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Discordant Phylogeographic and Biogeographic Breaks in California Halibut

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Abstract.—The range of the California Halibut, *Paralichthys californicus*, spans three biogeographic provinces along the coastline of Alto (United States) and Baja (Mexico) California. To assess population genetic structure of the California Halibut, we analyzed mitochondrial cytochrome *b* sequences from 375 individuals across a large portion of its native range. Nucleotide diversity was consistently low among sampling sites ($\pi = 0.0026 \pm 0.0017$), while haplotype diversity was consistently high ($h = 0.77 \pm 0.024$). We found that California Halibut were genetically homogeneous across sampled sites with an overall $\Phi_{st} = 0.0030$ ($p = 0.22$). We saw no evidence of genetic discontinuities at two previously recognized marine phylogeographic breaks in the Los Angeles region or across the California Transition Zone at Point Conception. We conclude that California Halibut are genetically homogeneous and experience substantial gene flow, at least over evolutionary time scales.

INTRODUCTION

The nearshore marine environment of coastal California (USA) has long been a playground for biogeographers owing to its dynamic composition of marine organisms that has undergone dramatic shifts during the past five decades or so, particularly among marine fishes (Horn, *et al.*, 2006). While southern California's marine ichthyofauna was once thought to share many elements of the cool water "Oregonian" faunal assemblage, a persistent warming trend since the early 1980s precipitated a change in southern California's marine ichthyofauna to a more temperate, sub-tropical fauna with established communities whose biogeographic affinities lie with faunal assemblages further south along the Pacific Coast (reviewed in Lea and Rosenblatt, 2000).

While the biogeographic history of southern California is dynamic, one geographic feature has consistently stood out as a potential dividing point between two distinct faunal provinces at Point Conception, a prominent headland that marks the beginning of the "California Bight" and the California Transition Zone (CTZ; Figure 1 [Valentine, 1966]). However, as detailed distributional data on California's marine fishes emerged, this biogeographic "break" appeared to be "leaky", and is now regarded as more of a gradual transition zone (Horn, *et al.*, 2006).

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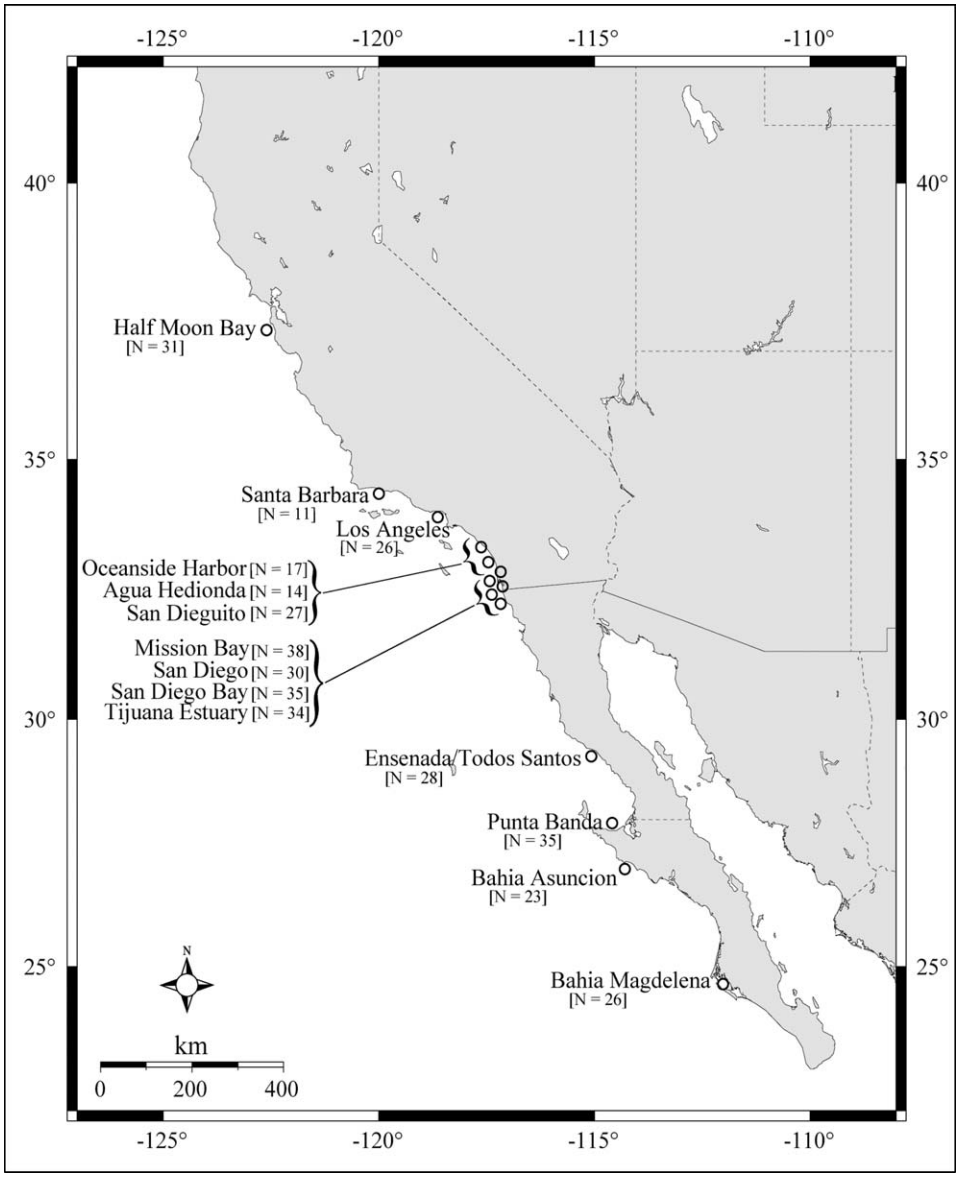

Fig. 1. *Paralichthys californicus.* Sampling locations and sample sizes for 375 individuals along the California coastline.

With the advent of the phylogeographic revolution in the late 1990's, many papers were written discussing the theoretical expectation of concordance between biogeographic boundaries and intra-specific, phylogeographical breaks (i.e., the concordance rule; see examples in Avise, 2000)). It was recognized that the genetic structure of a population may be influenced by a number of factors, including biogeographic barriers to dispersal (Bernardi, 2000; Bernardi, 2005; Blanchette and Gaines, 2007; Burton, 1998; Dawson, *et al.*, 2001), yet one assumption of the concordance rule that was not immediately recognized was that for a biogeographic boundary to function simultaneously as a

phylogeographic boundary, the expectation would be that sister species would exist on either side of the boundary due to the persistence of a common causal property of the geographic area restricting gene flow over evolutionary time scales. At that time, data from most studies highlighted the geographically similar locations of these phylogeographic and biogeographic breaks, particularly in the southeastern United States among marine organisms (e.g., Cape Canaveral, Florida). In coastal California, however, a pattern soon emerged in which geographical separations of marine faunal assemblages did not correlate with the geographic locations of phylogeographic breaks within species, and the generality of the ''concordance rule'' was challenged (e.g., Burton, 1998)

Further complicating the generality of California's hypothesized barrier was the realization that for some marine organisms, particularly those tied to aquatic inland habitats (i.e., estuaries and marshes), or with low dispersal potential (e.g., live-bearing fishes) a phylogeographic break was noted farther south in the Los Angeles region (LAR; Bernardi, 2000; Dawson, 2001; Dawson, *et al.*, 2002). Few studies to date have tested the functionality of either the LAR or CTZ in marine species with greater dispersal potential or vagility as adults, but notable examples include studies of rockfishes of the family Scorpaenidae (e.g., Hyde and Vetter, 2007; Hyde and Vetter, 2009).

The California Halibut (*Paralichthys californicus* Ayers 1859) is an ecologically and economically important flatfish species distributed from Washington State to southern Baja California with unsubstantiated records from the Gulf of California (R. N. Lea and R. Rosenblatt, pers. comm.). This range traverses the CTZ and the LAR. Contrary to early predictions, the California Halibut is known to utilize both embayments/estuaries and open coastal habitats for all stages of its life cycle (Fodrie, *et al.*, 2009). It is also a broadcast spawner with pelagic eggs and larvae. These characters provide an opportunity to examine the efficacy of the LAR and CTZ ''barriers'' for a species that is not restricted to aquatic inland habitats and that has higher dispersal potential than previous examples. Herein, we use mtDNA sequence data from the cytochrome *b* gene to examine the genetic architecture of California Halibut. We place these results within the context of recent and past genetic studies and show that California halibut provide yet another vexing example of the discordance between biogeographic and phylogeographic breaks in coastal California.

MATERIALS AND METHODS

Tissue samples from *P. californicus* were collected from 14 sites along the coast of California and Mexico throughout the entire effective range of the species (i.e., individuals are exceedingly rare North of San Francisco, California; Fig. 1). The northernmost site sampled was Half Moon Bay, while the southernmost site was Bahia Magdelena, Baja California Sur, Mexico. Samples were preserved in 100% ethyl alcohol and stored at room temperature.

Total genomic DNA was extracted using the DNeasy kit (Qiagen, Inc.) following manufacturer's protocol. Polymerase chain reaction (PCR) was initially performed using the primers (5′-GTGACTTGAAAAACCACCGTTG-3′) and (5′-AATAGGAAGTAT-CATTCGGGTTTGATG-3′), designed by Song *et al.* (1998) and Taberlet *et al.* (1992), respectively. Results were inconsistent with these primers, thus the species specific primers Para-CBF2 (5′- CTG ATG AAA CTT TGG CTC CCT -3′) and Para-CBR2 (5′- TAT GGG TGG AAG GGG ACT TTG TC - 3′) were designed which consistently amplified approximately 700 base pairs of the mitochondrial cytochrome *b* region. Twenty-five µl PCR reactions were prepared using BioMixRed (Bioline,USA) following manufacturer's

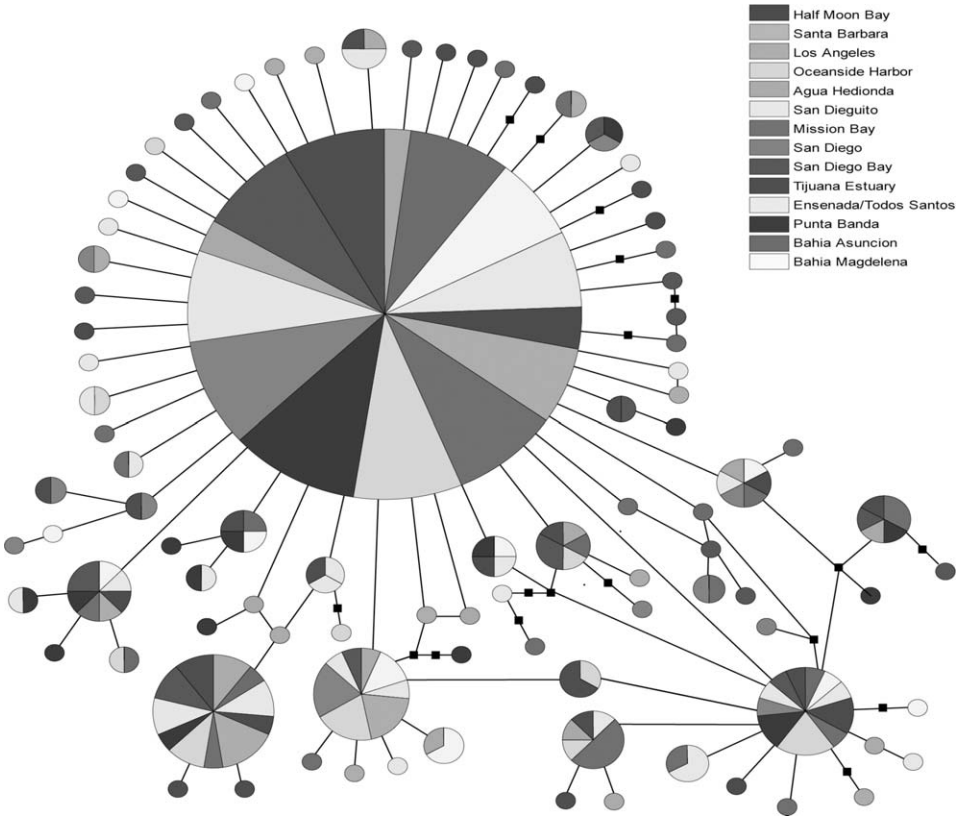

Fig. 2. *Paralichthys californicus.* Statistical parsimony network for 375 cytochrome *b* sequences. Small squares specify missing haplotypes; colors signify collection location. Circles are proportional to the number of individuals containing the haplotype with the smallest circles representing one individual.

protocols with the addition of 0.2 μM of each primer, and 10–100 ng DNA template. PCR amplifications were performed using the following cycling protocol: preliminary denaturing step for 2 min at 94°C, followed by 35 cycles of 30 s at 94°C, 45 s at 53°C, 45 s at 72°C, and a final continuous hold at 15 °C. Exonuclease I and shrimp alkaline phosphatase (ExoSAP) were used to eliminate non-incorporated oligonucleotide primers and excess dNTPs in successful amplification products. Direct sequencing of amplification products was performed in both directions using the PCR primers at the Hawai'i Institute of Marine Biology EPSCOR Sequencing Core Facility on an ABI3130 genetic analyzer.

Sequences were trimmed to a common length and collapsed to single stranded sequences using SEQUENCHER v. 4.1 (Sequencher® sequence analysis software, Gene Codes Corporation, Ann Arbor, MI USA), and aligned using CLUSTAL X (Larkin, *et al.*, 2007) with default settings. A statistical parsimony network of mtDNA haplotypes was created for *P. californicus* using the program TCS (Clement, *et al.*, 2000) under default settings (Fig. 2.). Hierarchical population structure was evaluated based on estimates of Φ_{st} for both the entire dataset and in a pairwise manner using ARLEQUIN (v. 3.11; Excoffier and Lisher, 2010). Values of haplotype and nucleotide diversity were obtained through ARLEQUIN. Departure from equilibrium conditions was assessed using Tajima's D and Fu's F_s (Table 2) as well as with mismatch distributions as calculated in ARLEQUIN. When

a unimodal distribution was found, we followed Li (1977) and Rogers and Harpending (1992), and fitted estimates of s, h_0 and h_1 to observed mismatch distributions to determine effective population sizes and time to coalescence. Coalescence analysis requires an estimate of generation time and rate of DNA evolution. Empirical values are not available for California halibut, so a range of values were used that bracket rates used in previous studies (Bowen, *et al.*, 2001). Mutation rates of 0.1–10% per million years within lineages and generation times of 1.5–10 yr were used.

A coalescence-based analysis of historical migration rates was performed using the program MIGRATE v. 3.1.6 (Beerli, 2009) to assess relative migration rates across the two hypothesized "barriers" (CTZ and LAR). The data were grouped into three pseudo-populations: North of Pt. Conception, Santa Barbara to the Tijuana Estuary, and Todos Santos to Bahia Magdalena. The Maximum Likelihood method was used under Markov Chain Monte Carlo (MCMC) search strategy of MIGRATE using default settings to estimate starting parameters for subsequent runs. A second MIGRATE analysis was performed using the estimates of Θ (N_e μ) and M (m/μ) from the first "run" as starting parameters. Estimates of Θ and M were within one order of magnitude and were thus accepted as good values following program documentation. Geographic distance between these pseudo-populations was not included in the analysis given the broad distances between individual sampling localities of the constituent members.

RESULTS

Overall, 681 base pair sequences of mtDNA cytochrome *b* were resolved for 375 individuals of *P. californicus*. Unique haplotypes were deposited in GenBank (JQ182307–JQ182398). Overall, there were 92 unique haplotypes found throughout all samples. San Diego Bay exhibited the highest number of unique haplotypes (N = 9) while Oceanside Harbor exhibited the least (N = 2). Overall nucleotide diversity was $\pi = 0.0026 \pm 0.0017$ and overall haplotype diversity was $h = 0.77 \pm 0.024$ (Table 1).

The statistical parsimony network showed a pattern consistent with the hypothesis that California Halibut represent a single, genetically homogeneous population with evenly dispersed haplotypes throughout the sampled range (Fig. 2). The fixation index (Φ_{st}) for the entire dataset was $\Phi_{st} = 0.0030$ ($p = 0.22$). In pairwise comparisons of the population, 5 out of 13 comparisons were statistically significant; however this significance was not apparent following Bonferroni correction for multiple comparisons (Table 2). Significant paiwise comparisons consistently included the open coast San Diego site. Tajima's D and Fu's F_s were negative and significant for nearly all sample locations and for the entire dataset (Table 1). Harpending's Ragedness index was $R = 0.01$ ($P = 0.98$; Fig 3).

Estimates of T, Θ_0 and Θ_1 are presented in Table 3. Estimated coalescence times did not vary depending on generation time (1.5–10yr) or mutation rate (0.1–10% per my). Coalescence times did vary, however, based on the mean, lower and upper limits of the estimated value of T (Table 3). The MIGRATE analysis indicated substantial effective migration among the three regions in a general North to South direction but not from South to North (Table 4).

DISCUSSION AND CONLCUSIONS

Point Conception has been a well-studied area due to its physical attributes and their implications for dispersal of marine organisms. Waters north of this region are characterized by strong, consistent upwelling and generally cooler surface waters, while those south of this region have weak, seasonal upwelling with relatively warmer surface

Table 1. *Paralichthys californicus.* Molecular diversity indices for 375 cytochrome *b* haplotypes. A single asterisk (*) indicates statistical significance at <0.05, double asterisk (**) indicates significance at <0.01.

Site	N	No. of Haplotypes	No. of Unique Haplotypes	Haplotype Diversity	Nucleotide Diversity	Tajima's D	Fu's F_s
California							
Half Moon Bay	17	11	5	0.8824 +/− 0.0718	0.002894 +/− 0.001925	−2.003*	−7.208**
Santa Barbara	11	7	3	0.8182 +/− 0.1191	0.002563 +/− 0.001816	−1.493	**−3.323****
Los Angeles	26	11	4	0.7785 +/− 0.0792	0.002548 +/− 0.001707	**−1.813***	**−5.633****
Oceanside Harbor	31	11	2	0.7269 +/− 0.0832	0.002078 +/− 0.001453	**−1.713***	**−6.167****
Agua Hedionda	14	10	5	0.9231 +/− 0.0604	0.003566 +/− 0.002307	−1.174	**−5.610****
San Dieguito	27	12	3	0.7350 +/− 0.0920	0.001991 +/− 0.001415	**−1.884***	**−8.713****
Mission Bay	38	19	8	0.8193 +/− 0.0621	0.003116 +/− 0.001972	**−2.251***	**−14.838****
San Diego	30	12	3	0.6805 +/− 0.0951	0.002093 +/− 0.001463	**−2.10***	**−7.805****
San Diego Bay	35	18	9	0.8185 +/− 0.0667	0.002833 +/− 0.001833	**−2.115***	**−14.841****
Mexico							
Tijuana Estuary	34	18	5	0.8093 +/− 0.0703	0.002947 +/− 0.001893	**−1.922***	**−14.662****
Ensenada/ Todos Santos	28	15	4	0.8201 +/− 0.0736	0.002785 +/− 0.001823	**−2.06***	**−11.162****
Punta Banda	35	16	6	0.7109 +/− 0.0869	0.002739 +/− 0.001786	**−2.287***	**−11.403****
Bahia Asuncion	23	9	3	0.5850 +/− 0.1222	0.001648 +/− 0.001242	**−2.269***	**−5.574****
Bahia Magdelena	26	12	4	0.7538 +/− 0.0900	0.002282 +/− 0.001569	**−2.099***	**−7.916****
All Samples	**375**	**92**	-			**−1.942***	**−8.918****

waters (Blanchette and Gaines, 2007; Diehl, *et al.*, 2007). Both the temperature difference and circulation patterns, along with discontinuities in hydrography, salinity, dissolved oxygen, and topography, suggest that marine organisms may experience restricted larval dispersal and thus increased potential for a decrease in gene flow Briggs, 1974; Seapy and Littler, 1980; Diehl, *et al.*, 2007). We found no evidence for a genetic break at Point Conception. Thus, it appears that none of the physical differences of this biogeographic boundary have affected the larval dispersal or gene flow of the California Halibut; instead they are best regarded as a single, genetically homogeneous population, at least over evolutionary time scales. These findings agree with numerous other studies examining the role of Point Conception in shaping the evolutionary history of marine organisms (Bernardi, 2000; Burton, 1998; Dawson, *et al.*, 2001; Lee and Boulding, 2007).

The California Halibut population was also continuous across the Los Angeles region (LAR). According to Dawson (2001), the LAR was fully or partially submerged before

Table 2. *Paralichthys californicus.* Population pairwise comparisons of Φ_{st} values of 375 cytochrome *b* sequences across 14 sample locations.

	Agua Hedionda	Half Moon Bay	Los Angeles	Mission Bay	Oceanside Harbor	San Deigo	San Dieguito	Santa Barbara	San Diego Bay	Bahia Asuncion	Bahia Magdelena	Ensenada/ Todos Santos	Tijuana Estuary	Punta Banda
Agua Hedionda	-	0.481	0.358	0.179	0.403	0.006*	0.230	0.395	0.155	0.072	0.029*	0.650	0.841	0.107
Half Moon Bay	−0.007	-	0.325	0.854	0.584	0.029*	0.391	0.767	0.538	0.312	0.234	0.952	0.727	0.799
Los Angeles	0.001	0.004	-	0.117	0.923	0.174	0.809	0.639	0.367	0.269	0.449	0.384	0.410	0.378
Mission Bay	0.014	−0.015	0.014	-	0.311	0.016*	0.091	0.916	0.288	0.125	0.069	0.745	0.393	0.295
Oceanside Harbor	0	−0.007	−0.018	0.003	-	0.059	0.662	0.521	0.344	0.288	0.381	0.862	0.721	0.437
San Diego	0.065*	0.030*	0.011	0.029*	0.020	-	0.199	0.299	0.327	0.458	0.690	0.011*	0.015*	0.063
San Dieguito	0.013	0.001	−0.015	0.016	−0.009	0.008	-	0.526	0.578	0.736	0.501	0.358	0.292	0.719
Santa Barbara	0.002	−0.018	−0.014	−0.028	−0.007	0.008	−0.006	-	0.775	0.431	0.705	0.519	0.605	0.814
San Diego Bay	0.018	−0.004	0.001	0.003	0.002	0.003	−0.004	−0.018	-	0.962	0.261	0.244	0.157	0.791
Bahia Asuncion	0.039	0.005	0.005	0.013	0.006	0	−0.011	0	−0.018	-	0.422	0.255	0.133	0.961
Bahia Magdelena	0.046*	0.010	0	0.018	0.001	−0.007	−0.002	−0.016	0.005	0	-	0.122	0.056	0.542
Ensenada/ Todos Santos	−0.012	−0.024	0	−0.008	−0.014	0.036*	0.001	−0.006	0.005	0.007	0.015	-	0.924	0.625
Tijuana Estuary	−0.022	−0.012	−0.002	0	−0.010	0.036*	0.004	−0.012	0.010	0.018	0.024	−0.014	-	0.204
Punta Banda	0.023	−0.013	0.001	0.003	−0.001	0.013	−0.007	−0.020	−0.007	−0.015	−0.003	−0.005	0.007	-

"*"indicates values are significant following Bonferroni correction. Values below diagonal are Φ_{st}, and above the diagonal are p values.

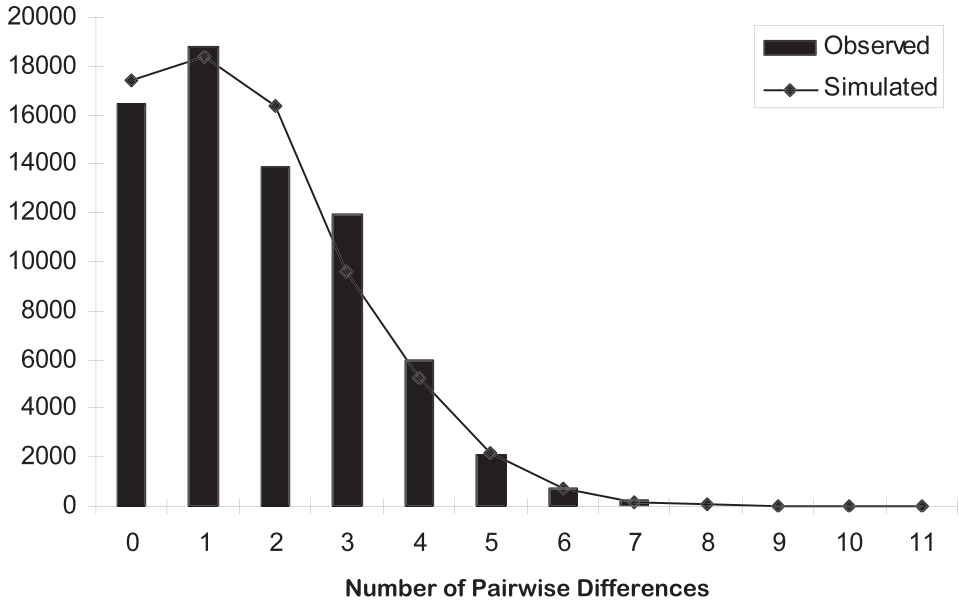

Fig. 3. Mismatch distribution for cytochrome *b* sequences of *Paralichthys californicus*. Harpending's "r" = 0.01 (P = 0.98).

the Late Pleistocene. Similar to the present day conditions, with a substantially-sized area submerged, there was an increase in shallow, coastal habitat available for marine organisms, particularly those that inhabit estuaries and bays. During the last ice age, the LAR subsequently emerged, leading to a significant loss of shallow coastal habitat. However given the complete loss of shallow coastal habitats elsewhere, the LAR may have provided glacial refuge given what little habitat remained in the LAR. This emergence most likely wiped out some coastal populations and created phylogeographic breaks in certain lineages (Ahnelt, *et al.*, 2004; Bernardi, 2005; Dawson, *et al.*, 2001; Dawson *et al.*, 2002), suggesting that historical fluctuations in sea level were likely key factors that contributed to these breaks (McGovern, *et al.*, 2010; Marko and Hart, 2011). Although populations of California Halibut may have been affected by this alteration in habitat across the LAR, we do not see evidence of a genetic break in the halibut population supporting this hypothesis. In addition, the estimated coalescence time for California Halibut of approximately 160,000 yr before present does not correlate with the last glacial cycle, an event that would have been recognized if populations were severely affected by the loss in habitat with the emergence of the LAR.

Table 3. Estimates of Tau (T), Theta naught (θo), Theta one (θ1), and Coalescence Times (CT; yr).

	Lower Bound	Mean	Upper Bound
T	0	2.175	5.262
θo	0	1.513	0.045
θ1	1.129	41215	Infinity
CT	13,656	159,691	330,837

Table 4. MIGRATE estimates of migrants (M) per generation, Θ, and likelihood scores (L). Top row indicates population from which migrants leave while left columns are recipient localities.

	L	Θ	North	Middle	South
North	1.993	0.0081	*	~0	31
Middle	1.993	0.0298	2920	*	~0
South	1.993	0.1154	2050	503	*

The MIGRATE analysis indicated that the three pseudopopulations were highly connected in a general North to South direction. This could represent longer-term gene flow over several thousand generations being affected by the general motion of the California Current. However, nearshore current fields, which may be those most expected to influence California halibut during their larval stage, are chaotic and generally do not echo the constant flow of the California current (Mitarai, *et al.*, 2009; White *et al.*, 2010).

Our results showed statistical pairwise differences of California Halibut in only the San Diego location. However, there are no obvious reasons for this phenomenon. For example, there are no differences in sizes or ages from the samples at San Diego which could suggest sampling a single cohort which may skew population signals and there are no geographic features which might be acting as a physical barrier.

The marine taxa that demonstrate phylogeographic structure in the LAR, mainly species of the family Gobiidae, share certain qualities that are susceptible to population bottlenecks during these periods, and these species tend to show deeper phylogeographic structure (e.g., they are egg layers, have low adult vagility and inhabit patchy supra-tidal or estuarine habitats, which presumably limits their dispersal capabilities). Halibut, however, have planktonic eggs and larvae, are more mobile as adults, and they also reside in continuous, sub-tidal habitats, factors that would suggest a refuge may not have been necessary or advantageous during Pleistocene sea level fluctuations and concomitant changes in habitat (Dawson, *et al.*, 2002). These differences in life history characteristics may explain why certain taxa show phylogeographic structure at LAR while others do not, including the California Halibut. In addition, other factors, including ecological parameters (e.g., kelp habitat and ocean circulation) may influence subtle genetic ''patchiness'' in California's marine species (Selkoe, *et al.*, 2010). The physical and biological factors mentioned above may thus work in concert with biological characteristics to design the genetic architecture of marine species in California.

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