

Genetic diversity and demographic history of *Dosidicus gigas* (Cephalopoda: Ommastrephidae) in the Humboldt Current System

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ABSTRACT: During the late Pleistocene-Holocene, the Humboldt Current System (HCS, Peru-Chile) was subject to important oceanographic variations that may have affected the abundance and distribution of marine populations, as well as their genetic structure and diversity. The fast growth and short life span of jumbo squid *Dosidicus gigas* make this squid a valuable model organism for evaluating how environmental fluctuations affect the genetic diversity of marine populations. We sequenced a 657 bp fragment of the mtDNA cytochrome *c* oxidase I (COI) gene of 169 jumbo squids from 6 locations in the HCS. We measured and compared genetic diversity among localities and performed neutrality tests to detect deviation from mutation-drift equilibrium. We inferred the demographic history of jumbo squids using Bayesian skyline analyses to estimate effective population size through time. A total of 23 haplotypes were found among the sequences. Haplotype and nucleotide diversity were low in all locations. *D. gigas* was characterized by an absence of population genetic structure and a star-like haplotype network. Neutrality test values were negative and statistically significant, and therefore consistent with a past population expansion. Similarly, Bayesian skyline analyses indicated a recent demographic expansion after the last glacial maximum. Our results suggest that *D. gigas* consists of a single, large population in the HCS, that may have experienced a dramatic demographic population expansion consistent with the oceanographic changes associated with the last glacial–interglacial transition.

KEY WORDS: COI · Jumbo squid · Population genetics · Expansion · Coalescent

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INTRODUCTION

The Humboldt Current System (HCS) is one of the most productive marine ecosystems on earth (Thiel et al. 2007). The general oceanography of the HCS is characterized by a predominant northward flow of surface waters of subantarctic origin and by strong upwelling of cool, nutrient-rich water. This upwelling results in a shallow Oxygen Minimum Zone (OMZ), especially in

the northern part of the HCS (Montecino et al. 2005, Thiel et al. 2007, Chavez et al. 2008, Montecino & Lange 2009). In this ecosystem, the principal marine resources (fishes, invertebrates and algae) show periodic changes associated with events at different time scales such as the El Niño Southern Oscillation cycles (ENSO), the Pacific-Decadal Oscillation (PDO) and beyond at millennial scales (Castilla & Camus 1992, Anderson & Rodhouse 2001, Arcos et al. 2001, Cubillos & Arcos

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2002, Chavez et al. 2003, Waluda et al. 2006, Thiel et al. 2007, Chavez et al. 2008). All these events result in similar correlated changes between sea-surface temperature variation, wind force intensity, productivity and geographic extension of the OMZ. These oceanographic changes increase in intensity from short to long time scales, from ENSO to PDO, stadial or interstadial, up to glacial and interglacial variations (Stott et al. 2002, Chavez et al. 2008). For instance, the HCS is less intense and northward surface water flows closer to the coast during interglacial episodes than during glacial periods (Molina-Cruz & Herguera 2002). Similarly, the bathymetric extension of the OMZ may contract during cool periods (glacial periods and stadials) and extend during warm ones (Holocene and interstadials) as proposed for the California Current System (CCS) (Cannariato & Kennett 1999). During the last 100 000 yr, primary productivity has varied with the precessional cycle (~20 000 yr) while sea-surface temperature exhibited large amplitude variation related to glacial-interglacial periods (Beaufort et al. 2001, Hebbeln et al. 2002, Feldberg & Mix 2003, Kaiser et al. 2005, Montecino & Lange 2009). In these highly variable environments, fluctuations in abundance and distribution of marine populations could impose distinctive genetic signatures on structure and diversity (Grant & Bowen 1998, Avise 2000, Lecomte et al. 2004, Hewitt 2004, Cárdenas et al. 2009a).

Cephalopods are characterized by fast growth, early maturity, high fertility, short life span and high variability in life history strategies (Boyle & Boletzky 1996). Such characteristics make cephalopod populations sensitive to environmental fluctuations; thus their abundance tends to fluctuate more than that of long-lived, slow growing species. Migration patterns, population size and geographic distribution of cephalopods are particularly susceptible to changes in oceanographic conditions (Anderson & Rodhouse 2001, Boyle & Rodhouse 2005, Dawe et al. 2007, Semmens et al. 2007). The jumbo squid *Dosidicus gigas* (d'Orbigny, 1835) is the most abundant squid in the HCS. The life span of *D. gigas* is about 1 yr, but the largest individuals can probably live for 3 yr, reaching up to 120 cm mantle length and 3 m total length (Roper et al. 1984, Nigmatullin et al. 2001, Keyl et al. 2011). This squid reaches velocities up to 20 km h⁻¹ during massive migrations of adults (Nesis 1970, Nigmatullin et al. 2001, Gilly et al. 2006b). It is a monocyclic species; it dies after one reproductive cycle (Rocha et al. 2001, Tafur et al. 2010). During the reproductive cycle, female jumbo squids undergo 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 to 4 m diameter) near the surface, embedded in a gelatinous

matrix and containing 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 3 to 10 d as a paralarva (Yatsu et al. 1999, Staaf et al. 2008), a life stage very similar to the subsequent adult stage. These characteristics of the early life stages may be related to a possible passive dispersal of this species.

In the HCS, *Dosidicus gigas* exhibits sporadic and short-term pulses in abundance related to environmental changes and recruitment patterns (e.g. ENSO) (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 and related to an expansion of the OMZ (Caddy & Rodhouse 1998, Zeidberg & Robison 2007, Bograd et al. 2008, Keyl et al. 2008). Moreover, the removal of top predators may have promoted the population increase of *D. gigas* by relaxing competition for their shared prey species, and by reducing mortality due to predation of juvenile squids (Zeidberg & Robison 2007).

The fast growth and short life span strategy of *Dosidicus gigas*, and evidence of temporal fluctuations in abundance, make this species a valuable model organism for evaluating how environmental fluctuations affect genetic diversity in marine populations, using the coalescent approach with a non-recombinant mtDNA marker. We predicted that (1) *D. gigas* should not exhibit any population genetic structure in the HCS due to its characteristic life history and ecology (e.g. pelagic eggs, active migrations), as has been found in other marine species with high dispersal capacity (Cárdenas et al. 2009a,b, Haye et al. 2010); and that (2) the *D. gigas* population should exhibit low genetic diversity after experiencing drastic fluctuations in distribution and abundance possibly associated with past oceanographic changes in the HCS.

MATERIALS AND METHODS

Sampling. Tissue samples from the mantle were collected from jumbo squids from 2 locations in Peru and 4 locations in Chile between 2005 and 2008 (Table 1, Fig. 1). Samples from Peru were taken from research cruises of the Instituto del Mar del Perú (IMARPE); mantle length ranged from 130 to 200 mm. The Chilean samples were obtained from artisanal fisheries dedicated to jumbo squid and as by-catch from the industrial mid-trawl fishery of Chilean hake *Merluccius gayi gayi*. Squids from these fisheries were adult individuals ranging from 400 to 700 mm mantle length.

DNA extraction and amplification. Total DNA was extracted following the saline extraction protocol (Aljanabi & Martinez 1997). We used the universal

Table 1. *Dosidicus gigas*. Sample size (N) and genetic diversity indexes of jumbo squid from the Humboldt Current System: (H) number of haplotypes, (S) number of polymorphic sites, (Hd) haplotype diversity, (π) nucleotide diversity, (Π) mean number of pairwise differences

Location	Coordinates	N	H	S	Hd	π	Π
Huarmey	10° 00'S, 73° 50'W	27	6	7	0.342	0.00079	0.519
Callao	12° 05'S, 77° 42'W	33	8	9	0.544	0.00120	0.848
Coquimbo	29° 57'S, 71° 22'W	29	8	7	0.430	0.00091	0.613
Valparaiso	33° 00'S, 71° 43'W	28	4	4	0.206	0.00043	0.286
Santa Maria	37° 00'S, 73° 35'W	29	6	5	0.320	0.00062	0.409
Isla Mocha	38° 23'S, 74° 04'W	23	5	5	0.324	0.00066	0.435
Total		169	23	24	0.370	0.00082	0.536

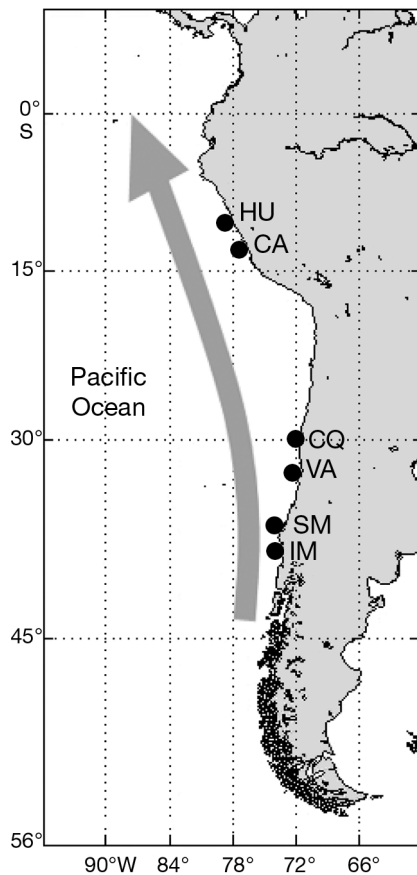


Fig. 1. The Humboldt Current System (grey arrow) and the 6 sampling sites: 2 in Peru, Huarmey (HU), Callao (CA); 4 in Chile, Coquimbo (CQ), Valparaiso (VA), Santa Maria (SM) and Isla Mocha (IM)

primers designed by Folmer et al. (1994) to amplify the mitochondrial cytochrome *c* oxidase I (COI) gene. PCR amplifications were carried out using, for each sample: 0.3 μ l of *Taq* DNA polymerase (1.5 units) and 2.5 μ l 10 \times (50 mM KCl, 10 mM Tris-HCl, pH 8.0) commercially supplied buffer, with 2 μ l deoxynucleoside triphosphates (dNTPs, 10 μ M), 1.0 μ l 50 mM MgCl₂, and 0.5 μ l (10 pg μ l⁻¹) of each primer (LCO1490 and HCO2198).

After an initial denaturation (3 min at 94°C), the reaction mixtures were subjected to 35 cycles at 94°C (40 s), 48°C (40 s) and 72°C (60 s) followed by a final extension at 72°C (7 min) using a thermal cycler. PCR products were purified with the Wizard™ Prep system (Promega) following the manufacturer's protocols. Purified PCR products were automatically sequenced (Macrogen Inc.). Sequences were edited and aligned by eye using ProSeq version 2.9 (Filatov 2002).

Population genetic analyses. From the 657 bp COI sequences, standard diversity indices such as the number of haplotypes (H), number of polymorphic sites (S), haplotype diversity (Hd), mean number of pairwise differences (Π), as well as nucleotide diversity (π) were estimated for each location using Arlequin version 3.11 (Excoffier et al. 2005).

The genealogical relationships among haplotypes were assessed with a haplotype network constructed using a median-joining algorithm as implemented in the software Network version 4.501 (Bandelt et al. 1999).

To test for population structure, we calculated pairwise F_{ST} (Wright's fixation index) among sampling locations. Significance of pairwise F_{ST} values was based on 10 000 permutations as implemented in Arlequin. Additionally, to detect geographical structure among samples we performed a spatial analysis of molecular variance (SAMOVA, Dupanloup et al. 2002) using SAMOVA software version 1.01. SAMOVA tests all possible ways to establish groups of populations that maximize the 'among-groups' component of the total genetic variance and reduce the 'among populations within groups' component. Significance of 'among locations' F_{ST} , 'among groups' F_{SC} and 'among locations within group' F_{CT} fixation index values was computed by a non-parametric permutation procedure with 10 000 iterations.

Demographic analyses. Using Arlequin software, we calculated Tajima's D and Fu's F_s indexes and their corresponding p-values to detect departures from Wright-Fisher mutation-drift equilibrium caused by population expansions or bottlenecks under neutrality hypotheses (Tajima 1989, Fu 1995). To further assess demographic change indicated by the mtDNA data, we constructed the mismatch distribution and estimated the parameters of the demographic expansion by a generalized non-linear least-squares approach (Schneider & Excoffier 1999, Excoffier 2004). Using this method we estimated the parameters of demographic expansion Theta Initial (θ_0 , before the population growth or decline), Theta Final (θ_1 , after the population growth or decline) and Tau (τ , the date of the growth or decline) measured in units of mutational time, as follows: θ_0 and

$\theta_1 = 2N_e u$ and $\tau = 2ut$, where N_e is effective population size, u is the mutation rate per sequence per year and t is the time in years. Confidence intervals for these parameters were obtained using a parametric bootstrap approach (Schneider & Excoffier 1999, Excoffier 2004) implemented in Arlequin.

The demographic history of *Dosidicus gigas* from the HCS was also inferred from Bayesian skyline analyses implemented in BEAST version 1.5.4 (Drummond & Rambaut 2007). The Bayesian skyline analysis utilizes Markov Chain Monte Carlo (MCMC) sampling of sequence data to estimate a posterior distribution of effective population size (N_e) through time and their Highest Posterior Density intervals (95% HPD) (Drummond et al. 2005). Bayesian skyline analyses were run using the HKY substitution model, which was identified as the best fitting model by Bayesian Information Criterion (BIC) implemented in jModelTest (Posada 2008) ($-\ln(\text{likelihood}) = 1087.02$, $\text{BIC} = 4379.85$). In this set of runs, the mean mutation rate was set with a prior normal distribution ($0.02 \times 10^{-6} \pm 0.005 \times 10^{-6}$ SD) based on values proposed by Pérez-Losada et al. (2007) for *Sepia officinalis*. The best model of molecular clock evolution (strict or relaxed) was evaluated by comparing Bayes Factors (Suchard et al. 2001). The relaxed molecular clock with uncorrelated exponential distribution was the model that best fitted the data (\log_{10} Bayes Factor = 5.217). The number of grouped intervals (m) was set to 10 and the Bayesian Skyline was performed in the piecewise-constant model. We ran 2 independent runs of 40 million iterations of the MCMC chains, sampling every 1000 generations; the first 2 million chains were discarded as burn-in. Each of the independent log files and tree files was combined using LogCombiner version 1.5.4 (Rambaut & Drummond 2009a), obtaining a chain of 72 000 000 steps. The Bayesian skyline plots were generated with the program Tracer version 1.5 (Rambaut & Drummond 2009b).

RESULTS

Population genetic analysis

A total of 23 haplotypes were found for the 657 bp fragment in the 169 individuals examined. Haplotype and nucleotide diversity were low in all locations (for pooled samples $Hd = 0.37$, $\pi = 0.00082$) (Table 1).

The median-joining network revealed a clear star-like pattern with a dominant central haplotype (H1) and a very short genealogy (Fig. 2). The central haplotype (H1) was the most common and the most widely distributed geographically; the other haplotypes were separated from H1 by one or 2 mutations (Fig. 2). This

network shape was consistent with a population undergoing demographic expansion and lacking genetic population structure (Slatkin & Hudson 1991).

Low and non-significant values of F_{ST} suggested that *Dosidicus gigas* exists as a large and genetically uniform population across all HCS localities sampled (Table 2). The only exception was a significant F_{ST} value for the pairwise comparison between the samples from Callao and Valparaíso (Table 2). This value, however, was not significant at the Bonferroni-corrected level. Moreover, SAMOVA performed for 2 to 5 groups showed low values and non-significant variation among groups (2.28 to 4.60%).

Demographic analysis

Values for Tajima's D and Fu's F_s were negative and significant ($D = -1.95$, $p = 0.0076$; $F_s = -4.23$, $p = 0.001$), and therefore consistent with a past population expansion. The distribution of pairwise differences among sequences was L-shaped, as a consequence of the large majority of individuals sharing the same haplotype (Fig. 3). The mismatch distribution did not differ from expected sudden growth-decline model (Raggedness, $r = 0.17$, $p = 0.64$, Fig. 2). Based on the expected values in growing and declining populations (Schneider & Excoffier 1999), sudden expansion time was estimated at 45 261 yr ago (95% CI = 0 to 86 360 yr). Bayesian skyline analyses indicated that population growth initiated approximately 25 000 yr ago in the HCS, increasing mean population size from around 10 000 individuals to a mean of 5.9 million individuals (95% HPD = 0.44 to 18.8 million) (Fig. 4). The mean Time to the Most Recent Common Ancestor (TMRCA) was estimated at 40 004 yr ago (95% HPD = 31 932 to 48 176 yr).

DISCUSSION

Population genetics

Our results suggest that *Dosidicus gigas* consists of a single population with high gene flow along the HCS, similar to the results reported for the gastropod *Concholepas concholepas*, the squat lobster *Pleuroncodes monodon* and the jack mackerel *Trachurus murphyi* (Cárdenas et al. 2009a,b, Haye et al. 2010). This absence of genetic structure in the HCS 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 in the HCS of up to 1000 km have been related to active feeding, migration and maturation (Nesis 1970,

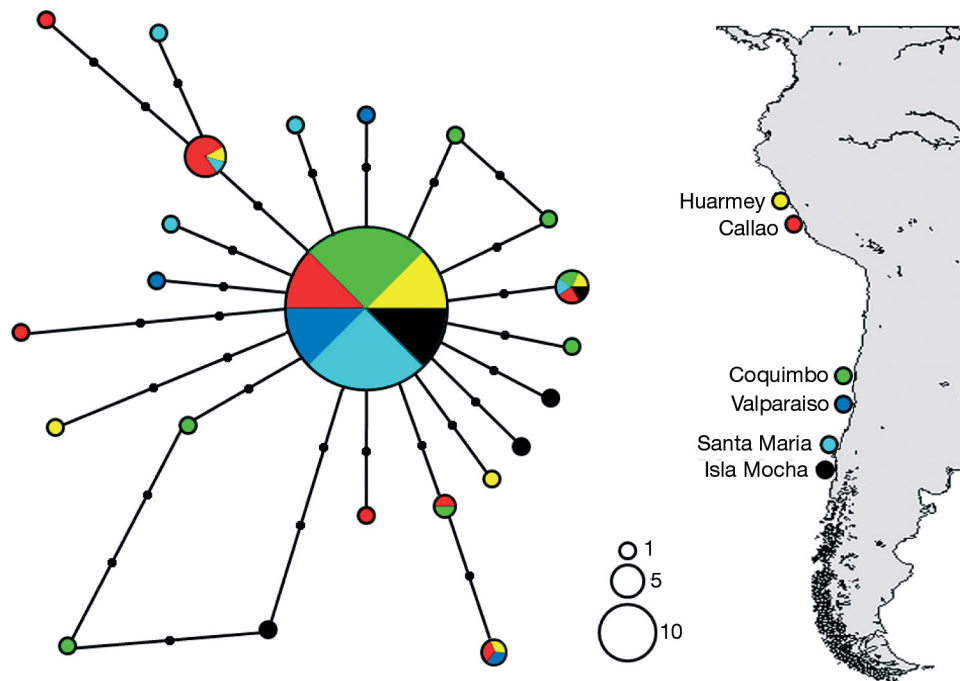


Fig. 2. *Dosidicus gigas*. Haplotype network of jumbo squid from the Humboldt Current System. Small black points in the network represent mutation steps and the size of the circles the number of individuals in each haplotype

Table 2. *Dosidicus gigas*. F_{ST} values (above the diagonal) and p-values (below) of jumbo squid from the Humboldt Current System

	Huarney	Callao	Coquimbo	Valparaiso	Santa Maria	Isla Mocha
Huarney		0.01204	-0.01566	-0.01059	-0.02446	-0.02384
Callao	0.21		0.00933	0.06665	-0.02318	0.0271
Coquimbo	0.86	0.23		0.01179	-0.01248	-0.01654
Valparaiso	0.57	0.02	0.29		-0.00863	-0.00911
Santa Maria	0.99	0.12	0.86	0.70		0.0215
Isla Mocha	0.99	0.14	0.85	0.69	0.99	

Nigmatullin et al. 2001, Ibáñez & Cubillos 2007, Keyl et al. 2008). These squids can move at a speed of 8 to 30 km d⁻¹ during their migrations, moving up to 200 km in 7 d (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. Fecundity of females can reach 15 to 18 million eggs (Nigmatullin & Markaida 2009) increasing the probability of dispersal along the Pacific Ocean. Recently, Staaf et al. (2008) reported the first discovery of a naturally deposited egg mass of *D. gigas* in the Gulf of California, with a volume of 3.13 m³ and an egg density of 0.6 to 2 million eggs per spawning batch. Finally, the huge fecundity, the presence of pelagic egg masses and paralarvae and the migration of adults may explain the genetic homogeneity observed for the COI gene along the ~3500 km of the Peruvian-Chilean

coastline. In a recent study, Sandoval-Castellanos et al. (2010) examined the diversity of the cytochrome *b* (Cytb) gene along the eastern Pacific, from Baja California to central Chile. While their main conclusion focused on the absence of phylogeographic structure in the study area, F_{ST} analysis detected the existence of genetic differentiation between

Central Chile and almost all other sites from Mexico and Peru. Our results based on the COI gene did not detect this genetic structure along the HCS. However, samples from Callao in Peru appeared as the most different compared to all other sites. Increase of sample size or the use of highly variable markers would be necessary to establish the existence of genetic differentiation in this area. The same COI haplotype H1 which is dominant in Chilean and Peruvian populations was also found in 43% of 315 squids captured along the North Pacific coast (GenBank accession no. DQ191367, Gilly et al. 2006a). The fact that jumbo squids from the Northern and Southern Hemisphere share the same dominant haplotype suggests that equatorial waters do not interrupt gene flow, in contrast to the Chilean and Californian jack mackerels (Poulin et al. 2004), and that *D. gigas* maintains genetic cohesiveness all along its distribution range from Alaska to southern Chile as

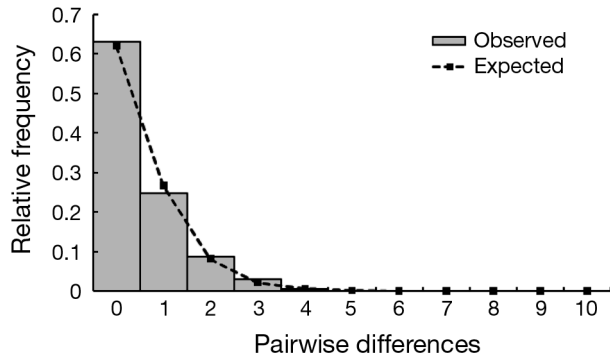


Fig. 3. *Dosidicus gigas*. Mismatch distribution of observed and expected pairwise differences among mtDNA COI sequences of jumbo squid from the Humboldt Current System

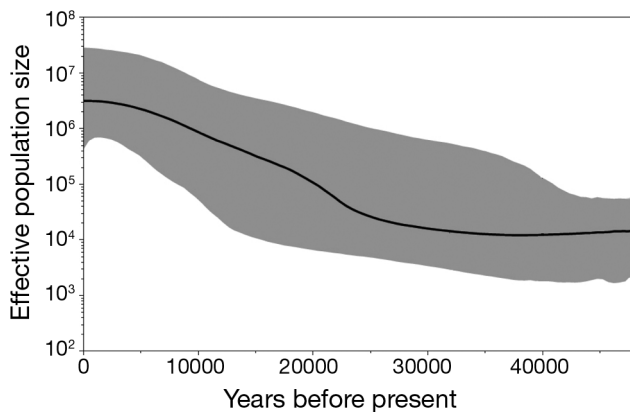


Fig. 4. *Dosidicus gigas*. Bayesian skyline plot showing changes in effective population size over time in jumbo squid. Time estimates along the x-axis were obtained by assuming an average pairwise sequence divergence rate of 2% per million years. Population size on the y-axis is given on a logarithmic scale. The thick solid line represents the mean estimate of population size; the grey shaded area shows the 95% HPD (highest posterior density) intervals

suggested by Sandoval-Castellanos et al. (2010). However, more variable molecular markers may identify finer genetic structure not detected because of the low variability of mitochondrial sequences in this species. Random Amplification of Polymorphic DNA (RAPDs) analysis of samples collected from Mexico, Peru, and Chile suggested the existence of 2 distinct genetic units separated by the equatorial currents and counter-currents (Sandoval-Castellanos et al. 2007, Staaf et al. 2010). Nevertheless, even if some genetic structure may occur among distant populations, our results support the existence of a single evolutionary unit for this species.

Similar results have been obtained from genetic studies in other pelagic squids but using other molecular markers such as allozymes and microsatellites. On the one hand, ommastrephid and loliginid squids showed high levels of genetic structure at large geo-

graphic scales (ca. 1000 to 10 000 km; Brierley et al. 1993, 1995, Reichow & Smith 2001, Herke & Foltz 2002, Katugin 2002, Shaw et al. 2004, Triantafillos et al. 2004, Sandoval-Castellanos et al. 2007, 2010, Shaw et al. 2010, Staaf et al. 2010). On the other hand, analyses at smaller geographic scale revealed weak and even absence of genetic structure (ca. 100 to 600 km; Carvalho & Loney 1989, Brierley et al. 1995, Adcock et al. 1999, Shaw et al. 2004, Buresch et al. 2006, Sandoval-Castellanos et al. 2007, 2010, Aoki et al. 2008, Shaw et al. 2010, Staaf et al. 2010).

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 it has a very large population size, *Dosidicus gigas* exhibits low diversity of the mtDNA COI, in agreement with a previous study based on Cytb (Sandoval-Castellanos et al. 2010). Such low mtDNA diversity has been observed in other studies for loliginid squids (Shaw et al. 1999, Herke & Foltz 2002, Aoki et al. 2008), indicating that this patterns of genetic diversity is not restricted to *D. gigas*. In the present study, only 23 haplotypes were found in 169 jumbo squids in the HCS, with 79% sharing the most common haplotype (H1). In the case of a constant population size under the Wright-Fisher model hypotheses, the haplotype diversity observed for *D. gigas* would be generated by an effective population size (N_e) of about 33 000 females, which is considerably smaller than the tens of billions of individuals expected from biomass estimations in the South Pacific Ocean (Nigmatullin et al. 2001). 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. Such a pattern of mtDNA diversity has been traditionally interpreted in 2 different ways. On the one hand, historical demographic variations may generate such characteristics. For example, a sudden population expansion following a bottleneck event or founder effect will produce a star-like genealogy because all coalescent events occurred at the same time, just before the expansion time (Slatkin & Hudson 1991). On the other hand, the existence of a selective sweep (the replacement of mtDNA sequences in the entire population with a phenotypically advantageous haplotype followed by an accumulation of new neutral variants) would produce a similar pattern of genetic diversity (Maruyama & Birky 1991, Skibinski 2000). Such ambiguity in the interpretation of very short-branched networks and an L-shaped mismatch distribution will per-

sist if no information is available about nuclear genetic diversity (Bazin et al. 2006). A selective sweep occurring in mtDNA should not involve nuclear diversity; by contrast, demographic variation should produce low diversity in the whole genome. In the case of *D. gigas*, a recent study using RAPD markers showed a low level of genetic diversity in this species (Sandoval-Castellanos et al. 2007). Because RAPD markers detect variation in short primer sequences in the whole genome, this low diversity should reflect a general tendency for nuclear diversity. These results, together with the low diversity of mtDNA genes, support the scenario of a recent demographic expansion over the selective sweep hypothesis. In this context, our results from neutrality tests (Tajima and Fu), and demographic inference analysis suggest that *D. gigas* experienced a dramatic population increase around 25 000 yr ago, based on the Bayesian approach or around 45 000 yr ago using the generalized non-linear least squares approach (Schneider & Excoffier 1999). Based on Cytb gene sequences from Mexico, Peru and Chile and using a similar substitution rate, Sandoval-Castellanos et al. (2010) estimated that population expansion occurred much earlier (between 230 000 and 280 000 yr ago). This discrepancy may be a consequence of the decision of these authors to pool all their sampling locations to infer a potential time of a global population expansion. Moreover, the Minimum Spanning Tree constructed from these sequences did not exhibit the typical star-like shape that characterizes a population that has passed through a sudden growth phase, and therefore did not support the hypothesis of a single expansion of *D. gigas* in the whole East Pacific. In contrast, our results at a regional scale clearly showed a robust star-like pattern and highly significant deviation in neutrality tests. Moreover, 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 yr (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 (Gilly et al. 2006a) 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). Higher frequency climate variability such as decadal oscillations or ENSO events should also affect population abun-

dance in a similar manner but with lower amplitude. However, because of the strong signal of population expansion detected at a millennium scale in our study, recent fluctuations in abundance on an annual or decadal scale would not leave an imprint on the mtDNA diversity. In the same way, past population dynamics of *Sepia officinalis* in northeast Atlantic Ocean and Mediterranean Sea indicates exponential population growth between the last 2 glacial maxima (130 000 to 20 000 yr ago, Pérez-Losada et al. 2007).

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