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Genetic assessment of diversity and population structure of *Dosidicus gigas*
(Cephalopoda: Ommastrephidae) in the Pacific Ocean

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ABSTRACT

The fast growth and short life span of *Dosidicus gigas* make this squid a valuable model to evaluate how environmental fluctuations affect the genetic diversity of marine populations. *Dosidicus gigas* is composed by two genetic units in the Pacific Ocean. The first one, conformed by individuals from Canada, USA and Mexico and the second one by squids from Peru and Chile. Each genetic unit was characterized by an absence of population genetic structure and a star-like haplotype network. Genetic diversity was related to the molecular marker, the mitochondrial ones showed low diversity compared with microsatellites. Neutrality test, genetic diversity and demographic analyses were consistent with a past population expansion related to oceanographic changes associated with the last glacial-interglacial transition.

KEY WORDS: Jumbo squid, Genetic diversity, Population genetics, Coalescent

INTRODUCTION

The jumbo squid *Dosidicus gigas* (d'Orbigny 1835) is the most abundant and biggest squid in the Pacific Ocean (Nigmatullin et al. 2001, Ibáñez et al. 2015). The life span of *Dosidicus gigas* is about 3 years, reaching up to 120 cm mantle length and 3 m total length (Keyl et al. 2010). This squid species undergoes multiple spawnings of 10 to 14 spawning batches with 32 million eggs or more; it has the highest fecundity of all cephalopods (Nigmatullin & Markaida 2009). Females spawn a large egg mass (3-4 m diameter) near the surface, embedded in a gelatinous matrix with 0.6 to 2 million eggs (Staaf et al. 2008). Like other cephalopods, *D. gigas* does not develop a true

larval phase but hatches after three to 10 days as a paralarva (Yatsu et al. 1999, Staaf et al. 2008), a life stage very similar to the subsequent adult stage.

Dosidicus gigas exhibits sporadic and short-term pulses in abundance related to environmental changes and recruitment patterns (e.g., ENSO) (Ichii et al. 2002, Waluda et al. 2006, Keyl et al. 2008, Zúñiga et al. 2008). Recently, after the 1997-98 ENSO event, *D. gigas* has experienced a range expansion in both hemispheres linked to an increasing abundance, related to expansion of the OMZ (Caddy & Rodhouse 1998, Zeidberg & Robinson 2007, Keyl et al. 2008, Bograd et al. 2008). Moreover, the removal of top predators may have promoted *D. gigas* population increase by relaxing competition for their shared prey species and may have reduced the mortality due to predation of juvenile squids (Zeidberg & Robinson 2007).

Genetic studies on jumbo squid revealed an absence of structuring at small distances (< 5000 km) and isolation at larger distances (> 5000 km) along Pacific Ocean (see review in Ibáñez et al. 2015). This pattern has been associated to their biological characteristics (e.g., horizontal migrations, dispersive egg masses and paralarvae) (Ibáñez et al. 2011).

This report is based on an exhaustive review of all literature available in relation to genetics studies of jumbo squids. This review is divided on: a) molecular markers, b) genetic diversity, c) population structure and d) demographic history.

Molecular markers

Most genetic studies in jumbo squid used mitochondrial DNA (Table 1). Among the different genes used, Cytochrome oxidase I (COI) is the more frequent, followed by Cytochrome b (Cyt b) and NADH dehydrogenase subunit 2 (ND2). Mitochondrial genes are important to coalescent inference since they have female heredity. For this reason, are useful to infer the Most Common Recent Ancestor (MCRA), expansion dates and divergence between lineages.

Molecular markers of high resolution like microsatellites and Single Nucleotide Polymorphisms (SNPs) are useful for recent changes in Effective population size (N_e) and population structuring. In jumbo squid only a few microsatellites have been used and resulted in similar evidence for population structure in South Pacific (Sánchez et al. 2016).

Genetic diversity

Thus far all studies conducted are consistent in the sense that low overall genetic diversity was found (Table 1), giving evidence to suggest that there has been a demographic expansion between the last glacial period and the present interglacial (Sandoval-Castellanos et al., 2010; Ibáñez et al., 2011).

Population structure

Studies at the intra-specific level suggest that there are two genetic units, one in the Northern Hemisphere (Mexico-USA) and the other in the Southern Hemisphere (Peru-Chile), which are explained by the isolation by distance model (Sandoval-Castellanos et al., 2007, 2010; Staaf et al., 2010). Some studies using the Cytochrome b mitochondrial gene (Cyt b) and RAPDs have found genetic differences between squids caught in Peru versus those caught in Chile (Sandoval-Castellanos et al., 2007, 2010). Conversely, using sequences of mitochondrial genes (COI, ND2) and microsatellites, there is evidence of high gene flow between populations in Chile and Peru (Ibáñez et al., 2011; Ibáñez & Poulin, 2014; Sánchez et al. 2016).

Demographic history

The historical fluctuations in the distribution range and population size of jumbo squid populations may be related to historical variation in productivity along the Pacific Ocean (Ibáñez et al., 2011; Ibáñez & Poulin, 2014). The divergence of the northern and southern populations of *D. gigas* along the Pacific coast is estimated to have been 39,000 years ago (Staaf et al., 2010). Demographic coalescent analyses indicated that southern population growth initiated approximately 25,000 years ago (Ibáñez et al. 2011, Ibáñez & Poulin 2014).

DISCUSSION

Population structure

Most of reviewed studies suggest that *Dosidicus gigas* consists of two populations corresponding to northern (Canada, USA and Mexico) and southern (Peru and Chile) hemispheres (Sandoval-Castellanos et al. 2007, 2010, Staaf et al. 2010). In both hemispheres each population have high

gene flow along their distribution. This absence of genetic structure inside each hemisphere is consistent with the life history of these species, especially with their high dispersal or migration capacities (long-lived planktotrophic larvae or migratory behavior). In the case of *D. gigas*, extensive seasonal active migrations up to 1,000 kilometers have been related to active feeding, migration and maturation (Nesis 1970, Nigmatullin et al. 2001, Ibáñez & Cubillos 2007, Keyl et al. 2008, Ibáñez et al. 2015). These squids can move at a speed of eight to 30 kilometers per day during their migrations, moving up to 200 km in seven days (Markaida et al. 2005, Gilly et al. 2006b). Furthermore, passive migrations of pelagic egg masses and paralarvae may contribute to high gene flow and long-distance dispersal along its distribution range.

Demographic history

Theoretically, a very large population size should maintain high levels of genetic variability because genetic drift is low and the rate of accumulation of mutations is high. Even though *D. gigas* has a very large population size, it exhibits low diversity of the mtDNA (Sandoval-Castellanos et al. 2010, Ibáñez et al. 2011). In addition to low haplotype diversity, *D. gigas* shows a star-like network characterized by very short branches as well as a marked L-shaped distribution of pairwise differences (Sandoval-Castellanos et al. 2010, Ibáñez et al. 2011). These results, together with the low diversity of nucDNA (RAPDs, microsatellites) support the scenario of a recent demographic expansion over the selective sweep hypothesis around 25,000 years ago. The estimated time of population growth coincides roughly with the rise in sea surface temperature and the reorganization of the OMZ in the last 30,000 years (Beaufort et al. 2001, Feldberg & Mix 2003, Kaiser et al. 2005, Montecino & Lange 2009) probably associated with the glacial-interglacial transition and may have been coupled with a latitudinal range expansion when the environmental conditions became more favorable for this species. The similarity in the genetic diversity pattern in both hemispheres may reflect a global impact of climatic changes in both HCS and CCS related to glacial and interglacial episodes (Herbert et al. 2001, Montecino & Lange 2009). However, such events should have affected both systems separately, generating regional population increases that could explain the shape of the global network shown by Sandoval-Castellanos et al. (2010) compared with Ibáñez et al. (2011).

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Table 1. Genetic studies on jumbo squid from Pacific Ocean.

Location	Markers	Diversity	Structure	References
Pacific Ocean (Costa Rica, Peru)	mtDNA (16S rRNA)	Low	2 units	Wada et al. 2005
Pacific Ocean (Mexico, Peru, Chile)	RAPDs	Low	2 units	Sandoval-Castellanos et al. 2007
Pacific Ocean (Mexico, Peru)	mtDNA (Cytb) & RAPDs	Low	NA	Sandoval-Castellanos et al. 2009
Pacific Ocean (Mexico, Peru, Chile)	mtDNA (Cytb)	Low	2 units	Sandoval-Castellanos et al. 2010
Pacific Ocean (Canada, USA, Mexico, Costa Rica, Peru, Chile)	mtDNA (COI, ND2)	High	2 units	Staff et al. 2010
South Pacific (Peru, Chile)	mtDNA (COI)	Low	1 unit	Ibáñez et al. 2011
South Pacific (Peru, Chile)	mtDNA (COI)	Low	1 unit	Ibáñez & Poulin 2014
South Pacific	Microsatellites	NA	NA	Liu et al. 2014
South Pacific (Peru, Chile)	mtDNA (ND2) & Microsatellites	Low	1 unit	Sánchez et al. 2016