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ORIGINAL PAPER

Genetic structure of *Octopus mimus* Gould, 1852 along three biogeographic marine provinces

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Abstract

The population genetic structure of a species is frequently shaped by biogeographic barriers that prevent the movement of individuals from one genetic population to another. Although *Octopus mimus* Gould, 1852 was reported to inhabit the shallow marine waters of the Peruvian province, recent studies suggest its synonymy with *O. hubbsorum* Berry, 1953 from the Panamanian and the Cortez provinces where it is the main octopus species caught in the artisanal fishery. The aim of the present study was to assess the genetic variability of *O. mimus* and to determine the presence of population structure across three sampled regions of the eastern Pacific Ocean using the mitochondrial marker cytochrome c oxidase subunit I. The hypothesis that the biogeographic boundary between the Panamanian and Peruvian provinces acts as a genetic break was further tested and recognized by the conformation of two phylogenetic clades and two haplogroups. Results indicate that these lineages are demographically independent populations of *O. mimus* and do not represent different species as evidenced by the Generalized Mixed Yule Coalescent method. The oceanographic processes have apparently allowed enough genetic flow along the Pacific coast yielding low but significant levels of genetic structure ($F_{ST} = 0.16$, $p < 0.05$) as seen in some fish populations.

Keywords COI · Biogeography · Dispersion · Octopodidae

Introduction

There are six biogeographic provinces in the eastern Pacific: California, Cortez, Panamanian, Galapagos, Peru-Chilean, and Juan Fernández (Briggs and Bowen 2012). All these provinces are defined by high endemism rates in a wide range of marine biotas and by genetic barriers in species boundaries. In previous genetic studies, the assessment of population structure in marine species has been addressed across the eastern Pacific, thus highlighting the importance of biogeographic barriers (Brante et al. 2012; Cárdenas et al. 2009; Ewers-Suacedo et al. 2016; Haye et al. 2014; Saarman et al. 2010). A study of *Hippocampus ingens* Girard, 1858 (Saarman et al. 2010) encompassed Cortez, Panamanian, and Peruvian provinces and evidenced low genetic differentiation among populations.

The Cortez province spans the Gulf of California. The Panamanian province extends from the mouth of the Gulf of California, Mexico, south to the Gulf of Guayaquil, Ecuador, where the Peruvian province begins down to the Taitao Peninsula (Briggs and Bowen 2012). The mixing of tropical and temperate waters and the convergence of the Humboldt

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and Panamanian currents in the Gulf of Guayaquil may interrupt gene flow between northern and southern organisms, while dynamic processes such as the seasonal shift of the Intertropical Convergence Zone and "El Niño" events could facilitate the dispersion of larvae (Saarman et al. 2010). Tropical invertebrates including cephalopods from the Panamanian Province have been recorded in Peru, an incursion thought to be associated to the El Niño event (Cardoso and Hochberg 2013; Paredes et al. 1998, 2004).

Octopus mimus Gould, 1852 inhabits shallow waters of the eastern Pacific including the three provinces mentioned above (Pliego-Cárdenas et al. 2016; Söller et al. 2000; Warnke et al. 2002). Söller et al. (2000) and later Warnke et al. (2002) using one mitochondrial gene (COIII) supported the distinction of *O. mimus* from *O. vulgaris* Cuvier, 1798 and indicated that the former was present off the coast of Central America. Later on, using sequences of three mitochondrial genes (COI, COIII and r16S), Pliego-Cárdenas et al. (2014) reported that *Octopus hubbsorum* Berry, 1953 and *O. mimus* belong to the same lineage. This finding suggests that they are synonymous and represent the continuum of a single species of *Octopus* present in both Central and South America western coasts. Subsequently, Pliego-Cárdenas et al. (2016) using the same three mtDNA markers showed that the populations of *O. mimus* from the eastern tropical Pacific and from the southeastern Pacific belong to distinct clades. They argued that different environmental conditions (warm North Pacific currents vs cold South Pacific currents) of the marine biogeographic provinces could be associated with the distinction of the two *O. mimus* groups, i.e., Panamanian and Peruvian, as a consequence of intraspecific genetic structure rather than of a speciation process. Thus, we refer to *O. hubbsorum* as *O. mimus* hereafter.

Octopus mimus is the main octopus fished along the eastern Pacific (Markaida and Gilly 2016). The fishery is artisanal, and octopuses are caught using "hooka" method (Sauer et al. 2019). Regional fishery management for this species includes minimum catch size and closed seasons in Mexico, Peru and Chile (Sauer et al. 2019). In Ecuador, the fishery has no official status (Markaida et al. 2018), and in Mexico, a national management plan for *O. mimus* is being developed (Diario Oficial de la Federación 2017).

The genetic population structure of *Octopus mimus* has been investigated separately in the northeastern (Domínguez-Contreras et al. 2018) and southeastern Pacific (Pardo-Gandarillas et al. 2018), using seven non-specific microsatellite *loci* and sequences of COIII, respectively. Both studies reported that *O. mimus* shows low levels of genetic diversity associated with the following: (a) a planktonic paralarval stage which can last for several days before the octopus settle on seabed, from 30 to 50 days in some species of *Octopus* (Villanueva and Norman 2008); (b) high fecundity, up to 200,000 oocytes per female (Warnke 1999; Pliego-Cárdenas et al. 2011); and (c) changes in oceanographic conditions (temperature and currents). However, each of the two study areas was restricted to a single biogeographic province (the Cortez province for the northeastern Pacific and the Peruvian province for the southeastern Pacific). Therefore, the aim of this study was to examine the genetic variability and structure of *O. mimus* across the three biogeographic provinces of the eastern Pacific: Cortez, Panamanian, and Peruvian. We hypothesize that oceanographic processes have allowed enough gene flow along the eastern Pacific coast yielding low levels of genetic structure as seen in some reef fishes (Muss et al. 2001; Saarman et al. 2010). Identifying population differentiation through genetic divergence will help to establish regional conservation management units and will give meaningful information to elaborate sustainability plans for *O. mimus*.

Materials and methods

Arm tissue samples of *Octopus mimus* were obtained from 28 localities covering four coastal countries of the eastern tropical Pacific: Mexico, Colombia, Ecuador, and Peru (see Fig. 1). Each locality was assigned to one of the biogeographic provinces (Cortez, Panamanian, or Peruvian). In total, 171 individuals were collected using fishery-dependent sampling between June 2010 and May–December 2014 (see Supplementary Material). All samples were stored in 96% ethyl alcohol and kept at − 4 °C for subsequent molecular analysis at the Laboratorio de Genética y Biología Molecular of the Universidad Autónoma Metropolitana, Unidad Iztapalapa, México.

Genomic DNA was extracted from arm muscle tissue and was subsequently purified using the PROMEGA Wizard SV Genomic DNA Purification System Kit following the established manufacturer procedure. DNA amplifications were carried out through polymerase chain reaction (PCR) using the mitochondrial cytochrome c oxidase subunit I (COI) primers, H2198: 5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′ and L1490: 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′ (Folmer et al. 1994), under a 25-μl total volume reaction, comprising 5× PCR buffer (Promega), 25 mM $MgCl_2$ (Thermo Scientific), 2 mM dNTPs (Thermo Scientific), 50 U *Taq* DNA polymerase (Bio-Rad), and 0.4 μM of each primer. PCR conditions consisted of 30 thermal cycles including the initial denaturation at 94 °C for 45 s, annealing at 49 °C for 45 s and final extension at 72 °C for 90 s. PCR products were run electrophoretically on a 1.5% agarose gel on TAE 0.5× buffer and were sequenced in both directions at Macrogen, Inc. (Seoul, Korea). Sequences of several species of *Octopus* as well as *O. mimus* from Chile (see Table 1) were retrieved from GenBank and aligned to the sampled sequences through the Clustal W method (Thompson

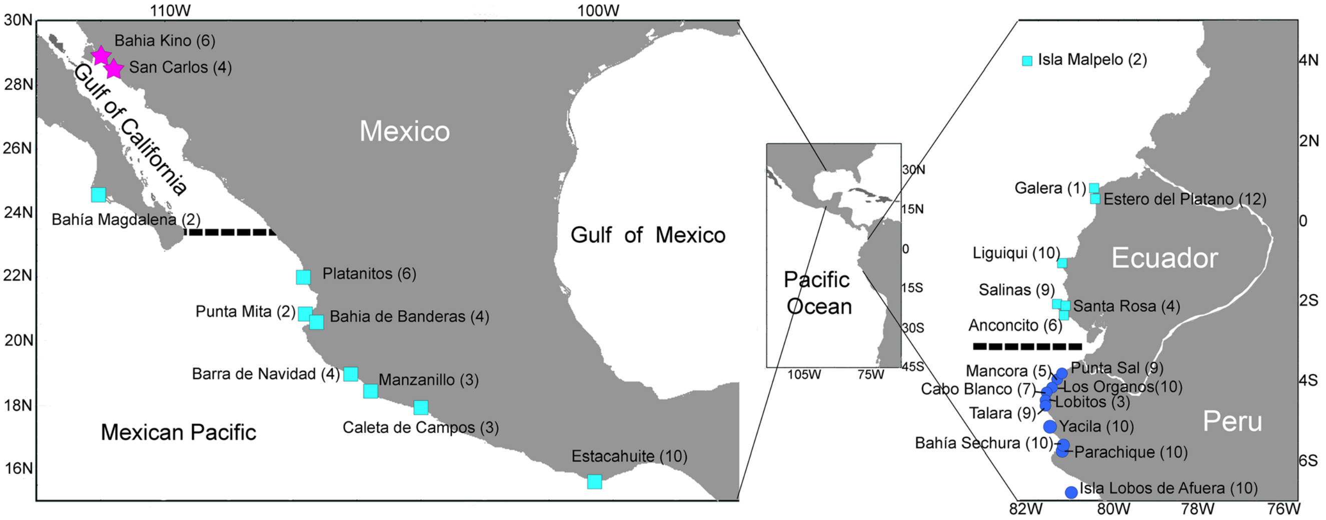

Fig. 1 Map showing the 28 localities where arm tissue samples of *O. mimus* were obtained. The sampling covered four coastal countries of the eastern tropical Pacific, Mexico, Colombia, Ecuador, and Peru, and three biogeographic provinces, Cortez (green stars), Panamanian (red squares), and Peruvian (blue circles). Black dashed lines indicate the provinces boundaries according to Briggs and Bowen (2012)

et al. 1994) in MEGA v7.2 (Kumar et al. 2015). The alignment was verified with the respective amino acid translation.

Genetic diversity was determined per province. The estimated parameters were the number of segregating sites (S), haplotypes (K), nucleotide diversity (π), and haplotype diversity (Hd) (DnaSP v5. Librado and Rozas 2009). The spatial distribution of genetic variation among the three provinces was examined using a hierarchical analysis of molecular variance (AMOVA) with significance levels set at $\alpha = 0.05$ and 10,000 random permutations as implemented in Arlequin (Excoffier and Lischer 2010). This method estimates the intraspecific genetic structure using haplotype frequencies (Excoffier et al. 1992). Genetic differentiation between pairs of regions was evaluated a posteriori by calculating pairwise F_{ST} (Excoffier and Lischer 2010). The genealogical relationship network among haplotypes was constructed using the median-joining method (Bandelt et al. 1999) in Network v5.0. A phylogenetic analysis was conducted in MrBayes v3.2. (Ronquist et al. 2012) using the GTR+G model, chosen by jModelTest (Darriba et al. 2012), and *Octopus insularis*

Table 1 GenBank accession numbers of sequences used in this study

Taxa	GenBank accession numbers	References
Octopus bimaculatus	KT335828	Pliego-Cárdenas et al. (2016)
Octopus bimaculoides	KF225006, MN180721	Pliego-Cárdenas et al. (2014); this study
Octopus insularis	KY492362, MH550425, MH550437	Flores-Valle et al. (2018); González-Gómez et al. (2018)
Octopus hummelincki	MH662556	This study
Octopus maya	GU362545,	Juárez et al. (2012)
	KY492363	Flores-Valle et al. (2018)
Octopus mimus	GU355923-GU355926, MN180702-MN180720	Acosta-Jofré et al. (2012)
		This study
Octopus oculifer	KT335831	This study
Octopus sinensis	AB430546	Kaneko et al. (2011)
Octopus tetricus	KJ605251	Amor et al. (2014)
Octopus vulgaris s. s.	HM104262,	Strugnell et al. (2014)
	KF844027, KF844042	Sales et al. (2013)
Octopus vulgaris type II	KF844031, KF844032, KF844040, KX611852-KX611854	Sales et al. (2013)
		Lima et al. (2017)

Leite & Haimovici in Leite et al. (2008) as outgroup (Pliego-Cárdenas et al. 2016). The Bayesian analysis was run for 10 million generations and sampling every 1000 generations. TRACER v1.6 was used to determine acceptable burn-in and to ensure the analysis had reached the stationarity (Rambaut et al. 2018).

We investigated whether the *Octopus mimus* clades recovered in the phylogenetic analysis are independent lineages or conspecific. To test this hypothesis, we used (a) the Generalized Mixed Yule Coalescent method (Fujisawa and Barraclough 2013), hereafter referred to as GMYC, which is a coalescent-based species delimitation method, and (b) a data set including 11 *Octopus* species (*O. bimaculatus* Verrill, 1883; *O. bimaculoides* Pickford & McConnaughey, 1949; *O. hummelincki* Adam, 1936*;* *O. insularis*; *O. maya* Voss & Solís-Ramírez, 1966, *O. mimus*, *O. oculifer* (Hoyle, 1904) *O. sinensis* D´Orbigny, 1834 In Férussac and D´Orbigny, 1834–1848 *O. tetricus* Gould, 1852; *O. vulgaris* and *O. vulgaris* type II D´Orbigny, 1840) and 40 sequences (see Table 1). The GMYC method is frequently used to delimit species based on a single locus. It is a likelihood method used to distinguish between inter- and intraspecific processes in a phylogeny by finding the maximum likelihood of a genealogical model (Fujisawa and Barraclough 2013). As good GMYC performance depends on several assumptions, we followed the recommendations of Talavera et al. (2013). Although our data set has singletons (a single haplotype for a species), this does not affect the good identification of species (Talavera et al. 2013). To include the most divergent haplotypes, the sampling covers most of the geographical range of the species. The ultrametric tree was created in BEAST v1.10 (Suchard et al. 2018) using a strict clock, a coalescent process, and a general time reversible (GTR) model, which best fit to the data as determined with the Akaike Information Criterion scores implemented in JModeltest. The chain ran for 15 million generations, sampled every 1000th generation. Tracer v1.6 was used to determine the convergence of chains. The analysis was performed two times, and log and tree files were combined with LogCombiner. Trees were then summarized using TreeAnotator discarding 10% of trees as burn-in. The GMYC model was tested using the splits package (Ezard et al. 2009) and a single threshold implemented in R.

Results

Table 2 Genetic diversity of *Octopus mimus* based on COI partial sequences from three Eastern Pacific regions. N = number of individuals, K = number of haplotypes, Hd = haplotype diversity, π = nucleotide diversity

Region	N	K	Hd	π
Cortez	10	3	0.511	0.0009
Panamanian	78	14	0.495	0.0013
Peruvian	83	11	0.707	0.0042
Total	171	19	0.66	0.0036

The 171 resolved sequences (605 bp) yielded 19 haplotypes, and a total of 20 polymorphic sites were identified. The populations from the three biogeographic provinces resolved from intermediate to relatively high haplotype diversity (Table 2; Hd = 0.495–0.707) and low nucleotide diversities (π = 0.0009–0.0042), with the Peruvian province showing the highest levels (Hd = 0.707; π = 0.0042) and the Panamanian, the lowest (Hd = 0.495; π = 0.0013). Overall AMOVA genetic differentiation using the F_{ST} index indicates low but significant differentiation ($F_{\mathrm{ST}} = 0.16$, $p < 0.05$), with most of the variation occurring within populations (83%) and 17% among groups (Table 3). Furthermore, the pairwise F_{ST} values support the hypothesis of population differentiation between the Panamanian and Peruvian provinces ($F_{\mathrm{ST}} = 0.16$, $p > 0.05$), and between the Cortez and the Peruvian provinces ($F_{\mathrm{ST}} = 0.13$, $p > 0.05$), but a differentiated population between the Cortez and the Panamanian provinces was not supported (Table 4).

The haplotype network showed the distribution of haplotypes in two well-defined groups (Fig. 2). Haplogroup 1 contains haplotypes from the three regions but with higher number of samples from the Panamanian region; therefore, hereafter, this haplogroup is referred as the Panamanian group. Haplogroup 2 contains predominantly specimens from the Peruvian province and only two specimens from Ecuador, thus, from hereafter is referred as the Peruvian group. These haplogroups are separated from each other by mutations at three sites. The most frequent haplotype, contained in the Panamanian group (H1, 55%), comprised 91 specimens from 22 sampled localities from the three provinces. It is followed by haplotypes 2, 3, and 4 (H2, H3, and H4, respectively) with frequencies > 5%. The haplotypes from Chile (GenBank accession numbers: GU355923-GU355926) were identical to H2 and H3 from the Peruvian group.

All haplotypes clustered together in one well-supported single monophyletic clade (Fig. 3) and were organized in

Table 3 Analysis of molecular variance (AMOVA) for cytochrome c oxidase subunit I (COI) in populations of *Octopus mimus*

Source of variation	d. f.	% Variation	Fixation index
Among groups	1	17	$F_{\mathrm{CT=}}0.19$
Among populations within groups	1	0	$F_{\mathrm{SC=}}0$
Within populations	168	83	$F_{\mathrm{ST}} = 0.16$*
Total	170	100	

*$p < 0.05$

Table 4 Pairwise fixation index calculated for COI partial sequences. Italicized values are significant ($p < 0.05$)

Province	Cortez	Panamanian
Panamanian	− 0.03684	
Peruvian	*0.13544*	*0.16324*

two main *Octopus mimus* subclades, one formed by specimens from the three regions and the other clustered specimens from the Panamanian (two individuals) and the Peruvian provinces. This finding is in agreement with the haplotype network.

The GMYC model recovered seven ML clusters (confidence interval 6–8) and 11 ML entities (confidence interval 10–13, $p < 0.05$) that correspond to the 11 *Octopus* species and support the conspecificity of the two lineages of *Octopus mimus* (Panamanian and Peruvian) (Fig. 4).

Discussion

Genetic diversity levels found in *Octopus mimus* along the three provinces are comparable to those observed for other *Octopus* species. Mean nucleotide diversity for *O. mimus* in this study (0.0036) is the same to that reported for this species in the Peruvian region (0.003) using COIII (Pardo-Gandarillas et al. 2018), and slightly lower than that for *O. vulgaris* using COI ($\pi = 0.005–0.021$, Sales et al. 2013). According to Pardo-Gandarillas et al. (2018), low levels of genetic diversity for *O. mimus* can be associated to demographic events caused by historic oceanographic changes.

It is well known that biogeographic boundaries act as genetic barriers precluding the gene flow between populations (Keigwin 1982). Two biogeographic barriers have been described along the tropical eastern Pacific Ocean, which subdivide populations of fishes and mollusks (Muss et al. 2001). These correspond to the transition zones among the biogeographic Cortez-Panamanian and Panamanian-Peruvian provinces (García-De León et al. 2018; Saarman et al. 2010). The mouth of the Gulf of California is characterized by strong salinity and seasonal temperature changes (Castro et al. 2000) that act like a barrier for some species but not for others (Bernardi et al. 2003; García-De Léon et al. 2018; Hurtado et al. 2007). The absence of genetic differentiation between the Cortez and the Panamanian populations could be caused by several factors, as a small sample size representing the Cortez province as well as by oceanographic processes. Fishes and mollusks show a similar pattern. Bernardi et al. (2003) found no differentiation between the populations of some species of fishes from the Gulf of California and the Pacific Ocean due to their dispersal potential. Similarly, Hurtado et al. (2007) attributed the panmixia of the snail *Nerita funiculata* Menke, 1850 along the eastern tropical Pacific to the longevity of its larvae which can be dispersed from Panama to the Gulf of California (about 5000 km). However, the use of more variable molecular markers in *O. mimus*, such as microsatellites and a larger sample size in the region, might help to resolve this issue in further studies.

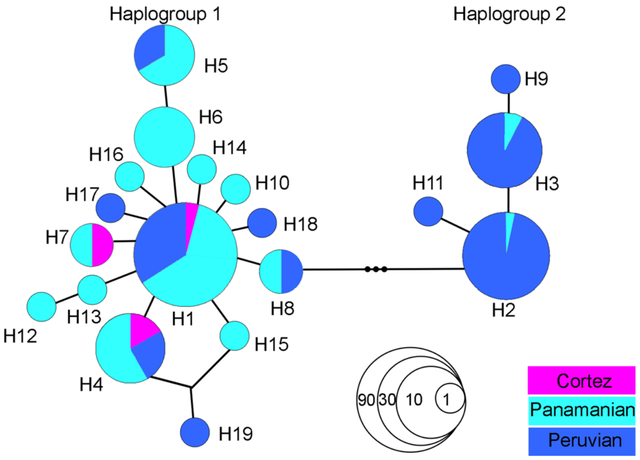

Fig. 2 The haplotype network resolved by the median-joining method. Haplotype circle sizes are proportional to the number of individuals

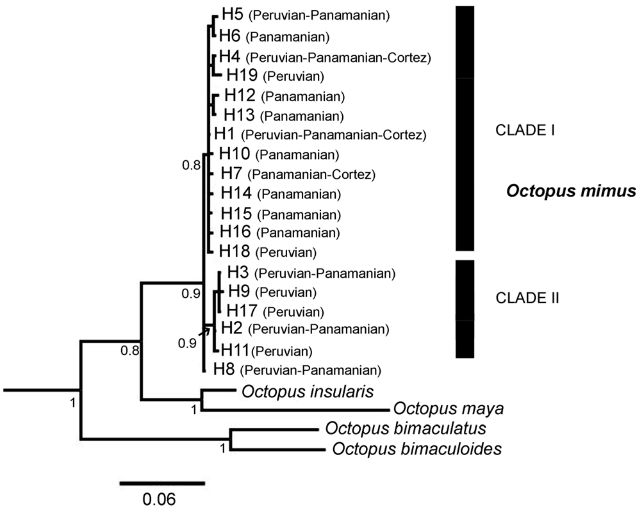

Fig. 3 Phylogenetic relations resolved by Bayesian analysis using the GTR+G model and *Octopus insularis* as outgroup. Values below nodes indicate Bayesian posterior probability

Contrary to the lack of distinction between lineages from the Cortez and the Panamanian provinces, pairwise F_{ST} values showed a low but significant genetic structure of the populations of *Octopus mimus* separated by the Panamanian-Peruvian biogeographic border, which is concordant to the hypothesis of oceanographic barriers to dispersal. It is possible that the association of the Pacific Ocean currents and the sea surface temperature (SST) of the region are enough to act like genetic barrier and to delimit two *O. mimus* populations. The Panama tropical current moving southward contrasts with the cold Humboldt current moving northward; thus, the SST in the Panamanian province typically exceed 20 °C while in the

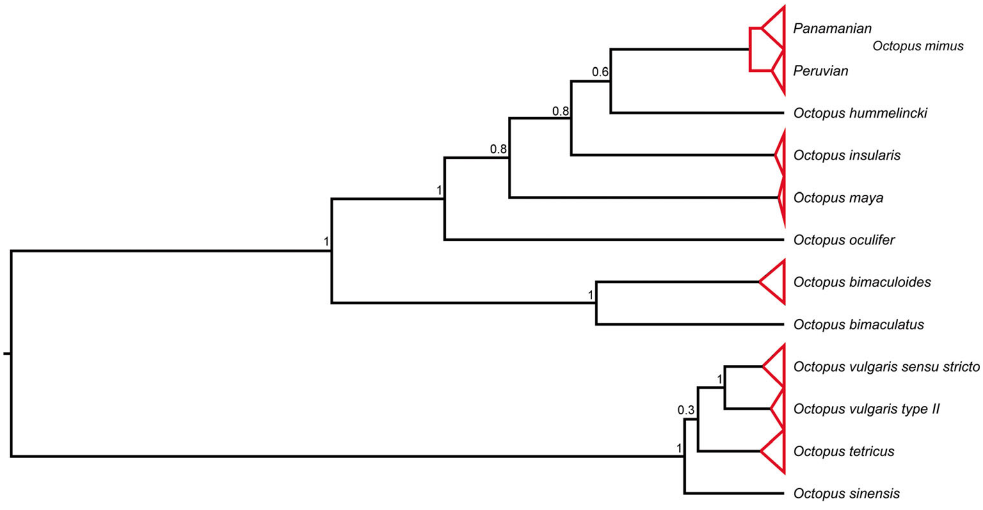

Fig. 4 Maximum likelihood clusters, recovered by GMYC model ($p < 0.05$), correspond to 11 *Octopus* species and the two lineages of *Octopus mimus* (Panamanian and Peruvian). Values above nodes indicate Bayesian posterior probability

Peruvian province the temperature is, usually, lower than 20° C (Hickman Jr. 2009; Montecinos et al. 2003).

The relatively low level of population differentiation detected between the populations of *Octopus mimus* is likely due to oceanic processes in the Pacific (Muss et al. 2001; Saarman et al. 2010) such as the El Niño Southern Oscillation (Cardoso and Hochberg 2013), which could favor the dispersal of paralarvae, which are tolerant to the warm temperatures (up to 24 °C) of El Niño (Warnke 1999). Cardoso and Hochberg (2013) recorded squids from the Panamanian province in Peruvian waters, and this incursion was attributed to tropical waters invasion into the Peruvian province during the El Niño event (Paredes et al. 1998, 2004). This oceanic process might explain the presence of the same octopus haplotypes in the Panamanian and the Peruvian provinces (Marin et al. 2018; this study).

Another example of an *Octopus* inhabiting more than one province is *O. insularis*, which has a wide distribution along the Western Atlantic, from Brazil to the Gulf of Mexico, spanning the Caribbean and the Brazilian biogeographic provinces (Briggs and Bowen 2012; Lima et al. 2017). The extensive distribution range of *O. insularis* is linked to the long-distance dispersal of paralarvae (González-Gómez et al. 2018), which allows gene flow among distant populations. Flores-Valle et al. (2018) support this hypothesis by finding octopuses from Mexico and Brazil sharing the same haplotype. In benthic octopuses with planktonic paralarvae, dispersion is ensured by ocean current transport far away from hatching localities. The paralarval stage of benthic octopuses, such as *O. mimus*, typically lasts from 3 weeks to 6 months (Villanueva and Norman 2008).

The use of the GMYC method in the present study allowed the identification of two genetic groups that coalesce in the same species group, *Octopus mimus*, and not as independent lineages, supporting the earlier findings by Pliego-Cárdenas et al. (2016). Nevertheless, it has to be considered that this study used a single marker, and, although the GMYC method is suitable when using a single locus (Fujisawa and Barraclough 2013) in species delimitation studies (Monaghan et al. 2009; Talavera et al. 2013; Vidigal et al. 2018), a multilocus analysis together with a morphological study could provide additional support to the COI sequences, since the phylogenetic tree cannot represent the evolutionary history of the species but, instead, represents the history of a single gene (Fujita et al. 2012).

Fishery management

As previously stated, there are no management plans for *Octopus mimus* fishery although in some countries seasonal closures and a minimum catch size have been implemented (Sauer et al. 2019). In Mexico, the closed season and minimum catch size have been implemented in a single Biosphere Reserve from the Gulf of California but not for the Mexican Pacific (Diario Oficial de la Federación 2017). The results from this study allow us to suggest that *Octopus mimus* should encompass two main fishery management units along eastern tropical Pacific (ETP), at least until data from microsatellite analysis become available. The occurrence of other known biogeographic barriers along ETP should be tested such as the border between the Gulf of California and the Mexican Pacific where a genetic break has been reported for the North Pacific hake and a threatened seahorse species (García-De Léon et al. 2018; Saarman et al. 2010). Efforts to study other aspects of population genetics and to investigate regional genetic structure will lead to (a) improved management plans and (b) a better understanding of how fisheries impact this species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies All samples were obtained by fishermen who have the necessary permits for sampling.

Data availability The data sets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Author contribution RPC, UM, and IBS conceived and designed research. RPC, SMP, and MAA conducted experiments. RPC and IBS contributed new reagents or analytical tools. RPC and SMP analyzed data. RPC, IBS, and SMP wrote the manuscript. All authors read and approved the manuscript.

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