, fatty acid biosynthesis, pentose phosphate, and N-glycan biosynthesis in the liver. However, after 28 days of starvation, these metabolic processes are reactivated (Xie et al. 2023). In gilthead seabream (*Sparus aurata*), the fructose-1,6-bisphosphatase (FBPase-1), a key enzyme in gluconeogenesis, increases its activity after 18 days of starvation and restores its reference levels before 20 days of refeeding (Metón et al. 2003).

The apparent reduction of RIL and ZI (without statistical differences) at the ESP in 4W treatment represents a modification of the weight and longitude of the intestine. Reports in Arctic charr (*Salvelinus alpinus*) showed the same tendency for intestinal somatic index recovery before reflecting a partial compensatory growth (Cassidy et al. 2018). The digestive somatic index decreases in sturgeon (*Acipenser*

naccarii) and rainbow trout (*Oncorhynchus mykiss*) after 72 days of starvation, although both species showed recovery after 60 days of refeeding (Furné et al. 2008). In Dabry's sturgeon (*Acipenser dabryanus*), the intestinal weight and length decrease after 14 days of starvation without recovery after 14 days of refeeding (Wu et al. 2021). Studies in herbivorous grass carp (*Ctenopharyngodon idella*), omnivorous channel catfish (*Ictalurus punctatus*), and carnivorous large-mouth bass (*Micropterus salmoides*) exposed to a short fasting period (7-10 days) followed by refeeding confirm that intestine experiences structural changes in the epithelium, including some degree of intestinal atrophy with shorter villi and a mucosa/submucosal decrease, reducing the effective intestinal surface area and hence may lessen performance, as an adaptative step to reduce energy maintenance coast (Day et al. 2014).

Ruíz-González et al. (2020) reported glucose levels of 51.467 mg dL^{-1} and protein levels of 3.936 ± 0.840 g dL^{-1} in wild catch *D. latifrons* juveniles previously fed for 30 days and three times a day with Purina® brand commercial diet (3.5 particle size with 35% protein, 8% fat). In the present study, fish at the ESP exposed to the 4W treatment showed the highest glucose value (~170 mg dL^{-1}), which concurs with high serum protein levels (~11 g dL^{-1}), around 3-fold higher than those values with 2W and 3W treatments. During starvation, glucose comes from glycogen by glycogenolysis or from non-glycoside substrates, such as lactate, glycerol, pyruvate, and some amino acids by gluconeogenesis (Polakof et al. 2012, Favero et al. 2017, Cassidy et al. 2018). The results of NFE in the muscle of *D. latifrons* always show a high level in 0W treatment, which may partially correspond to glycogen muscular reserves, which showed a depletion in all starvation treatments at the ESP. The high serum protein level found in *D. latifrons* at ESP exposed to treatment 4W comes from muscle reserves compared to 2W and 3W. However, 0W and 4W show the same muscle protein values. Nevertheless, these two treatments were in different nutritional conditions, where the 0W treatment presented higher muscular lipids and NFE reserves that had not yet been depleted.

Secor & Carey (2016) mention that switching from lipid to amino acid catabolism is a characteristic of a critical health status. On the contrary, fishes exposed to 2W and 3W produced the lowest glucose and serum protein levels at ESP, which agree with the lower hepatic lipid levels in both treatments, showing resistance to low levels of serum glucose during this starvation phase and the use of lipidic reserves. In this sense, blood triglycerides during the starvation showed no differences. Then, the use of lipids as an energy source is reinforced since the catabolism of triglycerides promotes the formation of ketone bodies from acetylCoA as characterized in sturgeon and common dentex (*Dentex dentex*) (Furné et al. 2012, Pérez-Jiménez et al. 2012).

Many studies characterize the metabolic energy mobilization aspects under starvation of fish; however, the high diversity of fish depending on feeding behaviors and adaptations is reflected in the high diversity of energetic metabolism under starvation and mainly depends on the specific fish strategy. Even glycogen levels in the liver and muscle were not measured, as reported in other fish species (Secor & Carey 2016, Favero et al. 2017, Dai et al. 2022); during the initial starvation period, *D. latifrons* used hepatic and/or muscle glycogen reserves as the main energy source, as previously reported in black carp (*Mylopharyngodon piceus*) (Dai et al. 2022). During the second and third starvation weeks, lipids from muscle and liver were used as the main source, and during the third and fourth starvation weeks, the use of endogenous protein to produce glucose as energy was observed. The increase in hepatic lipid levels registered in the 4W treatment at ESP agrees with reports in black seabream (*Acanthopagrus schlegeli*) (Deng et al. 2004) and common dentex (Pérez-Jiménez et al. 2012). It could be associated with the accumulation of lipids that became from lipogenesis by an excess of synthesized glucose (Polakof et al. 2012) or maybe from a hepatic re-esterification process in the liver into very low-density lipoproteins from free fatty acids derived from adipose tissue hydrolysis (Pérez-Jiménez et al. 2012).

The 1WR period is a key point in comparing the effect of the different starvation periods within the experimental design, where it is denoted that organisms can return to homeostasis in a short period. In this case, at 1WR, serum protein, glucose, triglycerides, total muscle protein, and total muscle lipid showed high variability between treatments, denoting that after refeeding, the return to homeostasis will depend on the time to replenish the energy expended during starvation. However, at the ERP, these parameters showed values like those registered with treatment 0W, where the glucose levels stabilize in all starvation treatments.

Serum proteins are divided into two groups (albumin and globulins); where albumin is required for transportation of organic substances with an important role in binding fatty acids and keeping them in a soluble form in the plasma, while globulins are essential for maintaining a healthy immune system (Kumar et al.

2013, Kulkarni 2021). No statistical differences were found in albumin levels at ESP. Meanwhile, globulin peaks (~10 g dL^{-1}) were detected with the 4W treatment. These results could be related to an increase in the innate immunity response that does not necessarily reflect the compromise of the physiological and health condition of fish, only reflecting the exposure to nutritional stress. At 1WR, another peak (~10 g dL^{-1}) in 3W treatment was registered; nevertheless, at the ERP, both parameters returned to normal levels in agreement with previous reports in the species (1.906; 2.391 g dL^{-1}, albumin, and globulins, respectively) (Ruíz-González et al. 2020).

RBCs function as gas transporters in blood, where hematocrit reduction during starvation could result from erythropoiesis depression (McCue 2010, Sakyi et al. 2020). Prolonged starvation in Trahira (*Hoplias Malabaricus*) affected blood parameters, where erythropoiesis decreased during the first 30 days of food deprivation and remained low even after 240 days of starvation, where the pre-existent red blood cells showed senescence and were not replaced during starvation (Rios et al. 2005). Previous reports in *D. latifrons* show hematocrit values of 39.1 ± 6.1% (Todd 1972), 28% (Ruíz-González et al. 2020), 32 to 36% between different density treatments without differences (Badillo-Zapata et al. 2022) and 42.7 ± 10% for males and 43.1 ± 8.8% for females, showing that hematological parameters depend on size and weight, where larger fish show higher values and smaller fish show lower values (Santana-Piñeros et al. 2023). Hence, hematocrit percentages between 34 and 38 could be considered a range for the species under constant feeding conditions for at least 2 weeks. RBC changes could be associated with changes in metabolic levels as a marker of oxygen transfer efficiency from respiratory organs to the tissues (Rahmati et al. 2016); therefore, starvation from 2 to 4 weeks induces a metabolic reduction in *D. latifrons* that restored at the first week of refeeding.

WBCs functions are defense and immunity (Sakyi et al. 2020). At the ESP, the highest WBC value was observed with the 2W treatments ($30.5 \pm 9.5 \times 10^3$ mm^3), which may result from starvation (stress). However, high variability was found without a clear tendency for starvation and refeeding. The MCV values in the present study are lower than previous reports, with values of 122.8 ± 7.0 (Todd 1972), 161.5 ± 34.9 (Ruíz-González et al. 2020) and 153.6 ± 44.9 for females and 152.7 ± 41.8 for males, with lower values associated to smaller fishes independent to sex (Santana-Piñeros et al. 2023). Although our results show lower values, the hematological parameters depend on several parameters such as size and weight, age, stress status, nutritional status, sexual maturity, water quality, temperature, oxygen level, and stocking density, among others (Fazio 2018, Santana-Piñeros et al. 2023). The NBT is used to evaluate the respiratory burst, which is used as a tool to reflect the immune response to disease or stress (Ruíz-González et al. 2020, Badillo-Zapata et al. 2022). The values reported in the present study are in the range of previous reports (Ruíz-González et al. 2020). At the ESP, the 2W and 3W treatments showed the lowest values, however, these treatments increase NBT values at ERP, representing an increase in the respiratory burst activity, providing a greater protection against infectious diseases.

Even though growth parameters were not the main objective of the present study, the results show that *D. latifrons* juveniles subjected to long-term starvation and refeeding periods show a physiological adaptation and recovery by a partial compensatory growth at the ERP compared to the control. In contrast, juveniles exposed to shorter starvation and refeeding periods (2 weeks) did not recover. Compensatory growth refers to a growth burst, usually induced by a period of reduced or no food availability (Secor & Carey 2016), which can occur partially when food-restricted fish exhibit accelerated growth after restarting normal feeding but do not reach the same body mass compared to continuously fed fish, which depends on the time of fasting and refeeding to which it is subjected, as well as, on the ability of the species to respond (Ali et al. 2003).

This compensatory growth phenomenon has been reported in *D. latifrons* when fishes decrease feed intake because of stress and depression caused by ectoparasite infection (*Argulus* sp.). After infection and treatment, when fish reach a normal healthy state, they recover their normal weight after 2 months (Vega-Villasante et al. 2017). Although the SGR after 3-4 weeks of refeeding was similar to that of the control, we can consider only a partial compensatory growth, since not even 4 weeks of refeeding were enough to obtain a WG similar to that of the control. Our results agree with those reported for hybrid striped bass (*Morone chrysops* × *Morone saxatilis*), where partial compensatory growth is reported after 1, 2, and 3 weeks of starvation and fed to satiation twice a day during the refeeding period (Turano et al. 2007). However, the opposite case was reported for grass carp (*Ctenopharyngodon idellus*) (Li et al. 2018b) and roach (*Rutilus caspicus*) (Abolfathi et al. 2012) fasted for 3 and 5 weeks of refeeding, where organisms did not

equal the growth values of the control group, showing the low capacity of these organisms to face long periods of fasting.

By examining the biochemical and physiological changes in *D. latifrons* during different periods of starvation and refeeding, this study offers insights into the species' nutritional and health condition, particularly its capacity to regulate glucose homeostasis. In conclusion, *D. latifrons* exposed to short-term starvation use hepatic and mesenteric fat reserves, increasing cholesterol plasma levels and maintaining triglyceride levels. However, gluconeogenesis was activated during the fourth starving week, representing the beginning of the long-term starving period using muscular protein as energy reserves. Nonetheless, all treatments tend to restore somatic indices, blood chemistry, and hematological parameters at the ERP. A tendency of an intestinal size decrease was found with the increase of the starvation period, denoted by the RIL and ZI values; however, in the 4W treatment, it was observed that the refeeding generated recovery from the first week. Hematological parameters such as hematocrit, RBC, albumin, and respiratory burst are not compromised under short and long-term starvation. However, with the 4W treatment at ESP, globulins increase while at ERP, the WBCs decrease, results that could reflect a long-term starvation break point, compromising *D. latifrons*'s health. The species shows partial compensatory growth under long-term starvation and refeeding, an effect not found in shorter starvation and refeeding periods.

Credit author contribution

K.N. Nieves-Rodríguez: conceptualization, methodology, formal analysis, investigation, writing an original draft; F. Vega-Villasante: investigation, funding acquisition, and review & editing; C.A. Álvarez-González: resources, methodology, and review and editing; M. Aréchiga-Palomera: methodology and formal analysis; L.E. Ruíz-González: investigation and formal analysis; D. Badillo-Zapata: resources, investigation, and review and editing; E.S. Peña-Marín: writing-conceptualization, project administration, and review and editing.

Conflict of interest

The authors have no conflicts of interest to declare regarding this work.

Data availability

Data are available upon request from the corresponding author.

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Ethical considerations

This study was carried out at the Laboratorio de Calidad de Agua y Acuicultura Experimental (LACUIC-CUCOSTA) of the Universidad de Guadalajara (UdG) and approved by the Animal Welfare Committee (CUCPV/ CBA/01/2023).

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