Research Article

Maximum critical temperature and oxygen consumption during thermoregulation in *Macrobrachium americanum* (Bate, 1868) adult prawns

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ABSTRACT. *Macrobrachium americanum* is a large prawn living in rivers and coastal water bodies of tropical and subtropical ecosystems of the Pacific side of the Americas. Water temperature and salinity are the main physicochemical variables determining its distribution. Temperature also influences its metabolic rate, which determines growth rate and reproduction. Because of this, preferred temperature, critical thermal maximum (CTMax), and O_2 consumption rates at four temperatures (20, 24, 28, and 32°C) were tested from wild prawns in laboratory assays. Those temperatures correspond to the annual temperature fluctuations at the sampling site. The final preferred temperature of this species is close to 26.4°C. The acclimatization temperature has an almost linear effect on the CTMax ($R^2 = 0.987$, $P < 0.05$), and the oxygen consumption routine rates increased as the acclimation temperature increased from 20 to 32°C.

Keywords: *Macrobrachium americanum*; thermoregulation; prawn; freshwater; aquaculture

INTRODUCTION

Macrobrachium prawns (Decapoda, Caridea, Palaemonidae) are among the most diverse and widely distributed genera of crustaceans (De Grave et al. 2008). Those prawns are important components for the ecological equilibrium in rivers and coastal lagoons because they eat dead animals and remove remains deposited on the bottom. They are also the prey of fish, reptiles, and birds. Some species within this genus are exploited worldwide by fisheries in rivers and coastal lagoons for human consumption. Particularly, species reaching large sizes are highly demanded as a culinary product, while small ones are used as a cheap source of protein for local communities living close to rivers and coastal lagoons. In contrast with Asia, in which there is a large industry on *Macrobrachium* prawns aquaculture, in Latin America, virtually all production comes from fisheries, and total production is low compared to Asian species (García-Guerrero et al. 2013a).

The exploitation in rivers and coastal lagoons in Latin America is unmanaged and excessive pollution, and habitat destruction are causing serious declines in their populations. Their absence could contribute to the loss of ecosystem equilibrium. One of the most affected species is *Macrobrachium americanum*, one of the prawns that reaches larger sizes and, therefore, one of the species that is mostly exploited. This prawn is initially distributed along the Pacific shore of America between Baja California (Mexico) and south Peru (García-Guerrero et al. 2013a). Adult *M. americanum* can travel long distances from the coast up into the rivers once they become juveniles (sometimes more than 150 km). Therefore, it could become a good biological index of ecological fitness, considering that domestic, agricultural, industrial and human wastes cause pollution at different scales. This prawn has become scarcer each year, and the status of its populations is unknown in most of its distribution areas. There has been increased interest in commercial far-

ming of this species in recent years among producers and research groups. However, there are still no efficient techniques for its culture, so its farming cannot be proposed in the near future (De Los Santos et al. 2021). Therefore, all current production relay on fisheries (García-Guerrero et al. 2015). The conservation of this species requires studies to understand their needs and limitations to propose conservation and exploitation measures. Studies on the growth rate, survival, and the detailed effect of most environmental variables that can affect this prawn, either in nature or in cultivation, are required. In most cases, water temperature is the physical variable that most affects its development because it influences the metabolic rate and its significant effect on O_2 consumption.

Understanding the physiological mechanisms underpinning thermal tolerance is essential to predict the impacts of current and future rises in global temperatures (Huey et al. 2012). In addition, global warming that might change annual temperature fluctuations in the atmosphere and water makes studying such phenomena in populations exposed to thermal stress a prime subject. In Decapoda, rising temperatures negatively affected growth increased metabolic rates, and challenged acid-base homeostasis (Klymasz-Swartz et al. 2019). According to Pörtner & Farrel (2008), subtle changes in water temperature, although not easily perceptible to humans, substantially affect aquatic life because temperature changes alter the life cycle speed and distribution of all the species that inhabit those places. The temperature study is fundamental to understanding the interval in which all metabolic activities and physiological processes can function efficiently (Ward et al. 2010); this also involves the study of O_2 consumption, which is determined by the metabolic rate and the energy flow required to maintain their homeostasis (Salvato et al. 2001, Das et al. 2005). O_2 consumption rates are often used as proxies for metabolism because of the difficulties in estimating actual metabolic rates (Glandon et al. 2019). The relationship between temperature and O_2 consumption and thermal limits are prime issues to study to understand the limitations and needs of aquatic species both in cultivation and in the wild.

Although the number of studies on the physiological effects of climate change is increasing, most research has been carried out on marine species. Coastal systems are some of the most productive regions on earth and are characterized by large and frequent fluctuations in environmental parameters, including temperature and O_2 (Glandon et al. 2019). Freshwater prawns, depending on species, spend the initial stages of their life in such ecosystems and have a limited capacity to cope

with extreme conditions. This limitation can interfere with their physiological functions, pushing them to their tolerance limits in the field and cultivation. Because of this, it is important to make studies that help understand its limits by knowing both the maximum and minimum critical temperatures and the most suitable temperatures. In addition, variations in O_2 consumption are among the main symptoms and one of the most determining factors in knowing how temperature changes affect all aquatic crustacea. Temperature changes also imply changes in O_2 consumption, and if temperatures are extreme, heat stress will be produced.

Progressively raising or lowering the temperature in laboratory studies from the acclimation temperature until thermal stress is manifested is a useful tool to recognize thermal limits (Diaz et al. 2002). One of the most accurate ways to evaluate thermal adaptive responses is to determine the critical thermal maximum (CTMax) and minimum (CTMin) as these limits are a measure of thermal tolerance (Reynolds & Casterlin 1979). The responses observed at maximal and minimal temperatures identify the temperature at which the first symptoms of stress appear without damage, directly resulting from how acclimation temperature modulates thermal tolerance (Angilletta et al. 2002). Several tools, such as the acclimation response ratio (ARR), assess thermal behavior. The acclimation response ratio can be calculated in most aquatic ectotherms as an index to determine the magnitude of thermal acclimation. Research on this topic may help create useful information that could predict and compare the possible consequences of warming events (Ern et al. 2020). It has been previously observed in various crustaceans, mostly decapods (Espina et al. 1993, Chen & Chen 1999, McGaw 2003, Re et al. 2005, González et al. 2010, Curtis & McGaw 2012, Padilla-Ramírez et al. 2015). The study of this phenomenon is particularly important in tropical and subtropical aquatic species since they are, presumably, close to their upper thermal limit and vulnerable to even small temperature increases (Ern et al. 2014).

Despite the importance of the subject, there are few studies dealing with the thermal behavior and its limits in the genus *Macrobrachium*. Previous examples studying this topic are the research by Hernández Sandoval et al. (2018a,b), who, with similar scope, addressed this same problem for two different *Macrobrachium* species, both from the western side of Mexico. One of those species, (*M. tenellum*) lives in the same area as *M. americanum* but is common only in warmer low areas and rarely travel into the upper areas of rivers where the water is regularly a little colder. The opposite pattern is commonly observed by *M. americanum,* mostly distributed as an adult in higher

portions of the river. This research shows how the water temperature directly affects thermal behavior, and this response is conditioned both by water temperature and previous acclimatization temperature.

We consider that a comparison between two species of the same genus and with similar distribution areas, but with different thermal needs and probably, different thermoregulatory responses, could provide useful information for a complete understanding of the thermoregulatory behavior of the American species of this genus. Due to the above, this study aims to determine the maximum and minimum critical temperatures in laboratory conditions of the freshwater prawn *M. americanum* and the effect of these temperatures on O_2 consumption.

MATERIALS AND METHODS

Collection and handling of specimens

Macrobrachium americanum specimens were caught with traps baited with dead fish in the Río Fuerte, Sinaloa, Mexico (26°02'34.45"N, 108°50'35.01"W). A bunch of 107 specimens was collected and transported to the Aquaculture Laboratory of the Universidad Autónoma de Occidente, Los Mochis Regional Unit, and placed in a 2500 L fiberglass pond for seven days. After a couple of days of acclimation, 80 specimens were selected (119.06 ± 14.44 g).

Experimental design for thermoregulatory behavior

Selected specimens were placed in 1000 L fiberglass circular ponds, with filtered freshwater, at a density of 10 per pond with PVC tubes as shelter. A 50% water exchange was performed every three days by siphoning while feces, food remains, and exuviae were removed. Food was provided once a day (18:00 h) consisting of fresh tilapia fillet and commercial shrimp pellets (Camaronina® 35% crude protein). Four temperatures were tested (20, 24, 28, and 32°C), consisting of the annual temperature interval at the sampling site (Hernández et al. 2018a). A blower (Pionner, 1 Hp, 115 V) was used to aerate and maintain the dissolved O_2 concentration always above 5 mg O_2 L^{-1} (Peraza-Gomez et al. 2022) measured with a YSI-55 oximeter (Yellow Spring, OH, USA). The temperature was kept constant with 500 W automatic heaters (Biopro® ± 0.5°C). In the 20°C treatment, an electric room cooler maintained the temperature. The temperature was monitored daily with a mercury thermometer (EW-03013-62; 0-250°C). All prawns were maintained under these conditions for 30 days for acclimatization as Manush et al. (2004) recommended.

Thermoregulation measurements

The acute method (Reynolds & Casterlin 1979) was used to find the optimal temperature or final *preferendum*. A horizontal thermal gradient as described by García-Guerrero et al. (2013b) was utilized, consisting of a hydraulic PVC tube 300 cm long and 20 cm in diameter with 20 subdivisions of 15 cm in length each. The depth of the water column was 15 cm, and the gradient was produced by placing two 500 W heaters at one end while the ice was placed in hermetic containers at the other end. The gradient had a temperature interval from 12 to 40°C (± 2.0°C). An air diffuser hose was placed at the bottom through the whole tube to maintain the dissolved O_2 concentration between 4.6-8.7 mg O_2 L^{-1} and avoid thermal stratification in the water. The temperature was measured in each segment with mercury thermometers. Thirty-one specimens were used (n = 8, 7, 8, and 8 prawns acclimatized to 20, 24, 28, and 32°C, respectively). They were placed individually in the section with a temperature equivalent to its acclimatization. The temperatures of the chambers chosen by the specimens were recorded every ten minutes for one hour and a half. According to Reynolds & Casterlin (1979), the final preference was determined graphically.

Critical thermal maximum (CTMax)

For the determination of the CTMx, five individuals (n = 20) of each acclimatization temperature (20, 24, 28, and 32°C) were used. They were placed one at a time in 50 L aquariums equipped with 200 W heaters (Steren®, WL-1300), a submersible pump (Evans® AQUA5W-110V), and an aerator stone to keep the temperature homogeneous. Prawns were placed 30 min before starting the experiment to reduce handling stress (García-Guerrero et al. 2011). Subsequently, the water temperature was increased by 1°C min^{-1} until balance loss (PE) was observed (Vinagre et al. 2015). Then, specimens were returned to their acclimatization temperature. The acclimatization response rate (TRA) was calculated from the CTMax divided by the acclimatization temperature (ΔCTMax / ΔT) (Claussen 1977).

Oxygen consumption rate

A semi-open respirometry system was used as described by Hernández-Sandoval et al. (2018b). Five specimens were selected from each experimental condition (n = 20). They were individually placed in 3-L respirometric chambers. An empty chamber was kept as a control to calculate O_2 consumption caused by bacteria. They were not fed 24 h before starting the experiments. The water flow remained open for 2 h in all chambers (Pérez et al. 2003). Then, initial O_2 concen-

tration was recorded, and the flow was closed for half an hour to prevent the concentration from decreasing below 30%, which might become a stress factor (Stern et al. 1984). Subsequently, a water sample was taken to quantify the final dissolved O_2 concentration. All measurements were made between 15:00 and 19:00 h with two repetitions at one hour. The water O_2 concentration was quantified at the beginning and at the end of the bioassay with a YSI 52 oximeter equipped with a polarographic sensor with a precision of ± 0.03 mL^{-1}. O_2 consumption was calculated as the difference between the initial and final concentrations of each chamber at each acclimatization temperature, expressed as mg O_2 kg^{-1} h^{-1} according to Padilla-Ramírez et al. (2015) using the following formula:

$$TCO = (C_t - C_0) \, V / (W \times T)$$

where: Ct is the change in the O_2 concentration in the chamber before and after the test; C_0 is the difference in O_2 in the control chamber; V is the volume of the chamber; W is the weight in kg of the prawn; T is time in hours, and TCO is the O_2 consumption rate.

Statistical analysis

Normality tests (Shapiro-Wilk, $P > 0.05$) and homo-geneity of variance (Levene, $P > 0.05$) were applied when required. Kruskal-Wallis ($P < 0.05$) was applied, and when significant statistical differences were shown, analysis of multiple *post-hoc* comparisons of Student Newman Keuls were executed ($P < 0.05$; Van-Emden 2008). Data were plotted in parallel boxes with Sigma plot v.12.5z software.

RESULTS

The final preferred temperature of this species is close to 26.4°C (Fig. 1). This figure shows how the acclimatization temperature directly affects the preferred temperature when the acclimatization temperature is low since, under such circumstances, prawns choose a lower preferred temperature. However, prawns acclimatized at 24°C or higher will choose a temperature close to the preferred tempe-rature. Figure 2 shows how the acclimatization temperature has an almost linear effect on the critical thermal maximum. The specimens acclimatized to 22°C are those with a lower critical temperature, while those acclimatized at 32°C had the highest. Figure 3 displays the average O_2 consumption rate of previously acclimatized prawns within the whole interval analyzed.
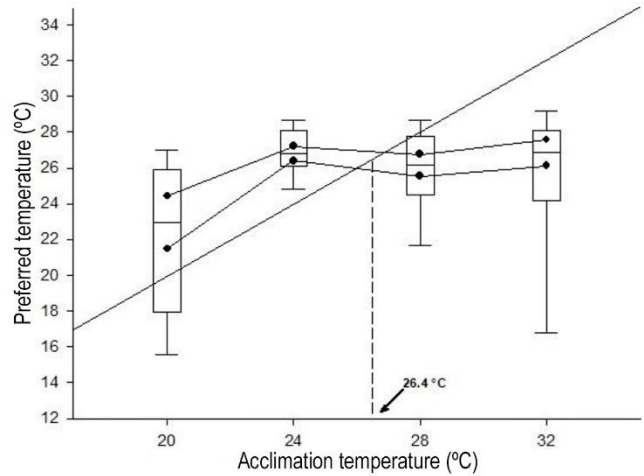

Figure 1. The preferred temperature of *Macrobrachium americanum* prawns (n = 40 per time point) acclimated to different temperatures. The zone between the solid lines represents the 95% confidence interval of the medians.
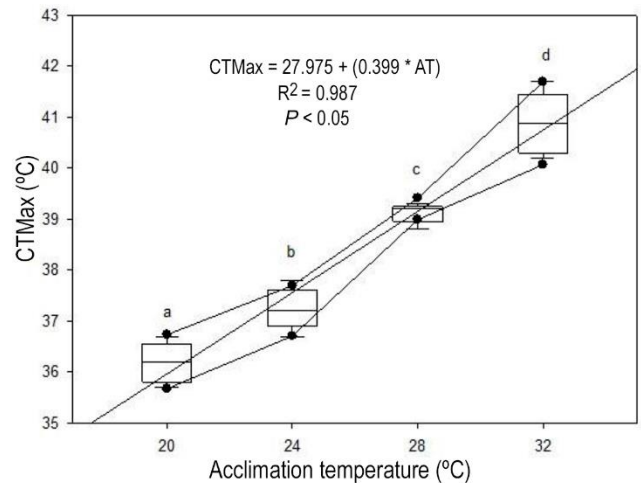
Figure 2. Critical thermal maximum (CTMax) of *Macrobrachium americanum* prawns (n = 40) acclimated to different temperatures. The. zone among the lines represents the 95% confidence interval of the medians. Different letters have significant statistical differences ($P < 0.05$).

DISCUSSION

Temperature is arguably the most important factor influencing the physiology of ectothermic organisms and a key determinant of geographic distribution (Miller et al. 2013). In the wild, temperature directly affects the distribution of all aquatic ectotherms even over other physicochemical water properties (Payette & McGaw 2003). Thermal behavior implies that the prawn will look for its preferred temperature, which is equivalent to that in which its metabolism is most
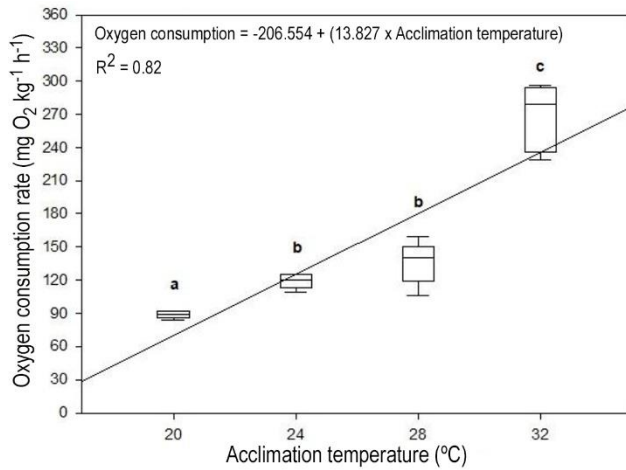
Figure 3. Average O₂ consumption rate of *Macrobrachium americanum* prawns previously acclimatized from 20 to 32°C. Different letters have significant statistical differences ($P < 0.05$).

efficient in terms of energy use (Nichelmann 1983, Díaz & Bückle 1993, Croll & Watts 2004, Ward et al. 2010, González et al. 2010). The results obtained in this research show up this effect in *Macrobrachium americanum* providing clues of how its thermal behavior makes them move to the most suitable temperatures. The present research observed that if specimens are acclimated to a temperature up to 24ºC, they will choose similar preferred temperatures between 26 and 27°C and regardless of having been acclimatized to 24, 28, or 32°C. Only specimens acclimatized at the lowest temperature will select a significantly lower temperature than the others, suggesting that as part of its thermal behavior, prawns might instinctively migrate or move to areas in which their homeostatic mechanisms are efficient, maintaining body temperature at suitable levels as initially proposed by Reynolds & Casterlin (1979). Likely, this behavior has a huge influence on its natural distribution area. Such behavior is part of species-specific adaptations displayed while experiencing temperature fluctuations over short periods, and this is common in subtropical and tropical ectotherms as previously mentioned by Díaz et al. (1998, 2002), Díaz & Re (2004), Kumlu & Kir (2005), Re et al. (2005) and Kir & Kumlu (2008). Thermal behavior also establishes limits since the prawns will avoid extreme conditions seasonally and spatially (Diaz et al. 2002). As a result, the preferred temperature is theoretically in which growth is optimal, and the critical thermal maximum establishes a limit that links a particular species' thermal biology with its ecology (Jobling 1981).

However, it is not always the same, even in species living in the same geographical basin. Present study

results slightly differ from Hernández-Sandoval et al. (2018b) for *Macrobrachium tenellum*. In that research, the same analytical criteria were used as in the present research, but it is observed that the low acclimatization temperature has a different effect on the preferred temperature. Low temperature acclimated *M. tenellum* also chooses a similar preferred temperature to those acclimated to higher temperatures. It seems that *M. tenellum* always chooses the same preferred temperature regardless of its acclimatization temperature.

In contrast, in *M. americanum,* this behavior seems to be conditioned by previous thermal history, particularly beyond 24°C, suggests that *M. americanum* has a better ability to stay in colder temperatures without the need for quick adjustments to speed up their metabolic rate once they could choose higher temperatures closer to their preferred one. In agreement with García-Guerrero et al. (2013b), *M. americanum* prawns tend to stay, especially the largest adults, at higher altitudes in the rivers, where the water stream temperatures are lower compared to the coast. In contrast, *M. tenellum* is a species that remains almost all the time in coastal lagoons or the lower sections of rivers, being rare 800 m above sea level when water is regularly colder. Therefore, *M. americanum* appears to have less need to adjust its metabolic need when kept at low temperatures, choosing a relatively low temperature when acclimatized in water several degrees below its preferred temperature, which might explain what occurs in Figure 1. In this case and in terms of energy use, it seems better to stay at a temperature only 2 or 3°C higher than that of acclimatization than move to warmer areas, at least in the short term. Because of this, *M. americanum* prawns are physiologically more capable of tolerating colder water, which is to be expected due to their frequent presence of 800 m above sea level in habitats where particularly large specimens live *M. tenellum* is absent in such spots.

On the other hand, it is shown in Figure 2 how the critical thermal maximum has a close relationship with the acclimatization temperature, so for *M. americanum,* there is an almost linear effect in which the lower acclimatization temperatures will imply lower critical temperatures, allowing the species to have a higher critical thermal temperature if acclimatization temperature is higher. When this graph is compared with the one showing the same results for *M. tenellum* in the research by Hernández-Sandoval et al. (2018b), it is observed that both species have similar behavior but with slight variations on the chosen temperature. Probably, this influences its preferred temperatures in the wild. The graph describing this phenomenon in Hernández-Sandoval et al. (2018b) research shows a

slightly more displaced linearity towards higher temperatures. The high critical temperature for this species is always a little higher than the highly critical of *M. americanum*, even if they were acclimatized to the same temperatures. It is suggested that this is directly related to the fact that in the wild, *M. americanum* is adapted to live in the lower interval of temperatures compared to *M. tenellum*, going preferably to higher altitudes, where water temperatures are lower.

In addition, another way of demonstrating the strong effect of temperature in prawn physiology or its distribution in the wild is by analyzing how O_2 consumption changes depending on water temperature. Animals depend on a continuous and adequate flux of O_2 for all metabolic tasks. If O_2 delivery does not satisfy metabolic requirements, this causes an impairment in the performance of all tasks. It often occurs at high metabolic rates caused by high temperatures because of an accelerated metabolism and because O_2 is more likely to become limiting under warmest conditions when its solubility on the water is lower (Hoefnagel & Verberk 2015). Under such circumstances, metabolic rate increases with temperature, reflecting elevated energetic costs associated with a high metabolic rate, which can be measured through O_2 consumption (Verberk et al. 2016). The maximum O_2 consumption rate detected in the present research might be close to maximum capacity and then the limit of the ability of organisms to meet the high energy demands associated with a high metabolic rate.

In contrast, the temperature where less O_2 is consumed in present research should be where energy expenditure is the lowest (Fig. 3). This figure displays the relationship between temperature and metabolic rate measured through variations in O_2 consumption and suggests an almost linear effect in terms of O_2 consumption as temperature rises. However, at higher temperatures, this consumption seems to alter the basic biological functions in most specimens, which can be deduced from the wide standard deviations in O_2 consumption occurring above 28°C. Above such temperatures, O_2 delivery seems insufficient to sustain aerobic energy production, as suggested by Ern et al. (2014). In contrast, a more stable consumption is observed when the prawns are kept between 20 and 25°C. This behavior is common in most invertebrates that depend on water temperature to sustain their metabolic rate (Salvato et al. 2001). In this sense, and as observed in many previous studies, measuring O_2 consumption is a direct and reliable way of knowing how the metabolic rate rises or falls depending on water temperature, given the direct relationship between the metabolic rate and the O_2 consumption in ectotherms.

Many previous studies show this same trend in crustaceans (Stern et al. 1984, Díaz & Re 2004, Manush et al. 2004, García-Guerrero et al. 2011, Padilla-Ramírez et al. 2015). García-Guerrero et al. (2011) observed, for *M. americanum*, the same trend in O_2 consumption, even in a wider temperature interval and considering that this prawn can tolerate lower temperatures compared with other co generics accustomed to warmer waters. García-Guerrero et al. (2011) also observed how, at high temperatures (28 to 30°C), prawns O_2 consumption rate becomes very high and irregular, as occurred in the present research. Deducted from its O_2 consumption, it is possible that, beyond such temperatures, these prawns can no longer properly control their metabolic functions as they are approaching their higher critical thermal limit. Determining the maximum sustainable rate of O2 consumption may also help understand this maximum temperature limit. According to Cerezo et al. (2009) the highest levels of oxygenation in the hemolymph are related to the greatest aerobic performance, occurring likely at the temperature at which the organism would perform at its maximum capacity. Over this interval, O_2 consumption will drop as the organism approaches its upper critical thermal limit.

Results like those in present research for thermal behavior and O_2 consumption have been observed in other crustaceans (Espina et al. 1993, Chen & Chen 1999, McGaw 2003, González et al. 2010, Curtis & McGaw 2012, Padilla-Ramírez et al. 2015), suggesting a common trend for the group. Differences could result from being native to regions with different climatic conditions or water hydrodynamics (Díaz & Bückle 1993, González et al. 2010). Other important aspect is their reproductive status since mature specimens during the reproductive season may instinctively choose water temperatures that stimulate reproduction rather than growth (Pascual et al. 1998, Pérez et al. 2001, Hernández-Díaz et al. 2003, Hernández-Sandoval 2008, González et al. 2010). Also, different trends could be explained by differences between species, physiological condition (fitness), or life history (Claussen 1977, Díaz et al. 1998, Chen & Chen 1999, Díaz et al. 2002, Re et al. 2005, González et al. 2010, Padilla-Ramírez et al. 2015). The ability to adapt to fluctuating thermal scenarios should be a factor that determines how a species copes with variations in water temperature through compensatory responses that allow them to overcome these changes (Díaz et al. 1998). Present results support such ability.

If laboratory studies are combined with field studies, a better understanding of the thermal requirements of any prawn species can be obtained. Knowledge of the high thermal tolerance limits,

thermal preferences, and thermal requirements for the growth of aquatic species could be useful in the selection of areas suitable for farming. It could also help better understand its population dynamics in the wild, its reproduction, and migration needs. Further research should consider the metabolic consequences of remaining at unsuitable temperatures, particularly those high. Also, to assess the potential impact of climate change on its populations.

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