

Genetic structure and diversity of squids with contrasting life histories in the Humboldt Current System

Estructura y diversidad genética de calamares con historias de vida contrastantes en el Sistema de Corrientes de Humboldt

Christian Marcelo Ibáñez and Elie Poulin

Instituto de Ecología y Biodiversidad, Departamento de Ciencias Ecológicas, Facultad de Ciencias,
Universidad de Chile. Las Palmeras # 3425, Ñuñoa. Chile
e-mail: ibanez.christian@gmail.com

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ABSTRACT

Dosidiscus gigas and *Doryteuthis gahi* are the most abundant squids in the Humboldt Current System (HCS). These species have contrasting life histories. To determine the genetic structure and diversity of these species, we collected samples from different places in the HCS and amplified a fragment of the mitochondrial cytochrome C oxidase I gene. The molecular analysis of *D. gigas* revealed low genetic diversity, absence of population structure and evidence for a demographic expansion during the transition from the last glacial period to the current interglacial. These results suggest that *D. gigas* is composed of one large population with high levels of gene flow throughout the HCS. In the case of *D. gahi*, the sequences indicated the presence of two population units in the HCS, one in south-central Chile and one in Peru. The Chilean unit had greater genetic diversity, suggesting that it is an old, relatively stable population. In the Peruvian unit there was less genetic diversity and evidence of a recent demographic expansion. The changes in distribution ranges and population sizes of the squid populations may be related to historical variations in productivity along the HCS. The different dispersion and migration capacities of these species may explain the differences in their structure; however, the genetic diversity of both species appears to be more related to historical variations in their distribution ranges and the biogeographic origin of each.

Key words: Genetic diversity, life histories, population structure, squids.

RESUMEN

Dosidiscus gigas y *Doryteuthis gahi* corresponden a los calamares más abundantes en el Sistema de la Corriente de Humboldt (SCH). Estas especies se caracterizan por tener historias de vida contrastantes. Para determinar la estructura y diversidad genética de ambas especies, se recolectaron muestras de diferentes lugares de SCH, y se amplificó un fragmento del gen mitocondrial citocromo c oxidasa I. Los análisis moleculares de *D. gigas* mostraron una baja diversidad genética, una ausencia de estructura poblacional y la evidencia de expansión demográfica durante la transición entre el último periodo glacial y el actual interglacial. Estos resultados sugieren que *D. gigas* corresponde a una única población caracterizada por alto flujo genético. En el caso de *D. gahi*, las secuencias revelaron la presencia de dos unidades poblacionales correspondientes al centro-sur de Chile y Perú. La unidad chilena mostró niveles más altos de diversidad, lo que sugiere que corresponde a una población antigua y estable. En la unidad peruana se detectó una menor diversidad genética y la evidencia de una reciente expansión demográfica. Los cambios de distribución y

abundancia de los calamares podrían estar relacionados a las variaciones históricas de la productividad. Las capacidades diferenciales de dispersión y migración de las dos especies podrían explicar las diferencias en estructura. Sin embargo, la diversidad genética de ambas especies parece relacionarse más con las variaciones históricas de sus rangos de distribución y del origen biogeográfico de cada una de ellas.

Palabras claves: Calamares, diversidad genética, estructura poblacional, historias de vida.

INTRODUCTION

The biological and ecological characteristics of organisms affect their dispersal ability and the amount of gene flow among their populations. Thus it is expected that species with little mobility will form genetically distinct populations, while more mobile species will maintain a genetic homogeneity by means of greater gene flow (Futuyma, 2009). However, sessile organisms and those with little vagility have other strategies which allow them to colonize distant sites (e.g., propagules, larvae, spores, seeds; Kinlan & Gaines, 2003; Cowen & Sponaugle, 2009). In the marine environment, invertebrates have a great diversity of life history strategies compared to terrestrial animals (Strathmann, 1990), which is a determining factor in geographic connectivity and genetic diversity. For example, gastropod species with planktonic larvae show lower levels of genetic structure and have greater diversity than those species with direct development (Kyle & Boulding, 2000; Johnson & Black, 2006; Lee & Boulding, 2009). However, this relationship between dispersal capacity and gene flow does not always hold, and oceanographic factors have been described as limiting for the dispersion of larvae or adults (Poulin *et al.*, 2002; Barber *et al.*, 2002). The geographic structure of genetic diversity may reflect historical processes generally associated with geographic breaks, as well as contemporary processes linked to the dispersal capacity of a species (Avice, 2000; Pecl *et al.*, 2009).

There are few studies of the genetic structure of the marine organisms of the Humboldt Current System (HCS). For species with a long-lived planktonic larvae (several weeks) such as the crab *Cancer setosus* (Molina, 1782), the gastropod *Concholepas concholepas* (Bruguère, 1789) and the squat lobster *Pleuroncodes monodon* (H. Milne Edwards, 1837), no spatial genetic structure was detected over at least 2000 km of the coast (Gomez-Uchida *et al.*, 2003; Cárdenas *et al.*, 2009a; Haye *et al.*, 2010). A similar result was found for fishes with a wide geographic range and long larval duration (several weeks) such as the Chilean hake *Merluccius gayi* (Guichenot, 1848) and the jack mackerel *Trachurus murphyi* Nichols, 1920 (Galleguillos *et al.*, 2000; Cárdenas *et al.*, 2009b). By contrast, the seaweeds *Lessonia nigrescens* Bory and *Mazzaella laminarioides* (Bory de Saint-Vincent) Fredericq and the gastropods *Chorus giganteus* (Lesson, 1831) and *Acanthina monodon* (Pallas, 1774) have a significant geographic structure associated with their reduced dispersal potential ($F_{ST} = 0.14-0.99$, Faugeron *et al.*, 2001; Gajardo *et al.*, 2002; Faugeron *et al.*, 2005; Tellier *et al.*, 2009; Sánchez *et al.*, 2011). These studies have all dealt with

individual species; there have been no comparative studies of sympatric taxa with different life history characters that share the same ecosystem in the HCS. Also, there is no information on the genetic structure of a number of important groups in the HCS such as echinoderms, polychaetes and cephalopods.

Within the cephalopods, the squids are a fundamental component of the pelagic ecosystems, due both to their abundance and their trophic role (Boyle & Rodhouse 2005; Thiel *et al.*, 2007). They are also interesting study models in population genetics and phylogeny because of their short life cycles, wide geographic ranges and contrasting life histories (Boyle & Rodhouse, 2005). The most common and abundant squids in the HCS are *Dosidicus gigas* (d'Orbigny, 1835) (Ommastrephidae) and *Doryteuthis gahi* (d'Orbigny, 1835) (Loliginidae). These species have contrasting body sizes, habitat use, migration patterns and reproductive strategies. In the case of *D. gigas*, its great dispersal potential associated with its large body size (> 2 m total length) and excellent swimming capacity (> 20 km/h) allows it to migrate actively distances of more than 1,000 km in the HCS, both in latitude and longitude (Nesis, 1970; Nigmatullin *et al.*, 2001; Ibáñez & Cubillos, 2007). Also, *D. gigas* spawns a large gelatinous mass of millions of eggs in the pelagic environment, which may be transported passively by currents to very distant places (Staaft *et al.*, 2008). Like other ommastrephids, *D. gigas* has a short embryonic development (around 6-9 days, Yatsu *et al.*, 1999). In contrast, *D. gahi* has a small body size (< 50 cm total length), and due to its reduced home range (continental shelf) only makes ontogenetic vertical migrations (Arkhipkin *et al.*, 2004). Additionally, *D. gahi* spawns on the bottom near the coast, capsules with hundreds of eggs which adhere to seaweeds or soft corals (Arkhipkin *et al.*, 2000; Villegas, 2001). Their embryonic development is completed in around 30 – 35 days (Guerra *et al.* 2001), a contrasting strategy compared to *D. gigas*. These differences between *D. gahi* and *D. gigas* could have consequences on their respective dispersal potentials, since only the paralarvae of the loliginids can contribute to passive dispersal, while both eggs and paralarvae of the ommastrephids may be transported by marine currents passively over 600 km from the spawning grounds (Bower, 1996; Boyle & Rodhouse, 2005). This information on the life history of the two squids allows predictions to be made about their spatial structure and genetic diversity. We hypothesize that the squids *Dosidicus gigas* and *Doryteuthis gahi* should have different patterns of spatial genetic structure in the Humboldt Current System, given their different life history strategies and migration patterns. *D. gigas* should show an absence of

population genetic structure as a consequence of its large migrations and pelagic spawning, while *D. gahi* should have a population genetic structure associated with its lower dispersal capacity and benthic spawning.

MATERIALS AND METHODS

This study is based upon data already published by Ibáñez *et al.* (2011, 2012), but here reanalyzed in a comparative context; thus the methodological details related to standardized laboratory protocols may be found in these publications. In summary, we collected between 23 and 33 tissue samples of the squids *Dosidicus gigas* and *Doryteuthis gahi* from several localities of Peru and Chile between 2005 and 2008 (Ibáñez *et al.*, 2011, 2012) (Table 1, Fig. 1) and sequenced the mitochondrial Cytochrome Oxidase I gene (COI).

To detect population structure in the squid species we estimated the number of clusters (k) and the posterior probability density (PPD) of belonging to a given cluster by means of Bayesian inference, in the software Geneland (Guillot *et al.* 2005), implemented in R software. We inferred the number of clusters from the modal value of k , running a Markov Chain Monte Carlo (MCMC) with 5×10^6 iterations, sampling parameters every 1000 iterations. After these runs we burn-in 500 resultant parameters in order to obtain posterior probabilities of population membership for each individual and each spatial domain. Each analysis was run 4 times to check the congruence. Additionally, to compare the levels of population structure in the squid species we calculated the F_{ST} index for each pair of localities using Arlequin version 3.11 (Excoffier *et al.*, 2005). Haplotype number and haplotype diversity (Hd) were calculated using Arlequin for each species and location.

Table 1. Sample size and haplotype diversity of the squids *Doryteuthis gahi* and *Dosidicus gigas*.

Species/location	N	Haplotype diversity	Number of haplotypes
<i>Dosidicus gigas</i>	169	0.370	23
Huarmey	27	0.342	6
Callao	33	0.544	8
Coquimbo	29	0.430	8
Valparaiso	28	0.206	4
Santa Maria	29	0.320	6
Isla Mocha	23	0.324	5
<i>Doryteuthis gahi</i>	116	0.730	15
Paita	26	0.508	5
Chimbote	32	0.343	6
Talcahuano	27	0.809	5
Chiloe	31	0.755	5

Finally, we inferred the demographic history of both squids from the HCS using Bayesian skyride (Minin *et al.*, 2008) analyses implemented in BEAST version 1.7.2 (Drummond *et al.* 2012). The Bayesian skyride uses Gaussian Markov random fields to achieve temporal smoothing of the effective population size (N_e) by means of a MCMC sampling of sequence data, to estimate a posterior distribution of N_e through time and its highest posterior density intervals (95% HPD) (Minin *et al.*, 2008). Bayesian skyride analyses were run using the Hasegawa–Kishino–Yano substitution model (HKY85), which was identified as the best fitting model by Bayesian decision criteria implemented in jModelTest (Posada, 2008). The relaxed molecular clock with uncorrelated exponential distribution was the model used. In this set of runs, the mean mutation rate was set with a prior normal distribution (0.02×10^{-6} , 10% SD). We ran 20×10^6 iterations, sampling every 1000 generations, while the first 10% were discarded as burn in. The Bayesian skyride plots were generated with the program Tracer version 1.5 (Rambaut & Drummond, 2009).

RESULTS

The Bayesian analysis of genetic structure georeferenced showed a maximum posterior probability of one group or population ($K = 1$) which is constituted *D. gigas* along its distribution range (Fig. 2a). This mean that the spatial configuration of the posterior probability map is constituted by individuals assigned to no more of one cluster (Fig. 2b), because this squids do not have spatial population structure. In the case of *D. gahi* the mode of number of clusters showed two genetic units in the HCS ($k = 2$, Fig. 3a). These units are located in Peru ($PP = 0.9$) and Southern Chile ($PP = 0.9$) (Fig. 3b). These results confirm the absence of geographic structure in *D. gigas* (Fig. 2), while in *D. gahi* the analysis showed two populations, corresponding to the Peruvian and Chilean locations (Fig. 3). The F_{ST} values of *D. gahi* (mean = 0.199 ± 0.15) were several orders of magnitude greater than in *D. gigas* (mean = 0.000261 ± 0.02).

A total of 15 haplotypes were found in the 683 bp fragment of COI among the 116 individuals of *D. gahi* examined, while in *D. gigas* there were 23 haplotypes in the 657 pb fragment of COI in the 169 individuals examined. The number of haplotypes in each location was similar, ranging between 4 and 8 (Table 1). The haplotype diversity of *D. gahi* was lower in the northern Humboldt ($Hd = 0.34-0.50$) than in the southern Humboldt ($Hd = 0.75-0.80$). For *D. gigas* the genetic diversity was low in all locations ($Hd = 0.20-0.54$) (Table 1). In general the haplotype diversity was greater in *D. gahi* than in *D. gigas* (Table 1).

Bayesian skyride analyses indicated that population growth of *D. gigas* initiated approximately 37,000 years ago in the HCS, increasing mean population size from around 10,000 individuals to a mean of 2 million individuals (Fig. 4). The mean Time to the Most Recent Common Ancestor (TMRCA) was estimated

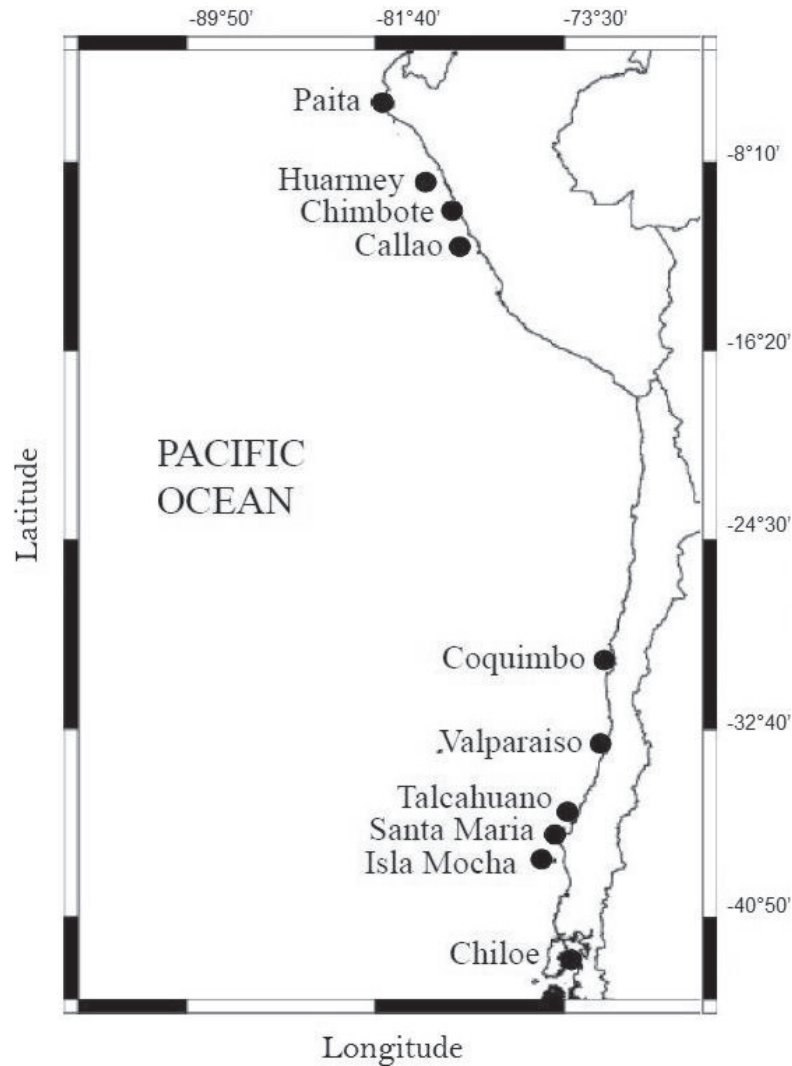


Figure 1. Map showing sampling locations of *Dosidicus gigas* and *Doryteuthis gahi* in the Humboldt Current System.

at 37,136 years ago (95% HPD 29,843 to 44,734 years). Bayesian skyride analyses of the Peruvian population of *D. gahi* indicated that population growth initiated approximately 35,000 years ago in the northern HCS and the mean time of TMRCA was estimated at 38,620 years (HPD 95% 30,762–45,995 years). The effective population size increased from 10,000 to 1,000,000 individuals in the last 35,000 years (Fig. 5a). The Chilean population showed a low increase of population size through time in the southern HCS from a mean population size of 10,000 to 100,000 individuals (Figure 5b). In this population the TMRCA was estimated at 96,956 years (HPD 95% 77,021–116,400 years).

DISCUSSION

This study found contrasting patterns of genetic structure in the two species. The neritic squid *D. gahi* had high values of genetic differentiation between populations collected in south-central

Chile and Peru (> 2,500 km), while *D. gigas* showed low values of structure in these same zones. However, both species showed an absence of genetic differentiation within the geographic zones (<1,000 km).

These results corroborate previous studies in these two squid families. The majority of the species of ommastrephids show an absence of genetic structure at scales of thousands of kilometers in the same biogeographic zone (e.g., Adcock *et al.*, 1999; Sandoval-Castellanos *et al.*, 2007, 2010; Ibáñez *et al.*, 2011). For these species, only major biogeographical breaks on the order of 10,000 km appear to be able to generate a spatial structure in their genetic diversity (e.g. Brierley *et al.*, 1993; Aoki *et al.*, 2008; Katugin, 2002; Sandoval-Castellanos *et al.*, 2007, 2010). In contrast, loliginid squids generally show genetic structure at a smaller geographic scale and appear to be influenced by local barriers such as the mouths of large rivers or abrupt changes in the sea floor (Brierley

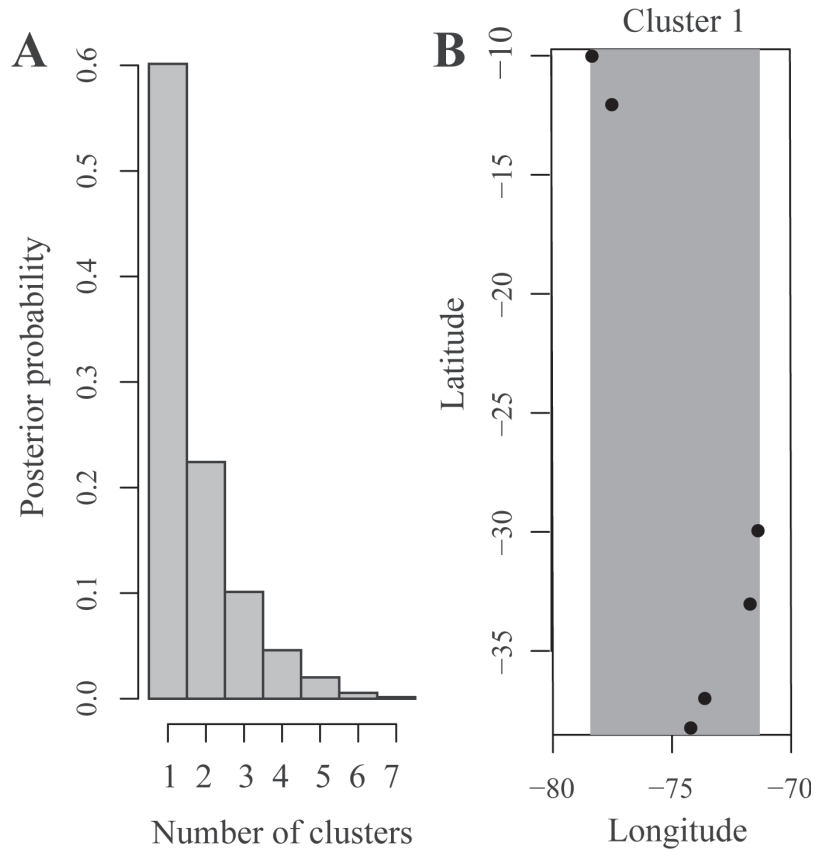


Figure 2a-b. *Dosidicus gigas*. a) Posterior probability density histogram, b) Spatial posterior probability of belonging to a cluster.

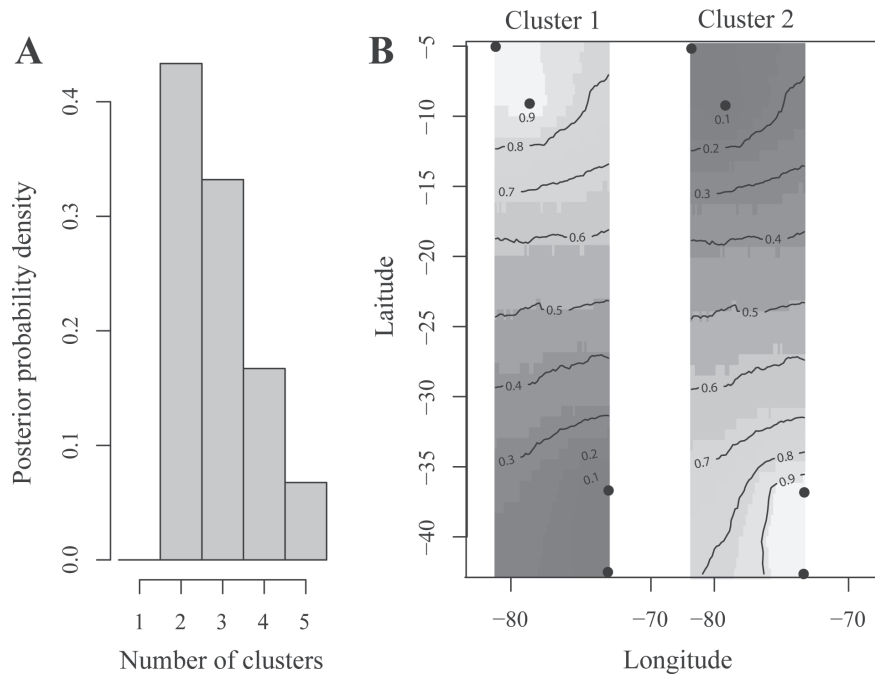


Figure 3a-b. *Doryteuthis gahi*. a) Posterior probability density histogram, b) Spatial posterior probability of belonging to a cluster.

et al., 1995; Shaw *et al.*, 1999; Herke & Foltz, 2002; Semmens *et al.*, 2007). In the absence of such barriers, these species are genetically homogenous up to a scale of hundreds of kilometers (e.g. Carvalho & Loney, 1989; Brierley *et al.*, 1995; Reichow & Smith, 2001; Shaw *et al.*, 2004; Buresch *et al.*, 2006; Shaw *et al.*, 2010).

This difference in patterns of genetic structure at the family level may be the consequence of the different life history strategies which characterize them, in particular those elements related to the dispersal potential of individuals (Shaw *et al.* 2010). The ommastrephids, which have little genetic structuring, are characterized by pelagic spawning and long migrations. According to the classification proposed by Rocha *et al.* (2001), the squids of the family Ommastrephidae are essentially monocyclic (animals reproduce once and then die), and some species such as *D. gigas* may spawn in batches (repeatedly). By contrast, squids of the family Loliginidae such as *D. gahi* have terminal spawning. Loliginid squids are neritic and spawn on the ocean floor, depositing their eggs in seaweeds or soft corals, while ommastrephids are oceanic and spawn masses of pelagic eggs (O'Dor, 1998).

Just as proposed in the literature (Boyle & Rodhouse, 2005; Shaw *et al.* 2010), these different life history strategies appear to have direct consequences on the patterns of gene flow and thus on the spatial structuring of the genetic diversity of these squids.

In terms of genetic diversity, both species had low numbers of recovered haplotypes, both in the northern and southern zones of the HCS. However, there were clear differences in the patterns of haplotype diversity (Hd) between the species, as well as between geographic zones within each species. Low levels of genetic diversity generally occur in populations that have undergone drastic fluctuations in population sizes, bottlenecks or founder

events, while high levels of genetic diversity are indicative of population stability or metapopulation dynamics (Grant & Bowen, 1998; Carvalho & Nigmatullin, 1998; Hoelzel, 1999; Lecomte *et al.*, 2004; Freeland, 2005). The spatial variation in Hd observed in this study may thus be related to past climatic changes in each geographic area and the way each species has responded locally, as the demographic analysis showed.

In the case of *D. gigas*, although there was low genetic diversity both in Peru and in Chile, the locations of the northern HCS had more diversity compared to the south. This low diversity, decreasing towards the south, may be due to a recent demographic expansion inferred by demographic analysis. Although the evidence at an ecological time scale shows latitudinal variations of *D. gigas*, usually attributed to El Niño Southern Oscillation (ENSO) or the Pacific Decadal Oscillation (PDO) (Keyl *et al.*, 2008), the genetic evidence shows signs of an older demographic process (37,000 years), probably linked to the drastic variations in the productivity of the eastern Pacific during the last glacial cycle (Hebbeln *et al.*, 2002). Based on our results we propose that *D. gigas* extended its distribution range towards the south during the transition between the last glacial maximum and the current interglacial period when the environmental conditions were more favorable. A similar phenomenon appears to have occurred in the California Current, in which its distribution was extended to more northern latitudes (Key *et al.*, 2008). In fact, 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).

The demographic history of *D. gahi* appears to have followed a completely different trajectory. In contrast to *D. gigas*, the high-

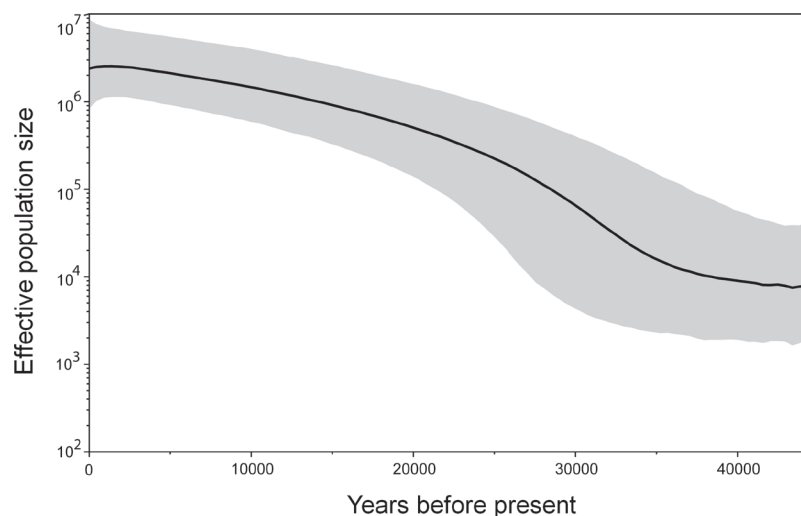


Figure 4. Bayesian skyride plot of *Dosidicus gigas* in the Humboldt Current System. Population size on the y-axis is given on a logarithmic scale. The thick solid line represents the mean estimate of population size; the grey area shows the 95% highest posterior density intervals.

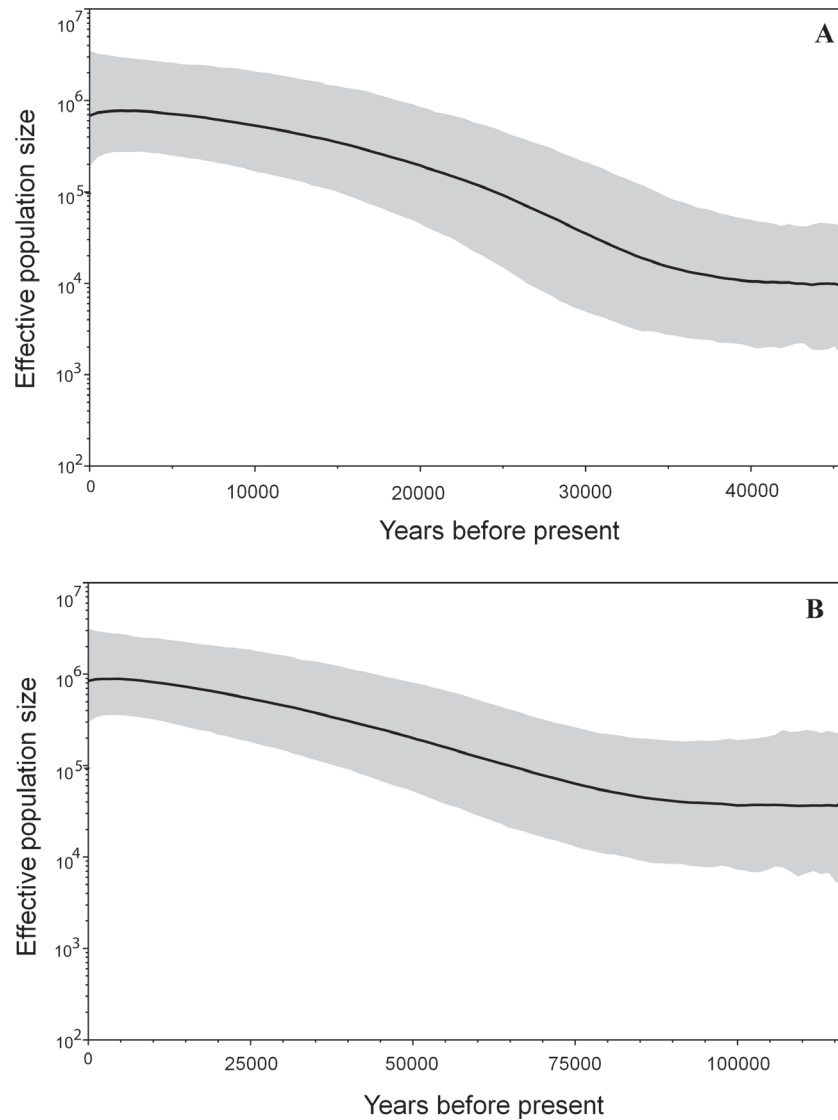


Figure 5a-b. Bayesian skyride plot of *Doryteuthis gahi* in the Humboldt Current System. Population size on the y-axis is given on a logarithmic scale. The thick solid line represents the mean estimate of population size; the grey area shows the 95% highest posterior density intervals. a) Peruvian population, b) Chilean population.

est diversity values were found in the southern HCS; only the population of Peru showed signals of a recent population expansion around 35,000 years ago. The greater genetic diversity and the low population growth estimated by demographic analysis in the southern HCS suggest that this population of *D. gahi* did not undergo major demographic fluctuations during the last glacial cycle. On the contrary, we suggest that it increased northward from the south of the South American continent to the northern zone of the HCS at the end of the last glacial period around 40,000 years ago when environmental conditions were more favorable.

The patterns of genetic diversity and effective population sizes do not appear to be linked to the life history strategies of these squids, and may reflect past demographic processes associated

with climatic changes over long time scales. However, these two species showed different responses to the changes which characterized the transition from the last glacial period to the current interglacial period. Changes in the productivity of the HCS over the last 30,000 years may be associated with the northward movement and intensification of the winds from the west which control the upwellings and practically all the climate in these latitudes (Lamy *et al.*, 1999; Hebbeln *et al.*, 2002). These environmental fluctuations may be responsible for the changes in the distribution and abundance of marine populations in the past, and the current observed patterns of genetic diversity are the result of processes of demographic expansion or bottlenecks inferred by means of the events of coalescence in the genetic lineages.

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