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Chronic Cadmium Exposure can Alter Energy Allocation to Physiological Functions in the Shrimp *Penaeus vannamei*

Juliana Rodrigues da Costa[1] · Mariana V. Capparelli[2] · Pedro Magalhães Padilha[3] · Emanuelle Borges[1] · Andressa C. Ramaglia[1] · Michelle Roberta dos Santos[1] · Alessandra Augusto[1,3,4,5]

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Abstract

Environmental stressors in aquatic organisms can be assessed using a bioenergetic approach based on the evaluation of changes in their physiological parameters. We evaluated the chronic effects of cadmium (Cd^{2+}) on the energy balance as well as the survival, growth, metabolism, nitrogen excretion, hepatosomatic index, oxidized energy substrate, and osmoregulation of the shrimp *Penaeus vannamei* with the hypothesis that the high energy demand related to the homeostatic regulation of Cd^{2+}could disrupt the energy balance and as a consequence, their physiological functions. The shrimp exposed to Cd^{2+} had higher mortality (30%), directed more energy into growth (33% of energy intake), ingested 10% more energy, and defecated less than control animals. Cd^{2+} exposure caused a tendency to decrease metabolism and ammonia excretion but did not alter the hepatosomatic index, type of energy substrate oxidized, and the hyperosmorregulatory pattern of the species. The Cd^{+2} exposure may have induced a trade-off response because there was a growth rate increase accompanied by increased mortality.

Penaeus vannamei is the most cultivated shrimp worldwide, with an annual production of nearly 6 million tons, representing 50% of all cultivated crustaceans (FAO 2022). This species is considered a good model for toxicity tests with contaminants, as they have a short life cycle, live and feed near sediments where there is a significant accumulation of toxins, and are responsible for much of the nutrient cycling and processing of organic matter in the environment (Loghmani et al. 2023). In general, *P. vannamei* farms are located in coastal areas and have contact with seawater that may be contaminated by various contaminants, including metals (Li et al. 2021; Fu et al. 2022). The effects of metals on crustaceans include oxidative damage and morphophysiological changes in tissues such as the gills and hepatopancreas (Das et al. 2019).

The integrity of animals exposed to metals can be assessed by investigating various physiological functions to detect their effects on individuals and populations. For example, the energy balance describes the energy gained by animals and its distribution among different physiological functions, such as growth, metabolism, nitrogen excretion, feces, and also exuviae in the case of arthropods (Mantoan

✉ Alessandra Augusto
alessandra.augusto@unesp.br

Juliana Rodrigues da Costa
juliana.r.costa@unesp.br

Mariana V. Capparelli
marivcap@gmail.com

Pedro Magalhães Padilha
pedro.padilha@unesp.br

Emanuelle Borges
emanuelle.borges@unesp.br

Andressa C. Ramaglia
andressa.cr.mota@unesp.br

Michelle Roberta dos Santos
michellesroberta@gmail.com

1 Aquaculture Center of UNESP (CAUNESP), São Paulo State University (UNESP), Jaboticabal, SP 14884-900, Brazil

2 Estación El Carmen, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de Mexico, Carretera Carmen-Puerto Real Km 9.5, 24157 Ciudad del Carmen, Campeche, Mexico

3 Department of Chemistry and Biochemistry, Institute of Biosciences, São Paulo State University (UNESP), Botucatu, SP 14884-900, Brazil

4 Department of Zoology, São Paulo State University (UNESP), Botucatu, SP 18618-689, Brazil

5 Laboratory of Sustainable Aquaculture, São Paulo State University (UNESP), São Vicente, SP 11380-972, Brazil

et al. 2021; Green and Hou 2024). Several factors can alter the energy balance of species, such as diet (Coelho et al. 2019; Mantoan et al. 2021), salinity (Xiong et al. 2020), and ontogenetic stages (Augusto et al. 2020). Furthermore, pollutants such as metals can affect any of the parameters of energy balance, from energy intake to energy channeled to growth and metabolism (Ferrari et al. 2011; Sadeq and Beckerman 2019; Hansul et al. 2021). Metals can impair the organism's ability to acquire energy from the environment, and animals may expend more energy to compensate for the adverse effects of the pollutant.

One of the metals becoming increasingly prevalent in coastal waters is cadmium ($Cd^{2+)}$. This metal is among the most toxic at low concentrations and has been used to manufacture batteries, phosphate fertilizers, cement, and electro-plating (Arisekar et al. 2022). Cd^{2+} has already been detected in the tissues of several crustaceans, such as *Callinectes danae* (Bordon et al. 2016), *Carcinus maenas*, and *Palaemon elegans* (Butler and Zou 2021). Although the response pattern is not uniform, this metal can cause energetic metabolism disturbances, changes in the molt cycle, and endocrine disruption (Hauser-Davis et al. 2022; Liu et al. 2022; Mourão et al. 2023). Knowledge about the effects of Cd^{2+} on crustaceans is of particular interest because they are significant invertebrates in the aquatic ecosystem, play an essential role in the food chain, are of economic interest, and are being fished and farmed in several regions of the world.

Therefore, given the ecological and economic importance of the marine shrimp *P. vannamei*, the present study aimed to evaluate the effects of chronic exposure to Cd_2 in a network of physiological processes such as energy balance, metabolism, growth, excretion, hepatosomatic index, and oxidized substrate type of this species. We hypothesize that the high energy demand related to the homeostatic regulation of Cd^{2+} could disrupt the energy balance and, consequently, the physiological functions of *P. vannamei*.

Material and Methods

Collection and Acclimation of Animals in the Laboratory

Juvenile marine shrimp *P. vannamei* (3.00 ± 0.11 g) were collected from farms in the state of Santa Catarina, Brazil (26°12′32.3″S 48°44′23.7″W), with the aid of tarrafa nets. The animals were transported in boxes containing water from the collection site with constant aeration to the Sustainable Aquaculture Laboratory/UNESP in São Vicente, Brazil (23°58′S 46°23′W). This lasted about six hours, and no animals died during the transport. Shrimps were acclimated to laboratory conditions in individual aquariums containing water with salinity (20‰) and temperature (30 °C) similar to the collection site for seven days. The water variables at the collection site, salinity, temperature, and ammonia total were verified daily, with a refractometer, thermometer, and colorimetry (Koroleff 1983), respectively. Pilot experiments in our laboratory (oxygen consumption, ingestion taxa) show that this acclimatization period is necessary to minimize the stress caused by transport and for the animals to get used to the characteristics of the laboratory. During this period, the animals were fed about 7% of their biomass daily with commercial marine shrimp feed (Guabi, 40% protein). All shrimp used were in the intermolt because pre- and postmolt stages can alter tissue hydration. The experiments were performed with a total of 10 animals per treatment ($N = 10$).

Exposure of *P. vannamei* to Cadmium

Penaeus vannamei were exposed to 0.1 mg L^{-1} (nominal concentration) of Cd^{2+} (CAS number, 7440-43-9) at an environmentally relevant concentration (Aguiarla et al. 2008) and at a chronic to sublethal dose for this species (Wu and Chen 2004). The control group remained in filtered brackish water and reconstituted without adding metal. Cadmium (Dinâmica® Contemporary Chemistry Ltda.) was diluted in filtered brackish water (20‰). The brackish water used in the experiments was prepared from fresh water and sea salt (Hiker Ocean Prosea Salt©, Qingdao Haike General Sea Salt). The animals were kept in individual aquariums containing 6 L of water with constant aeration, photoperiod of 12 h light–12 h dark, at 25 °C. The aquarium water was changed every three days to avoid increasing ammonia concentration and maintain control of the metal concentration. The animals were kept for 30 days under these experimental conditions so that the species' physiology could be evaluated. The animals were fed daily with commercial feed (Guabi, 40% crude protein, and 18.56 kJ) during this period.

Analysis of Cadmium in Water

The cadmium determinations in water samples were carried out by atomic absorption spectrometry in a graphite furnace, using a Shimadzu AA-6800 spectrometer (Osaka, Japan) equipped with a background absorption corrector with a deuterium lamp and a self-reverse system (SR), a pyrolytic graphite tube with an integrated platform and an ASC-6100 automatic sampler. A Shimadzu hollow cathode mercury lamp (Osaka, Japan) was used and operated at a current of 12 mA. The wavelength was 228.7 nm, and the spectral resolution was 0.5 nm. The inner walls of the pyrolytic graphite tubes with integrated platforms used in the mercury analyses were coated with tungsten. For this purpose, 25 μL aliquots of 1000 mg L^{-1} sodium tungstate solution (Merck, Darmstadt, Germany) were injected into the atomizer, which was then subjected to the program described by Bittarello et al. (2020). Tungsten ions were deposited on the graphite tube platform by heating it up to 500 °C, forming a tungsten carbide layer as a permanent chemical modifier. An analytical curve was done in the concentration range 1.0–5.0 µg L^{-1}, using Titrisol Merck standard (Merck, Darmstadt, Germany). Zirconium nitrate (Merck, Darmstadt, Germany) was added to the standard solutions to give final concentrations of 20 mg L^{-1} zirconium, which acted as a chemical modifier. Then, 20 µL of the standard solutions was injected into the spectrometer atomization system by using an autosampler. For the cadmium determinations, 20 µL aliquots of samples (composed of 10 µL of water samples with 4 µL of 100 mg L^{-1} zirconium nitrate and 6 µL of ultrapure water) were used. The 20 µL sample aliquots were injected into the spectrometer atomization system using an autosampler. Measurements were conducted in triplicate using the graphite tube heating program described as follows: Drying–160 °C/220 °C, 10 s/10 s; Pyrolysis–500 °C/800 °C, 10 s/10 s; Atomization–2100 °C, 3 s; Cleaning–2300 °C, 10 s. The absorbance values were measured in the peak area. The linear correlation coefficient (r) obtained for the analytical curve was 0.9999. The limits of detection (LOD) and quantification (LOQ) of the determination method, calculated based on the standard deviation of 10 readings of the standard solution blank and on the slope of the analytical curve (LOD = 3/slope and LOQ = 10/slope), as described by Currie (1999), were 0.011 and 0.037 µg L^{-1} respectively. The optimized experimental conditions for cadmium determinations were validated through analysis of Standard Reference Material—1640 Trace Elements in Natural Water (National Research Council Canada Measurement Science and Standards Research Centre, Ottawa—Canada) containing 22.79 ± 0.96 µg L^{-1}. The results obtained in the cadmium determination by GFAAS were 22.62 ± 0.26 µg L^{-1}. The determined values presented recovery percentages of 99.25%, demonstrating the excellent accuracy of the analytical method optimized for cadmium determination.

Evaluation of the Physiology of *P. vannamei* Exposed to Cadmium

Survival

During the 30 days of experiments, the survival of the animals in the aquariums was verified three times a day: at 8:00 a.m., 2:00 p.m., and 8:00 p.m. All animals that died were removed from the aquariums.

Ingestion and Egestion Rates

The ingestion and egestion rates were evaluated according to Augusto et al. (2020). The animals were fed daily at the end of the day with marine shrimp ration (Guabi, 40% protein), corresponding to 7% of their body biomass. After six hours, unconsumed food was removed from the aquariums by siphoning. Then, the foods were dried on filter paper, weighed (wet mass), dried in an oven at 60 °C for 48 h, and weighed again (Metler Toledo, 1 µg). Control food samples were weighed initially and placed in tanks without animals under the same experimental conditions to analyze the lixiviation rate. These values were used to correct uneaten feed. Diet ingestion was determined by the difference between the dry mass of the diet supplied and the unconsumed diet. The samples were stored in plastic tubes (15 ml) and frozen for later analysis of energy content. Feces were collected from the tanks, each 6 h with a plastic pipette, placed on aluminum plates, and dried at 60 °C for 48 h in an oven. They were then weighed on an analytical scale (Metler Toledo, 1 µg) and stored frozen until energy analysis using a calorimetric pump (IKA, C2000 basics).

Growth and Exuviae

The animals were weighed (Mars, AS 2000C) on the first and last days of the experiment (days 1 and 30). The seedlings of any ecdysis that occurred during the experimental period were collected and weighed so that the frequency of ecdysis could be associated with physiological data.

Metabolism, Nitrogen Excretion, and O/N Ratios

Oxygen consumption and ammonia excretion were evaluated on the last day of the experiment (30° day). The oxygen consumption was evaluated in 1200 mL closed individual respirometric chambers equipped with an oximeter (YSI, mod 52) and a probe with a precision of 0.01 mg L^{-1} (YSI, mod 5905). Every animal was subjected to 24-h starvation to reduce the calorigenic effect of food. After acclimation for 30 min under aeration, the first measurement of oxygen content within the chamber was made, and one hour later, another measurement was made. Control chambers were also used, and oxygen consumption was calculated. The excretion (TAN = unionized plus ionized ammonia, as nitrogen) of shrimps was measured from samples of water obtained from the respirometry chamber at the end of procedures to determine oxygen consumption. TAN concentration was determined by colorimetry (Koroleff 1976), and the effect of salinity upon ammonia-N readings was corrected using factor 1.06 (Koroleff 1983). The animals present in the respirometric chambers were killed by a freezing meter, weighed (wet mass), oven-dried at 60 °C for 48 h, and weighed again (dry mass). Oxygen consumption and TAN excretion were expressed as an individual rate (µg ind^{-1} h^{-1}) and dry mass rate (µg mg DM^{-1} h^{-1}). To calculate the energy channeled into metabolism, the calorigenic effect of food was added to the oxygen consumption rate, considering an increase of 70% (Zuniga-Romero 1983; Chu and Ovsianico-Koulikowsky 1994). Metabolic energy was calculated, assuming that 1 mg of O_2 consumed is equivalent to 1406 J (Gnaiger 1983) and the energy lost in excretion as 1 mg of TAN excreted is equivalent to 24.87 J (Gnaiger 1983).

The major metabolic substrate for the production of energy used by animals was estimated by the atomic ratio O/N calculated by dividing the number of gram atoms of oxygen consumed by the number of gram atoms of nitrogen excreted (Mayzaud and Conover 1988; Brown 2006; Augusto et al. 2020). According to Mayzaud and Conover (1988), pure protein catabolism will yield O/N ratios in the range 3–16, whereas equal amounts of lipid and protein catabolism will yield values between 16 and 60; above 60, there is a predominance of lipids.

Evaluation of the Hepatosomatic Index (HSI)

After the animals were euthanized, the hepatopancreas was dissected and weighed (Metler toledo, 1 µg) to determine the HSI based on the ratio below (Ramaglia et al 2018):

$$\text{HSI}(\%) = (\text{hepatopancreas mass} \times 100)/\text{body mass}.$$

Evaluation of the Hemolymph Osmolality

Hemolymph samples (30 µl) were taken from the region located at the cephalothorax to *P. vannamei* using an insulin syringe coupled to a #25-8 (Ramaglia et al. 2018). Hemolymph osmolality was measured using a vapor pressure osmometer (Wescor, Modelo 5500) and the results are presented in mOsm Kg^{-1} water.

Statistical Analysis

The effect of Cd^{2+} in the physiology of animals was evaluated for Test-*T*, followed by the Student–Newman–Keuls multiple means test (SNK) to identify significant differences between groups. The analyses were performed using Sigma Stat 3.5, and a minimum significance level of $P < 0.05$ was applied. The figures were presented using the data entered into the program Graphpad 5.01.

Results

Analysis of Cadmium in Water

Results were not detected (Recovery 99.02%) for the control and 0.152 ± 0.0018 mg L^{-1} (Recovery = 99.02%) for the nominal 0.1 mg L^{-1} of Cd2+. In this case, the nominal concentration was accepted because it was less than 1% different from the measured concentration.

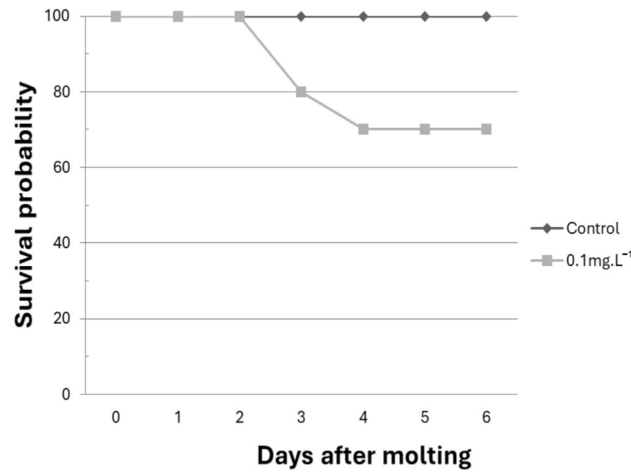

Fig. 1 Relationship between survival probability and days after molting of *Penaeus vannamei* exposed to cadmium at concentrations 0 and 0.1 mg L^{-1} for 30 days

Table 1 Energy content (kJ^{-1} g DW) of the body, feces, and feed of shrimp *P. vannamei* kept for 30 days in control water or with metal cadmium (0.1 mg L^{-1})

	Control	Cadmium	*P*
Body	18.10 ± 0.12	18.43 ± 0.17	0.114
Feces	8.57 ± 0.24	8.15 ± 0.162	0.204

(Mean ± SE; 7 ≤ N ≤ 10)

Mortality

Control animals had no mortality during the 30 days of the experiment, but those exposed to Cd^{2+} had a 30% death rate. These mortalities occurred about three days after molting. The relationship between survival rate and cycle molt is observed in Fig. 1.

Energetic Content of Body, Feces, and Diet

The energy content of the body and feces of the animals is shown in Table 1. There was no difference in the energy value of the animal's bodies (± 18 kJ g^{-1}) controls or exposed to Cd^{2+}. The energy value of the feed for both treatments was 18.56 ± 0.07 (kJ g^{-1} DW) (7 ≤ N ≤ 10).

Ingestion, Egestion, Growth, Metabolism, and Nitrogen Excretion of *P. vannamei*

The rates of ingestion, egestion, growth, metabolism, and nitrogen excretion of *P. vannamei* are shown in Table 2. In

Table 2 Daily rates of ingestion (C), defecation (F/C), growth (P), breathing (R), excretion (U), and O/N of *P. vannamei* kept in water control or exposed to cadmium (0.1 mg L^{-1}) for 30 days

	Control	Cadmium	*P*
C/WWi (%)	2.97 ± 0.23[a]	2.92 ± 0.26[a]	0.881
C (mg WW day^{-1})	102.02 ± 6.94[a]	106.15 ± 7.06[a]	0.694
F/C (%)	62.161 ± 1.39[a]	57.64 ± 1.45[b]	0.025
P/WWi (%)	23.14 ± 3.39[a]	43.57 ± 5.85[b]	0.021
P (mg WW day^{-1})	18.94 ± 1.84[a]	33.94 ± 4.29[b]	0.001
R (mg O_2 ind^{-1} day^{-1})	33.36 ± 2.33[a]	29.17 ± 1.85[a]	0.219
U (mg TAN ind^{-1} day^{-1})	4.30 ± 0.49[a]	3.45 ± 0.50[a]	0.250
O/N	3.99 ± 0.57[a] (protein)	5.25 ± 0.48[a] (protein)	0.250
HIS	6.73 ± 2.31[a]	6.49 ± 0.94[a]	1.000

Values are mean ± SE (7 ≤ N ≤ 10). Values with different letters in the same line differ statistically by test *T* followed by SNK test. Atomic ratio O/N indicates the major metabolic substrate for the production of energy used by animals

WW: wet weight, WWi: initial wet weight, P = protein

animals exposed to Cd^{+2}, the ingestion rate was similar to that of control animals (about 3% of its biomass) ($P = 0.88$). However, animals exposed to Cd^{+2} had a lower defecation rate (57% of the feed ingested) and an 80% higher growth rate. The animals suffered molt about three times during the experiments (30 days) (7 ≤ N ≤ 10).

Metabolism and Nitrogen Excretion

Oxygen consumption and nitrogen excretion in individual mass are shown in Table 2, and in specific dry mass (µg mg DW^{-1} h^{-1}) are shown in Fig. 2. Although both physiological parameters in specific dry mass show a tendency to decrease in animals exposed to Cd^{2+}, such alteration was not statistically proven, respectively ($P = 0.398$) ($P = 0.086$) (7 ≤ N ≤ 10).

Energy Budget

The energy ingested and channeled to the different physiological functions is expressed in percentage in Fig. 3. The animals exposed to Cd^{2+} ingested 2.07 ± 0.12 kJ ind^{-1} day^{-1}, corresponding to about 10% more energy than the control animals. Shrimp exposed to Cd^{2+} also channeled more energy into growth (33% of energy intake) relative to controls (20% of energy intake) (7 ≤ N ≤ 10).

Atomic Ratio, Hepatosomatic Index, and Hemolymph Osmolality

The O/N ratio in *P. vannamei* suggests the use of main proteins as energy substrate, the hepatosomatic index (about 6.6; $P = 0.872$), and the hemolymph osmolality (about 705 mOsm Kg^{-1} water) in *P. vannamei* did not change with the presence of metal in water (7 ≤ N ≤ 10).

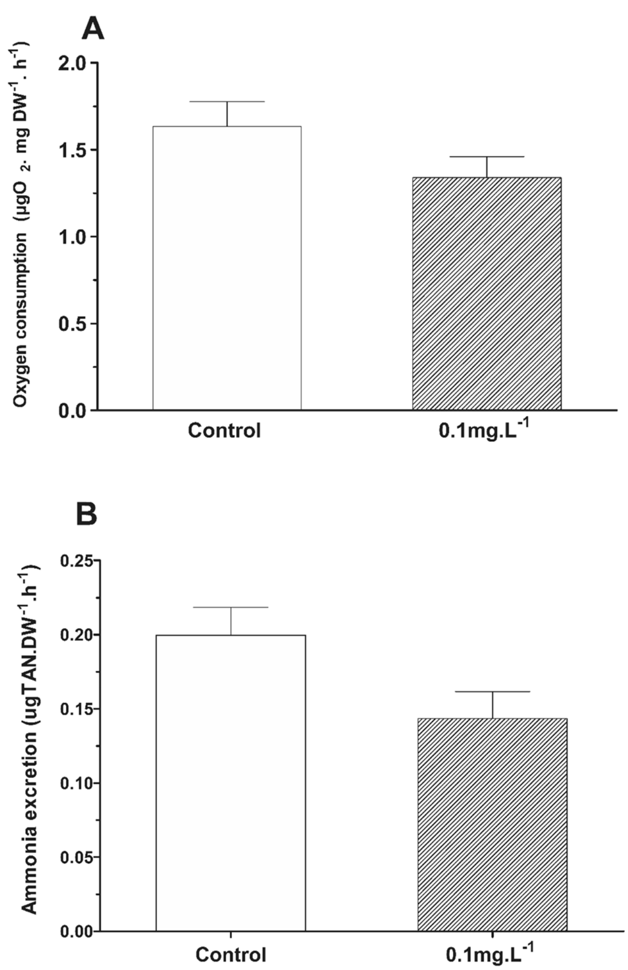

Fig. 2 **A** Oxygen consumption of *Penaeus vannamei* exposed to cadmium at concentrations 0 and 0.1 mg L^{-1} for 30 days ($P = 0.208$). **B** Nitrogen excretion of *Penaeus vannamei* exposed to cadmium at concentrations 0 (control) and 0.1 mg L^{-1} for 30 days. Data are presented as Mean ± Standard Error (7 ≤ N ≤ 10; $P = 0.054$)

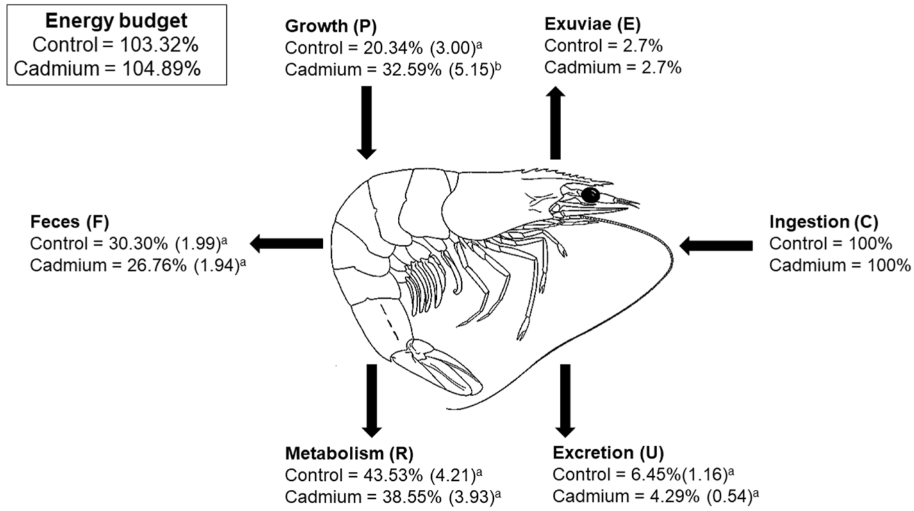

Fig. 3 Energy partitioning (expressed as a percentage of ingested energy) in *P. vannamei* for each treatment (control or exposed to cadmium–0.1 mg L^{-1}). Values are expressed as the mean and standard error of the mean in brackets ($7 \leq N \leq 10$). Values with different letters in the same category differ statistically by Test *T* followed by SNK. Figure of shrimp *P. vannamei* available in FAO (2009). Data from energy channeled to the molt were inserted in the figure according to Coelho et al. (2019)

Discussion

Mortality and Molting Cycle Relationship

The mortality rate in *P. vannamei* exposed to Cd^{2+} was observed around the third day post-molting. The endocrine system regulates the molting cycle of crustaceans, and studies have indicated that animals in the post-molt stage might be more susceptible to the toxic effects of chemical pollutants (Tumburu et al. 2012) due to alterations in epithelial permeability (Abidi et al. 2016). Some decapods experience increases in epithelial permeability during the post-molt phase, which typically lasts an average of five days and facilitates ion exchange and the hardening of the new exoskeleton (Rasmussen and Andersen 1996). However, there is evidence that body permeability might decrease in animals exposed to water containing metal cations as a defensive mechanism to prevent exchanges across membranes in an unfavorable environment, the decreased uptake hypothesis (Tumburu et al. 2012). Given the high post-molt mortality rate, it is plausible that this mechanism was active in *P. vannamei* exposed to Cd^{2+}. Decreased body permeability induced by Cd^{2+} may have limited the uptake of ions and minerals necessary for hardening the new exoskeleton. However, since the presence of the metals did not impact the osmolality of the hemolymph, it is also possible that during post-molting, there was a more significant influx of cadmium into the animals' bodies, and this caused greater mortality.

The Relationship Between Growth, Ingestion, and Defecation

Animal growth corresponds to the energy gained through food consumption and stored as bodily reserves. In the control group, growth was only 23% relative to the initial mass, while in the group exposed to Cd^{2+}, growth increased by approximately 44%. As a result, the animals directed more energy toward growth when exposed to Cd^{2+}, about 30% of their daily energy intake. Several hypotheses could explain this response. Although the Cd^{2+} concentration used in this study is comparable to levels found in contaminated waters (Aguiarla et al. 2008; Arcega-Cabrera et al. 2021), it is roughly ten times lower than the LC50 for *P. vannamei* (Wu and Chen 2004). This discrepancy might have triggered a biological response known as hormesis (Calabrese 2008), a phenotypic ability to shape the responses to environmental changes, such as metals, microplastics, pharmaceutical products, reduced pH, and variable temperatures (Hendry et al. 2008; Xiaoxue et al. 2014; Rix et al. 2022). This is a response to the disruption of homeostasis and is stimulated by low concentrations of contaminants (Jusselino Filho 2002). Such responses include increases in growth and reproduction rates, longevity, and disease resistance (Kmecl and Jerman 2000). Generally, the stimulating effect of hormesis may be 30% greater in animals exposed to the contaminant than in a control situation (Chapman 2001). However, to prove this hormesis hypothesis, future studies must be tested by exposing a dose–response curve *P. vannamei* exposure to Cd^{2+}. Although cadmium intoxication did not influence the value of the adenylate energy charge in shrimp *Palaemon serratus* (Théabalt et al. 1996), in *P.vannamei* PACAP (pituitary adenylate cyclase-activating polypeptide) promotes the growth of the animals (Lugo et al. 2013) and similar mechanism may have occurred here. In addition, for aquaculture, it is observed that the survival rate in cultivation is close to 89% within the considered ideal salinity range (between 15 and 25 ppt) (Furtado et al. 2016; Bray et al. 1994). Our work has shown that, although the growth is higher, their survival rate decreases to 70%, which could negatively affect the cultivation of *P. vannamei*.

Furthermore, Cd^{2+} might act as an endocrine disruptor related to growth and molting in *P. vannamei*, as has been suggested for other organisms (Cribiu et al. 2020; Chong 2022; Ortega et al. 2022). Future research should investigate whether the increased growth rate and molting frequency might be associated with an adjustment related to Cd^{2+} elimination through molting. In the crab *C. danae*, Cd^{2+} has been observed to deposit in the exoskeleton during the post-molt phase when mineralization occurs. Still, it adversely affects the formation of the exoskeleton's organic matrix (Butler and Zou 2021). Molting was considered a mechanism of depuration of metals in the fiddler crab *Uca pugnax* (Bergey and Weis 2007) and *Minuca burgers*i (Ramos and Leite 2022), and the shrimp, *Palaemonetes pugio* (Keteles and Fleeger 2001). Metals in the hemolymph migrate to the exoskeleton, which is discarded in the environment through the ecdysis process (Bergey and Weis 2007).

Animals exposed to Cd^{2+} ingested slightly more energy than control animals, at 2.1 and 1.8 kJ ind^{-1} day^{-1}, respectively, suggesting that Cd^{2+} exposure did not impact their ability to forage or handle food. This minor increase in intake rate might have promoted *P. vannamei* growth. Furthermore, the lower defecation rate implies improved utilization of ingested food. In this context, Cd^{2+} might have enhanced intestinal nutrient absorption through alterations in the microbiota or by increasing the expression of digestive enzymes produced in the hepatopancreas and intestine, changes that have already been observed in the crayfish *Procambarus clarkii* and the crab *Scylla paramamosain* when exposed to Cd^{2+} (Zhang et al. 2020; Zhu et al. 2018). Furthermore, Duan et al. 2021 found that exposure to Cd^{2+} increases and alters the composition of the intestinal microbiota of *P. vannamei*. This increase in diversity could contribute to neutralizing the adverse effects of Cd^{2+} exposure.

Metabolism and Nitrogen Excretion

Metabolism, broadly defined as the culmination of all chemical reactions within an organism, is often quantified by estimating an animal's oxygen consumption. Fluctuations in oxygen consumption generally occur when the homeostatic balance is disrupted, leading to an escalated demand for energy (Nicholls 2013; Rodriguez-Armenta et al. 2018). In *P. vannamei*, there was a tendency to decrease individual oxygen consumption and specific dry mass, but there were no significant statistical differences. Therefore, even though *P. vannamei* exhibited enhanced growth upon Cd^{2+} exposure, a condition that should theoretically increase energy demands, no corresponding rise in metabolic rate was observed. Juveniles of the shrimp *Exopalaemon carinicauda*, when exposed to the same concentration, also showed no statistical differences in their oxygen consumption (Zhang et al. 2014). Reduction in oxygen consumption has already been observed in juveniles of *P. vannamei* exposed to 0.3 mg L^{-1} of Cd^{2+} in salinity 15 (Wu and Chen 2004) and *Palaemon macrodactylus* exposed to 2.7 mg L^{-1} of Cd^{2+} in salinity 31 (Zhang et al. 2021). These differences between species may be due to different concentrations of the Cd^{2+}, ontogenetic stage, and salinity to which the animals were exposed. The Cd^{2+} exposure is believed to instigate cellular modifications or damage within the gills and disrupt oxygen-copper binding, the fundamental respiratory pigment in decapods (Ortega et al. 2017; Zhang et al. 2021).

Ammonia (unionized plus ionized ammonia) is the principal nitrogenous excreta of most aquatic animals. It results from the catabolism of free amino acids and is toxic in high concentrations, mainly due to its deleterious effect on enzyme activity. Quantifying nitrogen excretion is an important tool to assess the influence of abiotic factors and diet on animal protein metabolism (Uliano et al. 2010; Augusto et al. 2020). Like metabolism, nitrogen excretion in *P. vannamei* exposed to Cd^{2+} tended to decrease, but there were no statistical differences, suggesting that at low Cd^{2+} concentrations, as investigated here, physiological mechanisms related to changes in protein or free amino acid catabolism and excretion of nitrogenous compounds are not affected. Similar results were found in *Litopenaeus schmitti, Farfantepenaeus paulensis, Exopalaemon carinicauda* (Barbieri 2007; Barbieri et al. 2017; Zhang et al. 2014). Furthermore, the trend in reduced ammonia excretion could be related to the decreased utilization of amino acids as a strategy to channel more energy for growth, as observed in juvenile crabs *Portunus trituberculatus* when exposed to Cd^{2+} (Wang et al. 2022).

Hepatosomatic Index, Energy Substrate Oxidation, and Osmoregulation

In *P. vannamei*, exposure to Cd^{2+} did not affect processes associated with energy supply, such as the hepatosomatic index and the oxidation of energy substrates, nor did it impact the osmoregulatory capacity. The hepatopancreas in crustaceans plays vital roles in secreting digestive enzymes, absorbing nutrients, and storing and supplying energy essential for growth, reproduction, and metabolism. Under stress conditions, the energy reserves stored in the hepatopancreas can be mobilized to meet the increased energy demand (James et al. 2013). Additionally, the hepatopancreas is known to accumulate Cd^{2+} in crustaceans (Ghasemian et al. 2016), making the hepatosomatic index a potential biomarker of pollutant toxicity. In this study, no significant changes were observed in the hepatosomatic index of *P. vannamei*. This suggests that despite alterations in important parameters such as mortality and growth, the energy reserves stored in hepatopancreas were not accessed. In *Procambarus clarkii*, no statistically significant difference in the hepatosomatic index was observed following exposure to low concentrations of Cd^{2+} (Martín-Díaz et al. 2005). In shrimp *Macrobrachium nipponense*, hepatosomatic index increases when exposed to zinc and cadmium, respectively (Zhang et al. 2021). Some studies have shown that in shrimp exposed to high concentrations of Cd^{2+}, there is bioaccumulation of the metal in the hepatopancreas, especially in low salinities. For example, in *P. vannamei*, high Cd^{2+} toxicity was demonstrated during exposure to salinity of 5S, but not at 20‰ (Ardianshyah et al. 2012). In the shrimp *F. paulensis,* the Cd^{2+} was also toxic at high concentrations (40 mg L^{-1}), but only when the animals were kept at 5S (Barbieri and Paes 2011). Therefore, the salinity to which *P. vannamei* was exposed in the present study (20‰) may have influenced the results.

Moreover, the animals continued to oxidize proteins, regardless of the presence of Cd^{2+}. Changes in the oxidation of energy substrates may be linked to increased neoglucogenesis due to the heightened energy demand following Cd^{2+} exposure or to variations in the catabolism of free amino acids used in osmoregulation (Felten et al. 2008). The exposure to the pollutant did not alter the hyper-osmoregulatory capacity of *P. vannamei*, as indicated by the unchanged hemolymph osmolality. This may have happened because the animal is within its isosmotic point, keeping it in conditions close to its homeostasis (Jaffer et al. 2020). However, in other invertebrates such as shrimp, crabs, and mussels, exposure to dissolved metals like copper, cadmium, zinc, and nickel has been shown to modify osmoregulatory capacity, possibly due to intense competition for ion transporters such as Mg^{2+}, Ca^{2+}, and Na^{+} (Capparelli et al. 2017; Zhou et al. 2021).

Energy Balance

Most of the energy consumed by crustaceans is typically allocated to metabolism, which can vary depending on environmental conditions that challenge maintaining homeostasis (Xue et al. 2021; Mantoan et al. 2021). Both biotic and abiotic factors, including contaminants in the aquatic environment, can disrupt this process. Some authors suggest that environmental pollutants can affect individual-level energy balance and be used for predictions at the population level (Klok et al. 2012; Hansul et al. 2021). *Penaeus vannamei*, *M. amazonicum*, and *C. danae* allocate most of their energy intake to metabolism (approximately 40%), regardless of the treatment (Ramaglia et al. 2018; Augusto et al. 2020). The increased growth observed in Cd^{2+} exposed animals leads to a redistribution of the ingested energy. While control shrimps allocate 20% of the energy intake to growth, those exposed to Cd^{+2} allocate 33%. For example, Wang et al (2022) showed that shrimp *Fenneropenaeus chinensis* and crab *Portunus trituberculatus* exposed to cadmium occurred hormesis based on the alterations of enzymes as the superoxide dismutase, catalase, and reduced glutathione. Therefore, the hormesis mechanism may have influenced changes in the energy balance of the species. Hormetic dose–response relationships have been observed in various aspects of biology, but little is known about their effects on energy distribution within an organism's body (Calabrese 2008; Wang et al 2022). It has been suggested in the literature that crustaceans may reduce the energy allocated to certain functions at the expense of mechanisms involved in eliminating contaminants from the organism (Calow and Sibly 1990). This may be the case for *P. vannamei* if the high growth observed is related to removing Cd^{2+} through molting. Although using energy balance as a tool to understand the effects of pollutants is limited, studies have shown that exposure of the isopod *Porcellio scaber* to Cd^{2+} reduces the amount of energy intake (Sures and Taraschewski 1995) while exposure of the cladoceran *Alona guttata* to Pb^{2+} decreases the energy reserves devoted to reproduction and survival (Osorio-Treviño et al. 2019).

In conclusion, as hypothesized, the Cd^{+2} exposure may have induced a trade-off response because energy was reallocated for growth, compared to the control group, but accompanied by increased mortality. The trade-off allows animals to improve fitness in polluted environments but at reduced survival costs. For example, detoxification might use energy and alter resources, which are unavailable for other fitness traits such as survival. The observed changes in energetics and survival could substantially influence the population and community structure of *P. vannamei* exposed to Cd^{2}. Although the growth is higher, it is unknown whether it is sustained for extended periods (greater than 30 days) and the survival rate decreases to 70%, which could negatively affect marine biodiversity, fishing, and aquaculture, as it is among the most consumed shrimp in the world.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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