

Biogeography and Historical Demography of the Juan Fernández Rock Lobster, *Jasus frontalis* (Milne Edwards, 1837)

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Abstract

The genetic structure of present-day populations has been highly affected by glacial periods and physical oceanographic forcing, particularly with respect to species distributions and population gene-flow patterns. We assessed the current genetic composition of the *Jasus frontalis* population in the southeastern Pacific Islands off the coast of Chile to evaluate their connectivity modulated by contemporary and historic oceanographic processes. Population structure and demographical history for this species were assessed based on classic and Bayesian approaches using 84 sequences of cytochrome oxidase subunit I. In addition, we estimated the time of origin of *J. frontalis* in the different geographic zones. The analyses show a panmictic population with high gene flow between subcomponents and a lack of genetic structure ($F_{ST} < 0.008$). This high gene flow is mainly modulated by mesoscale oceanographic factors such as eddies and meanders. In a historical spatial context, the most probable common ancestor of *J. frontalis* could have colonized the region around 0.258 million years before present (MYBP), first becoming established in the Juan Fernández Archipelago and then expanding toward the Desventuradas Islands. The demographic history shows a consistent increase in the effective population size (N_e) starting approximately 0.130 MYBP, which is highly correlated with sea-level changes during the last glacial maximum.

Key words: *coalescence time, glaciations, Juan Fernández rock lobster, mesoscale oceanographic activity, phylogeography, skyride plot, southeastern Pacific Ocean*

The genetic structure of present-day populations and communities has been highly affected by glacial periods, particularly with respect to species geographic distribution, abundance, population genetic structure, and population gene-flow patterns (Hewitt 2000; Jansson and Dynesius 2002; Zhao et al. 2008; Johannessen et al. 2010). In marine environments, this climatic oscillation resulted in changes in temperature, current patterns, sea level, surging intensity, and coastal habitat extension (Petit et al. 1999; Lambeck et al. 2002). In the southern hemisphere, oceanic circulation and

sea level were modified during the glacial periods, principally due to the changes produced in global circulation patterns (McCulloch et al. 2000). A major change was the significant drop in sea level of approximately 130 m during the last glacial maximum (LGM), which occurred approximately 0.019 million years before present (hereafter MYBP; Huybrechts 2002). The effects of this severe environmental climate change on species can be studied using selectively neutral mitochondrial DNA markers, which provide a general image of gene flow, as well as other microevolutionary population

processes (Grant and Waples 2000; Hewitt 2000; Avise 2000, 2004). These studies are fundamental for understanding the underlying evolutionary processes that give rise to biodiversity in a geographic and ecological context. In particular, understanding the origin of the biogeographical patterns of genetic diversity is essential not only for inferring the history of natural populations but also for conserving biodiversity (e.g., Brasher et al. 1992; Frankham et al. 2003; Avise 2004) and for generating predictive models of the effects of global climate change on natural populations (Foll and Gaggiotti 2006).

The effect of physical oceanographic processes on populations depends on species' life-history traits, especially for marine benthic species whose populations are principally modulated by dispersal in early pelagic stages interacting with physical oceanographic forcing factors (McConaugha 1992; Largier 2003; Cowen et al. 2006). In conventional wisdom, many marine species connectivity is determined by dispersal potential because a prolonged larval stage can increase interconnections between distant areas (Shanks et al. 2003; Shanks 2009). In this sense, populations in island systems can be particularly impacted by physical oceanographic processes linked to the early life histories of sessile or low-mobility species, given their relative isolation. Consequently, species affected by factors that limit their dispersal tend to show greater genetic structure over time (Palumbi and Metz 1991; Hellberg 1996; Shaw et al. 1999; Palumbi 2003; Teske et al. 2005). Alternatively, current research establish that the larval duration may not be a good indicator of the spatial scale of connectivity as suggested by conventional wisdom (Bradbury et al. 2008; Weersing and Toonen 2009; Selkoe and Toonen 2011). In archipelagos, adult populations can be isolated due to discontinuous habitat and their restricted connectivity only to larval dispersal during early ontogenetic stages (Maurice et al. 2002; Sponaugle et al. 2002; Grantham et al. 2003; Shanks et al. 2003; Shanks 2009). In some systems, connectivity is primarily modulated by mesoscale oceanographic processes that act as dispersal agents establishing migration flows among remote areas (e.g., southeastern Pacific Islands, see Porobić et al. 2012).

The Juan Fernández Archipelago and the Desventuradas Islands, located off the Chilean coast (the former located about 667 km off the American continent), are a particularly interesting model system for studying the effects of historic (i.e., glacial) and contemporary (i.e., physical oceanographic) processes on the populations of benthic marine fauna, given their oceanographic characteristics and the high degree of endemism of their marine species (Rozbaczyllo and Castilla 1987; Pequeño and Sáez 2000). The large number of endemic species present on these southeastern Pacific Islands represents unique evolutionary histories, which are important for maintaining global biodiversity. Furthermore, geologically recent oceanic islands, such as the Juan Fernández Archipelago and the Desventuradas Islands, have been fundamental in the development and illustration of biogeographic and evolutionary theory (e.g., MacArthur and Wilson 1967; Emerson 2002; Burridge et al. 2006). These southeastern Pacific Islands include the Juan Fernández Archipelago,

a group of three islands (i.e., Robinson Crusoe, Santa Clara, and Selkirk), and the Desventuradas Archipelago (i.e., San Felix and San Ambrosio; Figure 1), which originated approximately 3–6 MYBP (Gonzales-Ferrán 1987). The benthic species that colonized and diversified in this system experienced diverse physical and biological historical processes whose effects on current population structure are still unknown.

One of the endemic species of this island system is the Juan Fernández rock lobster *Jasus frontalis* (Pequeño and Sáez 2000), which has great cultural and economic importance for the inhabitants of this archipelago (Arana 1987; Ernst et al. 2010). This lobster species is found at depths between 2 and 200 m and has a pelagic larval stage lasting approximately 1 year (Arana 1987), during which larvae are exposed to different oceanographic processes. Mesoscale eddies and meanders are important oceanographic features in the region that provide physical connectivity and establish a significant particle flow among the different island groups (Porobić et al. 2012).

In a macroevolutionary context, global climate change, tectonic and large-scale oceanographic processes have had profound impacts on species of the *Jasus* (George 1997, 2006; Ovenden et al. 1997). In fact, these factors have driven the speciation process of the subclade of *J. frontalis* and established its current distribution (George 1997, 2006). However, in a microevolutionary context, the effects of historic processes are unknown for this species.

The present study aims to assess the population structure of *J. frontalis* as a way to evaluate the connectivity among island groups mainly affected by oceanographic mesoscale activity (Porobić et al. 2012). We hypothesized that the larval duration of *J. frontalis*, together with active mesoscale oceanographic processes in the area, produced high gene flows among benthic subcomponents, resulting in a panmictic population. In addition, we evaluated effective population size of the ancestral population over time to infer potential historical processes associated with changes in effective population size (e.g., sea-level variation). Finally, based on the theory of expansion of the subgroup of *J. frontalis* proposed by George (1997, 2006), which states that the arrival of ancestors from the west was mediated by seamounts and the sub-Antarctic Islands, we hypothesize that the historical arrival of *J. frontalis* to the southeastern Pacific Island system began in the Juan Fernández Archipelago and later expanded to the Desventuradas Islands.

Materials and Methods

Data

Muscular tissue samples were collected from a total of 84 individuals of the species *J. frontalis* from the current known distribution of this species: 30 from Selkirk Island (AS; 33°48'S, 80°40'W), 30 from Robinson Crusoe/Santa Clara Islands (RC-SC; 33°36'S, 78°48'W), and 24 from the Desventuradas Island system (San Felix Island; 26°24'S, 80°00'W; Figure 1). The Juan Fernández samples were collected during the normal fishing activity of the Juan Fernández artisanal fleet

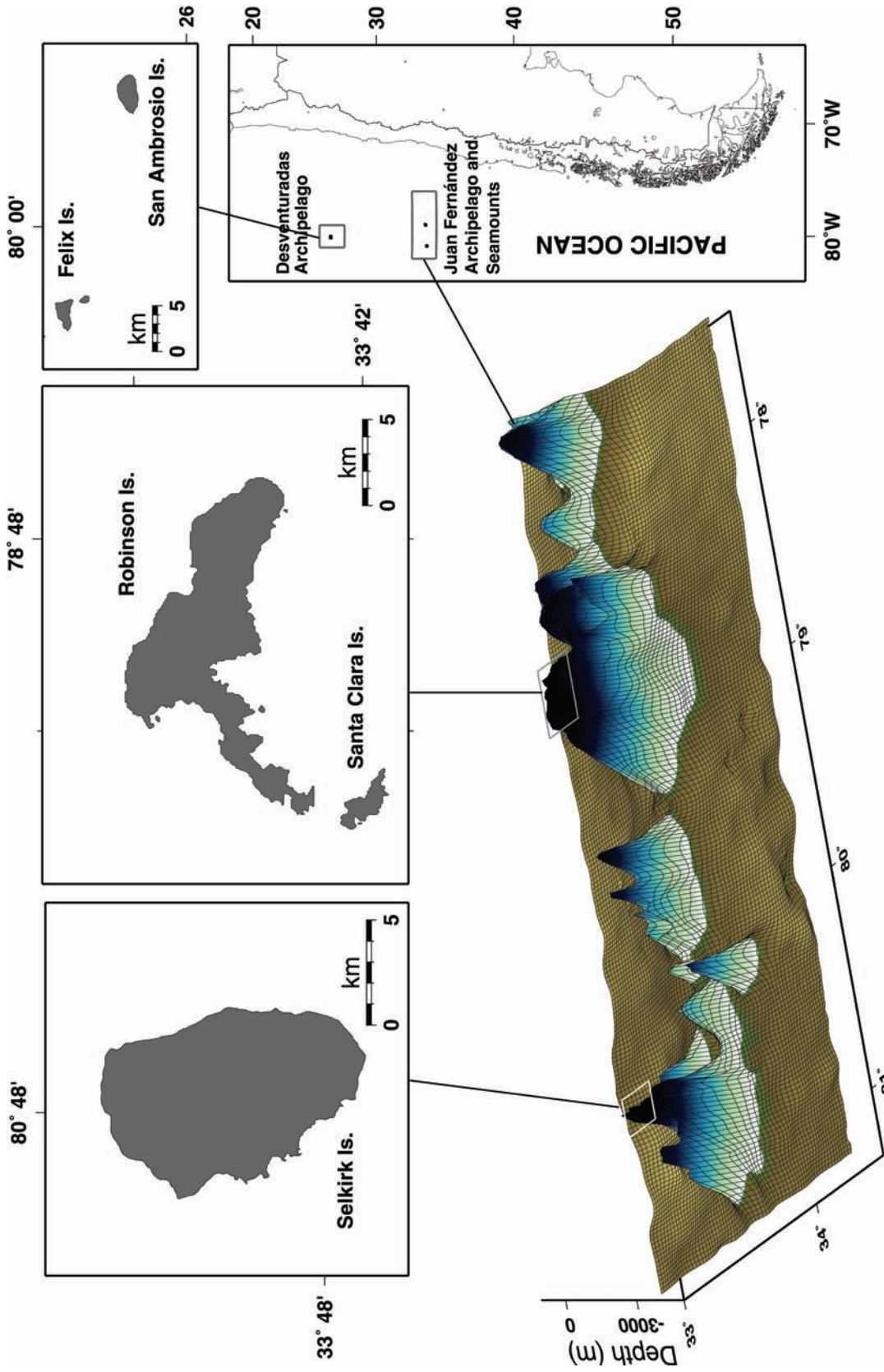


Figure 1. Map of the study area that includes the southeastern Pacific Islands of Robinson Crusoe/Santa Clara, Selkirk, the Desventuradas Islands, and seamounts.

between November 2004 and September 2008. Samples from San Felix Island were collected using regular Juan Fernández fishing traps on the “LM Ayayay” research vessel in October 2008. These samples were stored in 95% ethanol and refrigerated at -20°C for subsequent analysis.

Laboratory Analysis

Genomic DNA was extracted using the CTAB 2X protocol developed by [Crandall and Fitzpatrick \(1996\)](#). A fragment of the cytochrome oxidase subunit I (COI) gene was amplified in a final volume of 30 μ L, which contains 20 ng of template DNA for total, 1.5 mM MgCl₂ (Fermentas, Ontario, Canada), 0.1 mM dNTPs (Invitrogen, Carlsbad), 0.3 μ M of each primer ([Folmer et al. 1994](#)) and 1.2 U/ μ L of Taq DNA polymerase (Fermentas, Ontario, Canada). The amplification was conducted in a PCT-200 thermocycler (MJ-Research®) with the following conditions: 1 cycle at 95°C for 10 min, 60°C for 30 s, 72°C for 2 min, followed by 41 cycles of denaturation at 95°C for 30 s, annealing at 54°C for 45 s, extension at 72°C for 1 min, and a final extension at 72°C for 5 min. The PCR product was purified and sequenced using MacroGen® Inc. services. Sequences of ~650 bp were then examined, manually edited, and subsequently aligned using the multiple-sequence alignment program Clustal-W, implemented in the BioEdit program ([Hall 1999](#)). We used the mitochondrial gene, COI, because this is a region of mitochondrial DNA that has been widely used to assess population subdivision in closely related species (e.g., *Panulirus japonicus*, [Inoue et al. 2007](#)) and congeneric species (e.g., *J. edwardsii*, [Ovenden et al. 1992](#); *J. verreauxi*, [Brasher et al. 1992](#); *J. lalandii*, [Matthee et al. 2007](#); *J. tristani*, [von der Heyden et al. 2007](#)).

Population Genetic Analyses

To evaluate the presence of population structure in *J. frontalis* within the Juan Fernández Archipelago and Desventuradas Islands, we used the program GENELAND version 1.0.7 ([Guillot et al. 2005a, 2005b, 2008; Guillot 2008](#)) in the R-Package ([Ihaka and Gentleman 1996](#)), which implements a statistical population model with Bayesian inference based on a set of georeferenced individuals. This model allows us to infer and locate the genetic discontinuities between populations of georeferenced genotypes. We transformed the sequences using the transformation proposed by [Guillot et al. \(2009\)](#), where the nucleotide bases were codified as alleles assigning whole numbers (i.e., A = 1, T = 2, C = 3 and G = 4). To estimate the most probable number of *K* populations, a preliminary estimate was performed using 5×10^6 Markov chain iterations, where we found the highest probability values for *K* = 1, which indicates the existence of a single large population. To evaluate the existence of a ghost population, we made a second run with *K* fixed to the value obtained in the first run, obtaining the same result. Considering this result, no further analysis with this method was performed on population structure. Additionally, a classic evaluation of population differentiation was performed by calculating the Wright fixation index (F_{ST}) ([Weir and Cockerham 1984; Slatkin 1995](#)) between localities (by pairs)

of *J. frontalis* using the program Arlequin 3.1 ([Excoffier et al. 2005](#)), and the significance level was calculated based on 10 000 permutations.

To determine whether there is isolation by distance, we calculated the correlation coefficient *r* between the genetic distance (GenD) and the geographical distance (GeoD) matrix in zt_win software ([Bonnet and Van de Peer 2002](#)). Significance level was calculated based on 10 000 permutations.

The network genealogy of the haplotypic structure was graphically analyzed with the median joining algorithm, implemented in the program NETWORK, version 2.0 ([Bandelt et al. 1999](#)). The parameters used were calibrated by assigning the transition/transversion rate to 14.5, which was previously calculated using the program MODELTEST, version 3.7 ([Posada and Crandall 2001; Posada and Buckley 2004](#)). The calculated number of haplotypes, haplotypic diversity, and nucleotide diversity were estimated in DNAsp, version 5 ([Librado and Rozas 2009](#)).

Historical Demography and Biogeographical Analysis

In order to evaluate possible events of population expansion, *D* test of neutrality by [Tajima \(1983\)](#) and F_S test by [Fu \(1997\)](#) were calculated using the software Arlequin 3.0 ([Excoffier et al. 2005](#)). To assess the temporal fluctuation dynamics of the effective population size (N_e), we used the Gaussian Markov random field Bayesian Skyride Plot (BSRP) approximation ([Minin et al. 2008](#)), implemented in the program Beast, version 1.6 ([Drummond et al. 2006; Drummond and Rambaut 2007](#)), with all data combined as a single site. The BSRP uses a fast-mixing sampling procedure of a Markov Chain Monte Carlo algorithm (MCMC), designed for a highly structured Gaussian model, to estimate a posteriori distribution of the variation of N_e over time and incorporates the uncertainty of the genealogy from a DNA sequence sample given by a model of specific nucleotide substitutions. This methodology, in contrast to other methods of reconstruction of population sizes, can successfully recover the “true” population size trajectories without evoking strong prior assumptions ([Drummond et al. 2005; Opgen-Rhein et al. 2005; Minin et al. 2008](#)). The running conditions include 10 million iterations and 20 000 trees burned before the convergence zone. To evaluate the mutation rate, the type of molecular clock, and the different types of models implemented, we used the Bayes Factor (BF), which measures the weight of the evidence in the proposed model against another candidate model ([Goodman 1999](#)). Finally, we used a model with a mutation rate of 2.3% per million years, which has been previously calculated for decapods ([Schubart et al. 1998; Albrecht et al. 2006](#)). Based on the BF, the selected model was a general model of reversible time with invariable sites and gamma distribution (GTR + I + G), implemented under a log-normal relaxed molecular clock ($BF \approx 20$; [Drummond and Rambaut 2007; Ho 2007](#)). Both the calculation of BF and the BSRP graph were generated using the program TRACER, version 1.4 ([Rambaut and Drummond 2007](#)). In order to evaluate the hypothesis of the effect of sea level on N_e , the Pearson correlation coefficient was calculated

for N_e and historical sea level for the time range between 0.132 MYBP and present. This time span used for calculating the correlation is defined by the confidence intervals of time using the BSRP estimation method. Historical sea levels were obtained from Miller et al. (2005).

To estimate the time and the geographic zone of origin of *J. frontalis*, the time of the most recent common ancestor was calculated using Bayesian phylogenetic reconstruction based on coalescence theory in the Beast Program (Drummond and Rambaut 2007), using the Yule Speciation Model (Drummond et al. 2006). To implement this model, individuals were grouped into one group because there was no significant genetic subdivision among samples, and time of origin was determined using the previously described mutation rate (2.3% million years). The model was run using the conditions previously indicated for BSRP construction. To evaluate the geographic zone of the origin of *J. frontalis*, we used the ancestral state reconstruction package available in the Multistate module of BayesTraits 1.0 software (Pagel and Meade 2007), evaluating the area of most recent common ancestor at the root of the Bayesian consensus tree. For this, we used both the topology and the branch lengths (i.e., time) obtained from the sample of phylogenies in Beast software. For reconstruction of the ancestral characters states, we used the continuous-time Markov k-state model (Pagel 1994; Lewis 2001) estimating states under Bayesian MCMC framework. We ran the MCMC analysis with a uniform prior distribution on the rate coefficients with a range from 0 to 100. Several values of the Rate Deviation parameter were used to avoid spurious acceptance between successive MC steps (i.e., appropriated acceptance values are in the range 0.2–0.4; Andrew Meade, personal communication). We ran 50 000 000 MCMC iterations, discarding the first 50 000 iterations to avoid results outside the likelihood convergence.

Calculation of Actual and Potential Historical Bathymetric Distribution

We used all the bathymetric information for the two island systems available from the literature; unfortunately, there are no such data for Alejandro Selkirk (AS) Island. Nevertheless, this island represents a small proportion in comparison with the other four islands. Bathymetric information of three

seamounts adjacent to Juan Fernández Archipelago (JF1, JF1.1, and JF2; Figure 1) was obtained from Niklitschek et al. (2010). Finally, using this information, we generated bathymetric depth contours for 100, 200, and 300 m and calculated the areas of the polygons between 0 and 200 m (i.e., the current bathymetric preference of *J. frontalis*) and between 100 and 300 m (i.e., the potential historical bathymetric range for *J. frontalis* during the LGM). Bathymetric and coastline information were incorporated into GIS/ESRI software. Areas of different polygons were computed on a two-dimensional basis using standard built-in routines.

Results

Mitochondrial DNA Sequence Variation

A sequence of ~650 bp of a COI fragment was obtained for each one of the 84 analyzed individuals of *J. frontalis*. The sequences showed a total of 54 haplotypes with an average haplotypic diversity of 0.95 and average nucleotide diversity of 0.0064 (Table 1), which corresponds to diversity values commonly found in other crustaceans, consisting in high haplotypic diversity (Hd) and moderate nucleotide diversity (Pi) (Stamatis et al. 2004). Of the 54 haplotypes found, only 1 is shared by the 3 island systems (RC-SC, AS, and Desventuradas Islands); the rest of the haplotypes are either unique (found only once) or are only shared between 2 island systems (Figure 2).

Population Structure

The probability distribution estimated by the GENELAND program for the K parameter showed highest values for $K = 1$ and no presence of ghost populations (Guillot et al. 2005b; Coulon et al. 2006). This strongly suggests there is a single population with high gene flow among island systems, and therefore the genetic composition has not been structured. Along with this, the haplotype network did not show clear structure among the island systems (Figure 2). This fact, together with the low observed population differentiation indicated by F_{ST} values, confirms the result obtained with GENELAND. The correlation coefficient to test for isolation by distance was $r = -0.051$, which indicates no relationship between genetic distance and geographic distance.

Table 1 Genetic diversity index (numbers of individuals N , number of haplotypes h , observed haplotypic diversity Hd_{obs} , observed nucleotide diversity Pi_{obs} , estimated haplotypic diversity Hd_{est} , estimated nucleotide diversity Pi_{est}) and demographic parameters (D , F_S) with their corresponding significance values (P -value) for *J. frontalis*

Location	Sequence diversity						Demographic parameters			
	N	h	Hd_{obs}	Hd_{est} (C.I.)	Pi_{obs}	Pi_{est} (C.I.)	Tajimas' D	P -value	Fu's F_S	P -value
AS	30	19	0.940	0.812 (0.58–0.92)	0.0067	4.418 (1.14–10.8)	-1.113	0.131	-12.645	<0.0001
RC-SC	30	22	0.947	0.799 (0.50–0.92)	0.0062	4.053 (1.00–9.96)	-1.810	0.016	-15.678	<0.0001
Desventuradas	24	19	0.975	0.788 (0.44–0.92)	0.0058	3.633 (0.85–8.91)	-1.714	0.028	-16.006	<0.0001
All islands	84	54	0.951	0.805 (0.56–0.91)	0.0064	4.169 (1.20–10.49)	-2.180	<0.01	-64.381	<0.0001

Hd_{est} , Pi_{est} , and confidence intervals (C.I.) were estimates based on 1 000 coalescent simulations.

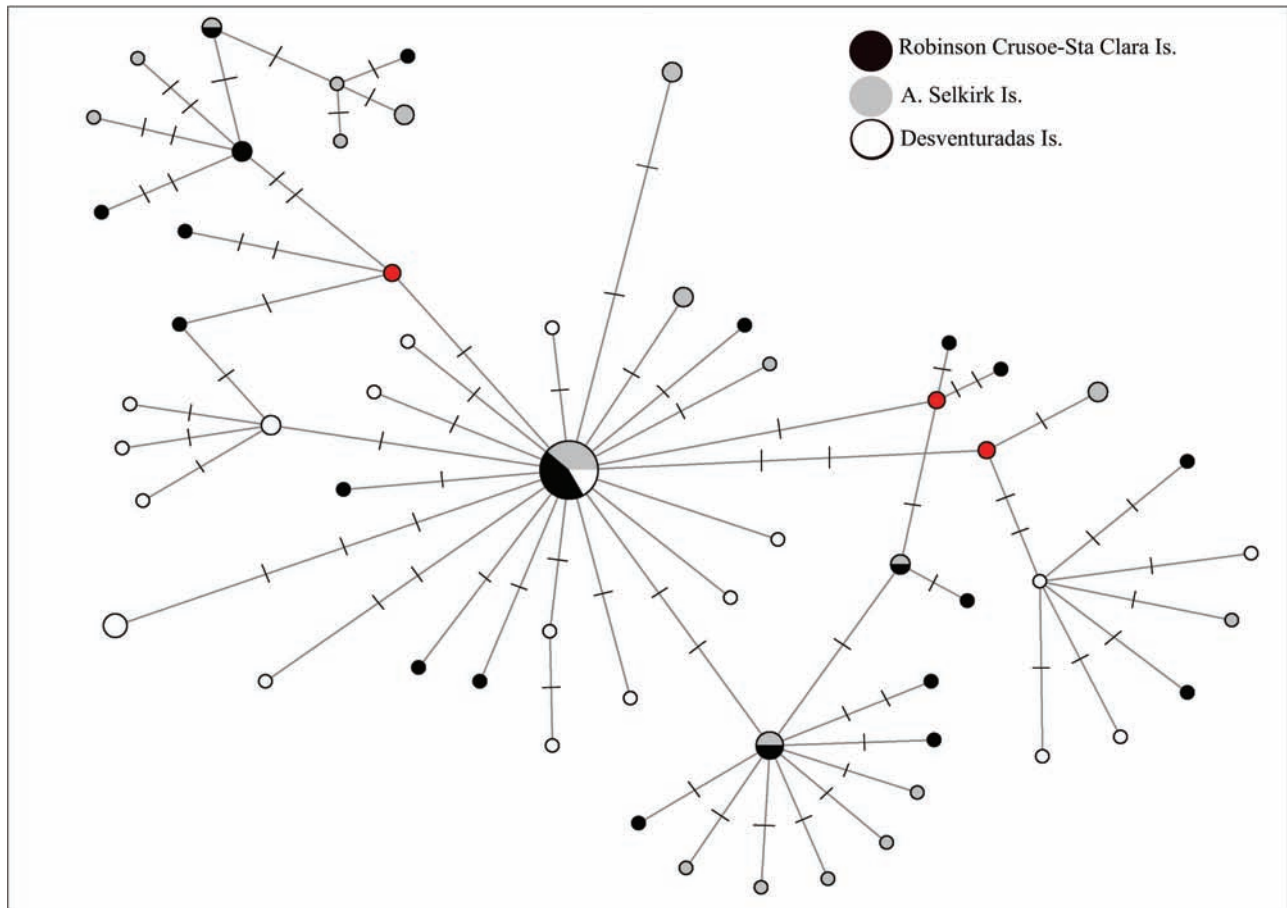


Figure 2. Network of haplotypes obtained from sequences of COI from *J. frontalis* in the 3 studied localities. The size of the circle represents the frequency of the haplotype, and the different shades represent the frequency in each locality. Transverse lines represent the number of mutational steps between haplotypes. The small red circles are the missing haplotypes.

Historical Demography

F_S test by Fu (1997) and D test by Tajima (1983) provided significant negative values for all islands except the Tajima's test of Selkirk Island (Table 1). These results suggest historical demographic processes of population expansion for *J. frontalis*. The demographic history of *J. frontalis*, in reference to the population size estimated by BSRP, shows a continuous increase in effective population size (N_e) approximately 130 thousand years ago (Figure 3a). Additionally, this increase in N_e shows a high inverse correlation ($r = -0.80$; $P < 0.001$) with sea level between 0.132 MYBP and present time (Figure 3b).

From the reconstruction of ancestral area, we found that all of the actual lineages of the *J. frontalis* descended from an AS Island ancestor (Figure 4) approximately 0.258 (± 0.0582) MYBP.

Discussion

Population Structure

The Juan Fernández rock lobster population is not structured in its geographic realm, presenting high connectivity

among the different systems and functioning as a single, large population with high gene flow among the different regional groups. This result is not unexpected, considering that the phyllosoma larva of *J. frontalis* lives approximately 1 year in a pelagic environment (Arana 1987) and is the fundamental dispersing unit of this species (von der Heyden et al. 2007). The extended planktonic stage has been an important explanatory factor for the lack of population structure observed in congeneric species, for which either no genetic differentiation (e.g., *J. edwardsii*, Ovenden et al. 1992) or low genetic differences were found (e.g., *J. verreauxi*, Brasher et al. 1992; *J. lalandii*, Matthee et al. 2007; *J. tristani*, von der Heyden et al. 2007). In this sense, the high degree of connectivity within the southeastern Pacific system could be determined by 2 principal factors: 1) local-scale advection of the phyllosoma larva during its approximately 12 months in the plankton as suggested by Shanks et al. (2003) and Grantham et al. (2003) for marine invertebrates. Indeed, according to the relationship of permanence in the plankton and distance traveled proposed by Shanks et al. (2003), theoretically the *J. frontalis* larvae could cover more than 1000 km from their location of origin prior to settling, which is greater than the maximum

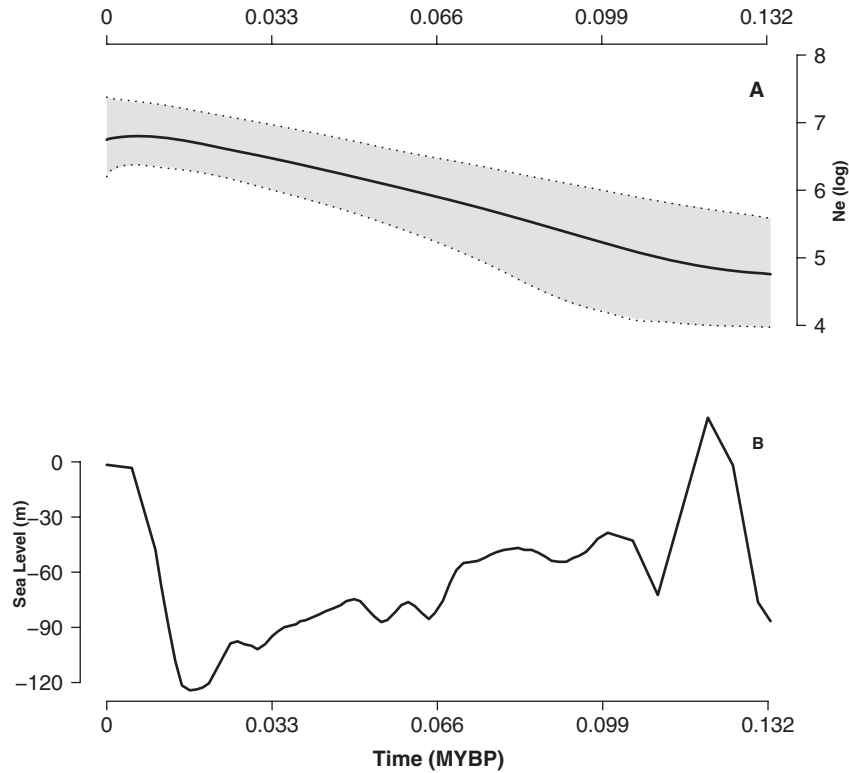


Figure 3. Logarithm of the effective population size N_e (A) and changes in sea level (B) during the last 0.132 MYBP. The dashed lines represent the 95% limit of probability based on the sample of Bayesian parameters.

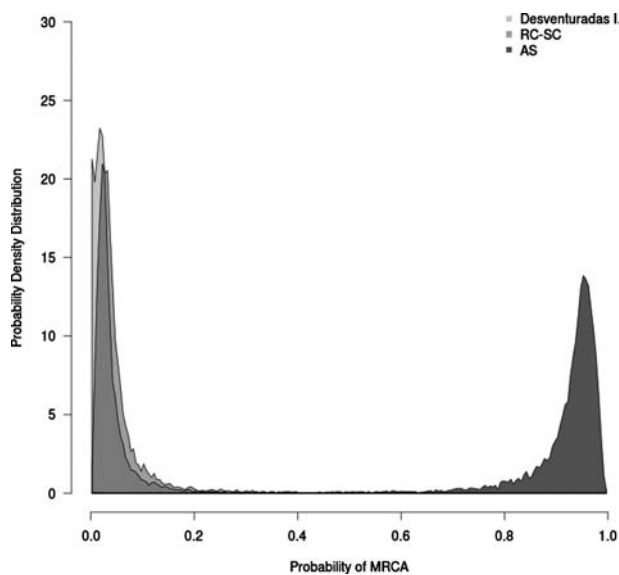


Figure 4. Probability density distribution of the geographical location for the most recent common ancestor (MRCA) of *J. frontalis*. Each of the geographic areas is identified with a color: light gray for Desventuradas Island; medium gray for Robinson Crusoe and Santa Clara islands (RC-SC); and dark gray for Alejandro Selkirk Island (AS).

distances between the Juan Fernández and Desventuradas Archipelagos; 2) mesoscale physical oceanographic factors that could act as vectors for larval dispersal (McConaughy 1992; Largier 2003; Cowen et al. 2006). Although oceanographic studies in the archipelagos are incipient, authors such as Hormazabal et al. (2004) describe important eddy activity around 30° S latitude, whereas other authors establish the presence of meandering structures within the area bounded by the islands, structures with a predominantly northerly direction Vásquez et al. (unpublished data). Current work to establish the physical and biological mechanisms that determine the connectivity of *J. frontalis* populations indicates that the connectivity is mainly modulated by oceanographic forcing such as eddies and meanders, especially in conjunction with biological factors related to the reproductive process. In this sense, we conclude that the distance between the different islands is not a biogeographical barrier to dispersal, resulting in a panmictic population.

Historical Demography and Biogeography

The effective population size (N_e) of *J. frontalis* showed a continuous increase since approximately 0.13 MYBP (Figure 3a). This period is coincident with the decrease in temperature during the last glacial period and with an approximately 90–120 m drop in sea level (relative to current values; Figure 3b; Miller et al. 2005). These conditions have resulted

Table 2 Current and historical (i.e., during the LGM) total area in square kilometres available on the shelf between 0 and 200 m depth for the system of islands and nearby seamounts (JF1, JF2, JF1.1)

	RC-SC	Desventuradas	Subtotal	Seamounts	Total
Current	343977	75707	419684.2	59.5	419743.7
Historical	367941	77147.3	445088.2	49782.2	494870.4
Increment (%)	6.97	1.90	6.05	83×10^3	17.90

The increment represents the percentages of the historical area with respect to the actual suitable area for the *J. frontalis* population.

in the emergence of a large amount of subtidal area, and an increase in potential benthic habitat available for *J. frontalis* (Table 2), which shows a marked bathymetric preference that goes from 0 to 200 m depth (Arana 1987). In fact, considering a decrease in sea level of 100 m during the LGM, for only 4 of the islands where *J. frontalis* populations currently inhabit (i.e., RC-SC, AS, and Desventuradas Islands), could have produced an increase of total suitable area of 6.05%. Moreover, if we also consider the nearest seamounts in the area (i.e., JF1, JF2, and JF1.1), the total increase in suitable area could be expanded to approximately 18% during the LGM (Table 2). Thus, the total potential area available for colonization by *J. frontalis* is conditioned by a drop in sea level due to the LGM.

We propose the hypothesis that the increase in the potential suitable habitat for *J. frontalis* with the emergence of the seafloor areas, due to the drop in sea level, could have had a positive effect on the population size (N) and the effective population size (N_e) of the Juan Fernández rock lobster. Other authors have previously described that an increase in habitable area provokes an increase in N , which in turn results in an increase in N_e (Jesus et al. 2006). This hypothesis suggests that the LGM could be related to an increase in N_e of *J. frontalis*, given an increase in potential subtidal marine habitat above 200 m. These ideas differ from those reported for land environments where glacial periods reduced populations and fragmented the habitable area (Hewitt 2000, 2004; Jansson and Dynesius 2002; Jesus et al. 2006). However, our hypothesis should be further evaluated based on new information on habitat availability and the preference of *J. frontalis*. It is, nevertheless, important to note that after the LGM, an increase in sea level (which provokes a decrease in the amount of suitable habitat for *J. frontalis*) is not associated with a decrease in N_e . This result is possibly explained by the potential loss of genetic variability of the population over the last 20 000 years, which has not been enough to show a drop in N_e in the islands, as would be expected due to the decrease in population size (N) (Frankham et al. 2003; Palstra and Ruzzante 2008) caused by the immersion of part of the suitable habitat.

Some authors have proposed that the appearance of *J. frontalis* is related to the establishment of the circumpolar current (George 1997, 2006; Ovenden et al. 1997), which would allow the arrival of ancestors from the west mediated by submarine seamounts and sub-Antarctic Islands, around the Late Myocene (<10 MYBP; George 1997). This hypothesis suggests that it is highly probable that the genus diversified following the direction of the West Wind Drift

(WWD; George 1997, 2006; Ovenden et al. 1997). On the other hand, other authors suggest a possible route of transoceanic dispersal, also in the direction of the WWD, passing by the Juan Fernández and Desventuradas Islands, following the Foundation Chain located on the Pacific Plate (Burrige et al. 2006). Our results support this latter hypothesis of colonization given that we obtained a high probability that the most recent common ancestor inhabited Selkirk Island (Juan Fernández Archipelago, Figure 4) approximately 0.258 (± 0.0582) MYBP. However, the speciation processes of the genus *Jasus* in the southeastern Pacific Ocean is older and probably linked to past vicariant events as proposed by George (1997, 2006) and Ovenden et al. (1997).

In conclusion, *J. frontalis* would have originated by the migration of the ancestral population, following the Foundation Chain, in the direction of the circumpolar current, establishing the most recent ancestral population on the Juan Fernández Archipelago during the last million years. This ancestral population would have subsequently colonized the Desventuradas Islands as the most recent historic colonization in a general Stepping Stone model (Whittaker 1998) of species dispersal, possibly due to constant advective flow toward this area. Currently, the *J. frontalis* population presents strong gene flow between the different islands, showing no population differentiation. This should be modulated by mesoscale eddies and meanders that could be advecting larvae with long permanence in the water column from one system to another, thus establishing a panmictic population with high genetic flow among island groups.

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