Genetic monitoring of the Mexican four-eyed octopus *Octopus maya* population: New insights and perspectives for the fishery management

Oscar E. Juárez[a], Luis Enríquez[b], Faustino Camarena-Rosales[c], Leticia Arena[d], Clara E. Galindo-Sánchez[a], Fabiola Lafarga-De la Cruz[e], Laura López-Galindo[a], Karina Nambo[e], Carlos Rosas[d,f,*]

[a] *Departamento de Biotecnología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada, B. C. Carretera Tijuana-Ensenada 3918, Fraccionamiento Zona Playitas, Ensenada, Baja California, México*
[b] *Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada 3917, U.A.B.C., Ensenada, Baja California, México*
[c] *Facultad de Ciencias, Universidad Autónoma de Baja California, Carretera Tijuana-Ensenada 3917, U.A.B.C., Ensenada, Baja California, México*
[d] *Unidad Multidisciplinaria de Docencia e Investigación, Sisal, Universidad Nacional Autónoma de México, Puerto de abrigo s/n, Sisal, Yucatán, México*
[e] *Departamento de Acuicultura, Centro de Investigación Científica y de Educación Superior de Ensenada, B. C. Carretera Tijuana-Ensenada 3918, Fraccionamiento Zona Playitas, Ensenada, Baja California, México*
[f] *Laboratorio Nacional de Resiliencia Costera (UNAM, -CONACYT)*

ABSTRACT

The *Octopus maya* fishery is one of the most important among the octopod fisheries in America. Recent studies about the wild population of this species, have contributed to understand that population variations and dynamics are highly influenced by temperature. The distribution area of this species could be divided in two well-differentiated thermal zones: an eastern zone influenced by the upwelling pulses, and a western zone with no upwelling influence. There is evidence suggesting that variations in population parameters could be linked to these thermal zones. However the fishery is still managed as one single unit, and there is no control of the capture limit. In this study we analyzed the multilocus microsatellite genotypes of wild *O. maya* across its distribution area to find out if the population is structured, and if the structure matches the mentioned thermal zones. Additionally, the heterozygosity was compared between samples from 2010 and 2015 to monitor changes related to the high fishing pressure. Results show that *O. maya* population is structured in two clusters that match with the different thermal zones in the distribution area. Moreover, significant genic differentiation was detected between these thermal zones. On the other hand, despite the high fishing pressure over this species, there is no significant difference in heterozygosity between 2010 and 2015 samples, and no inbreeding was detected, showing that genetic diversity is still high. We recommend the continuous monitoring of heterozygosity in this species, and a separate fishery management for Campeche (western) and Yucatan (eastern) subpopulations.

1. Introduction

The octopus fishery in the Yucatan Peninsula (Mexico) is the largest in the American continent; this fishery relies on two species, *Octopus maya* and *O. vulgaris,* and however *O. maya* represents the major part of the total catch (Galindo-Cortés et al., 2014; Gamboa-Álvarez et al., 2015). *O. maya* is a very well-studied species, and evidence suggest that there are differences in some population parameters between the western zone (in front of Campeche State), and the eastern zone (in front of Yucatan State), such as: size (Cabrera et al., 2012), abundance, catchability (Gamboa-Álvarez et al., 2015), sexual maturation (Ángeles-González et al., 2017) and reproductive season (Ávila-Poveda et al.,

2016). Moreover, a preliminary genetic analysis working with 4 heterologous microsatellites showed 2 loci with significant differentiation between eastern and western locations (Juárez et al., 2010). Another difference is that El Niño Southern Oscillation (ENSO) has an influence in the productivity of the western fishery locations but not in the eastern locations (Gamboa-Álvarez et al., 2015; Ángeles-González et al., 2017). Therefore, differences between western and eastern population features may be influenced by the different thermal conditions between these regions (Ángeles-González et al., 2017). The eastern edge of Yucatan Peninsula differs from the western zone, by the presence of upwelling pulses along the year. In summer, the upwelling maintains lower sea surface temperature (SST) offshore along the Yucatan State

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* Corresponding author at: Unidad Multidisciplinaria de Docencia e Investigación, Sisal, Universidad Nacional Autónoma de México, Puerto de Abrigo s/n, Sisal, Yucatán, México.
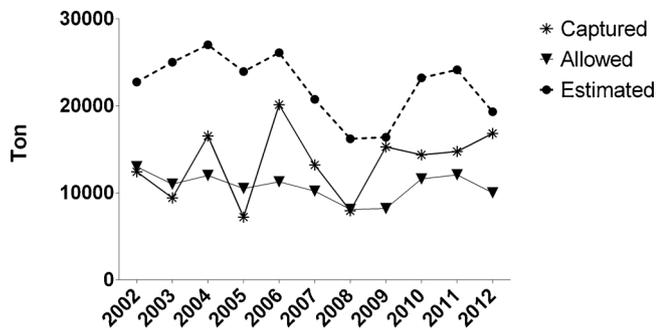*E-mail address:* crv@ciencias.unam.mx (C. Rosas).

Fig. 1. Comparison of total estimated biomass, allowed biomass to be captured, and captured biomass for *O. maya* during 10 fishing seasons.

(23–27.5 °C) in comparison with the western zone with no influence of the upwelling (Zavala-Hidalgo et al., 2006; Enríquez et al., 2013; Noyola et al., 2015). In the western zone the offshore SST in summer can reach 30 °C (Noyola et al., 2015). Recently, it was observed in experimental conditions that temperatures above 27 °C, can reduce the reproductive success of females (Juárez et al., 2015), but also the metabolic performance of embryos and hatchlings (Caamal-Monsreal et al., 2016; Juárez et al., 2016). This could explain why thermal anomalies such as ENSO have a stronger effect over the fishery productivity in the western zone. However, in spite of the differences detected in the *O. maya* population features between western and eastern zones, the fishery has been managed as one single unit. Additionally, another management challenge, but related to the high fishing pressure, is that the maximum quote allowed has been frequently exceeded (Galindo-Cortés et al., 2014) (Fig. 1). In fact, in 2009 the estimated total biomass and the captured biomass was almost the same (SAGARPA, 2013). Such fishing pressure could cause changes in the genetic diversity of the population. So it is important to monitor this population parameter in order to detect a possible reduction. In this sense, and considering that only 4 neutral loci have been analyzed in this population (Juárez et al., 2010), it is necessary to go further in the monitoring of population dynamics using neutral markers as microsatellites. This kind of genetic markers have been successful in the identification of population structure and in the assessment of genetic diversity and heterozygosis of many cephalopod species around the world (Shaw et al., 1999; Adcock et al., 1999; Greatorex et al., 2000; Murphy et al., 2002; Casu et al., 2002; Pérez-Losada et al., 2002; Cabranes et al., 2007; Doubleday et al., 2009; Juárez et al., 2010). Therefore, in response to the mentioned management challenges, the aim of this study is to assess if the population is genetically structured, by incrementing the number of neutral loci analyzed. Moreover, the number of alleles and heterozygosity between samples of 2010 and 2015 from Sisal were also compared, to detect if the high fishing pressure has caused a reduction in the genetic diversity of this species in that lapse of time. Previous results planted the hypothesis that Sisal zone is a place of passage of octopus, migrating from the warmer zones to the cooler ones, where the upwelling has influence (Gamboa-Álvarez et al., 2015; Ángeles-González et al., 2017), making Sisal a key marine area to assess the genetic diversity of *O. maya* population.

2. Method

2.1. Sampling

Octopuses were captured by artisanal fishing gear during 2010 fishing season from 2 locations in the Campeche State representing the region without the upwelling influence: Sabancuy (n = 33) and Campeche (n = 33); as well as 3 locations in the upwelling-influenced region in the Yucatan State: Sisal (n = 36), Dzilam (n = 30) and Río Lagartos (n = 26) (Fig. 2). An additional sample of 27 individuals was obtained from Sisal in the 2015 fishing season. Captures were carried

out approximately at 10 m depth.

2.2. Genotyping

For all samples, DNA was extracted from arm muscle tissue. For the 2010 samples, the genomic DNA was extracted via the phenol:chloroform method; for the 2015 samples genomic DNA was extracted by using the DNeasy Blood and Tissue kit (Qiagen) following manufacturer's instructions. DNA was quantified in a NanoDrop spectrophotometer (Thermo Fisher Scientific). The DNA integrity was assessed by electrophoresis in 1.5% agarose (85 V for 40 min). The amplification of eight microsatellite loci (accession numbers: KC602399.1, KC602400.1, KC602402.1, KC602403.1, KC602405.1, KC602406.1, KC602407.1, KC602409.1) were carried out in a thermal cycler (Eppendorf Mastercycler) using fluorescent labeled forward primers, following same PCR conditions as described in Juárez et al., 2013. Two positive controls and one negative control from each population were included in the genotyping analysis for verifying genotyping consistency. For allele visualization, PCR products were analyzed by commercial fragment analysis service (SeqXcel Inc., USA for 2010 samples and Carver Biotechnology Center, University of Illinois, USA for 2015 samples).

2.3. Data analysis

The sampling locations were grouped in two thermal zones. The group one is composed by Sabancuy and Campeche which represent the no-upwelling (western) zone and where SST can reach 30 °C. The group two is composed by Sisal, Dzilam and Río Lagartos representing the upwelling-influenced (eastern) zone, where temperature is below 27 °C most of the year (Fig. 2). A data matrix was built with the multilocus genotypes of each indivudual. This matrix was first analyzed with Microchecker v2.2.3 to detect null alleles and scoring errors. Then, departures from the Hardy-Weinberg (HW) equilibrium were tested for all locations in Arlequin v3.5.2.2, and for each locus in GenePop v4. The number of alleles in each sampling location were compared by using a one-way ANOVA, and multiple comparisons were corrected by using the Tukey test. The Fis index was estimated for all locations and Fst was estimated for the grouped locations with Fstat v2.9.3.2. A hierarchical AMOVA was performed in Arlequin v3.5.2.2 for the grouped locations, and the statistical significance was tested by bootstrapping. An exact test of genic differentiation was performed among the groups with GenePop v4. P values < 0.05 were considered significant in all the analyses. Finally, each individual was probabilistically assigned to a population by using Structure v2.3.4, inferring migrants from the data matrix by implementing the admixture model, and simulating from 1 to 5 clusters (k) with 30 replicates. The ΔK statistic (Evanno et al., 2005) was implemented to identify the number of k that best fits the data, by using Structure Harvestrer v0.6.94 (Earl and von Holdt, 2012).

3. Results

In spite of the presence of null alleles in the locus Omy4-11 (accession number KC602405.1), each analyzed locus is in H-W equilibrium (Table 1) as well as the multilocus genotypes in all the locations, including the 2015 sample from Sisal (Fig. 3, all values in Supplementary material 1). There are no significant differences in the number of alleles observed among the locations, and no significant differences between Sisal 2010 and Sisal 2015 (Fig. 4). Specific Fis indices per location were not significant (Table 2). When locations were grouped by thermal zones (zone one: Sabancuy-Campeche, zone two: Sisal-Dzilam-Río Lagartos) the Fst was significant between these zones. Moreover, the exact test of genic differentiation was also significant between these zones (Table 3). The probability for the number of clusters (k) composing the population was highest for k = 2 (Supplementary material 2). The assignment of individuals to putative clusters,
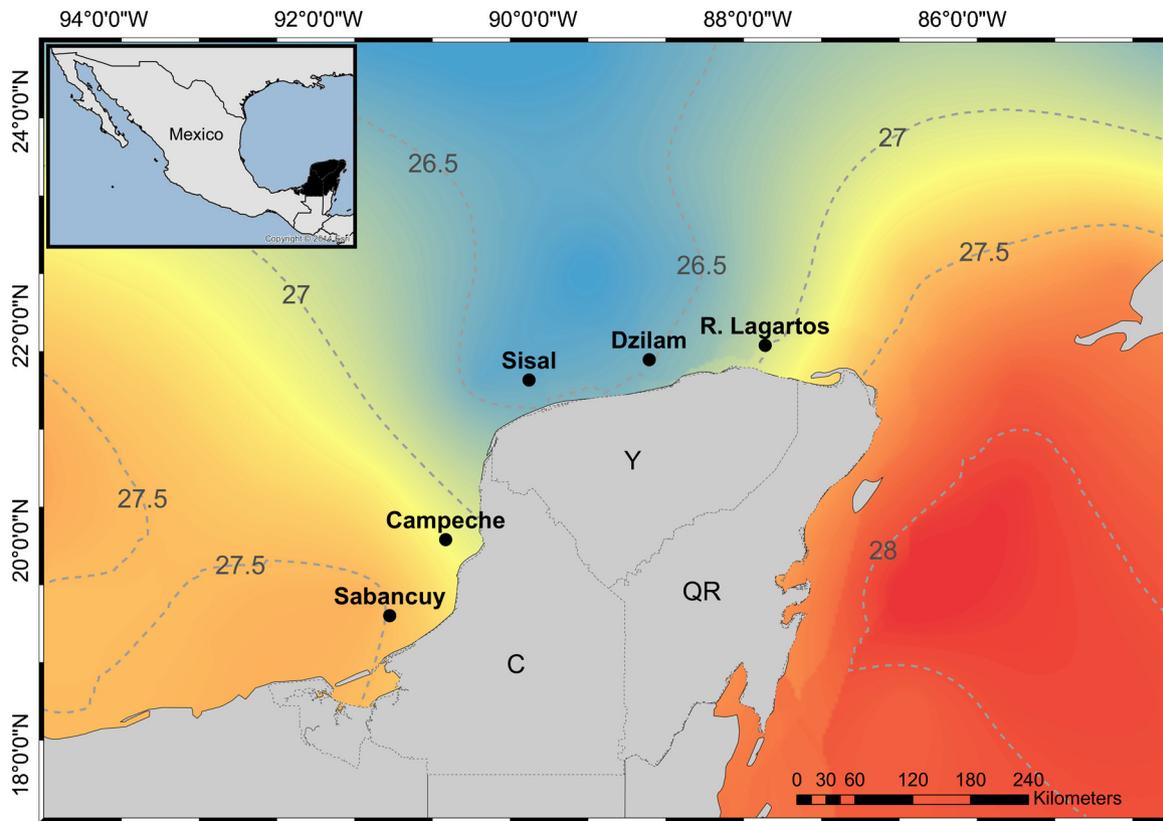
Fig. 2. Sampling locations and mean sea temperature at 10 m depth during the fishing season. Octopuses were captured approximately at this depth. Temperatures below 27 °C, which are beneficial for spawning and embryonic development are present in coasts of Yucatan State (Y) most of the year. Temperature data available from: https://gulfatlas.noaa.gov.

Table 1
Heterozygote deficit test by locus for all locations (Hardy-Weinberg equilibrium). SE = standard error. No significant heterozygote deficit was detected.

Locus	Accession	P value	SE
O2-02	KC602399.1	0.0571	0.007
O2-07	KC602400.1	0.3801	0.008
O2-37	KC602402.1	0.0797	0.0054
O4-01	KC602403.1	0.072	0.006
O4-11	KC602405.1	0.3794	0.0088
O4-18	KC602406.1	0.5541	0.0089
O4-20	KC602407.1	0.1473	0.0091
O4-40	KC602409.1	0.497	0.0112

Fig. 4. Number of alleles in each sampling location during 2010 fishing season, and including a sample from Sisal of the 2015 fishing season.

Table 2
Specific Fis in each location. No significant Fis was detected.

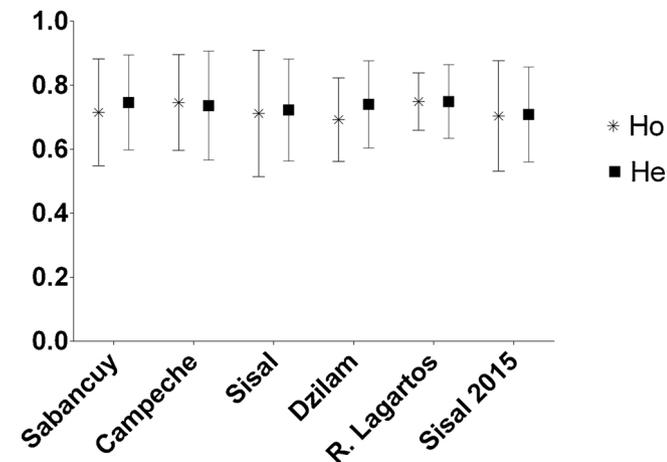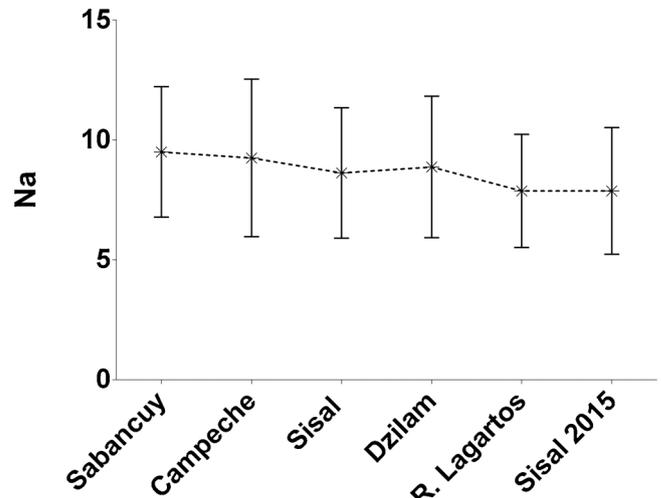|	Fis	P value
Sabancuy	0.0197	0.2933
Campeche	−0.0615	0.9697
Sisal	−0.0036	0.5728
Dzilam	−0.0081	0.6119
R. Lagartos	−0.0057	0.5953
Sisal 2015	0.0072	0.4457

Fig. 3. Heterozygosity values in sampling locations during 2010 fishing season, including a sample from Sisal of the 2015 fishing season.

Table 3
Fst (below diagonal) and Genic differentiation (above diagonal) P values between thermal zones: Zone 1 = Sabancuy-Campeche, Zone 2 = Sisal-Dzilam-Rio Lagartos. Both P values are significant.

	Zone 1	Zone 2
Zone 1	*	0.0064
Zone 2	0.0270	*

shows that Sabancuy-Campeche individuals are more likely to belong to cluster one, and Sisal-Dzilam-Río Lagartos individuals are more likely to belong to cluster two (Fig. 5). However, some admixture was detected between clusters, the estimated number of migrants between locations was 9.93, and between thermal zones was 12.06.

4. Discussion

4.1. Population structure

The results obtained in this study are coincident with other studies in remarking that *O. maya* population is structured in at least two clusters, in coasts of Campeche and Yucatan States respectively (Cabrera et al., 2012; Gamboa-Álvarez et al., 2015; Ávila-Poveda et al., 2016; Ángeles-González et al., 2017). A possible explanation for the observed population structure is that temperatures below 27 °C, which are beneficial for spawning, embryonic development and hatchlings metabolic performance (Juárez et al., 2015; Caamal-Monsreal et al., 2016, Juárez et al., 2016) are present in the coast of Yucatan State (eastern zone) most of the year thanks to the upwelling pulses (Zavala-Hidalgo et al., 2003; Zavala-Hidalgo et al., 2006; Ángeles-González et al., 2017). By contrast, in the coast of Campeche State (western zone), spawning is favored only in winter (Markaida et al., 2016) when temperature decreases. This generates asynchronous cohorts along the distribution area (Arreguín-Sánchez et al., 1993) that possibly do not interbreed due to size and reproductive stage differences (Cabrera et al., 2012; Ávila-Poveda et al., 2016). In this regard, there is an increment in the individual size from west to east along the coast of Campeche State, and also from west to east along the coast of Yucatan State. Therefore, around the border between Campeche and Yucatan States we can find bigger octopuses at the Campeche side and smaller octopuses at the Yucatan side (Cabrera et al., 2012). That difference in size between octopuses from adjacent locations, also implies a difference in age and in the sexual maturation stage (Ávila-Poveda et al., 2016; Ángeles-González et al., 2017); resulting in a separate distribution of adult octopuses in Campeche and juvenile octopuses in Yucatan during the

fishing season (Gamboa-Álvarez et al., 2015). Adult and juvenile octopuses do not interbreed due to different maturation stages, and juveniles could even move away from adults probably avoiding the cannibalistic behavior observed in cephalopods (Ibañez and Keyl, 2010; Hernández-Urcera et al., 2014). This can explain the significant Fst and genic differentiation observed between eastern and western regions. On the other hand, it has been observed a seasonal inversion in individuals' size along the area. Big octopuses are more common in Campeche (western zone) during the fishing season; but in the closed season, this pattern inverts and big octopuses are found around Río Lagartos (eastern zone) (Gamboa-Álvarez et al., 2015). This can be attributed to the asynchrony of the different cohorts; however, some authors have proposed that there could be a west to east migration of adults (Cabrera et al., 2012; Ángeles-González et al., 2017), to explain the seasonal shift in sizes along the distribution area. This migration is plausible even when it may imply a counter-current movement of the individuals, because summer temperatures at the western zone can reduce the reproductive success; by contrast, the eastern zone offers better thermic conditions for *O. maya* reproduction, embryonic development and juvenile biological performance (Juárez et al., 2015, 2016; Caamal-Monsreal et al., 2016). The estimated number of migrants between thermal zones could be a consequence of this migration pattern.

4.2. Genetic diversity

The expected and observed heterozygosity values were very homogeneous along the distribution area during fishing season 2010, and no significant differences were observed in the Sisal samples from 2010 and 2015. The same homogeneous pattern was observed for the number of alleles. In general, heterozygosity levels were high and the fixation indices (Fis) were not significant in all locations. Additionally all loci, including 2010 and 2015 samples, are in HW equilibrium. From these results it can be inferred that population is big enough to avoid inbreeding. Actually, the population size may be bigger than previously reported. According to the fishing reports and the estimated biomass for the population each year (SAGARPA, 2013; Galindo-Cortés et al., 2014), in 2009 the total biomass and the captured biomass was almost the same (Fig. 1). Such an event, might left a trace in the genetic diversity, in terms of a heterozygote deficit or the fixation of alleles. However, our results show the opposite, that alleles are not fixed and that heterozygosity is still high. From this, emerges the hypothesis that the biomass could be underestimated. Since 2002 until 2012, the biomass was estimated based on the number of encounters registered by scuba divers, who carried out the sampling only in shallow waters along the coast of the Yucatan Peninsula (SAGARPA, 2013). However, deeper
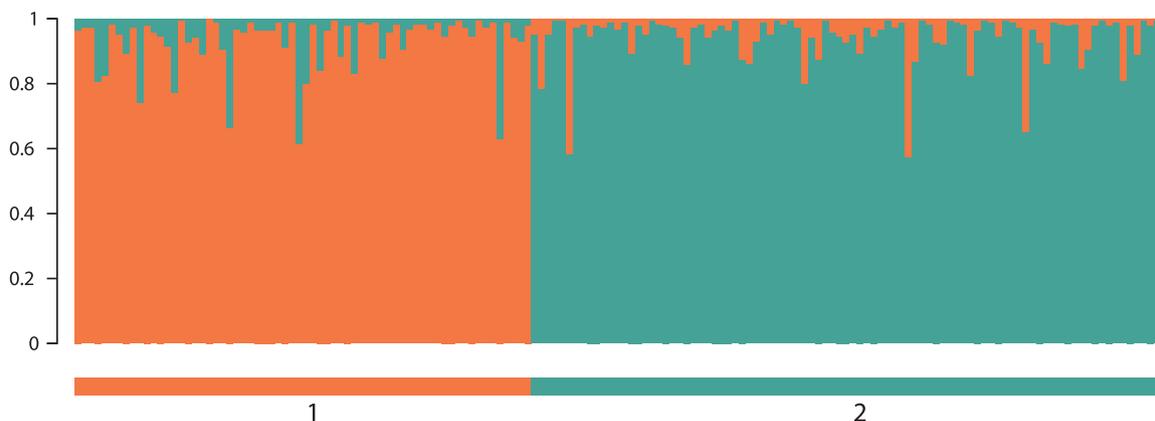

Fig. 5. Assignment of individuals into *k* clusters, simulation of *k* = 2. The individuals are grouped according to the influence of the upwelling in the distribution area of *O. maya*. At the left the no-upwelling zone including Sabancuy and Campeche individuals, at the right the upwelling-influenced zone including individuals from Sisal, Dzilam and Río Lagartos. The probability for belonging to cluster 1 is shown in red and for cluster 2 is shown in green, for each individual. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

zones were not included in the analysis even when is well known that this species is found at up to 60 m deep (Pérez-Pérez et al., 2006). Although it was previously proposed that migration of octopuses along the coast of the Yucatan Peninsula could occur in west to east direction, in an attempt of the individuals to reach cooler temperatures; octopuses from the western zone (without upwelling influence) may also migrate to deeper areas. In this sense, other studies should be done to know if in deeper areas of the western zone there are all the other environmental conditions that *O. maya* requires for its growth and survival (refuges, preys, etc.). Deeper (cooler) areas may represent an important refuge from high temperatures, which reduces fitness in this species (Juárez et al., 2015; Juárez et al., 2016; Caamal-Monsreal et al., 2016), but it also represent a good refuge from human pressure, because artisanal fishing fleets do not fish at high depths.

On the other hand, high heterozygosity levels are common among octopuses and in other octopus species, the heterozygosity levels are even higher (Greatorex et al., 2000; Murphy et al., 2002; Cabranes et al., 2007; Doubleday et al., 2009). Heterozygosity tend to be high in octopuses, possibly due to the polygamous reproductive strategy that they present. Multiple paternity has been demonstrated in different octopus species such as: *Graneledone boreopacifica* (Voight and Feldheim, 2009), *Octopus vulgaris* (Quinteiro et al., 2011) and *Enteroctopus dofleini* (Larson et al., 2015). This reproductive strategy has been observed as well in other cephalopods like *Loligo forbesi* (Shaw and Boyle, 1997), *Loligo pealei* (Buresch et al., 2001), *Loligo bleekeri* (Iwata et al., 2005), *Sepia apama* (Naud et al., 2005), and *Sepioteuthis australis* (Van Camp et al., 2004). So among cephalopods is common to find high heterozygosity levels, therefore it is very important to keep monitoring this parameter through time (even when heterozygosity levels in this study seem to be high). Comparing this parameter among different species will be necessary in order to detect real heterozygosity reductions in the future, which could be derived not only from fishing pressure, but also from environmental challenges like ocean warming.

5. Conclusion

The *O. maya* population shows significant structure and significant genic differentiation between western (no-upwelling) and eastern (upwelling-influenced) regions. These two subpopulations may differ in features such as reproductive season, so it is necessary to adjust management policies to the different population dynamics in each region to improve fishery productivity. Heterozygosity levels are still high, in spite of the high fishing pressure over the population, however this is a common feature among cephalopods. We recommend to continue the genetic monitoring of this population and to compare its diversity levels with other octopus species through time, in order to prevent a real reduction in its genetic diversity.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.fishres.2018.05.002.

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