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# Effect of maternal temperature stress before spawning over the energetic balance of *Octopus maya* juveniles exposed to a gradual temperature change

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ABSTRACT

*Octopus maya* supports an important fishery in Yucatan Peninsula (YP) where this species is highly abundant. Considering that temperatures in the tropics are increasing (IPCC, 2013), there are several scenarios that can modify the dynamic of the *O. maya* population in YP: i) prolonged summer and short winter seasons, and/or ii) fast temperature increases and high temperatures after a winter season, both affecting the survival of hatchlings and the performance of juveniles. The present study was designed to evaluate the effect of maternal temperature stress over hatchling and juvenile performance in terms of their energetic plasticity and thermoregulatory behaviour, when they were exposed to a gradual temperature increase (TI) from 24 to 30 °C and compared with hatchlings maintained at preferred and constant temperature (24 °C). Hatchlings from stressed females were smaller, and had a lower growth rate compared to those from unstressed females providing evidence that temperature stress experienced by females has consequences on the performance of hatchlings, with effects on the biomass production and survival. Results also demonstrated that hatchlings exposed to TI (24–30 °C) had a growth rate and oxygen consumption similar to those maintained at preferred temperature (24 °C), in both female groups indicating that a gradual temperature increase of 1 °C every 5 days is probably enough to allow the organisms to make physiological adjustments without an excessive energetic cost.


## 1. Introduction

Cephalopods are strongly influenced by temperature, as it play an important role in the regulation of embryo development, growth patterns and reproduction (Katsanevakis et al., 2005a, 2005b; André et al., 2009; Uriarte et al., 2012; Zuñiga et al., 2013). In cephalopods, respiratory metabolism has a central role in the survival and physiological performance, due to the high demand of energy that those organisms have for growth (Petza et al., 2011; Semmens et al., 2011) and locomotion activity (Wells and Clark, 1996). Temperature is the main environmental factor that controls the respiratory metabolism in cephalopods; therefore, it is considered the most important factor controlling the energy turnover and the fitness of cephalopods (Mangold, 1983; Farías et al., 2009; Noyola et al., 2013b).

Temperature defines the distribution limits of marine animals and determines how they perform in the ecosystem (Clarke, 1996; Stillman and Somero, 2000; Somero, 2010; Tepolt and Somero, 2014); beyond these limits, growth and reproductive capacity decrease, thereby increasing vulnerability both in vertebrates and invertebrates (Pörtner and Knust, 2007; Sokolova et al., 2012; Magozzi and Calosi, 2015). These limits and their relationship with phenotypical plasticity (Pigliucci et al., 2006) allow us to know how possible climate changes could negatively affect marine populations in their natural distribution zones; those results are of particular interest when experiments are designed to resemble the temperature variations of the environment where the species inhabits (Clarke, 1996; Pörtner, 2002).

Angilletta et al. (2002) proposed that the evolution of thermal sensitivity in ectothermic organisms relates body temperature with the environmental temperature. This relationship is not a coincidence, as the environment has selected organisms which performance is maximal at those temperatures. Therefore when the temperature chosen by the animal matches the naturally occurring temperature in an experimental

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gradient, it can be considered as the optimum temperature (Brett, 1971; Beitinger and Fitzpatrick, 1979; Magnuson et al., 1979; Hochachka and Somero, 1984; Angilletta et al., 2002; Noyola et al., 2013a). In *Octopus maya* juveniles a preferred temperature of 23.4 °C was identified (Noyola et al., 2013a). Results of growth and energetic balance indicate that, juveniles of *O. maya* maximise their efficiency to transform the ingested energy into body biomass in a temperature range of 22–26 °C, confirming that the theoretical value of final preferred temperature coincides with the range of temperatures in which the juveniles exhibit their maximum performance (Noyola et al., 2013b). These results provide evidence and relevant information related to the adaptive mechanism involved in the temperature tolerance of this species; however their interpretation is limited, because the animals were acclimated at constant temperatures that are far to those occurring in cultured or wild conditions.

According to Pigliucci et al. (2006), the genotype generates phenotypes that are capable of responding to environmental changes, due to the fixation of characters during the evolutionary history of an organism, shaping its phenotypic plasticity. Examining the effects of temperature on the variation of a phenotype allows us to explore the interaction between an environmental change rate, performance scope and genetic variation within a population (Clarke, 1996).

The Yucatan Peninsula (YP), located in the northern hemisphere of the American continent, is a transition site between the Caribbean Sea and the Gulf of Mexico. Oceanographic studies performed in this region show that the temperature of the adjacent continental shelf is regulated, at least partially, by the presence of a seasonal upwelling in summer. According to Enriquez et al. (2013), the upwelling arises in pulses, provoking temperature fluctuations between 22 and 26 °C. Although this upwelling has an influence on wide zones of the Gulf of Mexico, at the western edge of the continental shelf of YP, benthic temperatures can reach 30 °C during the summer, including areas where *O. maya* inhabits (Zavala-Hidalgo et al., 2006; Enriquez et al., 2013; Centre for Atmospheric Science, 2014). Juárez et al. (2015) demonstrated that the temperature is the stimulus that triggers the onset of spawning in *O. maya*. In their study, fertilised females were exposed to different possible thermal scenarios: a) high summer temperature (31 °C), b) winter temperature (24 °C) and c) a temperature decrease (TD) at a rate of 1 °C every 5 days from 31 to 24 °C, which resembles the summer-winter transition in the continental shelf of YP at the beginning of the *O. maya* spawning season. Juárez et al. (2015) observed that a temperature of 31 °C is enough to inhibit the spawning of *O. maya* females (only 13% of females spawned). The few fertilised eggs spawned died 2 weeks later, indicating that the high temperature was also deleterious to embryos. Females exposed to TD only spawned after the temperature was 27 °C and below (86% of females spawned). At the end of the experiment, a mean value of 530 eggs per spawn was observed in these females. They also observed that all females maintained at 24 °C spawned, with a mean value of 1208 eggs/spawn. From such results, it was evident that 27 °C is the threshold temperature that determines the *O. maya* spawning and that those higher temperatures provoke enough stress in the females to reduce the reproductive success. Their results suggest that *O. maya* females are adapted to avoid spawning at high temperatures because of the low survival of the embryos and hatchlings (Juárez et al., 2015). Considering that temperatures in the tropics are increasing (IPCC, 2013), there are possible scenarios that can affect the dynamics of *O. maya* population: i) prolonged summer and short winter seasons that reduce the time of low temperatures in the continental shelf, allowing the spawning of octopus females, but exposing them to temperature stress during maturation process; ii) fast temperature increases after the winter season, as a consequence of atmospheric elevation of temperature, affecting the benthic temperatures early in the year, and exposing hatchlings to gradual increases of temperature in their distribution zone; iii) reduction of the upwelling pulses, provoking higher temperatures (i.e., 30 °C; Centre for Atmospheric Science, 2014) than observed when regular upwelling pulses arise (i.e., 24 °C; Enriquez et al., 2013).

The strongest ocean warming is projected for the surface in tropical and northern Hemisphere subtropical regions, with an increase between 0.6 and 2.0 °C by the end of the 21st century, with scenarios where the atmosphere will be warming (IPCC, 2013). In such circumstances, a reduction on cold days could be expected, besides an increase in the number of hot days, generating gradual temperature increases in the *O. maya* hatchling zone. The present study was designed to evaluate if hatchlings spawned by females that experienced a thermal stress (after being exposed to TD), are affected in terms of their energetic physiology and thermoregulatory behaviour when they are exposed to a gradual temperature increase.

## 2. Method

### 2.1. Origin and acclimation of animals

The study was carried out in the Experimental Cephalopod Production Unit (ECPU) at the UMDI-UNAM, Sisal, Yucatan, Mexico, following the procedures of Rosas et al. (2008) and Moguel et al. (2010) for collecting and maintaining egg-laying females of *O. maya*. Octopuses were caught using artisan lines, with live crabs as bait, in front of Sisal harbour (Yucatán, Mexico). The octopuses were transported from the port to the laboratory, which is situated 300 m inland, in a 120 L circular tank containing seawater. A total of 50 octopuses were used for the experiments. For all treatments, octopuses were acclimated outdoors during 14 days, in a semi-open aquaculture system consisting of 22 $m^3$ circular liner tanks (maximum 30 animals per tank), keeping a 1:1 sex ratio. The system temperature ranged from 20 to 29 °C; with salinity of 36 psu and dissolved oxygen (DO) concentration around 5 mg $L^{-1}$. Each octopus was fed fresh *Callinectes sapidus* (half of crab at the morning and half at the afternoon) with a mean weight of 130 g. Uneaten food and faeces were removed daily. During acclimation octopuses paired freely.

Fertilised females (15 per treatment) were individually reared in 80 L tanks in a recirculating aquaculture system. Each tank included a fibreglass box that served as a refuge for the female and for spawn settlement. For stressed females, the initial system temperature was 31 °C, which was maintained for 10 days, and then the temperature dropped 1 °C every 5 days until the system reached 24 °C for a total of 40 days treatment. These conditions were selected because 24 °C is the preferred temperature and has been recommended as the best condition for the spawn (Noyola et al., 2013a; Rosas et al., 2014). The water was heated by a 1200 W titanium immersion heater connected to a digital temperature sensor, both at a system reservoir. The water was cooled using air conditioning, according to the temperature required. Salinity, aeration, diet and cleaning were kept the same as the conditions used during the acclimation for all treatments. Unstressed females ($n = 15$) were kept at 24 °C for 40 days with the same salinity, aeration, diet and cleaning as used in the treatment of stressed females. Spawns of both stressed and unstressed females were incubated at 24 ± 1 °C until hatching.

Hatchlings from three females of each group were mixed and used in the experiment (48 hatchlings from stressed females and 48 from unstressed females); they were separated in four groups, each group with 24 hatchlings, such that hatchlings with the same thermal history were maintained at 24 ± 1 °C or exposed at a temperature ramp (Ramp) of 24–30 °C with increment of 1 °C every 5 days.

Hatchlings were individualised in 500 mL containers and fed ad libitum with fresh crab–squid paste (Martinez et al., 2014) for 45–46 days. Every day, the food was added by opening the cap of the container without disturbing the animals. A clean *Megalongena corona bispinosa* shell was placed in each container as a refuge.

The containers included windows covered with mesh and were placed into 40 L tanks connected to a flow-through seawater system