Preferred Temperature, Critical Thermal Maximum, and Metabolic Response of the Black Sea Urchin *Arbacia stellata* (Blainville, 1825; Gmelin, 1791)

PREFERRED TEMPERATURE, CRITICAL THERMAL MAXIMUM, AND METABOLIC RESPONSE OF THE BLACK SEA URCHIN *ARBACIA STELLATA* (BLAINVILLE, 1825; GMELIN, 1791)

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ABSTRACT Populations of the black sea urchin *Arbacia stellata* present in the Gulf of California and outer Pacific Coast area are probably the result of colonization from the Panamic region. In the Pacific Coast of Baja California, this species experiences seasonal fluctuations of temperature. It was determined the preferred temperature (PT), critical threshold limits represented for Critical Thermal Maximum (CTMax) and oxygen consumption rate in organisms acclimated to 16°C, 19°C, 22°C, and 25°C in controlled conditions. The PT of *A. stellata* was determined in organisms using the acute method. As the acclimation temperature increases, the PT also increases significantly ($P < 0.05$) and decreases to 22.8°C. In the acclimation temperature of 25°C, PT for black sea urchins was 23.3°C ± 0.3°C. A direct relation was determined between the CTMax and acclimation temperatures being of 36.48°C ± 0.6°C, 37.64°C ± 0.76°C, 38.08°C ± 0.94°C, 38.42°C ± 0.71°C. The end point of CTMax was stage E4, where the sea urchins stop moving, relax the large spines but activity continues with light movements of small spines and when the organisms lose the ability to remain attached to the substrate. The oxygen consumption rates increased significantly ($P < 0.05$) from 5.59 to 11.5 mg O_2 kg/h wet weight (w.w.) as the acclimation temperature increased from 16°C to 25°C. The range of temperature coefficient (Q_{10}) between 16°C and 25°C (lowest) was 1.90, indicating that within that range of acclimation temperature, organisms are adapted to maintain homeostasis. This corresponded with the interval of PT of the species. These results may partially explain their distribution pattern in Baja California Coast.

KEY WORDS: preferred temperature, thermal stress, oxygen consumption, black sea urchins, *Arbacia stellata*

INTRODUCTION

Temperature is one of the most important environmental factors controlling development in ectotherms including echinoderms, which progress faster through their developmental stages as temperature increases (Hoegh-Guldberg & Pearse 1995). Organisms have evolved a variety of strategies for controlling their body temperature. These strategies fall in three broad categories: behavioral, physiological, and morphological regulation. Behavioral responses includes body reorientation, effective in avoiding potentially damaging body temperatures and these strategies are commonly used by a variety of ectotherms (Gaitan-Espitia et al. 2013).

To demonstrate the preferred temperature of different aquatic organisms in the laboratory, the use of thermal gradient studies has been widely used (Díaz et al. 2015). The preferred temperature has been determined considering the temperature at which organisms spend most of the time within the thermal gradient at which they have been exposed (Reynolds & Casterlin 1979, Díaz et al. 2011, 2015).

The thermoregulatory behavior has been reported in aquatic ectotherms as a homeostatic mechanism, because the organism attempts to keep its internal temperature similar to that of its environment. This allows optimization of physiological and biochemical processes for maximal efficiency (Hutchison &

Maness 1979, Nichelmann 1983, Díaz et al. 2002, Tepler et al. 2011, Díaz et al. 2015).

Most studies on the impacts of temperature on echinoids have focused on upper thermal thresholds of embryos and larvae, but it is also important to understand thermal thresholds in adults to predict how marine species may respond to changing ocean conditions (Hoegh-Guldberg & Pearse 1995, Pörtner et al. 2007, Díaz-Perez & Carpizo-Ituarte 2011).

Critical Thermal Maximum (CTMax) is the first response proposed to link animals' thermal physiology with ecology, is a behavioral stress response, and is defined as the arithmetic mean of collected thermal points at which locomotory activity becomes disorganized to the point that the organism loses its ability to escape conditions that will promptly lead to its death (Cox 1974). Thermal limits have received much attention, because its investigation provides an insight into how climate shapes variation in the ecology, distribution, and physiological responses of the species (Pörtner 2001). Critical limits are positively related to optimal performance temperatures and are relatively simple to measure, and they considered both upper and lower temperatures (Huey & Bennett 1987). Critical thermal limits are considered ecologically relevant, because they provide an indication of the activity range for a population under acute exposure conditions such as upwelling cold winters or hot long summers (Somero 2005).

It has been widely used to investigate thermal limits in ectothermic animals and has been applied in the context of global warming (Lutterschmidt & Hutchison 1997, Stillman 2003).

In the context of long-term climate warming, a key characteristic of an ectotherm's performance is the difference between its CTMax and the current range of temperatures that organisms experience in their habitat, which is recognized as their warming tolerance (WT) (Deutsch et al. 2008).

Among the physiological parameters that can be correlated with environmental changes (temperature or salinity), metabolic rate is relevant, because it helps determine the energetic costs that these abiotic parameters have on the performance of the organism (Lemos et al. 2001, Altinok & Grizzle 2003, Brougher et al. 2005). The oxygen consumption (VO_2) is intimately associated with the metabolic work and the energy flow that an organism can use for homeostatic control mechanisms (Salvato et al. 2001, Das et al. 2005).

As a rule, shallow-water epifaunal sea urchin genera are either entirely tropical or entirely temperate, with limited overlap in the subtropics. Only one genus of sea urchins, *Arbacia*, is unique among epifaunal shallow-water echinoid genera in containing species that extend from the northern temperate zone into the tropics, and also species in the Southern Hemisphere that are restricted to the temperate and sub-Antarctic zones (Lessios et al. 2012). The genus *Arbacia* is one of the shallow-water Panamic echinoid genera that originated in the West Indies probably during the Eocene and invaded the Panamic Province of the Eastern Pacific before the Pliocene rising of the Isthmus of Panama. Populations of *Arbacia stellata* present in the Gulf of California and outer Pacific Coast area are probably the result of colonization from the Panamic region (Olguin 2004).

In the eastern Pacific, *Arbacia stellata* is found from Baja California to Peru at <10 m depth. In the Pacific coast of Baja California, this species experiences seasonal fluctuations of temperature, ranging from 19°C to 25°C in summer and from 15°C to 23°C in winter (Olguin 2004).

The aim of the present study was to examine the possible relationship between acclimation temperature and physiological responses as the preferred temperature, thermal tolerance, and oxygen consumption rate (OCR) of adults the black sea urchin *Arbacia stellata*, near their northern limit of distribution in Baja California coast.

MATERIALS AND METHODS

Adult black sea urchins *Arbacia stellata* weighing 33.02–68.19 g were collected in February 2014 by sea hookah diving at 5–10 m in the area of Tres Hermanas in Punta Banda, Baja California, México (31° 42′ Lat. N; 116° 45′ Long. W). Organisms ($n = 220$) were kept for 30 days in laboratory conditions in four 2000-l fiberglass tanks, in 35‰ salinity and at 20°C ± 1°C in a flow-through water system to simulate the conditions at the collecting site. The photoperiod was maintained in 12–12 h light–dark cycles with 30 min transition periods between them. Black sea urchins were fed fresh kelp *Macrocystis pyrifera* daily during the acclimation period. The reservoirs were washed weekly to reduce the accumulation of fecal matter and associated bacteria.

To determine the preferred temperature, we used 80 black sea urchins previously acclimated for 4–6 wk in 2000-l reservoirs at temperatures of 16°C, 19°C, 22°C, and 25°C ± 1°C according to the methods described by Percy (1972). Forty-eight hours before beginning each experiment, organisms were individually tagged with a plastic mark placed on a spine. The preferred temperature experiments were performed in a thermal horizontal gradient (Fig. 1) constructed from a 400-cm-long and 20-cm-wide PVC tube, which was divided into 20 virtual segments each 20 cm long, with a total volume of 150 l as described by Díaz et al. (2006) and Padilla-Ramirez et al. (2015). A Neslab thermoregulator model HX 150 (Newington, NH) was connected to the right side of the gradient to cool the water to 10°C; a 1000-W heater was placed at the left side, which was connected to a temperature-controlled heater to heat the water to 30°C, generating a stable temperature gradient ($y = 6.50 + 1.68\ x$, $r^2 = 0.98$, where x = segments of gradient and y = temperature of the gradient segments). An aeration system that consisted of a high-efficiency diffuser hose was placed along the gradient to maintain dissolved oxygen concentrations between
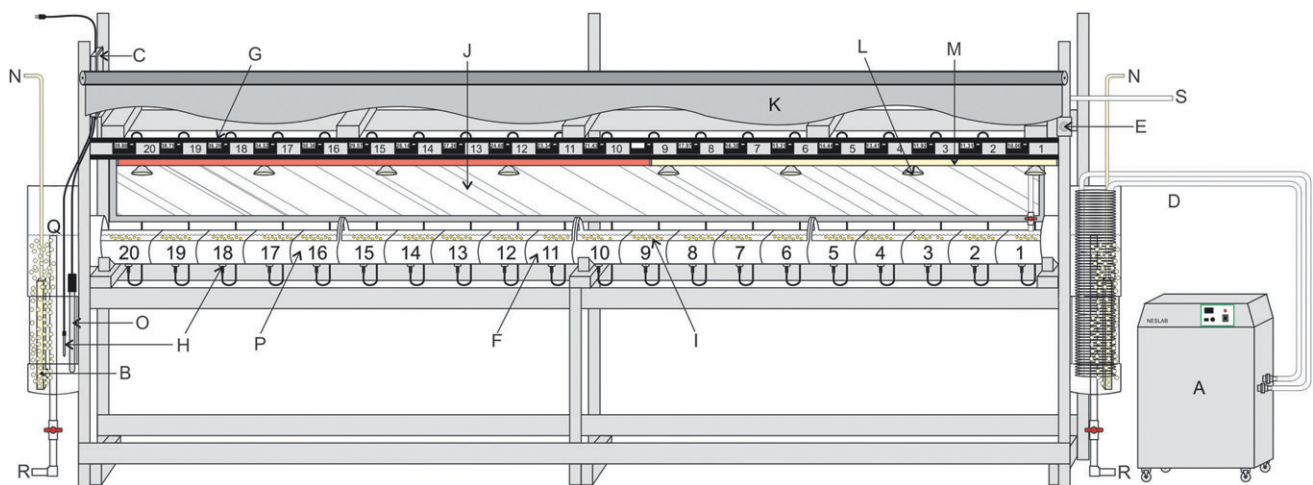
Figure 1. Diagram of horizontal temperature gradient apparatus used for determination of the preferred temperature in *Arbacia stellata*. **(A)** Digital recirculating chiller, **(B)** air stone, **(C)** heater temperature controller, **(D)** titanium heat exchanger, **(E)** dimmer, **(F)** gradient of 400 cm length and 20 cm of diameter, **(G)** digital thermometers, **(H)** temperature sensor, **(I)** air stones, **(J)** mirror, **(K)** curtain, **(L)** fluorescent lamps, **(M)** incandescent lamps, **(N)** air lines, **(O)** titanium heater, **(P)** gradient segments, **(Q)** water level, **(R)** drain tubes, **(S)** water drainage, **(T)** refill line.

6.4 and 8.5 mg/l and to eliminate vertical thermal stratification of the water column. The water column depth in the gradient was 9 cm and to maintain high water quality, it was refilled at a rate of 13.0–14.0 l/h.

The acute method described by Reynolds and Casterlin (1979) was used to determine the preferred temperature. Five organisms, randomly chosen and, within the same weight range, were introduced to the gradient at the virtual segment where the water temperature was the same as acclimation temperature. The location of the organisms and the temperature where the sea urchin was located in the gradient were recorded using a digital IR thermometer (Steren HER-425), every 10 min for 120 min. The final preferred temperature was determined by the intersection of the preferred temperatures by the organisms from each acclimation temperature, with the equality line. For each experimental condition, four repetitions were done [N (total) = 20]. The black sea urchins were not fed during the 24 h prior to testing according to recommendations by Nelson et al. (1985) and Beamish and Trippel (1990).

As a control group, 15 individuals were placed in the gradient system (in groups of three and previously acclimated to different temperatures), with the heater and chiller turned off (resulting in a constant temperature of 20°C along the gradient, which was the temperature that water had entered the system). This control experiment allowed to determine that final location was indeed due to temperature selection and not a preference for any particular site inside the tube.

To determine the CTMax, 16 black sea urchins were acclimated in each of the four 2000-l reservoirs at temperatures of 16°C, 19°C, and 22°C, and 25°C ± 1°C, [N (total) = 64) and a salinity of 35‰ for 4 wk. They were not fed in the 24 h prior to testing. The black sea urchins were then placed in 40-l aquaria provided with a 1000-W immersion heater and permanent aeration to maintain a uniform temperature. The water was maintained at the experimental temperature for 30 min to reduce stress caused by handling (Pérez et al. 2003). Temperature was raised from the acclimation temperatures of 16.0°C, 19.0°C, 22.0°C, and 25°C ± 1°C at a rate of 1°C per min according to Lutterschmidt and Hutchison (1997), to allow the core temperature of the organism to equilibrate to the surrounding water temperature. All determinations of CTMax were made between 09:00 and 14:00 h. The description of the behavioral response to thermal stress of Hernández et al. (2004) for the red sea urchin *Mesocentrotus franciscanus* (formerly *Strongylocentrotus franciscanus*) was used. A series of the responses in the red sea urchin to increasing temperatures are described as follows: E1, the sea urchin moves actively toward the bottom of the aquarium with the tube feet extended to the maximum; E2, retraction and decrease of the tube feet movement also followed by decrease of the spines movement; E3, with the tube feet retracted, the sea urchins increase the movement mostly using the large and small spines; E4, the sea urchins stop moving, relax the large spines but activity continues with light movements of small spines; and E5, the sea urchins stop movement with all spines and tube feet relaxed, and in some specimens anus opened up. Visual monitoring was performed and recorded to define the time and temperature at which *Arbacia stellata* reached stage E4, which was the end point of CTMax according to criterion described by Hernández et al. (2004) and they became detached from the aquarium floor. Immediately after experiencing the stress produced by the

increasing temperature regime established, sea urchins were removed from the aquarium and returned to their acclimation temperature where their survival was monitored for 96 h, the organisms were only used once. The data obtained from sea urchins that did not fully recover after returning to acclimation temperatures were discarded.

Warming tolerance and thermal safety margin (TSM) of sea urchin was calculated according to Deutsch et al. (2008) as

$$(WT = CT_{max} - T_{hab}) \tag{1}$$

and

$$(TSM = T_{opt} - T_{hab}) \tag{2}$$

where CT_{max} = critical thermal maxima, T_{hab} = temperature habitat, and T_{opt} = optimal temperature.

The oxygen consumption rate was measured in an intermittent respirometer system as described by Díaz et al. (2007), consisting of 15 acrylic chambers of 2,500 ml each. Black sea urchins were acclimated for 30 days at 16.0°C, 19.0°C, 22.0°C, and 25°C ± 1°C. Fifteen urchins from each acclimation temperature were individually introduced into the respiratory chamber 24 h before initiating measurements, to minimize the effect of stress caused by handling. All measurements were taken between 09:00 and 13:00 h. To minimize the possible influence of body weight on oxygen consumption, urchins within a narrow weight range were used [wet weight (w.w.), 50.4 ± 2.6 g; mean ± SE].

The water flow in the chambers remained open for 2 h before it was turned off, and one water sample was taken by filling a plastic balloon with water to avoid the sample to be in contact with air. To measure the initial concentration of dissolved oxygen, a YSI 52 oxymeter (Yellow Spring Instruments Co., Yellow Springs, OH) equipped with a polarographic sensor with an accuracy of ± 0.03 mg/l was placed inside an acrylic hermetic chamber with a 10-ml capacity. Subsequently, the acrylic chambers remained closed for only 1 h to avoid a decrease of the dissolved oxygen higher than 25%–30% of the initial oxygen concentration in the chamber. Lower values could constitute an additional stress factor according to Stern et al. (1984). Before re-establishing the water flow, one water sample was taken to measure the final concentration of dissolved oxygen.

The OCR was calculated according to Eq. 3 (Cerezo Valverde et al. 2006, Zheng et al. 2008).

$$OCR = \frac{(C_t - C_0)V}{(W \times T)} \tag{3}$$

where C_t is the change in the oxygen content in the respirometric chambers before and after the test, C_0 the change of the oxygen content in the blank (control), V the volume of the chamber, W the weight of sea urchins in kilogram wet biomass, and T the time duration in hours.

The 16th acrylic chamber was used as a control to measure oxygen consumption of the microorganisms present in the water, and the necessary corrections were made. Two repetitions were carried out for each test. Results of the OCR are given in mg O_2 h/kg w.w.

Calculation of the thermal coefficient for the metabolic rate of the sea urchins (Q_{10}), which represents the organism's

sensitivity to temperature variation, was derived by Eq. (4), proposed by Schmidt-Nielsen (1997):

$$Q_{10} = \left(\frac{\text{Rate}_2}{\text{Rate}_1}\right)^{(10/\text{Temp2}-\text{Temp1})} \qquad (4)$$

A one-way analysis of variance test was used to determine differences in preferred temperature, CTMax, and OCR (Zar 1999).

RESULTS

When water temperature was maintained constant (control treatment), adults of *Arbacia stellata* were found distributed freely along the gradient (400 cm) after 2 h, indicating they showed no preference for any particular segment.

Acclimation temperature significantly affected the thermal preference of sea urchins ($P < 0.05$) and this will increase from 19.9°C to 23.8°C as the acclimation temperature increases from 19.0°C to 22.0°C and diminishes to 22.8°C in organisms acclimated to 25°C. The preferred temperature obtained was 23.3°C (Fig. 2). A positive relationship between acclimation temperature and CTMax was obtained the thermal tolerance increased significantly ($P < 0.05$), as acclimation temperature increased obtained in 16°C, a CTMax value of 36.48°C, whereas for 25°C, CTMax was 38.4°C (Fig. 3).

The value obtained for WT for *Arbacia stellata* had an interval of 14.5–16.4°C for temperatures experimented in its habitat during the winter and 17.5–19.4°C for the summer. For TSM, the values for summer temperatures were 3.0°C and for winter 4.3°C.

The OCR of the sea urchins increased significantly ($P < 0.05$; $y = -5.51 + 0.62\ x$, $r = 0.966$) as acclimation temperature incremented from 16°C to 25°C. The sea urchin *Arbacia stellata* reached a maximum of 11.5 mg O_2 kg/h w.w. in a higher acclimation temperature (Fig. 4). The range of temperature coefficient (Q_{10}) of the sea urchins between 19°C and 22°C (highest) was 2.1, and between 22°C and 25°C (lowest) was 1.9.
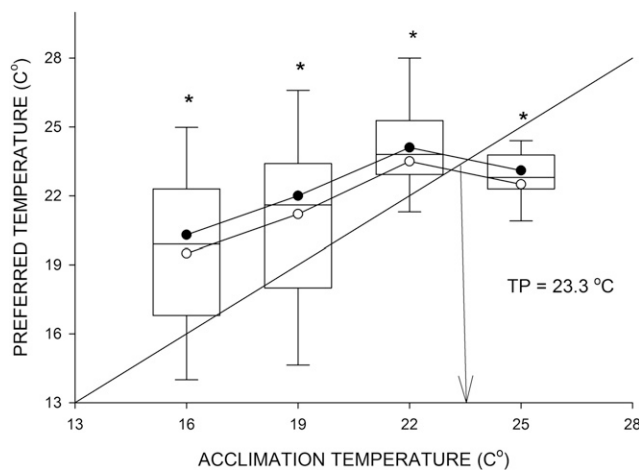

Figure 2. Preferred temperature of adults of *Arbacia stellata* acclimated to different temperatures. The zone, bordered by circles, represents the 95% confidence interval of the median. The bars include 50% of the organism's distribution. The 45° construction continuous line represents the point where preferred and acclimation temperatures are equal. The asterisk denotes significant differences.
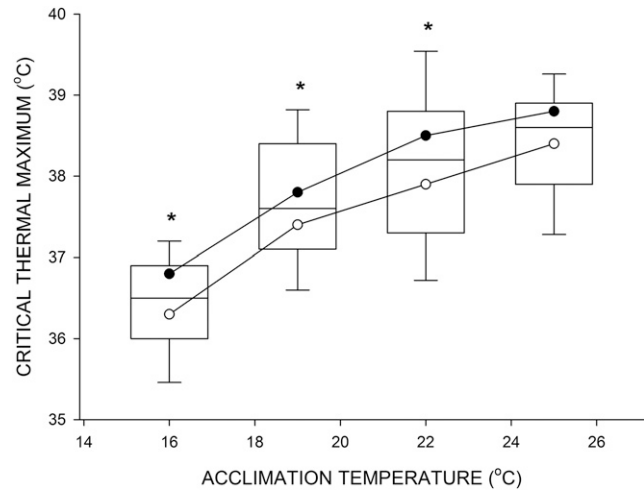

Figure 3. Thermotolerance of adults of *Arbacia stellata* acclimated to different temperatures. The zone bordered by circles represents the 95% confidence interval of the median. The bars include 50% of the distribution and the vertical lines represent the quartiles. The asterisk denotes significant differences.

DISCUSSION

The results show that black sea urchin *Arbacia stellata* was thermotactic, meaning that they moved toward the source of the thermal stimulus. When initially exploring the thermal environment in the gradient they moved back and forth, and this movement decreased, which was indicative that they were in the preferred temperature range. In contrast, organisms exposed to an environment with uniform temperature were distributed freely until the end of the experimental period. For *Hemigrapsus nudus* (MacGaw 2003), *Cancer borealis* (Lewis & Ayers 2014), *Cancer anntenarius* (Padilla-Ramirez et al. 2015), and *Hemigrapsus crenulatus* (Cumillaf et al. 2016), using thermal gradients, the authors reported a similar behavior when exposed to the temperature gradient.

Marine organisms have a variety of temperature-preference relationships that can be categorized into three classes on the basis of whether they are positive, independent, or negative function of the acclimation temperature (Johnson & Kelsch 1998). The temperature-preference relationships obtained for black sea urchins were a positive function over the range of acclimation temperatures from 16°C to 22°C. Similar results were obtained by Cherry et al. (1977) in *Oncorhynchus mykiss*, Kelsch (1996) in *Lepomis macrochirus*, Padilla-Ramirez et al. (2015) in *Cancer antennarius*, and Cumillaf et al. (2016) in *Hemigrapsus crenulatus*. This seems to be an adaptive response to changing temperatures that sea urchins experienced in their natural habitat. According to Olguin (2004), *Arbacia stellata* in Baja California is exposed to seasonal temperature fluctuations of 15–23°C in the winter and 19–25°C in the summer. This response is typical of species experiencing thermal cycles of relatively high amplitude and duration in their habitats (Johnson & Kelsch 1998).

Therefore, the final preferenda can be used as a measure of the temperature selected by the black sea urchins as an index of the magnitude of temperatures to which the species is adapted (Johnson & Kelsch 1998). This result demonstrates that *Arbacia stellata* was able to thermoregulate in the gradient, selecting
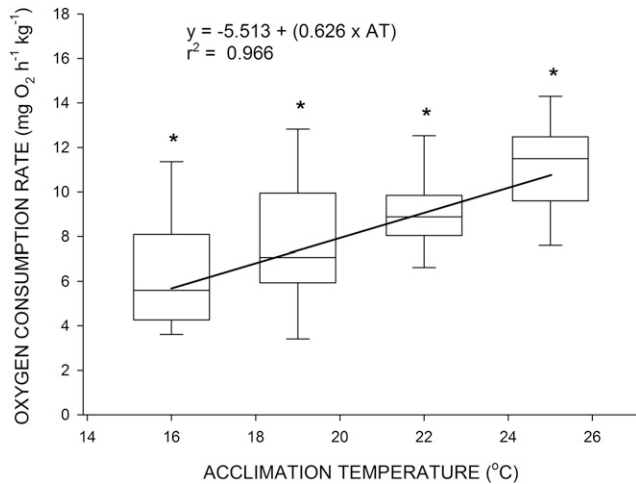
Figure 4. Effect of acclimation temperature on OCR in adults of *Arbacia stellata*. The bars involve 50% of the distribution and the vertical lines represent the quartiles. The asterisk denotes significant differences.

advantageous temperatures available within the mosaics of environmental conditions that were offered. It was conclude that, the black sea urchins were able to regulate their body temperature using behavioral thermoregulation, which may partially explain their pattern of spatial distribution in the intertidal and subtidal zone northern limit of distribution along the coast of Baja California.

To determine CTMax, black sea urchins were subjected to a continuous and constant linear increase in temperature until an endpoint was reached. This was considered equivalent to stage E4, according to Hernández et al. (2004), and is characterized by the ceased movement, relaxed large spines, but continued small movements by the smaller spines, and when the organisms lost their ability to remain attached to the substrate. In *Arbacia stellata*, a CTMax interval of 36.5–38.4°C was obtained for organisms acclimated from 16°C to 25°C. Hernández et al. (2004) reported for *Mesocentrotus franciscanus* an interval of CTMax values of 33.2–33.6°C for organisms acclimated from 18°C to 21°C. The differences in CTMax values for both species of sea urchin, which are distributed along the Pacific coast of Baja California, may be that the population of *A. stellata* present in the Baja California Peninsula is probably the result of a recent colonization from the Panamic region, therefore the population has a physiological reminiscence of its tropical origin, which has been mentioned by Olguin (2004).

The sea urchins' ability to attach themselves to substrates comes from their multiple independent adhesive organs, the tube feet. Each tube foot consists of an enlarged and flattened distal extremity, the disc, which makes contact and attaches to the substratum, the epidermis of the disc encloses a duo-gland adhesive system comprising two types of cells, the ones releasing adhesive secretions and those releasing de-adhesive secretions, allowing sea urchins to attach themselves to substratum (Santos & Flammang 2007). The flexibility of the water vascular system allows the sea urchins to adjust the number of attached tube feet very quickly, and thus continuously adapt their attachment force to the temperature increase. Variation of tenacity according to temperature has already been reported in various marine invertebrates including limpets (Grenon & Walker 1981), mussels

(Crisp et al. 1985), sea cucumbers, (Flammang et al. 2002), sea urchins (Santos & Flammang 2007), wavy turban snail (Díaz et al. 2011), a marine snail gastropod (Salas-Garza et al. 2014), and the giant keyhole limpet (Díaz et al. 2015). As temperature increases, tube feet in *Arbacia stellata* lose the ability to adhere to the substrate. A similar response was observed in the sea urchin *Strongylocentrotus droebachiensis* by Percy (1973). Increasing temperatures have an effect on the tenacity at which the organism remains attached, thus making its escape from increasing temperature conditions more difficult and ultimately leading to its death; the tenacity of thermal attachment in response to thermal conditions is, therefore, a sea urchin response that reflects the effect of temperature on the organism.

In the present study, it was proposed that the values reported for CTMax for *Arbacia incisa* correspond to the critical threshold temperature at which the scope of metabolic activity is zero. That explains why organisms at their threshold temperature can stay alive for a short time, during which the animals enter to an acclimation reparation period (Pörtner 2010). The intervals between 16°C and 25°C correspond to acclimation in functional capacity where the maximum performance can be observed (Pörtner 2010).

Deutsch et al. (2008) mentioned that WT represents the average of environmental warming an ectotherm can tolerate before performance drop to a fatal level. Lugo et al. (2016) reported that species that inhabit the Gulf of California such as *Conasperella perplexus* and *Conasperella ximenes* had greater "high thermal" tolerance, which is typical of species that are distributed throughout tropical climates, whereas those that inhabit the Pacific Coast such as *Conasperella californicus* had a lower "high thermal" tolerance; similar results were obtained for *Arbacia incisa*, indicating that they are distributed throughout temperate climates (Olguin 2004).

Thermal safety margin represents an index that indicates that species living in environments that are already close to their physiological optimum have small value of this index, like the ones obtained for *Arbacia stellata* of 3.0–4.3°C. Sherman (2015) obtained values of TSM for *Diadema antillarum* of 5.67°C and *Echinometra lucunter* of 3.66°C. Lugo et al. (2016) reported values for *Conasperella perplexus* of 2.5°C and *Conasperella ximenes* of 0.25°C, which are species distributed in Gulf of California. In contrast, species such as *Conasperella californicus* presented higher TSMs, with values of 7.2°C, which represent environments that are on average cooler than optimal (Deutsch et al. 2008).

Once the black sea urchin was in a temperature of 25°C, there was an increase of 13% in the OCR, indicating higher oxygen supply requirements at this temperature. Several reports using different species of invertebrates, including the sea urchins, *Mesocentrotus franciscanus*, *Strongylocentrotus purpuratus*, *Strongylocentrotus droebachiensis*, and *Strongylocentrotus fragilis*; the sea cucumber *Apostichopus japonicus;* the California sea hare *Aplysia californica*; and the intertidal snail *Tegula regina*, obtained higher rates of oxygen consumption when organisms were exposed to higher temperatures (Percy 1972, Ulbritch & Pritchard 1972, Ulbricht 1973, Dong et al. 2011, Re et al. 2013, Salas Garza et al. 2014). According to Dong et al. (2011) and Miller et al. (2013), this pattern suggests that high thermal tolerance may come with a significant fitness and energetic cost.

The temperature coefficient (Q_{10}) reported in black sea urchins is lower, in the range of 22–25°C (1.90), indicating that

within that range of acclimation temperature, organisms are adapted more efficiently to maintain homeostasis (Gonzalez et al. 2010). According to Kita et al. (1996), Das et al. (2005), Debnath et al. (2006), and Padilla-Ramirez et al. (2015), the point where the Q_{10} falls compared with the acclimation temperatures corresponds to the optimum temperature for growth and reproduction as because the decrease in the Q_{10} indicates that the metabolism was reduced and that more energy was available for growth. In the present study, the temperature interval of 22–25°C coincided with the preferred temperature obtained for *Arbacia stellata* (25.1°C). The optimum temperature coincides with the temperature range at which adults of *A. stellata* had a smaller Q_{10} value.

According to Brothers and McClintock (2015), populations in habitats with higher seawater temperature may live closer to their upper thermal tolerance than populations living in habitats at lower seawater temperatures, and therefore may be more vulnerable to climate-induced elevated seawater temperature. Populations the *Arbacia stellata* in Baja California may able to gain refuge from elevated seawater temperatures by expanding their biogeographical range or by moving to deeper water.

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