# Temperature modulates spatio-temporal variability of the functional reproductive maturation of *Octopus maya* (Cephalopoda) on the shelf of the Yucatan Peninsula, Mexico

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## ABSTRACT

Laboratory studies have demonstrated that high temperatures inhibit spawning of *Octopus maya*; therefore, in oceanic warming scenarios the population dynamics may be affected. The aim of the present study was to go beyond laboratory studies under controlled temperatures to examine the possible relationship between large-scale thermal patterns and reproductive season (represented by functional maturation) of *O. maya* in the wild on the continental shelf of the Yucatan Peninsula, where it is endemic. The macroscopic maturity index (MaMI) was obtained in females, and reproductive complex index (RCI) and number of spermatophores in males. Associations between these indices and environmental temperature regime were inferred by sampling octopuses in an upwelling zone (Z-I), a transition zone (Z-II) and a nonupwelling zone (Z-III). The reproductive condition of *O. maya* differed between Z-I and Z-III. In all zones, the proportion of adults showing functional maturity was highest in both females (MaMI: 36–71% of values ≤0.2) and males (RCI: 12–40% of values ≥0.9; 41–49 spermatophores per octopus) during the season of winter storms ('nortes' season, November–February), when the sea-surface temperature oscillates around 25 °C. In Z-I, some individuals were functionally mature throughout the year, likely due to low temperatures maintained by summer upwelling. Zone-I had the greatest proportion of functionally mature males (up to 40% of adults in 'nortes' season) and the greatest number of spermatophores (mean 43–49 spermatophores per octopus in all seasons). Females in Z-III (without upwelling) were functionally mature mainly in the 'nortes' season when water temperature decreased, with only a small proportion mature in the rest of the year when water temperatures reached 31 °C. As predicted by laboratory studies, water temperature below 27 °C appears to be favourable for the functional reproductive maturation of wild *O. maya*.

## INTRODUCTION

Octopuses are cosmopolitan cephalopods of commercial importance that inhabit continental shelves and oceanic waters (Solis-Ramírez, 1997). They are important components of trophic webs due to their role as predators, prey or competitors of fishes and crustaceans (Gartner *et al.*, 2008; Briceño *et al.*, 2016). In Mexico, the octopus fishery is the ninth most important fishery by volume landed and the fourth most important fishery in terms of economic value (Pérez-Pérez *et al.*, 2011). Yucatan and Campeche contribute about 90% of the national octopus fishery, which mainly targets *Octopus maya* (Voss & Solis Ramirez, 1966) (red octopus) and

*O. vulgaris* (common octopus). The fishery of *O. maya* is already at the maximum allowable catch; therefore, a maximum annual catch of 20,000 t, minimum size of 110 mm dorsal mantle length (DML) and minimum fresh body weight (BW) of 450 g were set to manage the fishery (Pérez-Pérez *et al.*, 2011).

*Octopus maya* is a coastal species that inhabits shallow waters adjacent to the continental shelf of the Yucatan Peninsula (states of Campeche, Yucatan and Quintana Roo). This species is often associated with areas covered by sea grass (*Thallassia testudinum*), coral fragments and empty shells of gastropods (Voss & Solis Ramirez, 1966). The red octopus is one of the most studied

species in the region (Solis-Ramírez, 1997; Arreguín-Sánchez, 2000; Hérnandez-Flores *et al.*, 2001; Rosas *et al.*, 2014; Gamboa-Alvarez, López-Rocha & Poot-López, 2015).

The catchability of *O. maya* is variable along the continental shelf; compared with the east coast of the Yucatan Peninsula, the west coast is characterized by greater abundance of smaller individuals during the fishing season (August–December) (Gamboa-Alvarez *et al.*, 2015; Markaida, Méndez-Loeza & Rosales-Raya, in press). However, the greatest abundance of *O. maya* in the Yucatan Peninsula occurs when the fishing season is closed (December–July) (Gamboa-Alvarez, López-Rocha & Poot-López, 2015).

Variations in octopus landings are associated with thermal anomalies resulting from El Niño–Southern Oscillation (ENSO) events (Fig. 1) (Comisión Nacional de Pesca y Acuacultura, 2016). For example, production of the octopus fishery is negatively affected in the western zone of the Yucatan Peninsula when the temperature increases 2 °C above average during an ENSO event. This has led to the hypothesis that the ENSO anomaly causes migration of octopuses from the western to the eastern zone, where temperature increase is limited by seasonal upwelling (Zavala-Hidalgo, Morey & O´Brien, 2003; Zavala-Hidalgo *et al.*, 2006; Enriquez *et al.*, 2013; Ruiz-Castillo *et al.*, 2016). According to this hypothesis, adults are favoured by the presence of summer upwelling that maintains the bottom shelf temperature below 27 °C. This temperature has been identified as the critical threshold for reproduction and embryonic development in *O. maya* (Juárez *et al.*, 2015, 2016; Caamal-Monsreal *et al.*, 2016). Temperatures above 27 °C inhibit the spawning of *O. maya* in captivity (Juárez *et al.*, 2015). Embryos maintained at temperatures above 26 °C had malformations or died (Caamal-Monsreal *et al.*, 2016; Sánchez-García *et al.*, 2017). *Octopus maya* juveniles spawned from females exposed to thermal stress during the last phase of gonad maturity had higher metabolic rates and lower initial weights than those from females that were not thermally stressed (Juárez *et al.*, 2016). These findings suggest that a temperature threshold of around 27 °C may control reproductive success of *O. maya*. Similarly, upper thermal limits have been reported in reproduction and embryo development for other cephalopod species (Villanueva *et al.*, 2003; Sen, 2005; Staaf *et al.*, 2008).

The aim of the present study was to go beyond previous laboratory studies under controlled temperatures, in order to examine the possible relationship between temperature and reproductive season (represented by functional maturity) of *O. maya* in the wild. Therefore, we compared functional maturity throughout the year in three climatic zones on the continental shelf of the Yucatan Peninsula, where contrasting thermal regimes arise from local upwelling patterns.

Functional maturation refers to the process by which gonads attain maturity and become ripe for spawning, i.e. for the gamete transfer process (Arkhipkin, 1992). In females, this process involves formation of additional oocyte coverings and the process of transferring oocytes into the organs from which spawning will take place; in males, it involves the formation of spermatophores. It is distinct from anatomical maturation, which refers to the anatomical development of the entire reproductive system. Functional maturity is therefore the better measure of reproductive condition.

## MATERIAL AND METHODS

### Sampling sites

The Campeche Bank is the continental shelf of the Yucatan Peninsula, adjacent to the states of Yucatan and Campeche in southeastern Mexico (Fig. 2). This shelf covers $104,000 \, \text{km}^2$ at the entrance of Gulf of Mexico and is characterized by four well-defined terraces (see contours of isobaths, Fig. 2) located at 2–18, 29–36, 51–63 and 90–134 m depth (Mendoza & Ortíz-Pérez, 2000). Oceanographic conditions on the shelf, and the presence of local upwelling and rain events (Enriquez *et al.*, 2013), allow differentiation of three environmental zones with contrasting temperature regimes, where a total of seven sites (fishing harbours) were sampled (Fig. 2). Zone I (Z-I) is located in Yucatan State and includes the two sites Ria Lagartos (21°38′N, 88°10′W) and Dzilam de Bravo (21°24′N, 88°53′W). Zone II (Z-II) is a transition zone that includes Progreso (21°18′N, 89°39′W) and Celestun (20°52′N, 90°24′W). Zone III (Z-III) is located in Campeche State and includes the city of Campeche (19°51′N, 90°32′W), Seybaplaya (19°38′N, 90°41′W) and Champoton (19°21′N, 90°43′W). The main upwelling event occurs from July to September in Z-I, but is less marked in Z-II and absent in Z-III (Merino, 1997).

Three seasons can be identified in the Yucatan Peninsula: (1) the winter storm season ('nortes'; November–February) with low atmospheric temperatures (mean 23 °C) and moderate precipitation of
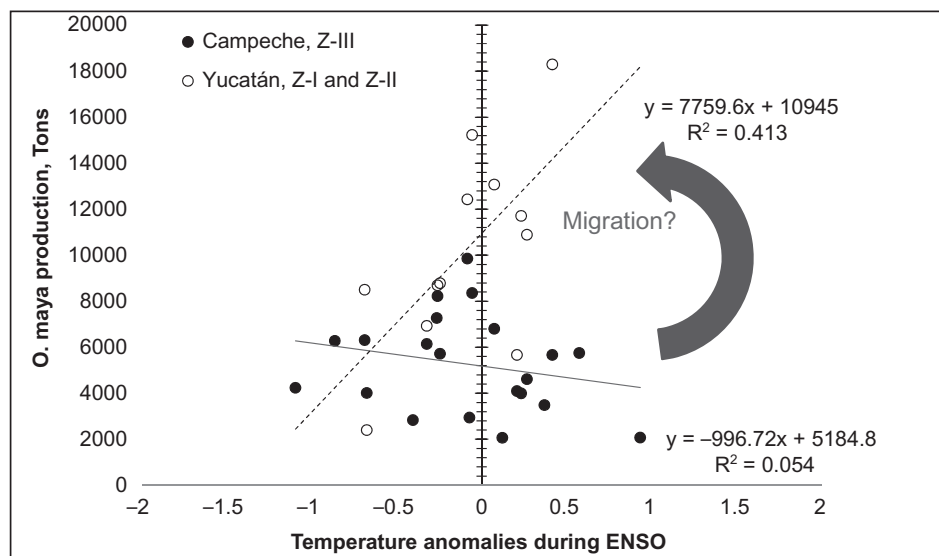


**Figure 1.** *Octopus maya* fisheries production in the western (Z-III; Campeche) and eastern (Z-I and Z-II; Yucatan) areas of the Yucatan Peninsula as a function of temperature anomalies recorded during El Niño–Southern Oscillation events in the period 2006–2015 (NOAA, 2016). Fisheries data from National Mexican Fisheries and Aquaculture Commission (Comisión Nacional de Pesca y Acuacultura, 2016).
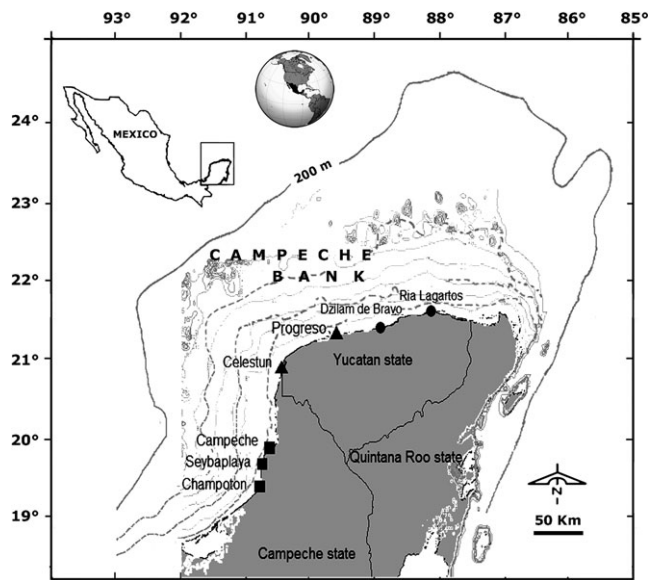
**Figure 2.** Sampling sites along the coast of the Yucatan Peninsula, Mexico, for zones Z-I (solid circles), Z-II (triangles) and Z-III (squares). Summer upwelling occurs in Z-I but not in Z-III, while Z-II is transitional.

40–150 mm/month; (2) the dry season (March–May) with atmospheric temperatures around 36–38 °C and low precipitation of 0–30 mm/month and (3) the rainy season (June–October) with atmospheric temperatures higher than 38 °C and precipitation greater than 220 mm/month, or higher than 350 mm/month if hurricanes occur (Herrera-Silveira, Ramírez & Zaldivar, 1998).

### *Octopus sampling and reproductive status*

A total of 2,145 sexually mature adults of *Octopus maya*, i.e. anatomically ready with a developed reproductive system, were sampled. The animals were considered to be mature adults on the basis of their size; for males, total BW was >242 g and/or DML >74 mm; for females, BW was >335 g and/or DML >126 mm (Avila-Poveda *et al.*, 2016; Markaida *et al.*, in press). Sampling was done using the local fishing method known as 'gareteo'. This method consists of leaving the boat (up to 8 m in length) to drift, releasing 10–12 lines that are tied to the side of the boat and to 5-m-long canes, known locally as 'jimbas', fixed to the bow and stern of the boat. The bait preferentially used by fishermen is the blue crab *Callinectes sapidus* or spider crab *Libinia dubia* (Solis-Ramírez, 1997). Using this method, artisanal octopus fishing is carried out over the first two terraces, between 10 and 25 m deep, where *O. maya* has its greatest abundance (Gamboa-Alvarez *et al.*, 2015).

Monthly collection of *O. maya* was carried out from August 2009 to June 2010 (except March to May in Z-II when a harmful algal bloom occurred) in an attempt to survey the three seasons and three zones along the Yucatan Peninsula. Of the total octopuses caught, 691 were sampled from Z-I (383 females and 308 males), 679 from Z-II (302 females and 377 males) and 775 from Z-III (336 females and 439 males).

Individuals were dissected and the wet weight of the reproductive organs was recorded to the nearest 0.001 g. Weight measurements included: BW, reproductive complex weight (RCW, defined as accessory glands without gonad—i.e. spermatophoric complex, Needham's sac and vas deferens in males and oviducts and oviducal glands in females), gonad weight (GW), reproductive system weight (RSW, defined as gonad with ducts and accessory glands; i.e. RSW = RCW + GW). The number of spermatophores stored

in the Needham's sac of each male was counted to estimate the immediate potential of males to inseminate females.

The reproductive status was determined using the macroscopic maturity index (MaMI = RCW/RSW) in females (Hayashi, 1970; Guerra, 1975) and the reproductive complex index (RCI = [RCW/(BW – RCW)] × 100) in males (Markaida & Sosa-Nishizaki, 2001). These indices are considered the best descriptors of reproductive condition (Avila-Poveda *et al.*, 2015, 2016). Values of MaMI ≤0.2 in females and RCI values ≥0.9 in males indicate functional maturity, i.e. animals that are in full reproductive condition (Avila-Poveda *et al.*, 2016).

### *Data analysis*

The relationships between reproductive indices and monthly sea-surface temperature (SST) were examined. Monthly SST data at 8 km resolution off each harbour to 100 m depth were obtained from the National Geophysical Data Center (National Oceanic and Atmospheric Administration, NOAA, 2016). Monthly SST was also compared with bottom depth temperature data from Enriquez *et al.* (2013) and Zavala-Hidalgo *et al.* (2006).

To test for statistical differences ($P < 0.05$) in reproductive condition (i.e. MaMI in females and RCI in males) and male capacity to inseminate (number of spermatophores) among sampling zones (Z-I, Z-II and Z-III) and among seasons (winter storms 'nortes', dry and rainy), the Kruskal-Wallis test was followed by Dunn's test (with Šidak correction) for unequal sample sizes as a 'post hoc' test (Zar, 1999). Statistical analyses were carried out using R v. 3.2.2 (R Core Team, 2012) and Statistica 10.

## RESULTS

### *Living weight*

The mean BW of mature adult males and females of *Octopus maya* oscillated between 570 and 1,200 g, with a few individuals weighing as little as 150 g or up to 1,500 g (Fig. 3). There were no statistical differences in BW between sexes of sampled animals ($P > 0.05$), so monthly data were pooled.

### *Seasonality of reproduction*

Values of MaMI for females for all zones and seasons ranged between 0.01 and 1 (Fig. 4). There were no significant differences among MaMI values in the three seasons in Z-I. In Z-II and Z-III, significantly lower values were observed during the 'nortes' season than other seasons ($P < 0.002$; Fig. 4). At least 40% of the animals were functionally mature in each season in Z-I (i.e. MaMI values <0.2; Fig. 5), whereas in Z-II and Z-III 40% functional maturity was exceeded only in the 'nortes' season and was only 8–18% in other seasons (Figs 4, 5). Of the total number of animals collected in the 'nortes' season, 45% of the females from Z-II and 70% of the females from Z-I and Z-III were functionally mature (Fig. 5).

Values of RCI for males for all zones and seasons ranged between 0.02 and 2.8 (Fig. 6). RCI values observed in the rainy season in Z-I and Z-II were significantly lower than those in the dry and 'nortes' seasons ($P < 0.01$; Fig. 6). Significantly higher RCI values were obtained in Z-III during the 'nortes' than in dry and rainy seasons ($P < 0.007$; Fig. 6). The proportion of males showing functional maturity (i.e. RCI values ≥0.9) in the 'nortes' season was highest in Z-I (24%) compared with Z-II and Z-III (8 and 12%, respectively; Fig. 7). During the dry season, 40% of the males from Z-I and 8% of the males in Z-III were functionally mature (Fig. 7). Functional maturity of males was below 2% in all sampled zones during the rainy season (Fig. 7).

The number of spermatophores counted in the Needham's sacs was highly variable among seasons and sampling months, ranging between 2 and 120 spermatophores per male (Fig. 8). However, a
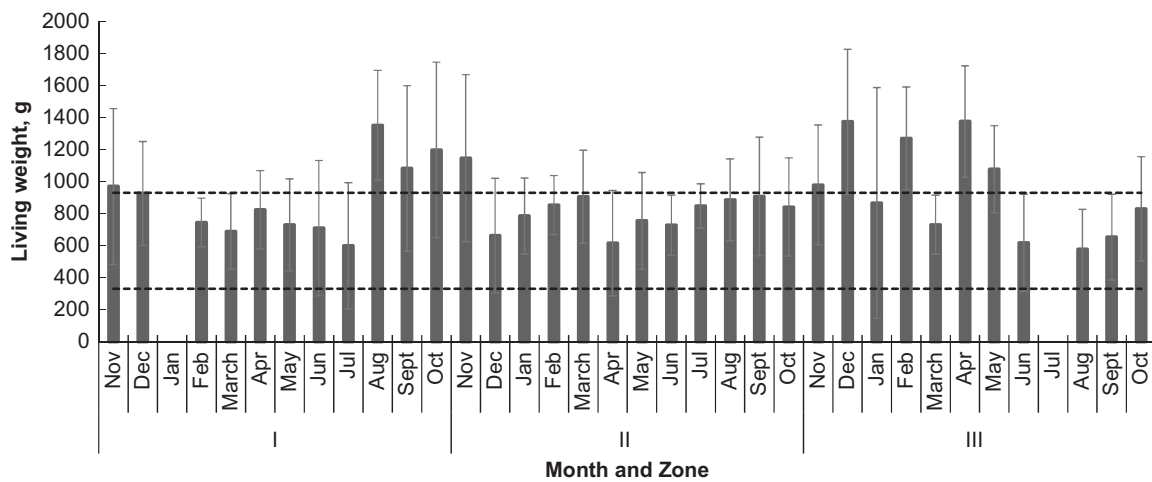
**Figure 3.** Living weight of *Octopus maya* adults (males and females) sampled around the Yucatan Peninsula monthly for 1 year. Values are mean ± standard deviation. Lower (Avila-Poveda *et al.*, 2016) and upper (Markaida *et al.*, in press) dashed lines indicate the body weight interval of mature animals.
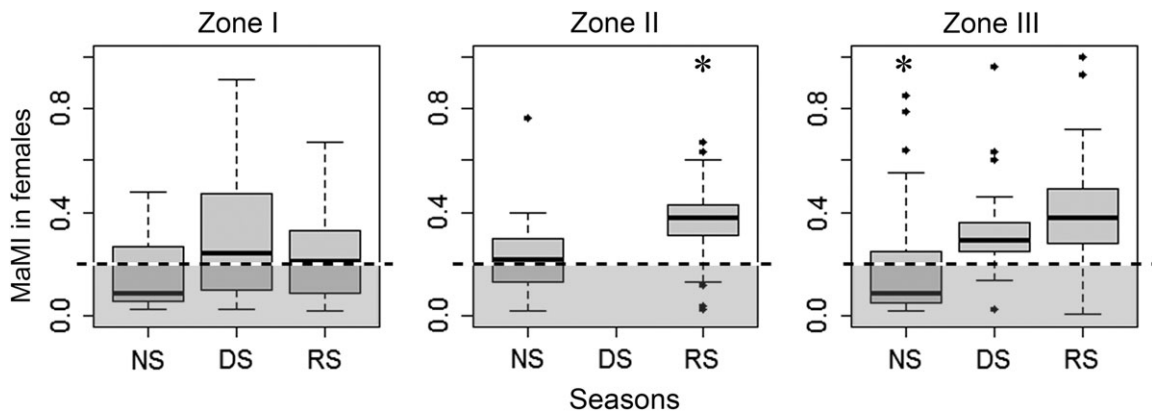


**Figure 4.** Spatio-temporal variation of macroscopic maturity index in female *Octopus maya* around the Yucatan Peninsula. Asterisks denote significant differences from other seasons within each zone ($P < 0.05$). The threshold of functional maturity in females (macroscopic maturity index MaMI $\leq 0.2$) is shown by the dotted line; i.e. females in shaded grey area are functionally mature. Values are median ± quartile deviation (bold line and box) with range (whiskers) and outliers (dots). Seasons: NS, 'nortes' (winter storms); DS, dry season; RS, rainy season. Zones: see Figure 1; summer upwelling occurs in Z-I but not in Z-III, while Z-II is transitional.

decreasing number of spermatophores was observed from Z-I to Z-III ($P < 0.05$; Fig. 8). The lowest average number of spermatophores was found in animals sampled in Z-III during the dry and rainy seasons (12 ± 9 and 26 ± 13 spermatophores, respectively; Fig. 8). These differences did not appear to be a consequence of differences in BW because, across all sampled animals, the number of spermatophores was not correlated with BW ($P > 0.05$; Fig. 9).

*Sea-surface temperature*

The seasonal variation in SST was different between zones (Fig. 10). Mean SST was highest between June and September (rainy season), reaching >30 °C in Z-III, while SST of only 29 °C was recorded in Z-II. In the same months, SST in Z-I showed a gradual increase from 27–27.5 °C in June and July to 29 °C in September and October, indicating the influence of the summer upwelling that produces a thermal gradient from west to east for much of the year (Fig. 10). Benthic temperatures measured in Z-I were lower than SST, but likewise showed a drop during the rainy months, suggesting that upwelling affected not only the SST, but also the benthic zone where the octopuses live (Fig. 10).

## DISCUSSION

As in other octopus species, reproduction of *Octopus maya* is modulated by many variables, some internal (size at maturity, hormonal control, multiple paternity, nutritional condition, among others), while others are dependent on the ecosystem dynamics and characteristics (food availability, temperature, pollution, light, ocean currents, etc.) (Zuñiga, Olivares & Ossandón, 1995; Rosa, Pereira & Nunes, 2005; Keay, Bridgham & Thornton, 2006; Estefanell *et al.*, 2010; Quintana, Rosas & Moreno-Villegas, 2011; Caamal-Monsreal *et al.*, 2015). Of these factors, size at maturity and temperature are considered to be of key importance; their synchrony modulates the timing of reproductive activity and determines the environment in which embryos develop until hatching (Otero *et al.*, 2007; Krstulović-Šifner & Vrgoč, 2009; Perales-Raya *et al.*, 2014; Juárez *et al.*, 2015).

Several studies of *O. maya* in the Yucatan Peninsula have investigated size at maturity and, as a result, it is well attested that females heavier than 375 g are mature (Moguel *et al.*, 2010; Caamal-Monsreal *et al.*, 2015, 2016; Juárez *et al.*, 2015, 2016; Tercero-Iglesias *et al.*, 2015; Sánchez-García *et al.*, 2017), whereas males mature at a smaller size (Avila-Poveda, Colin-Flores & Rosas, 2009; Avila-Poveda *et al.*, 2016). This species reaches maturity at a wide
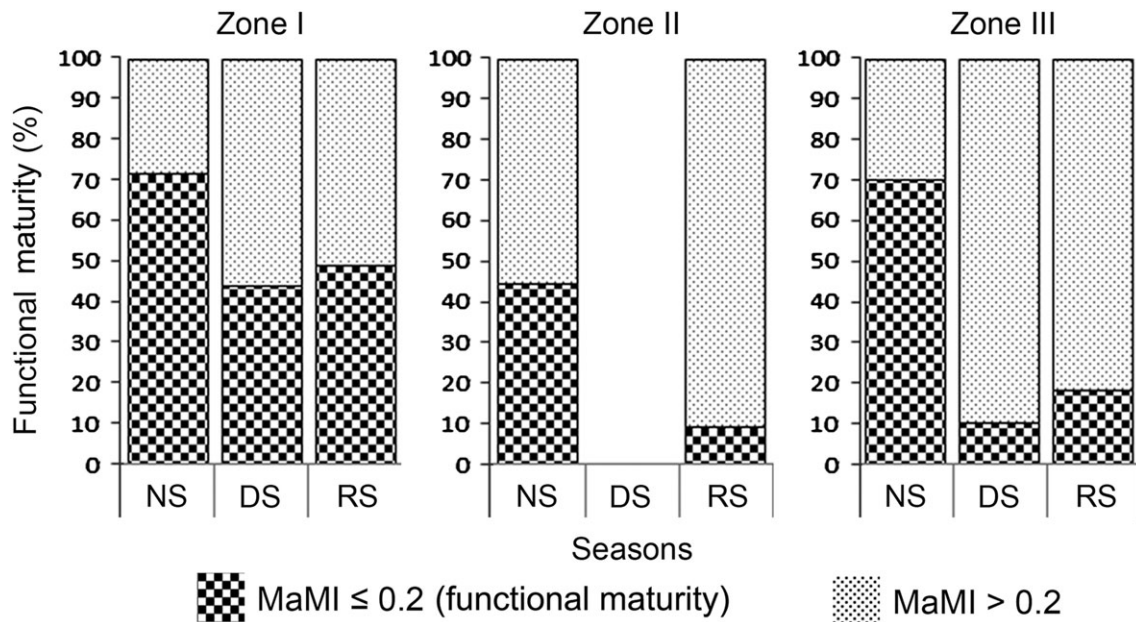
**Figure 5.** Proportion of female *Octopus maya* that are functionally mature (macroscopic maturity index MaMI ≤0.2) during each season around the Yucatan Peninsula. Seasons: NS, 'nortes' (winter storms); DS, dry season; RS, rainy season. Zones: see Figure 1; summer upwelling occurs in Z-I but not in Z-III, while Z-II is transitional.
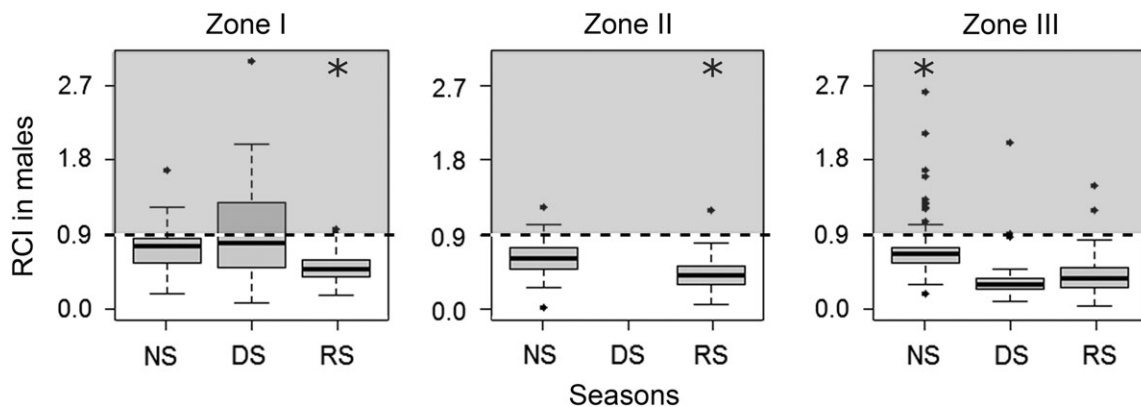


**Figure 6.** Spatio-temporal variation of reproductive complex index in male *Octopus maya* around the Yucatan Peninsula. Asterisks denote significant differences from other seasons within each zone ($P < 0.05$). The threshold of functional maturity in males (reproductive complex index RCI ≥0.9) is shown by the dotted line; i.e. males in shaded grey area are functionally mature. Values are median ± quartile deviation (bold line and box) with range (whiskers) and outliers (dots). Seasons: NS, 'nortes' (winter storms); DS, dry season; RS, rainy season. Zones: see Figure 1; summer upwelling occurs in Z-I but not in Z-III, while Z-II is transitional.

range of body sizes for, in a study that sampled 37,000 animals from five localities in Z-III during the rainy and part of the 'nortes' seasons for 4 years, Markaida *et al.* (in press) observed mature and spent individuals in the size range taken in commercial catches, 45–60 to 200 mm ML or 140–180 g to 2,500 g BW. However, according to our results, differences in functional maturity of *O. maya* between seasons and zones were not correlated with differences in size and anatomical maturity among samples, because all the octopuses were anatomically mature adults and no significant differences in adult size were found between seasons and zones. Therefore, we suggest that temperature, a recognized factor governing physiological condition in aquatic ectotherms (Clarke & Fraser, 2004), controls the spawning seasons and sperm production of wild *O. maya* around the Yucatan Peninsula. This postulate is based on both the observed seasonal differences in functional maturity (and number of spermatophores) and its modulation according to location around the peninsula, which can be explained by the cooling

effects of localized summer upwelling. The Yucatan Peninsula lies between the Caribbean Sea and the Gulf of Mexico. Summer upwelling events in Z-I and in part of Z-II (on the east side of the peninsula) limit the temperature of the benthic ecosystem in the area (Zavala-Hidalgo *et al.*, 2003, 2006). The cold water flows westward until it is mixed with warm water from the Gulf of Mexico (Enriquez *et al.*, 2013). In Z-I, where temperatures are below 27 °C for much of the year, more than 40% of females were functionally mature in all three seasons, while in Z-III mature females were found mainly in the winter 'nortes' season (November to March), which is the only period when temperatures are similarly low. Similarly, male spermatophore numbers were high all year in Z-I, while in Z-III the animals had a similarly high number of spermatophores only in the 'nortes' season. The pattern in the functional maturity of males was less clear. In Z-II, both females and males showed values of reproductive condition that were intermediate between the other two zones (although data for the dry season were
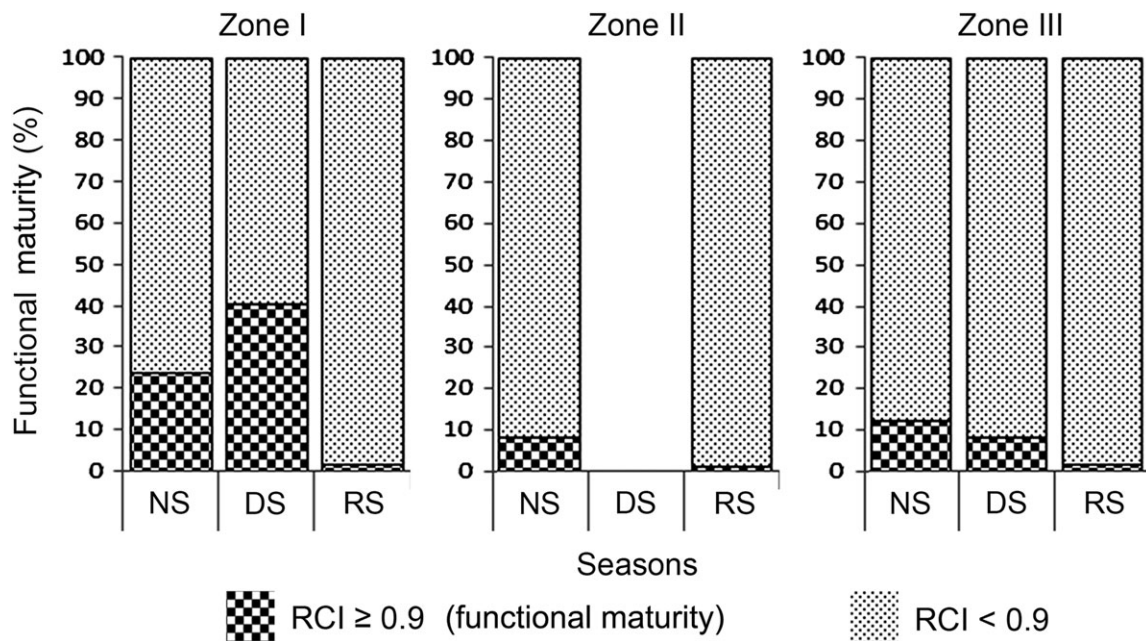
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**Figure 7.** Proportion of male *Octopus maya* that are functionally mature (reproductive complex index RCI ≥0.9) during each season around the Yucatan Peninsula. Seasons: NS, 'nortes' (winter storms); DS, dry season; RS, rainy season. Zones: see Figure 1; summer upwelling occurs in Z-I but not in Z-III, while Z-II is transitional.
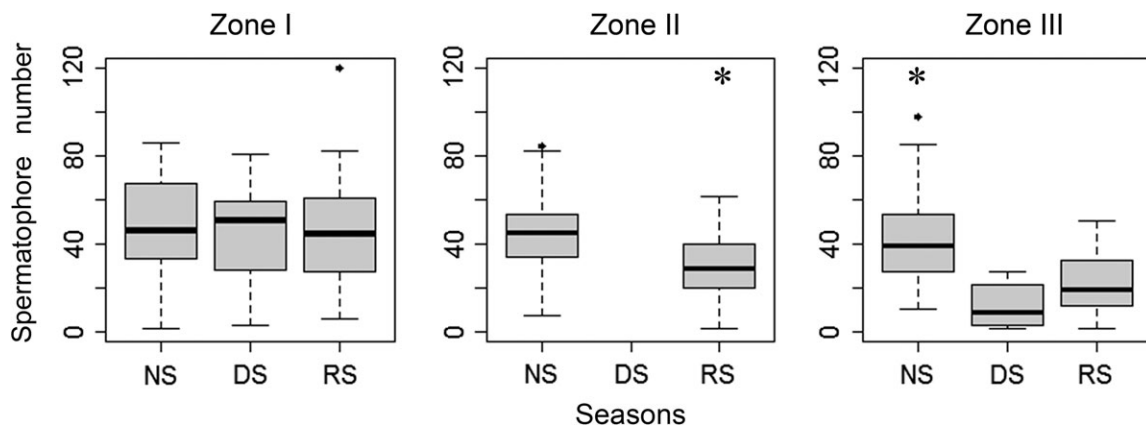


**Figure 8.** Number of spermatophores in male *Octopus maya* during each season around the Yucatan Peninsula. Values are mean ± standard deviation. Asterisks denote significant differences from other zones within each season ($P < 0.05$).

lacking), suggesting a reproductively transitional zone in the northeastern Yucatan Peninsula.

The mean monthly SST recorded during the 'nortes' season in all three zones (when reproductive condition is at a peak) was below 27 °C. This is consistent with laboratory studies, which have demonstrated that an upper temperature threshold limits reproduction in *O. maya*. In the laboratory, female *O. maya* do not spawn at temperatures above 27 °C (Juárez *et al.*, 2015). Moreover, juveniles spawned by females that were exposed to temperatures higher than 27 °C had a smaller BW and double the oxygen consumption compared with juveniles spawned by females maintained at temperatures lower than 27 °C (Juárez *et al.*, 2016). The redox system of the embryos appears to be unable to operate above 27 °C due to high levels of reactive oxygen species caused by the raised metabolic rate at high temperature (Sánchez-García *et al.*, 2017). Therefore, the 27 °C threshold appears to be important for *O. maya*. Observations on other cephalopod species have also indicated that there are upper thermal limits for reproduction

and embryonic development. For example, egg masses of *Dosidicus gigas* are found in the Gulf of California at a depth between 16 and 20 m, where temperatures are between 26 and 27 °C (Staaf *et al.*, 2008). The physical and chemical properties of the jelly determine that the egg mass rests at a depth that offers a reasonably oxygenated and thermally adequate environment for embryonic development. In *Loligo vulgaris*, an upper temperature threshold of 24 °C has been reported for embryonic development (Villanueva *et al.*, 2003; Sen, 2005).

The reproductive capacity of males was estimated using the number of spermatophores as a proxy. Sperm production in this and other octopus species is continuous (Qian *et al.*, 2016), but it would not be expected that males accumulate a full stock of spermatophores, because they start inseminating females immediately once they reach maturity. The maximum of 70 spermatophores per octopus recorded in this study is comparable with previous records of *O. maya* from Z-III with up to 80 spermatophores (Santos-Valencia & Re-Regis, 2000).
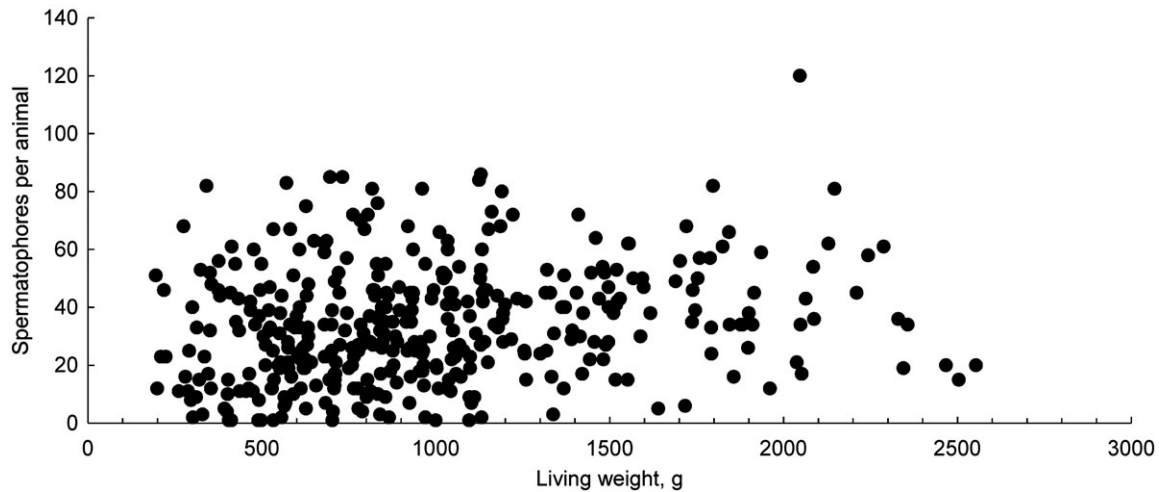
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**Figure 9.** Relationship between living weight and number of spermatophores for animals sampled around the Yucatan Peninsula monthly for 1 year.
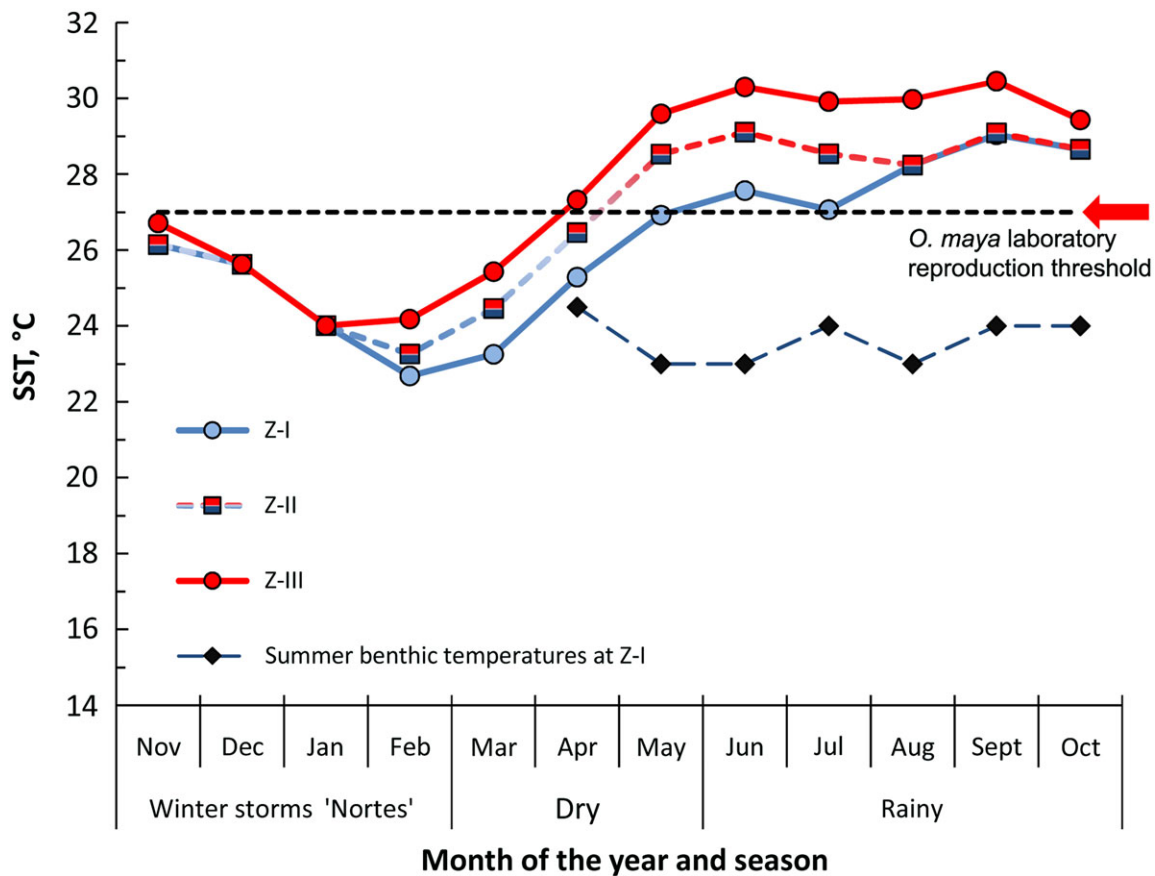


**Figure 10.** Monthly mean sea-surface temperature around the Yucatan Peninsula for zones Z-I, Z-II and Z-III and benthic temperature in Z-I (see Fig. 2). Sea-surface temperature from National Geophysical Data Center (period 2006–2015) (NOAA, 2016); benthic temperature from Enriquez *et al.* (2013) and Zavala-Hidalgo *et al.* (2006).

The effects of temperature on sperm production, quality and spermatophore transfer have not been reported for *O. maya* and laboratory studies are required. However, a 50% decrease in the number of fertilized eggs was observed in females maintained at temperatures higher than 27 °C, compared with fertilized eggs of females maintained at 24 °C (Juárez *et al.*, 2015). According to Juárez *et al.* (2015), temperature may affect sperm viability in the oviducal gland when females are exposed to high temperature. Testicular damage due to increased temperature was recently demonstrated in *O. tankahkeei* (Long *et al.*, 2015).

Heat-shock protein-70 increased in heat-treated octopus and the nuclei of testis cells became abnormal. Taking into account the thermal sensitivity of *O. maya* males, similar effects of high temperature in this species could be expected.

### *Possible sensitivity of* O. maya *to climate change*

This study suggests that temperatures below 27 °C offer favourable conditions for reproduction (functional maturity) of wild *O. maya*.
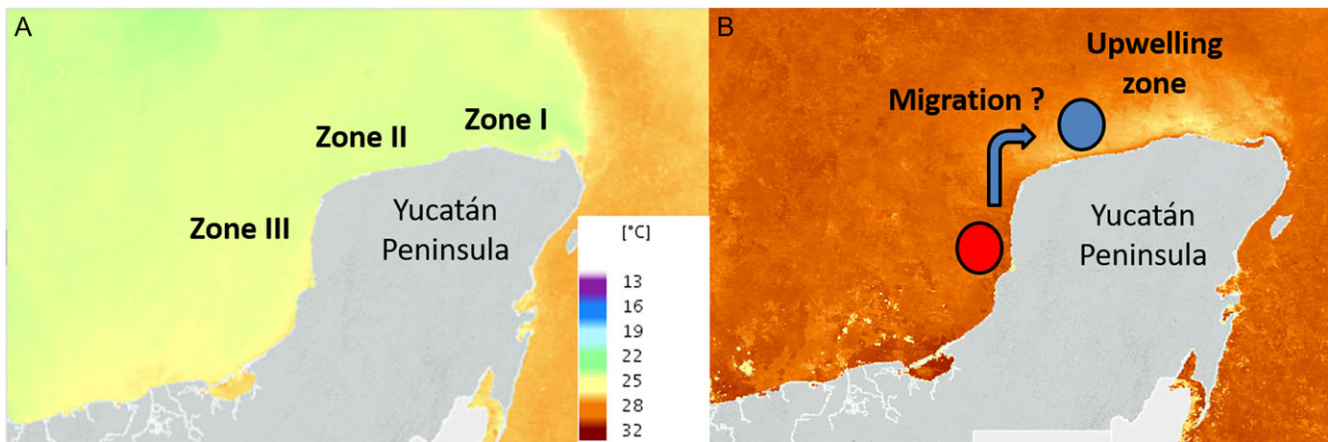
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**Figure 11.** Sea-surface temperature in the Gulf of Mexico during January 2013 (**A**) and September 2013 (**B**). Note the influence of the seasonal upwelling during summer (September) that favours temperatures below 26 °C off Yucatan (Centro de Ciencias de la Atmósfera, 2014). If temperature increases as predicted (IPCC, 2014), will the *Octopus maya* population concentrate in the zone where the upwelling regulates thermal condition of the benthic community?

We suggest that the *O. maya* population could be migrating eastward when the temperature in Z-III is higher than 27 °C (Fig. 11). This agrees with the hypothesis that migration occurs when ENSO anomalies are present (Zavala-Hidalgo *et al.*, 2003, 2006; Enriquez *et al.*, 2013; Ruiz-Castillo *et al.*, 2016). If this is the case, then in a climatic warming scenario the *O. maya* population could be concentrated in the upwelling zone, where lower temperatures favour its reproduction. Thus, changes in distribution of populations of this commercially exploited species could potentially be used as an indicator of the effects of global climate change on the western continental shelf of the Yucatan Peninsula, where the summer upwelling is not present. The potential impact of climate change on distribution of the global fisheries catch has been reviewed by Cheung *et al.* (2010). In this context, there are other questions that arise. For example, in a warming scenario, are there enough refuges and prey to sustain the total *O. maya* population (estimated at more than 50 million individuals) (Salas *et al.*, 2012) in the upwelling zone?

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