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Genetic variability and historic stability of the California spiny lobster *Panulirus interruptus* in the Gulf of California

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ABSTRACT

The California spiny lobster *Panulirus interruptus* ranges from California into the Gulf of California in Mexico. In Mexico, the lobster supports an economically important fishery. Lobsters in the Gulf of California may belong to a small and genetically distinct population. We determined the genetic diversity and population structure of *P. interruptus*, using mitochondrial DNA sequences of the control region and the 16SrRNA gene. Samples were collected in the Gulf of California, the west central and southwest coast of the Baja California Peninsula, and the United States. We found a slightly higher genetic diversity in the Gulf of California populations than in the Pacific, but no significant genetic differentiation was shown by an analysis of molecular variance. Using a spatial clustering model and Bayesian methods, the weak population structure was consistent with the absence of a phylogeographic pattern and genetic admixture analysis. However, mismatch distribution analysis suggests that lobster from the gulf represents a more stable and older population than the Pacific, which fitted a model of sudden population expansion. The clinal trend in several genetic parameters between the Gulf of California and the Pacific suggests a historical separation that has not yet resulted in a significant genetic differentiation by genetic drift, mainly because of the large size of the population. Implementation of independent fisheries management practices between these regions could be justified; however, biological and ecological information should be used to support genetic data.

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1. Introduction

The California spiny lobster *Panulirus interruptus* is an important fishery along the west coast of the Baja California Peninsula (Vega-Velázquez, 2010). It is distributed within the temperate–subtropical environment of the California Current ecosystem, between 35° to 23.5°N, from San Luis Obispo, California to north of Bahía Magdalena on the west coast of the Baja California Peninsula (Vega-Velázquez et al., 2003). A small population has been reported within the eastern coast of the Baja California Peninsula around Bahía de Las Animas (Fig. 1). However, there are no records of this species from prospective surveys in the central to southern gulf from Guaymas to San Jose del Cabo (Campos 2007; Vega-Velázquez et al., 2012). Thus, it is a potential isolated population that is maintained by strong tidal currents and upwellings that carry high concentrations of nutrients in this region (Alvarez-Borrego, 1983; Escalante et al., 2013). This could have originated during the rise in sea level rise of the late Miocene (Campos, 2007).

Commonly, marine species having a prolonged pelagic larval stage with low intra-specific genetic differentiation (Palumbi, 1992; Avise, 1994). The California spiny lobster has a long planktonic larval stage of 7.75–12 months, passing through 11 phyllosoma molts (Johnson, 1960; Phillips et al., 2013). This long stage, coupled with ocean currents most of the year (Johnson, 1960) generates populations with poorly defined edges. Restriction fragment length polymorphism analysis of the mtDNA control region support the hypothesis of a panmictic population (García-Rodríguez and Perez-Enriquez, 2006). Allozyme (Perez-Enriquez et al., 2001) and microsatellite (Iacchei et al., 2013) analyses report genetic differences among several sites along the coast of California and western

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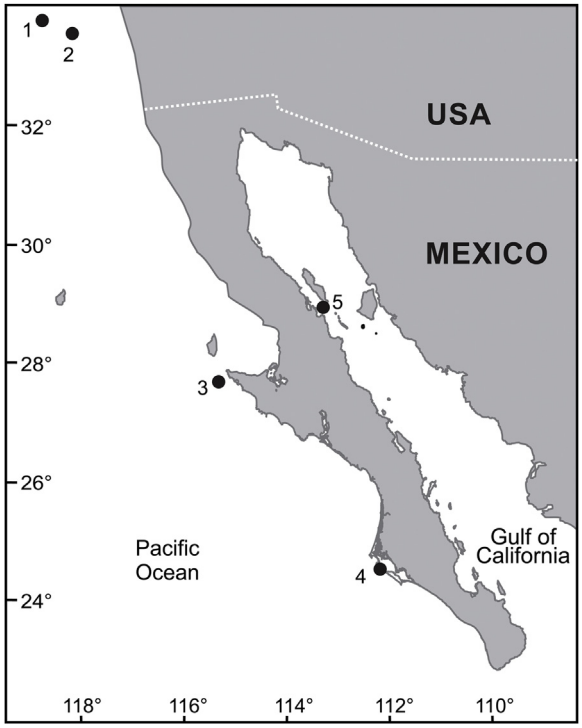

Fig. 1. Sampling sites. Locations in the U.S.A.: Santa Catalina Island (1) and Santa Barbara (2). Locations in Mexico: Punta Eugenia (3), Bahia Magdalena (4), and Bahía de las Animas (5).

coast of the Baja California Peninsula, which were associated with chaotic genetic patchiness (Hedgecock, 1994) rather than a limited gene flow.

Even though lack of genetic differences occurs in other lobster species (Inoue et al., 2007; García-Rodríguez and Perez-Enriquez, 2008; Kennington et al., 2013; Dao et al., 2015; Jeena et al., 2016; Watson et al., 2016), there are examples that show population differences at the extremes of their range, indicating that oceanographic and biological barriers may limit gene flow between localities leading, not only to a clear population structure, but also to the formation of subspecies (Marshall et al., 2009). Such is the case of *P. argus* (Sarver et al., 1998; Diniz et al., 2005), *P. delagoae* (Gopal et al., 2006), *P. elephas* (Palero et al., 2008), and *P. penicillatus* (Chow et al., 2011; Abdullah et al., 2014a,b).

Understanding the degree of genetic connectivity of *P. interruptus* between the Gulf of California and the Pacific is relevant for the population's viability, which depends on complex intrinsic and extrinsic interactions (Hallerman, 2003), either from recent climate fluctuations or if a fishery develops (Vega-Velazquez, unpublished data). If lobsters in the Gulf of California belong to a distinct population from the Pacific, a significant different genetic composition and lower genetic diversity in the Gulf of California than in the Pacific would be expected. In this study, we used genetic analysis, based on the sequences of two mtDNA fragments, to test the isolation hypothesis and discuss possible current and historical processes of genetic lineages in the California spiny lobster.

2. Materials and methods

Samples from the west coast of the Baja California Peninsula from the commercial fishery came from Punta Eugenia (PE-1999, n = 50 and PE-2001, n = 54), and Bahía Magdalena (BM-1999, n = 49). Samples from the Gulf of California were collected in 2006–7 at Bahía de las Animas (BA) with lobster traps (n = 70). Samples from the coast of California [Santa Catalina Island (SCI, n = 29) and Santa Barbara Island (SBI, n = 50)], were obtained from the commercial fishery in 2003 and 2007, respectively. Final sample size was slightly reduced because some samples failed during amplification (Table 1). Sampling sites are shown in Fig. 1. Muscle tissue samples were stored in 90% alcohol until analysis.

Total genomic DNA was extracted with proteinase-K for 18 h at 37 °C and a standard phenol-chloroform procedure (Perez-Enriquez and Taniguchi, 1999). DNA was suspended in 100 μL TE buffer (10 mM Tris-HCl, 1 mM EDTA) at pH 7.6 and stored at 4 °C. We initiated our study on samples from the extremes of *P. interruptus* distribution (SCI, PE-1999, and BA) of an 825 bp segment of the mtDNA containing the control region (CR); because each individual showed a different haplotype (see Results), a less variable mtDNA fragment [a 492 bp segment of the 16SrRNA (16S) gene] was analyzed on a second set of samples (SBI, PE-2001, BM, and BA; SBI and BA being from the same year). The CR was amplified using primers LanCR-F (5′-GCGTTTAGCTTATTATTCG; García-Rodriguez and Perez-Enriquez, 2006) and LanespRC-R (5′-TGGTGTGATCCCGTTACTTG; García-Rodríguez et al., 2008). The 16S was amplified with primers 16SarL (Palumbi et al., 1991) and 16Slang-b 5′-GCTGCTGCACCATAAAGGTT; this last primer was designed for this study from a sequence in GenBank, (accession number EF546597), using the program PRIMER3 (Rozen and Skaletsky, 2000). PCR amplification was performed with a total volume of 35 μL, mixing 0.48 μM of each primer, 1 × PCR buffer (#10342046, Invitrogen, Carlsbad, CA), 0.2 mM dNTP mix, 4.0 mM $MgCl_2$, and 0.05 U μL^{-1} Taq DNA polymerase ((#10342046, Invitrogen). Thermocycling involved denaturation for 2 min at 94 °C, 30 cycles for 1 min at 94 °C, 1 min annealing (59 °C for CR and 61 °C for 16S), extension at 72 °C (2 min for CR and 45 s for 16S), and final extension for 4 min at 72 °C.

The sequences were edited and arranged in Sequencher 4.5 software (Gene Code, Ann Arbor, MI) and alignment was done, using the MUSCLE algorithm in MEGA 6.0 (Tamura et al., 2013). Edited sequences were deposited in the GenBank (accession numbers KX787120–KX787315 for 16S KX787316–KX787429 for CR). Two previously deposited 16S sequences from BM were also used (accession numbers EF546599 and EF546600). The haplotype frequencies were obtained using DnaSP 5 software (Librado and Rozas, 2009). We calculated haplotype diversity (H) and nucleotide diversity (π) for each locality with Arlequin 3.5 software (Excoffier and Lischer, 2010). AMOVA was performed to test genetic variation within and among populations. We also estimated the values of Φst (analogous to *Fst*) for pairing of locations. The statistical significance for these tests was based on permutation tests of 10,000 replications, using Arlequin 3.5. Because nucleotide diversity, global Φst (for AMOVA), and pairwise population Φst represent molecular distances, we used jModelTest 2.0 (Darriba et al., 2012) to determine the most appropriate nucleotide substitution model incorporated in Arlequin 3.5. Based on the Akaike information criterion, we determined that the Tamura and Nei (1993) model with gamma parameter of 0.395 for CR and 0.451 for 16S was the best model for these fragments.

The phylogeographic analysis used a minimal spanning network of multi-state data, part of the Network 4.2.0.1 software (Bandelt et al., 1999). The network was constructed using the median joining method, based on Kruskal's algorithm and Farris's maximum-parsimony heuristic algorithm. To support the phylogeographic analysis, a genetic mixture analysis was performed with a spatial clustering model (Cheng et al., 2013) in BAPS 6.0 software (Corander et al., 2013). This analysis was based on DNA sequences and coordinates data obtained for each sampling site from Google Earth (http://earth.google.com). We ran a range of K (cluster: 1–10) values multiple times to increase the probability of finding the best partition (Corander et al., 2013).

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