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Response to Hyperthermia and Hypoxia Stress during Compensatory Growth in *Penaeus vannamei*

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Abstract

This study evaluated oxidative stress and resistance to abiotic stress factors of juvenile *Penaeus vannamei* during compensatory growth. Shrimp underwent two dietary treatments in a 50-day experiment: a reference group (REF) fed *ad libitum* and a restricted group (T50) fed 50% of the REF diet for 10 days, followed by 40 days of *ad libitum* refeeding. During refeeding, shrimp from both groups were exposed to two abiotic challenges: 1) hyperthermia (34°C) for 12 hours and 2) hypoxia (1.5 mgO_2 L^{-1}) for 9 hours, followed by reoxygenation for 3 hours (5 mgO_2 L^{-1}). Compensatory growth in the T50 group was evidenced by increased specific growth rate, hyperphagia, and improved feed efficiency. Moreover, the malondialdehyde content (MDA) and catalase activity in the shrimp hepatopancreas increased during compensatory growth, indicating oxidative stress. This result converges with the increased metabolism assessed by metabolic chambers. While hyperthermia caused oxidative stress, as indicated by the increase in MDA content in both groups, shrimp under compensatory growth demonstrated similar resistance to the REF group. Exposition to hypoxia and reoxygenation did not generate significant oxidative stress. Compensatory growth induced oxidative stress in *P. vannamei* without compromising resistance to hyperthermia or hypoxia events.

Introduction

The Pacific white shrimp, *Penaeus vannamei*, is the most widely farmed aquaculture species, with production reaching 5.8 million tonnes in 2020 (FAO, 2022). Between 2015 and 2020, its production increased by almost 35% worldwide, implying an intensification of farming (FAO, 2022). As production rises, the challenge of feeding shrimp has grown, and research to improve feed management is highly active. However, despite these efforts, feeding costs still represent up to 50% of total shrimp production costs (Debbarma et al., 2019; Engle et al., 2017). Temporal feeding restriction has received great interest since it can lead to compensatory growth, a physiological process allowing organisms to display accelerated growth when returning to optimal conditions after a growth decline caused by a stressful event (Ali et al., 2003). This mechanism can be triggered in response to various types of stress and has been observed in *P. vannamei* after a period of thermal stress (Barajas-Sandoval et al., 2023), high stocking density (Liu et al., 2022) or dietary restriction (Rocha et al., 2019). Numerous studies have focused on developing feeding strategies to optimize the degree of compensatory

growth response in shrimp (Py et al., 2022). Full compensatory growth occurs when accelerated growth allows previously restricted organisms to reach the weight of continuously fed ones (Ali et al., 2003). Conversely, when accelerated growth fails to reach the weight of control organisms, it is known as partial compensatory growth (Ali et al., 2003). It is worth mentioning the distinction between full compensatory growth and catch-up growth, where organisms regain their growth trajectory to reach the control weight (Jobling, 2010; Hector & Nakagawa, 2012). In *P. vannamei*, the application of various continuous or cyclic dietary restrictions has already led to full compensatory growth and allowed for a 25% savings in feed (Abgoun et al., 2023; Lara et al., 2017). Furthermore, applying fasting/feeding cycles for 36 days to *P. vannamei* resulted in full compensatory growth and considerably reduced the amount of nitrogen and phosphorus discharged (Zhu et al., 2016). Compensatory growth is facilitated by mechanisms of hyperphagia upon return to regular feeding or improved feed conversion efficiency (Ali et al., 2003). The intensity and duration of food restriction affect the degrees of compensatory growth response. Moreover, accelerated growth appears more intense in the initial days of refeeding and tends to return to normal after 10 to 15 days of refeeding in shrimp (Quintino-Rivera et al., 2023; Rocha et al., 2019; Wu et al., 2001). For example, after applying different quantitative feeding restrictions (12%, 8%, and 4% of biomass) for 10 days to the Chinese shrimp, *Fenneropenaeus chinensis*, all treatments led to hyperphagia and accelerated growth in the first 10 days of refeeding before returning to baseline levels (Wu et al., 2001).

It is well-established that implementing dietary restrictions to induce compensatory growth yields major economic and ecological benefits. However, before considering the implementation of compensatory growth in shrimp farms, it is advisable to consider possible physiological costs associated with this phenomenon. Indeed, accelerated growth has already been mentioned as a factor causing oxidative stress in the damselfly *Lestes viridis* (De Block & Stoks, 2008) and in the fish *Gasterosteus aculeatus* (Kim et al., 2019). Oxidative stress is a serious threat as it can lead to cell apoptosis and even necrosis (Lushchak, 2014), highlighting the importance of considering it as a potential knock-on effect of accelerated growth.

Moreover, farmed shrimp are regularly exposed to stressful events related to fluctuations in water parameters. The use of high shrimp densities and overfeeding can lead to a decrease in dissolved oxygen concentration due to anaerobic degradation of leftover feed and feces (Avnimelech & Ritvo, 2003) and poor management of water quality (Emerenciano et al., 2022). Organisms are considered to be exposed to hypoxia when dissolved oxygen concentration drops below 2 mg L^{-1} (Diaz, 2001), and it has been shown that short-term exposure of *P. vannamei* to 1.5 mg L^{-1} of dissolved oxygen, followed by reoxygenation, can lead to oxidative stress (Li et al., 2016). Oxidative stress is defined as an imbalance between the production of reactive oxygen species (ROS) and their elimination by the antioxidant system (Halliwell, 2007). *P. vannamei* possesses an efficient antioxidant defense system, including key enzymes such as superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (Gpx), which constitute the first line of defense against ROS (Ighodaro & Akinloye, 2018). SOD, known as the most potent cellular antioxidant, facilitates the dismutation of the first ROS produced, superoxide anion (O_2^-). The resulting hydrogen peroxide (H_2O_2) is neutralized by CAT and Gpx (Ighodaro & Akinloye, 2018; He et al., 2017). Previous studies showed that the antioxidant system of *P. vannamei* is disrupted upon exposure to hyperthermia (Duan et al., 2018; Estrada-Cárdenas et al., 2021). Native to the east coast of the Pacific, *P. vannamei* has an optimum temperature range between 20 and 30°C (Ponce-Palafox et al., 1997). In shrimp farms, it is common for temperatures to rise above 30°C, reaching 38°C in some parts of the world (Hoang et al., 2020). It has been observed that Pacific white shrimp exposed to a temperature of 33°C were already under oxidative stress (Duan et al., 2018). In this regard, evaluating the shrimp's response to stress involves assessing the activities of antioxidant enzymes, such as SOD, CAT, and GPx (Duan et al., 2018; Estrada-Cárdenas et al., 2021; Parrilla-Taylor & Zenteno-Savín, 2011). Additionally, lipid peroxidation is a key indicator of oxidative stress, being one of its major consequences (Barim-Öz, 2018; Repetto et al., 2012). In this study, oxidative stress assessment focused on the shrimp hepatopancreas, as it appears to be the organ most susceptible to stress factors due to its high metabolic rate and central detoxification role (Estrada-Cárdenas et al., 2021; Han et al., 2018; Trasviña-Arenas et al., 2013).

This study aims to elucidate whether the potential oxidative stress caused by compensatory growth in shrimp compromises the capacity of their antioxidant response to additional oxidative stress factors, such as hyperthermia and hypoxia/reoxygenation.

Material and Methods

Experimental Animals

Penaeus vannamei post-larvae (0.019±0.01 g) were obtained from a commercial laboratory and stocked in a 1500-L fiberglass tank. Shrimp were maintained for 3 weeks under laboratory conditions (28±0.5°C, pH at 8±0.3, and D.O.>4.5 mg L^{-1}) and were fed twice a day with a commercially balanced feed (Nutrimar®, 35% of protein and 8% of lipids). Shrimp were subjected to a photoperiod of 12:12 hours light:dark and to daily water exchange (30% of tank volume). The seawater (37 UPS) was first passed through a 1-mm mesh and sterilized with a UV light.

Feed Formulation

The balanced feed used in the experimental trial was manufactured according to the following formula: 33% fish meal, 30.8% wheat flour, 28% soybean paste, 4% soybean lecithin, 2.5% fish oil, 1% sodium alginate, 0.1% vitamin C, 0.5% vitamin-mineral premix (Peña-Rodríguez et al., 2020), and 0.1% choline chloride. The feed was elaborated by mixing the dry ingredients and then adding the oil-based ingredients and hot water (350 mL kg^{-1} of feed). After homogenization, the mixture was passed twice through a 2 mm die meat grinder. The pellets were dried at 50°C for 8 hours and then stored at 4°C until use.

The proximal composition of the experimental feed was determined in triplicate, measuring dry matter (AOAC, 2005; Method 930.15), crude protein content according to the combustion method developed by Dumas (Ebeling, 1968), lipid content (AOAC, 2005; Method 2003.05), crude fiber content (AOAC 2005; Method 978.10) and ash content (AOAC 2005; Method 942.05). By difference, nitrogen-free extracts (NFE) were estimated. The experimental diet shows a moisture content of 5.2%, crude protein content of 37.5%, lipids content of 8.2%, crude fiber content of 0.8%, ash content of 8.5%, and NFE of 34.9%.

Experimental Design

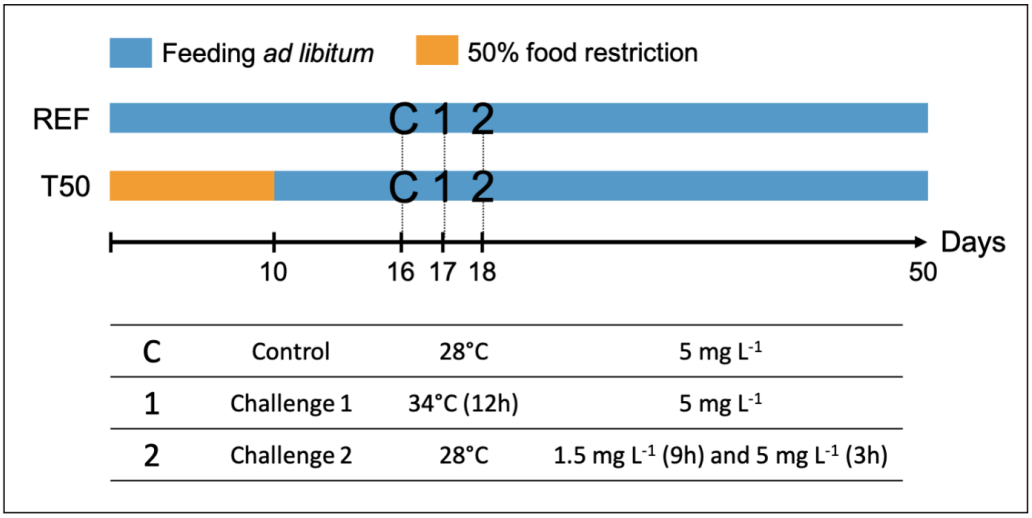
The experiment included two dietary treatments over a 50-day period, during which two punctual abiotic stress challenges and one control group were conducted (Figure 1). A total of 120 juvenile *P. vannamei* weighing an initial average of 0.81±0.05 g were randomly distributed into 12 fiberglass tanks of 50L (55 shrimp m^{-2}). Two dietary treatments, each represented by 6 replicates of 10 organisms, were applied: the reference treatment (REF) and the restriction treatment (T50). In the REF group, shrimp were fed *ad libitum* for the 50-day experiment. In contrast, in the T50 group, shrimp were subjected to a 50% restriction (of the REF ration) for 10 days before being refed *ad libitum* for the next 40 days. The initial feeding rate of shrimp in the REF group was 9% of their biomass, and the daily food portion was offered in two meals (9:00 a.m. and 4:00 p.m.). Before the morning feeding, any uneaten feed and faeces were siphoned off, allowing the daily feeding rates to be adjusted. If uneaten feed was collected, the portion was reduced by 1% of shrimp biomass, and if no feed remains were observed, the portion was increased by 1%. The temperature and dissolved oxygen concentration were monitored daily with a multiparameter (YSI 556 mps, Yellow Springs, USA). Seawater treatment and photoperiod were kept constant throughout the experiment, as mentioned in section 2.1. Ammonium concentration was regularly monitored (API Marine, ammonia test kit, Oldsmar, FL, USA), and a daily water change (50% of the tank volume) was carried out to ensure levels did not exceed 0.5 mg L^{-1}. Shrimp survival was recorded daily, and biometrics of the shrimp's wet weight were performed every 10 days, including survival rate, weight gain (WG), specific growth rate (SGR), feed intake (FI), and feed conversion rate (FCR) as follows:

Survival (%) = final number of shrimp/initial number of shrimp × 100. (Cruz-Suárez et al., 1993)

WG (%) = 100 × (Final weight – Initial weight) / Initial weight. (Cruz-Suárez et al., 1993)

SGR (% day^{-1}) = 100 × (ln Final weight – ln Initial weight) / number of days. (Ricker, 1975)

FCR = Total feed provided per shrimp during the feeding trial / (Final mean weight – Initial mean weight). (Cruz-Suárez et al., 1993)



C	Control	28°C	5 mg L^{-1}
1	Challenge 1	34°C (12h)	5 mg L^{-1}
2	Challenge 2	28°C	1.5 mg L^{-1} (9h) and 5 mg L^{-1} (3h)

Figure 1. Experimental protocol. The colored bars represent the dietary treatment applied to *P. vannamei* shrimp (Blue for *ad libitum* feeding -REF- and orange for 50% food restriction -T50-). The arrow indicates the timeline of the experiment. Labels C, 1, and 2, respectively, indicate the time points at which the control and challenges 1 and 2 were applied, described in the table.

Abiotic Challenges

During the refeeding period, a 12-hour control group and two 12-hour challenges were successively performed on days 16, 17, and 18 in respirometers (Figure 1). For the control and each challenge, 10 shrimp from each treatment (REF and T50) were individually placed into a 450 mL metabolic chamber; additionally, four chambers left without shrimp were used as a blank for water parameter measurements. Shrimp were acclimatized for 12 hours to minimize handling stress (Ulaje et al., 2020). The respirometers were sealed and connected to inlet and outlet tubes to create a continuous flow chamber system. Seawater (37 UPS, filtered through a 5-µm mesh) entering the metabolic chambers was previously stored in an 800-liter tank where water parameters (°C and D.O.) were controlled by a computerized system as described by Ulaje et al. (2020). A peristaltic pump maintained the water flow at 40-45 mL min^{-1} throughout the experiment, and metabolic chambers were placed in a water bath to ensure a stable water temperature.

After the 12 hours of acclimatization, the optimum conditions of temperature and oxygen concentration (28±0.2°C and 5 mgO_2 L^{-1}) were maintained during 12 hours for the control group. For challenge 1 (hyperthermia), the temperature was gradually increased from 28°C to 34°C within 4 hours and maintained at 34°C until the end of the 12-hour challenge. Dissolved oxygen concentration was maintained at its optimum (5 mgO_2 L^{-1}). For challenge 2 (hypoxia and reoxygenation), nitrogen gas was bubbled into the water, entering the metabolic chambers to reduce dissolved oxygen concentration. The concentration was dropped to 1.5 mgO_2 L^{-1} and maintained for 9 hours, followed by 3 hours of reoxygenation at 5 mgO_2 L^{-1}.

Shrimp were fed 6 hours after the challenge started (5% of the biomass). Dissolved oxygen concentration was measured after 8 (post-prandial condition) and 10 hours (resting condition) of challenge onset using a 50 µm fiber optic oxygen sensor (Microx TX2, PreSens, Regensburg, Germany). Water samples were taken from the respirometers at 8 and 10 hours of the challenge and stored at -40 degrees to measure the ammonium (NH_4^+) concentration afterward. At the end of each 12-hour control and challenge, the 20 shrimps were sacrificed, and the hepatopancreas was sampled and stored at -40°C until analysis.

Oxygen Consumption and Ammonium Excretion Rate

In order to calculate the oxygen consumption and ammonium excretion rate of shrimp during the control and each challenge, 20 shrimp from the feeding trial were weighed (wet weight) and dried in a lyophilizer for 24 hours to obtain the wet weight/dry weight ratio. The amount of food administered to the shrimp was also placed in blank respirometers to account for bias caused by food decomposition in the calculations. Oxygen consumption values were calculated by subtracting the dissolved oxygen concentration in the shrimp chambers from the blank chamber concentrations in relation to shrimp dry weight according to the following equation (Rosas et al., 1998):

$$VO_2 = ((O_{2C} - O_{2shrimp}) \times Fr) / DW$$

Where VO_2 represents the oxygen consumption values (mgO_2 $g^{-1}h^{-1}$), O_{2c} is the dissolved oxygen concentration at the outlet of the metabolic chambers used as a blank (without shrimp) (mg L^{-1}), $O_{2shrimp}$ is the dissolved oxygen concentration in the chambers with shrimp (mg L^{-1}), Fr is the flow rate (mL h^{-1}), and DW is the dry weight of the shrimp (g).

The sodium salicylate ammonium quantification method was used to measure the ammonium concentration (NH_4^+) in water samples from respirometers (Bower & Holm-Hansen, 1980). The ammonium excretion rate ($mgNH_4$ g^{-1} h^{-1}) was calculated by measuring the production of ammonium by water flow in the chamber in relation to the dry weight of organisms.

Antioxidant Enzyme Analysis

For the control and each challenge, 4 hepatopancreas samples from shrimp in each dietary treatment (REF and T50) were weighed and homogenized in 1250 µL of phosphate buffer (K_2HPO_4, 0.1 M, pH 7.5). The mixture and beads were run through a Fastprep-24 (MP Biomedicals, Sta. Ana, CA, USA) for 2 cycles of 5 seconds at 30,000 g. The homogenized samples were centrifuged for 4 cycles of 10 minutes at 3500 g, and the supernatant was recovered at each centrifugation stage to proceed to the next. During the process, samples were handled on ice to preserve enzymes from degradation. The collected hepatopancreas extracts were frozen at -40°C until analysis of the antioxidant enzymes.

The total protein content of samples was measured using the Bicinchoninic Acid Assay (BCA) method described by Smith et al. (1985), with incubation of the microplate at 60°C for 15 minutes and reading at 562 nm absorbance. Antioxidant enzymes activities were measured using a superoxide dismutase assay kit (catalogue no. 706002, CAYMAN, USA), a catalase assay kit (catalogue no. 707002, CAYMAN, USA), and a glutathione peroxidase assay kit (catalogue no. 7031012, CAYMAN, USA).

Lipid Peroxidation

Lipid peroxidation was assessed by measuring each challenge's malondialdehyde (MDA) content of 4 shrimp hepatopancreas samples from each dietary treatment (REF and T50). The method of Draper et al. (1993) was

standardized for use on shrimp hepatopancreas. Organs were weighed, homogenized in phosphate buffer (K_2HPO_4, 0.1 M, pH 7), and fast-poured with beads. Each sample was processed in triplicate. Trichloracetic acid (TCA, 10%) and saturated aqueous thiobarbituric acid (TBA) were added to crude homogenates. The mixture was plunged into a 100°C water bath for 20 minutes and then immersed in ice to stop the reaction. After two cycles of centrifugation (3000g, 10 min, 4°C), absorbance was read at 532 nm. Malondialdehyde content of hepatopancreas was calculated using a standard malondialdehyde curve performed in parallel to the samples, and the results are expressed in nmol per gram of tissue^{-1}.

Statistics

Results of growth, oxygen consumption, and ammonium excretion were compared between the REF and T50 groups by a Student t-test for each sampling point. Before this, data were assessed for normality with the Shapiro-Wilk test and homogeneity of variance with the F-test. A Kruskal-Wallis test and a Dunn's post hoc test were performed to compare the oxygen consumption and ammonium excretion values of the REF or T50 group between the different challenges.

The results of antioxidant enzyme and malondialdehyde content analyses were subjected to Shapiro and Barlett tests to ensure the normal distribution and homoscedasticity of the data. Then, a two-way ANOVA was run with the dietary treatment (REF, T50) as the first factor and the control conditions or the challenge induced as the second factor (hyperthermia, hypoxia/reoxygenation). When the effect of treatments was significant, a Tukey's test was applied with a significance level of 0.05. All statistical analyses were performed using R software (v4.2.3).

Growth and Shrimp Performance

Water temperature and dissolved oxygen concentration averaged 27.8±0.1°C and 5.4±0.3 mgO_2 L^{-1}, respectively, over the experiment and did not differ significantly between tanks (P>0.05). The survival rate of organisms was 95% in the REF group and 93% in the T50 group at the end of the experiment, showing no significant difference (P>0.05). As shown in Table 1, shrimp weight was similar between treatments at the start of the experiment (P>0.05). Shrimp from T50 had a significantly lower mean weight than shrimp from REF on days 10, 20, and 50 of the experiment (P<0.05). The shrimp weight gain was lower under the T50 treatment during the initial 10 days of restriction compared to the REF treatment (P<0.05) (Table 1). During the initial days of refeeding, the weight gain was significantly higher in the T50 group than in the REF group (P<0.05). Between days 21 and 50, no significant difference in weight gain was observed between the two treatments (P>0.05). Over the entire duration of the experiment (day 1 to day 50), there was no significant difference between the weight gains of the REF and T50 groups (P>0.05). During the restriction period, the specific growth rate of REF shrimp was significantly higher than T50 shrimp (P<0.05) (Figure 2). Over the 10-day refeeding period, shrimp from T50 exhibited a significantly higher SGR than those from REF (P<0.05) (Figure 2). The SGR of both treatments decreased during the last 30 days of the experiment, but it remained significantly higher in the T50 group (P<0.05) (Figure 2). During the initial 10 days of the experiment, there was no significant difference in the FCR between the two groups (P>0.05), while, at other times during the experiment, the feed conversion ratio of shrimp from T50 was significantly lower than that of shrimp from REF (P<0.05). The mean biomass feeding rate was significantly higher in the REF

Table 1. Weight, Weight gain, Feed Conversion Ratio (FCR), and mean feeding rate according to the biomass of shrimp (%) during the experimental trial

	Days	REF	T50	Level of significance
Weight (g)	Initial	1.24±0.02	1.25±0.06	ns
	10	2.14±0.03	1.75±0.04	***
	20	2.95±0.03	2.78±0.06	**
	50	5.72±0.03	5.58±0.05	**
Weight gain (g)	1-10	0.90±0.02	0.51±0.06	***
	11-20	0.83±0.06	1.02±0.06	**
	21-50	2.77±0.04	2.80±0.04	ns
	1-50	4.48±0.05	4.33±0.11	ns
FCR	1-10	1.21±0.02	1.08±0.12	ns
	11-20	1.64±0.07	1.35±0.08	**
	21-50	1.56±0.02	1.50±0.03	*
	1-50	1.51±0.02	1.41±0.02	***
Mean feeding rate (%biomass)	1-10	7.74±0.07	3.98±0.15	***
	11-20	6.75±0.13	8.06±0.17	***
	21-50	4.87±0.12	5.04±0.12	ns
	1-50	5.96±0.06	5.46±0.11	***

Values are presented as the mean of replicates ± standard deviation. Significant differences (Student t-test) are indicated with asterisks: * (P<0.05); ** (P<0.01); *** (P<0.001). ns means that the difference was not significant (P>0.05).

treatment than in the T50 treatment during the first 10 days of the experiment (P<0.05). In contrast, this parameter was significantly higher in T50 during the first 10 days of refeeding (P<0.05). Between days 21 and 50, there was no significant difference in the mean biomass feeding rate between the two groups (P>0.05).

Respiration, Excretion Rate, and Feed Consumption

Oxygen consumption (OC) and ammonium excretion rate (AER) of shrimp during abiotic challenges are presented in Table 2. In the control, T50 shrimp showed a significantly higher respiration rate than REF shrimp (P<0.05) and a significantly higher ammonium excretion rate after 8 and 10 hours of challenge (P<0.05). Throughout exposure to hyperthermia, physiological rates did not show significant differences between dietary treatments (P>0.05). After 8 hours of hypoxia, shrimp from T50 showed a significantly higher OC and AER than shrimp from REF (P<0.05). Under reoxygenation, OC was also significantly higher in the T50 group than in the REF group (P<0.05).

Shrimp from REF exhibited significantly higher OC and AER after 8 hours (post-prandial condition) of hyperthermia challenge than in control conditions (P<0.05). Over 8 hours of hypoxia challenge, the OC of REF shrimp was significantly lower than in the control conditions (P<0.05). Similarly, in the T50 group, OC was significantly higher after 8 hours of exposure to 34 degrees and significantly lower after 8 hours of hypoxia exposure compared to control conditions (P<0.05).

After 10 hours of challenge (resting condition), OC and AER of shrimp from REF appeared significantly lower in control conditions than in hyperthermia (P<0.05).

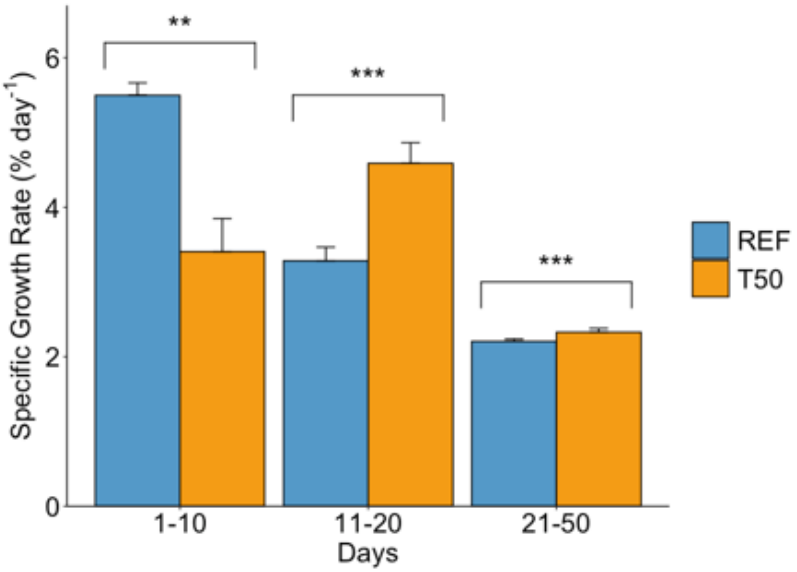


Figure 2. Specific Growth Rate (SGR % day^{-1}) of shrimp during the experiment. Each bar represents the mean ± standard error. Significant differences between treatments (Student t-test) are indicated with asterisks: * (P<0.05); ** (P<0.01). ns means that the difference was not significant (P>0.05).

Table 2. Oxygen consumption and excretion rate of *P. vannamei* under abiotic challenges in the respirometry chambers.

	Challenge	Hours of challenge	REF	T50	Student test
Oxygen consumption (mgO_2 g h^{-1})	Control	8	2.24 ± 0.44^{B}	3.05 ± 0.55^{B}	**
		10	1.40 ± 0.62^{b}	2.16 ± 0.54^{b}	*
	Hyperthermia	8	3.39 ± 0.81^{A}	3.86 ± 0.55^{A}	ns
		10	3.27 ± 0.53^{a}	3.21 ± 0.60^{a}	ns
	Hypoxia	8	0.73 ± 0.42^{C}	1.09 ± 0.44^{C}	*
	Reoxygenation	10	2.12 ± 0.66^{b}	3.14 ± 0.66^{a}	**
Ammonium excretion rate ($mgNH_4^+$g h^{-1})	Control	8	0.0615 ± 0.018^{B}	0.1074 ± 0.034^{A}	**
		10	0.038 ± 0.02^{b}	0.0790 ± 0.03^{a}	**
	Hyperthermia	8	0.1591 ± 0.06^{A}	0.1656 ± 0.07^{A}	ns
		10	0.1186 ± 0.04^{a}	0.1176 ± 0.05^{a}	ns
	Hypoxia	8	0.0508 ± 0.02^{B}	0.0995 ± 0.04^{A}	*
	Reoxygenation	10	0.0906 ± 0.05^{a}	0.1162 ± 0.03^{a}	ns

Values are presented as the mean of replicates ± standard deviation. Significant differences between treatments (Student t-test) are indicated with asterisks: * (P<0.05); ** (P<0.01). Different upper cases show a significant difference (P<0.05) between challenges within the same dietary treatment 8 hours after the challenge starts (Kruskal-Wallis and Dunn tests). Different lower cases show a significant difference (P<0.05) between challenges within the same dietary treatment 10 hours after the challenge starts (Kruskal-Wallis and Dunn tests).

Shrimp in the T50 group had higher OC under hyperthermia and reoxygenation than under control conditions (P<0.05); however, AER was similar between the control and each challenge (P>0.05).

The shrimp consumed all the food 1 hour after it was provided in control and hyperthermia challenges, regardless of dietary treatment. In contrast, during the hypoxia/reoxygenation challenge, the offered feed was not consumed until oxygenation returned.

Antioxidant Enzyme Activities and MDA Content

Activities of antioxidant enzymes SOD and GPx were not significantly affected by the dietary treatments (REF and T50), by the abiotic challenges (hyperthermia and hypoxia/reoxygenation), or by the interaction of both (P>0.05) (Figure 3; Figure 4).

CAT activity was not significantly affected by the effect of dietary treatment (P>0.05) (Figure 5). However, CAT activity was significantly affected by the effect of abiotic challenges and by the interaction of abiotic challenges and dietary treatment (P<0.05). In the control conditions, T50 shrimp showed significantly higher CAT activity than REF shrimp. CAT activity was significantly increased after 12 hours of exposure to hyperthermia in organisms from REF group.

Malondialdehyde (MDA) content in shrimp hepatopancreas was significantly affected by the dietary treatment, abiotic challenge, and the interplay of the two factors, as illustrated in Figure 6. In the control conditions, T50 shrimp presented significantly higher MDA content than REF shrimp (P<0.05). Exposure to hyperthermia caused a significant increase in MDA content independently of the dietary treatment compared to the REF group in the control conditions (P<0.05). In contrast, exposure to hypoxia and reoxygenation did not result in a significant increase in MDA content in either the REF or T50 treatments (P>0.05).

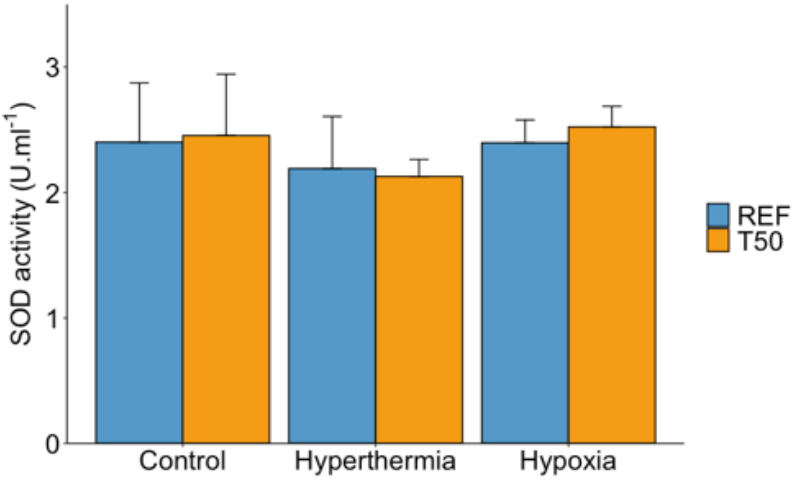


Figure 3. SOD activity in the hepatopancreas of *P. vannamei* under abiotic challenge in the metabolic chamber. Each bar represents the mean ± standard error. No letters indicate a non-significant difference between the means (two-way ANOVA, P>0.05).

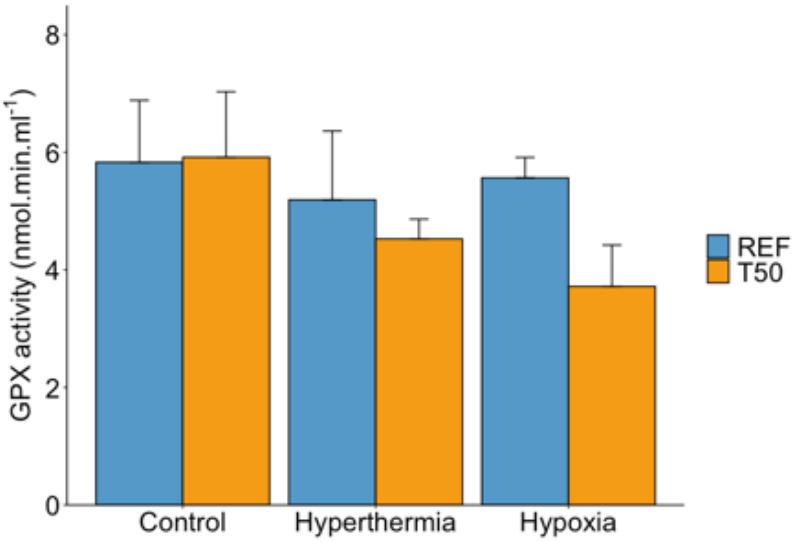


Figure 4. Gpx activity in the hepatopancreas of *P. vannamei* under abiotic challenge in the metabolic chamber. Each bar represents the mean ± standard error. No letters indicate a non-significant difference between the means (two-way ANOVA, P>0.05).

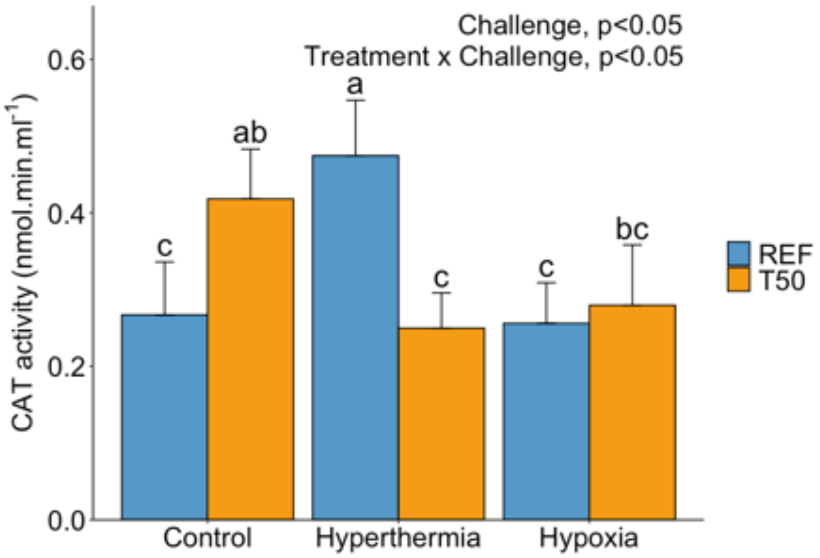


Figure 5. CAT activity in the hepatopancreas of *P. vannamei* under abiotic challenge in the metabolic chamber based on a two-way ANOVA. Each bar represents the mean ± standard error. Different letters indicate a significant difference between the means under the effect of the Treatment x Challenge intercept (two-way ANOVA and Tukey test, P<0.05).

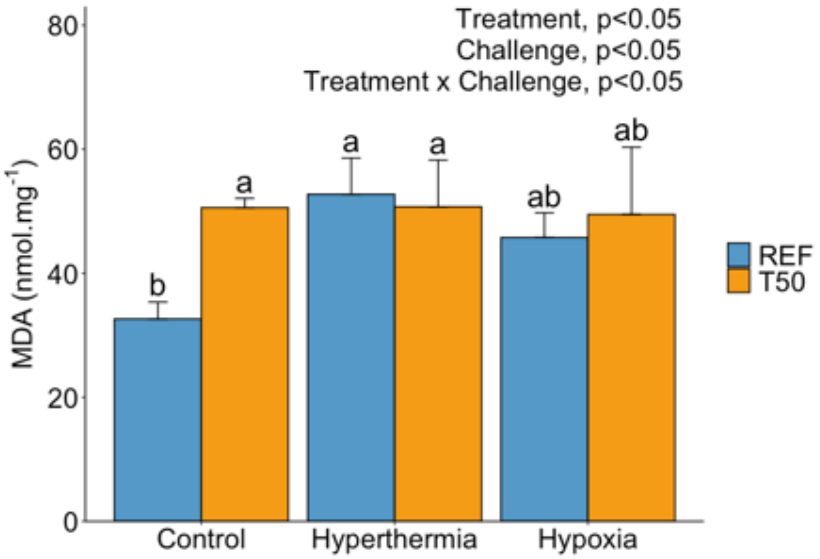


Figure 6. Malondialdehyde content in the hepatopancreas of *P. vannamei* under abiotic challenge in the metabolic chamber based on a two-way ANOVA. Each bar represents the mean ± standard error. Different letters indicate a significant difference between the means under the effect of the Treatment x Challenge intercept (two-way ANOVA and Tukey test, P<0.05).

Discussion

Compensatory Growth Response

Shrimp can withstand food restriction by utilizing energy reserves and lowering metabolism (Abgoun et al., 2023; Sánchez-Paz et al., 2007), resulting in slower growth than regularly fed shrimp, as observed in shrimp restricted for 10 days in this study. However, severe food restriction, combined with high density, can lead to cannibalism (Lara et al., 2017; Shao et al., 2020). In this study, applying a 10-day 50% food restriction did not result in mortality in juvenile *P. vannamei*. Upon return to regular feeding, organisms exhibited accelerated growth, known as compensatory growth, commonly evaluated by the specific growth rate (SGR) (Quintino-Rivera et al., 2023; Wu & Dong, 2002; Zhu et al., 2016). Additionally, studies in fish and crustaceans have shown that compensatory growth can also be identified by the mechanisms of hyperphagia and/or improved food efficiency (Luo et al., 2022; Prates et al., 2023). In the initial 10 days of refeeding, the SGR and weight gain were significantly higher in shrimp from T50 than in shrimp from REF. This result is consistent with other studies showing compensatory growth in shrimp after quantitative restriction (Lara et al., 2017; Prates et al., 2023; Wu et al., 2001). Between days 20 and 50, while SGR remained consistently different, weight gain was

similar between the two groups, confirming compensatory growth is more pronounced in the initial days of refeeding (Rocha et al., 2019; Wu et al., 2001). Concurrently with accelerated growth, shrimp undergoing refeeding demonstrated improved FCR and increased food consumption. The enhanced FCR observed during the 40 days of refeeding suggests improved food digestion and absorption, likely linked to increased digestive enzyme activity upon returning to continuous feeding (Rahman et al., 2020; Zhu et al., 2016). This aligns with previous findings where improved FCR is regularly observed in shrimp undergoing compensatory growth (Quintino-Rivera et al., 2023; Rahman et al., 2020; Yildirim & Aktaş, 2019; Zhu et al., 2016). During the initial 10 days of refeeding, shrimp in the T50 group showed a markedly increased appetite, consuming an average of 8.06% of their biomass, compared to 6.75% for continuously fed shrimp. Other studies have demonstrated a hyperphagic response in crustaceans after food restriction or deprivation (Quintino-Rivera et al., 2023; Wang et al., 2019; Wu et al., 2001). The increased nutrient influx allows energy reserves to be replenished and enhances the frequency of ecdysis (Álvarez & Nicieza, 2005; Wu et al., 2001), leading to accelerated growth. Furthermore, the immediate hyperphagic response indicates that dietary restriction did not affect the shrimp's digestive system (Gao et al., 2015; Zhu et al., 2003). In the present study, the observed compensatory growth in juvenile *P. vannamei* was driven by the hyperphagic response and improved FCR. Nevertheless, T50 shrimp did not achieved the final weight of REF shrimp during the 40 days of refeeding, reflecting only a partial compensatory growth (Ali et al., 2003).

Oxidative Stress during Compensatory Growth in Controlled Conditions

Shrimp's respiration and ammonium excretion rate were used as proxies for the metabolic rate (Barbieri et al., 2016). The oxygen consumption and excretion rate of shrimp undergoing compensatory growth (T50) were significantly higher than REF shrimp in post-prandial and resting conditions. As ROS are inevitable by-products of respiration, a rise in metabolic rate inexorably leads to their increased production (He et al., 2017). Increased metabolism during compensatory growth is consistent with activating anabolic pathways to catch up with somatic growth and recover depleted energy reserves (Won & Borski, 2013). Organisms are endowed with an antioxidant system, including SOD, CAT, and Gpx, charged to continuously eliminate the ongoing production of ROS and avoid oxidative stress (He et al., 2017). CAT and Gpx reduce hydrogen peroxide (H_2O_2), which is the product of the dismutation of superoxide anion (O_2^-) by SOD (Halliwell & Gutteridge, 2015). The acceleration of respiration must have led to greater production of superoxide anion during compensatory growth (De Block & Stoks, 2008); however, SOD activity did not differ between the two shrimp groups at this sampling point. Nevertheless, some studies have shown that under stress, the increase in antioxidant enzyme activity can be quite short-lived in shrimp (Duan et al., 2015, 2018; Zheng et al., 2019). As found in this study, the SOD enzyme may have exhibited a peak of activity in response to stress, but it might have been short-lived and not observable during the sampled times. In the current study, CAT activity was significantly higher in compensatory-growth shrimp than in REF shrimp. The increase in CAT activity indicates the establishment of an antioxidant defense strategy in response to increased production of H_2O_2. While Gpx has the same primary function of detoxifying H_2O_2, the enzyme differs from CAT by its higher affinity for the ROS, allowing it to activate with lower quantities than CAT (Duan et al., 2018). Thus, it seems consistent to assume that in this study, the Gpx peak possibly occurred before the CAT one.

Oxidative stress is a serious threat as free radicals are unstable molecules that can attack proteins, lipids, and DNA (Halliwell & Gutteridge, 2015). It was previously suggested that compensatory growth may be related to oxidative stress due to the high cellular activity associated with it (Costantini et al., 2018; Monaghan et al., 2009). Regarding this, lipid peroxidation, commonly measured by malondialdehyde content (Florescu et al., 2021; Gou et al., 2023), was found to be significantly higher in the hepatopancreas of T50 shrimp undergoing compensatory growth than in shrimp from REF in control conditions. The higher activity of CAT, in response to the increased production of ROS during metabolic acceleration, was insufficient to prevent oxidative stress during compensatory growth. Our results support recent studies on fish, which have also demonstrated oxidative damage in fishes undergoing compensatory growth (Florescu et al., 2021; Gou et al., 2023; Kim et al., 2019; Sakyi et al., 2021). For example, in sturgeon *Acipenser stellatus*, subjected to 14 days of fasting and 14 days of refeeding, MDA content in the gut was significantly higher after the refeeding period (Florescu et al., 2021).

It is important to note that some studies have highlighted the generation of oxidative stress after the application of a fasting period in fish (Liao et al., 2021; Wu et al., 2022) and crustaceans (Barim-Öz, 2018; Cai et al., 2021; Włodarczyk et al., 2019). Oxidative stress generation during fasting does not seem intuitive as metabolism decreases to support the lack of food; however, the overproduction of ROS, in this case, does not appear to be linked to metabolism but to mitochondrial degeneration caused by malnutrition (Włodarczyk et al., 2017, 2019). However, to our knowledge, it has not been demonstrated that partial food restriction induces oxidative stress in aquatic animals. Nevertheless, it cannot be completely excluded that oxidative stress during compensatory growth in *P. vannamei* could be a late consequence of dietary restriction.

Oxidative Stress in Response to Abiotic Stress Factors

This study aimed to evaluate the resistance capacity of *P. vannamei* shrimp to abiotic stress factors during compensatory growth. Since applying dietary restriction and refeeding strategy causes oxidative stress in shrimp, it can be expected that shrimp undergoing compensatory growth will not respond to abiotic stress in the same way as their correctly fed counterparts.

Hyperthermia is a stressor known to generate oxidative stress in crustaceans (de Souza et al., 2016). Our results confirm the acceleration of shrimp metabolism during exposure to hyperthermal stress (Spanopoulos-Hernández et al., 2005; Ulaje et al., 2020). The increase in respiration leads to a rise in superoxide anion production and an increase in MDA in *P. vannamei* exposed to a temperature of 33°C for 6 to 72 hours (Duan et al., 2018). In this study, CAT activity increased in shrimps from REF after a 12-hour exposure to hyperthermia. Other studies have shown antioxidant response to heat stress in shrimp (Duan et al., 2018; Estrada-Cárdenas et al., 2021; Zheng et al., 2019). The significant increase in MDA content in the hepatopancreas of shrimp exposed to hyperthermia demonstrates the failure of the antioxidant strategy employed to prevent oxidative stress (de Souza et al., 2016; Duan et al., 2018; Zheng et al., 2019). In our study, the CAT activity of shrimp from T50 did not increase during hyperthermia, suggesting that compensatory-growing shrimp focused their energy on growth, which could have prevented an increase in CAT activity during the hyperthermic challenge. However, this lack of antioxidant response did not generate more lipid peroxidation during heat stress in shrimp undergoing compensatory growth (T50).

Exposure to hypoxia and reoxygenation may also lead to oxidative stress in *P. vannamei* (Han et al., 2018; Li et al., 2016). In the present study, the SOD, CAT, and Gpx activities did not appear to be altered after 9 hours of hypoxia at 1.5 mg O_2 L^{-1} and 3 hours of reoxygenation. It has already been mentioned that hypoxia may not necessarily increase the production of ROS. Indeed, to combat the lack of oxygen, organisms can reduce their metabolism, which reduces the flow of electrons into the mitochondria (Kniffin et al., 2014; Ulaje et al., 2020). Our results align with this claim, as respiration was lower in shrimp exposed to hypoxia than in shrimp under control conditions for both dietary treatments. This confirms that *P. vannamei* can adapt to a drop in dissolved oxygen concentration (Ulaje et al., 2020). However, it is often mentioned that oxygenation restoration is more threatening, as the influx of oxygen can cause an overproduction of ROS (Parrilla-Taylor & Zenteno-Savín, 2011; González-Ruiz et al., 2023), leading to increased MDA content in the hepatopancreas of *P. vannamei* (Li et al., 2016) and in the liver and brain of fish *Pelteobagrus fulvidraco* (Wang et al., 2021). The present results showed that MDA content in shrimp hepatopancreas from REF and T50 increased after exposure to hypoxia/reoxygenation compared to REF shrimp under control conditions, although not significantly. The Pacific white shrimp is known for its tolerance to oxygen variations, given its natural ability to adapt between marine and estuarine environments throughout its life cycle (Prates et al., 2023) and its capacity to the mechanism of preparation for oxidative stress (Kniffin et al., 2014; Parrilla-Taylor & Zenteno-Savín, 2011). As shown in this study, the shrimp probably adapted well to hypoxia and short-term reoxygenation, as previously demonstrated in the same species (Han *et al.*, 2018).

Conclusion

In a nutshell, shrimp undergoing compensatory growth (T50) showed similar oxidative stress consequences to shrimp fed continuously (REF) when an additional stress factor was applied. Thus, applying dietary restrictions followed by refeeding would reduce costs without threatening production in case of hyperthermia or hypoxia events. However, our results showed that compensatory growth was associated with the generation of oxidative stress in the Pacific shrimp, which entails physiological consequences. This highlights the importance of exploring other physiological costs associated with accelerated growth before its potential application on an industrial scale.

Ethical Statement

All applicable international, national, and institutional guidelines for the care and use of animals were followed by the authors.

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Author Contribution

Clara Adèle Py, Sergio Alan Ulaje and Diana Barajas-Sandoval: Experiment execution, formal analysis, and Writing; María Teresa Sicard: Conceptualization, Methodology, Supervision; Alberto Peña-Rodríguez and Regina Elizondo-González: Conceptualization, Methodology, Supervision, Resources, Writing- Reviewing and Editing, Funding acquisition.

Conflict of Interest

The authors declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

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