BOLETÍN DEL CENTRO DE INVESTIGACIONES BIOLÓGICAS
VOLUMEN 37. NO. 2, 2003, PP. 103 - 117
UNIVERSIDAD DEL ZULIA, MARACAIBO, VENEZUELA

PREFERRED AND AVOIDED TEMPERATURES OF THE PRAWN *Macrobrachium acanthochirus* (CRUSTACEA, PALAEMONIDAE)

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Abstract. This study determined thermoregulatory behavior of prawns (*Macrobrachium acanthochirus*) in relation to thermal conditions of their natural environment (20-28°C). Preferred temperatures (PT) and avoided temperatures were measured in a thermal gradient for organisms acclimated to 23, 26, 29, and 32°C. The acute thermal preference (25.7°C) was obtained graphically and by linear regression: PT = 36.304 - 0.414 AT ± 0.15°C, where AT is the acclimation temperature. The model was highly significant ($P = 0.028$, $R^2 = 0.996$). To define the relationship between high avoided temperatures (HAT) and low avoided temperatures (LAT) and AT, the following regressions were calculated: HAT = 43.333 - 0.567 AT ± 0.39°C ($P = 0.010$, $R^2 = 0.980$), and LAT = 38.0 - 0.60 AT ± 0.63°C; ($P = 0.024$, $R^2 = 0.953$). Prawns acclimated at low AT had high PT values and vice-versa. At intermediate temperatures, the differences between AT and PT were negligible. A similar pattern was observed for the avoided temperatures. Specific thermal efficiency (STE) of the prawns is 77.5%.

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Recibido: 19 Marzo 2003 / Aceptado: 20 Noviembre 2003
Received: 19 March 2003 / Accepted: 20 November 2003

Therefore, cultivation of *M. acanthochirus* is recommended at locations where most frequent temperatures are near the thermal preferendum for this species. The range of *M. acanthochirus* expands 250 km northward to Jalisco State and altitudinally to 600 m. Previously, the species was known to occur from the State of Oaxaca to the southern part of Colima State.

Key words: Acute thermal preferendum, avoided temperatures, *Macrobrachium acanthochirus*, Palaemonidae, prawn, range expansion, thermoregulatory behaviour.

TEMPERATURAS PREFERIDAS Y EVITADAS DEL LANGOSTINO *Macrobrachium acanthochirus* (CRUSTACEA, PALAEMONIDAE)

Resumen. Se determinaron las temperaturas preferidas y evitadas del langostino *Macrobrachium acanthochirus* en relación a las condiciones térmicas de su ambiente natural (20-28°C). Las temperaturas se midieron en un gradiente térmico en organismos aclimatados a 23, 26, 29 ó 32°C. El preferendum térmico agudo (27,5°C) se obtuvo gráficamente y de la regresión lineal: TP = 36,304 – 0,414 AT ± 0,15°C; modelo que fue significativo (p = 0,028; R^2 = 0,996). Con el fin de definir la relación entre las temperaturas evitadas altas (TEA) y bajas (TEB) y TA se calcularon las regresiones: TEA = 43,333 – 0,567 TA ± 0,39°C (p = 0,010; R^2 = 0,980) y TEB = 38,0 – 0,60 AT ± 0,63°C (p = 0,024; R^2 = 0,953). Los langostinos aclimatados a bajas temperaturas prefirieron temperaturas altas y viceversa, mientras que a temperaturas intermedias la diferencia entre TP y TA fue insignificante. Se observó un patrón similar en las temperaturas evitadas; y la eficiencia térmica específica (ETE) de los langostinos fue 77,5%. Para el cultivo de esta especie se recomiendan sitios donde las temperaturas más frecuentes se encuentren alrededor del preferendum térmico. *Macrobrachium acanthochirus* previamente se encontró desde el Estado de Oaxaca hasta la parte sur del Estado de Colima. En este estudio se encontró en el Estado de Jalisco, lo cual significa que su distribución se expandió 250 km hacia el norte y sobre los 600 msnm.

Palabras clave: Comportamiento termorregulador, expansión de distribución, langostino, *Macrobrachium acanthochirus*, Palaemonidae, preferendum térmico agudo, temperaturas evitadas.

INTRODUCTION

Several prawn species inhabit rivers of the central Mexican Pacific coast, including *Macrobrachium americanum*, *M. occidentale*, *M. michoacanus, M. hobbsi*, *M. tenellum*, *M. digueti* and *M. acanthochirus* (Villalobos 1966, Wicksten 1989, Nates and Villalobos 1990). These species are caught indiscriminately, because all are highly-valued by consumers. During the rainy season, when rivers rise, these organisms are swept by currents to estuaries, where larvae hatch. It is during these massive migrations when prawns are captured, and *M. occidentale* and *M. acanthochirus* comprise 60% of the commercial catch. In Mexico, the genus *Macrobrachium* is widely distributed, but little is known about its thermal behavior.

Temperature influences vital processes of organisms and may be a lethal factor. However, organisms are able to withstand adverse temperatures via thermal acclimation. This process involves compensatory changes that occur during the lifetime of the animal (Claussen 1980). In natural environments, organisms may be exposed to unfavorable temperatures, but have mechanisms to detect and avoid such temperatures. Avoided temperatures are temperatures in which organisms spend the least time; organisms are less active in thermally neutral environments. Thermal preference and avoidance of certain temperatures modulate the functional relationships between the organism and its environment, thus affecting the survival of the species (Giattina and Garton 1982). Optimum values of physiological processes occur within the interval of preferred temperatures, e.g. the species improves its performance when living within the interval (Giattina and Garton 1982). The concept of performance includes optimum rates of ingestion and assimilation, growth, health, environmental adaptation and functions of control systems. The optimum temperature is the ambient temperature where organisms experience least stress (Nichelman 1983). Because thermal preference is influenced by several factors, organisms in natural environments do not always live within the optimum temperature interval. Like any other environmental stressor, adverse temperatures inhibit ingestion rates, causing decreased growth rates (Nichelman 1983). The author emphasizes that both exploitation and management of aquatic organisms must be based on detailed understanding of their biology. Thus, study of relationships between organisms and their environment is important to implementing their successful cultivation. The purpose of this work is to study the thermoregulatory behavior of *Macrobrachium acanthochirus* and its relationship with thermal conditions of the natural environment. This information makes it possible to define the most favorable thermal conditions for cultivating the species.

MATERIALS AND METHODS

Macrobrachium acanthochirus prawns were caught at sites in Jalisco State, Mexico, and each site was located by using a geographic positioning system (Magellan Model NAV 5000DX). These sites were at 19°37’30"N, 104°32’73"W in the Purificación river at Hermenegildo Galeana, Lo Arado, Casimiro Castillo Municipality; at 19°19’14"N, 104°53’32"W at El Rebalse de Apazulco, La Huerta Municipality; and at 19°13’10"N, 104°38’14"W in the Seco river in Cihuatlán Municipality. Prawns were caught using cone-shaped creels made of reed or bamboo, placed on river bottom with the cone opening toward the current. Most of the samples were nocturnal during the dry season and diurnal during the rainy season, when the organisms were swept by the currents in the swollen rivers (Hernández-Díaz 2003). Prawns were transported to the laboratory in plastic containers filled with water taken from the collecting site and aerated with portable air pumps. Zeolite was placed on the bottom of containers to partially eliminate nitrogenous waste (Hernández-Díaz 2003). In the laboratory, water was gradually changed until organisms were released into 2500 L fiberglass tanks containing unchlorinated aerated water and 1” PVC refuge tubes. The following physicochemical characteristics of the water were maintained with weekly monitoring: temperature: 23 ± 1°C (Brannan thermometers; ± 0.1°C); pH: 7.9 (Conductronic 20; ± 0.01

units); oxygen concentration: 5.8 - 6.2 mg O_2/L (oxymeter and polarographic sensor; HACH 16046-00 YSY 5739; 0.1 mg O_2/L); hardness: 136.75 and alkalinity: 111.50 mg $CaCO_3$/L (APHA 1992). The photoperiod was a 12:12 h light-dark cycle. Prawns were fed daily with a balanced commercial diet (35% protein) at 3% of body weight. Water was partially changed weekly, and organisms remained in these conditions for 30 days.

Subsequently, the prawns were divided into four groups (20 organisms each) and placed in 150-L fiberglass aquaria. The first group was maintained at 23°C, while water temperature of other groups were increased 1°C/day, using a 200 W heater, until obtaining 26, 29, or 32 ± 1°C. The acclimation period lasted 15 days.

Experimental temperatures (23-32°C) were chosen considering the high and low temperatures at the site where the prawns were caught. The mean annual temperature in the area is in the 20-28°C range, with a minimum of 10°C in January and February, and a maximum of 40°C in the months of June, July, and August (Estación Metereológica Chamela 2000).

Thermal preference of organisms, acclimated to the different experimental temperatures, was measured in a horizontal trough (300 cm length and 20 cm diameter) where a thermal gradient was stabilized from 5 to 45°C (Espina *et al*. 1993). At one end of the tube, the water was cooled with a Frigo Thermomix system (VWR ± 0.02°C), whereas higher water temperatures at the opposite end were produced by heating with a 1000 W titanium heater (± 0.2°C). The 15 cm water column was kept permanently aerated using a plastic tube (with multiple perforations) placed on the bottom of the trough, thus preventing thermal stratification. The tube was covered with plastic mesh which served as substrate for the organisms. The 300 cm tube was marked into 15 chambers whose temperatures were recorded using thermocouples connected to a digital thermosensor (Digi-Sense 8528-10, Cole Parmer). Organisms were placed in the trough in groups (N = 4-5) in the sector corresponding to their acclimation temperature. Four trials were conducted for each acclimation temperature (N = 16-20). Only prawns in the intermolt stage and starved for 24 h were included in the experiment. Prior to the experiment, color-coded tags were affixed to the backs of the animals with cyanoacrylate adhesive. Positions of prawns in the various chambers and temperatures therein were recorded every 10 min during 180 min. Measurements started 30 min after transfer; and were taken via a mirror to avoid perturbing the organisms. The experiments were performed between 08:30 and 12:00 h.

Median preferred temperatures were plotted against acclimation temperatures. Medians and their confidence intervals ($P<0.05$) were calculated according to the Exploratory Data Analysis approach (Hoaglin *et al*. 1983). Linear regression was also performed on the relationship between the acute preferred temperature (PT) and the acclimation temperature (AT). Acute thermal preferendum was obtained, in both cases, from the intersection of the preferred temperature curve, and the 45° line. The model for this relationship was: PT = 36.304 - 0.414 AT ± 0.15°C, p = 0.028 and accounted for 99.6% of the variation ($R^2 = 0.996$).

Temperatures avoided by the prawns were calculated from the confidence intervals of the median values of the thermal preferenda (Hernández-Díaz 2003). Linear regressions between avoided temperatures and the acclimation temperature were also performed. The relationships for high avoided temperatures (HAT) and low avoided temperatures (LAT) were as follows: HAT = 43.333-0.567 AT ± 0.39°C, p = 0.010, $R^2 = 0.980$ and LAT = 38.0-0.60 AT ± 0.63°C, p = 0.024, $R^2 = 0.953$. Differences between avoidance temperatures were also calculated, in order to estimate specific thermal efficiency (STE). Curves were fitted using least squares method (Zar 1999). Statistical significance of data ($P<0.05$) was determined by analysis of variance.

RESULTS

Mortality during acclimation to 29°C was 20% and 30% at 32°C. This was attributed partly to cannibalism of newly-molted organisms.

Weight of organisms ranged from 15.13g to 25.24g (Table 1) and significant differences ($P<0.05$) in weight were observed between the group acclimated to 29°C and other groups. Within the thermal gradient, all groups preferred temperatures different from their acclimation temperatures (Fig. 1, Table 1). Considering expected values, prawns acclimated to 23°C preferred temperatures 14.2% higher, whereas prawns acclimated to 32°C preferred temperatures 41.2% lower than AT (Table 2, Fig. 2).

Median and mean values were similar, indicating that data approached a normal distribution (Table 1). From the box plot data on

TABLE 1. Preferred temperatures of *Macrobrachium acanthochirus* acclimated to different temperatures (°C).

Elements and Estimators	Acclimation Temperatures (°C)			
	23	26	29	32
M	27.5	26.5	23.3	22.7
Hs	31.4	29.5	29.1	26.0
Hi	23.6	21.7	20.2	20.2
ΔH	7.8	7.8	8.9	5.8
Cs	43.1	41.2	42.4	34.7
Ci	11.9	10.0	6.8	11.5
CI	24.51,	23.67	19.79,	20.16,
	30.49	29.33	26.81	25.24
X	26.60	25.40	24.30	23.50
SE	± 1.23	± 1.08	± 1.26	± 1.06
Weight (g)	22.3 (20.23, 24.37)	21.1 (19.8, 22.4)	16.0 (15.13, 16.87)	18.0 (20.16, 25.24)
(N)	(17)	(19)	(16)	(13)

Parallel box plot, elements and estimators: M = Median, Hs = upper forth, Hi = lower forth, ΔH = forth-spread, Cs = upper outer cutoff, Ci = lower outer cutoff, X ± SE = mean ± standard error, (N) = number of organisms.

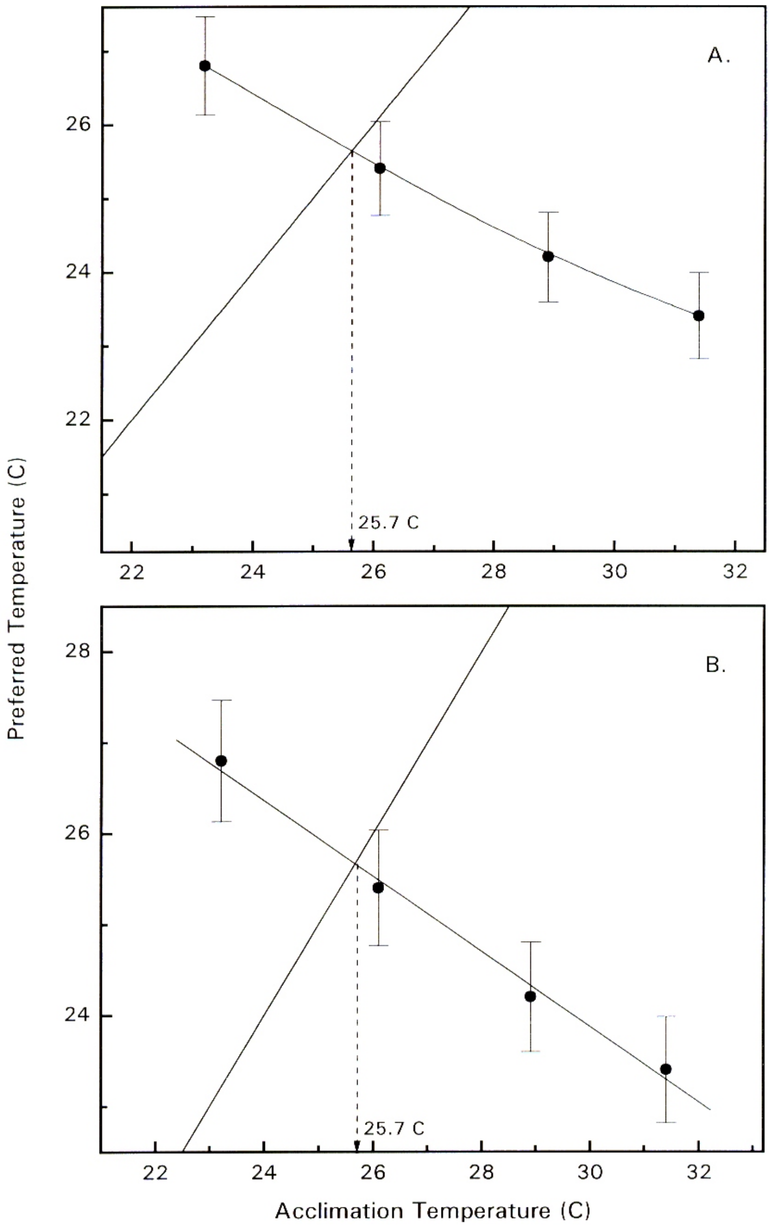

FIGURE 1. Relationship between preferred and acclimation temperatures (°C) of *Macrobrachium acanthochirus.* A. Visual inspection adjustment, B. Linear regression adjustment. Arrow shows acute thermal preferendum.

TABLE 2. Expected values of preferred and avoided temperatures (°C) of *Macrobrachium acantochirus* acclimated to different temperatures.

AT	PT	(PT-AT)	LAT	(LAT-AT)	HAT	(HAT-AT)	(HAT-LAT)	STE
23	26.8	3.8	24.2	1.2	30.3	7.3	6.1	0.68
26	25.5	–0.5	22.4	–3.6	28.6	2.6	6.2	0.69
29	24.3	–4.7	20.6	–8.4	26.9	–2.1	6.3	0.70
32	18.8	–13.2	18.8	–13.2	25.2	–6.8	6.4	0.71
*25.7	*25.7		*22.6		*28.8		*6.2	*0.69

AT = acclimation temperatures. PT = preferred temperatures. LAT and HAT = low and high avoided temperatures. STT = scope for thermal tolerance.
*Estimated values associated to the acute thermal preferendum.

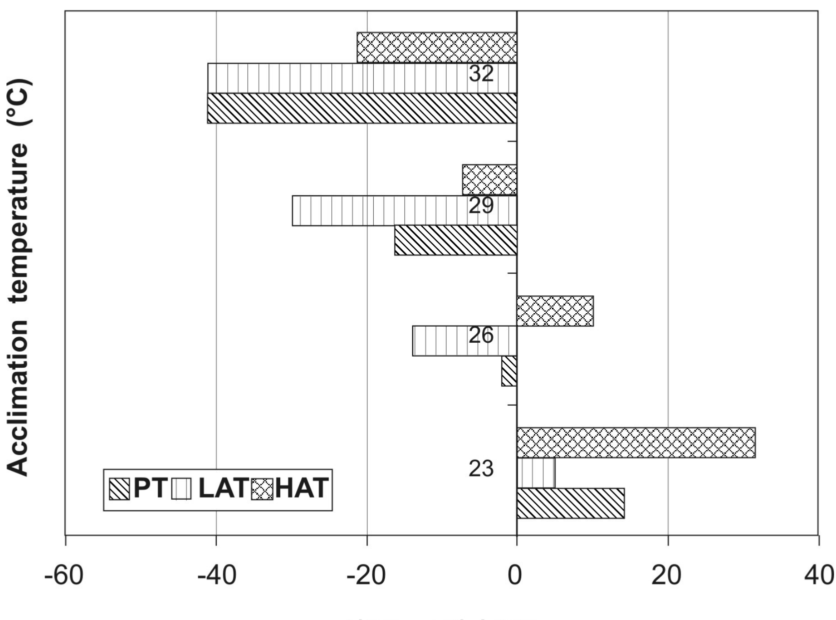

FIGURE 2. Relative change (%) in temperature response (TR) of *Macrobrachium acanthochirus* with respect to acclimation temperature (AT). HAT: high avoided temperature, LAT: low avoided temperature.

upper and lower limits (H_S and H_I), it is estimated that prawns did not make incursions into the gradient sectors with extreme temperatures (Table 1). In general, organisms chose temperatures 23% lower than the upper limit and 36% higher than the lower limit.

The final preferendum or point where preferred and acclimation temperatures are equal (Mathur *et al.* 1982), was determined graphically (Fig. 1A) and from regression between acute preferred temperature (PT) and acclimation temperature (AT) of specimens (Fig. 1B). The values obtained by both methods were 25.7°C.

Expected values for preferred temperatures, obtained using the model, are included in Table 2. Differences between these values and those of acclimation temperatures are in the range +3.8 to –13.2°C.

As with the preferred temperatures, avoided and acclimation temperatures differed; relative values are shown in Fig. 2. Differences between low avoided temperatures (LAT) and acclimation temperatures range from +1.2 to –13.2°C, while differences between high avoided temperatures (HAT) and acclimation temperatures ranged from +7.3 to –6.8°C.

Regardless of amplitude of such ranges, prawns did not make incursions into lethal temperatures, remaining in thermal spaces 23% lower than the average theoretical upper limit (42°C) and 36% higher than the average lower limit (10°C) (Table 2). As with preferred temperatures, avoided and acclimation temperatures differed; relative values are shown in Figure 2.

DISCUSSION

High mortality among prawns maintained at 29°C and 32°C may be partly due to the possibility that such temperatures are extreme for these organisms when in captivity, causing an increase in their activity. The average annual temperature in their natural habitat ranges from 20-28°C. In addition, prawns in their natural environment take refuge on river bottoms, where temperatures are lower. On

Compared to the preferenda of other species, the acute thermal preferendum of *M. acanthochirus* (25.7 ± 0.40°C) is identical to the nocturnal preferendum obtained for *Procambarus clarkii* (26.7 ± 0.13°C) by Bückle *et al*. (1994). These authors reported that the final diurnal preferendum of the crawfish was 24.0°C, which is similar to the acute preferendum of the same species (Espina *et al*. 1993) and 12% lower than the acute preferendum of *M. acanthochirus*.

Temperature controls physiological processes as well as behavior and distribution of exothermic organisms (Hutchinson and Maness 1979). Therefore, behavioral responses allow organisms to increase their thermal tolerance interval and exploit a heterothermal medium by enlarging their environmental space. Prawns (*M. acanthochirus*) were observed by Villalobos (1966) in the State of Oaxaca and as far as the southern part of Colima State. In this work, prawns were found at locations in the State of Jalisco, thus increasing substantially the distribution of *M. acanthochirus* to 250 km northward and to 600 m altitudinally (Hernández-Díaz 2003).

This geographical expansion is interpreted from results obtained for the thermal space limited by the temperatures avoided by the prawns. Giattina and Garton (1982) state that preference and avoidance are inseparable aspects of the thermoregulatory behavior of species and that the area limited by the avoided temperatures is equivalent to the tolerance area. In *M. acanthochirus*, like in other organisms, avoided temperatures were inversely proportional to acclimation temperatures. This agrees with what has been observed in other organisms (Mathur *et al*. 1982, Espina *et al*. 1993). Thermal space between the avoided temperatures corresponding to the preferred temperature was 6.2°C (Table 2). On the other hand, the average ambient temperature ranges from 20 to 28°C. Based on these data, the specific thermal efficiency (STE) (Bückle *et al*. 1996) of prawns is 77.5%. However, considering the thermal interval that exists throughout the year between minimum and maximum temperatures (40°C-10°C), the STE is only 21%. These data explain the low population levels of *M. acanthochirus* in rivers in Jalisco State and in the Purificación and Arroyo Seco rivers during the hot, dry season, and abundance of these organisms following the rainy season (Hernández - Díaz 2003). It is likely that during very hot or very cold periods the prawns use natural refuges at appropriate temperatures, as observed in *O. causeyi* by Loring and Hill (1976).

The thermal tolerance interval of prawns ranged from 68% to 71% in the 23-32°C acclimation interval, with a mean value of 70%, which approaches the value calculated considering the animals' acute preferendum. In contrast, in the 20°C to 28°C interval, the theoretical efficiency is 77%. Although the maximum critical temperature has not been measured, it is possible that 32°C is stressful for *M. acanthochirus*. Thus, these results may be important to successfully cultivate this species.

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