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Metapopulation structure informs conservation management in a heavily exploited coastal shark (*Mustelus henlei*)

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ABSTRACT: The identification of historical, environmental and biological factors influencing metapopulation connectivity is important for informing management policies and for designing conservation areas to protect biodiversity. The brown smooth-hound shark *Mustelus henlei* is a key component of the Mexican commercial shark fisheries, one of the largest in the world. However, Mexico lacks conservation management policies for this heavily exploited species. We conducted phylogeographic and population genetic analyses using data from mitochondrial and nuclear DNA markers and from oceanographic variables to assess metapopulation connectivity in *M. henlei* from the Gulf of California and the Pacific coast of Baja California. We report on historical range expansion during the Pleistocene, probably associated with the last stages of formation of the Gulf of California. From a contemporary perspective, there is significant population structure explained by spatial distance (but not by environmental factors), which contrasts with expectations of high dispersal capacity for this shark. Population- and individual-based genetic analyses suggest that both female philopatry and male-biased dispersal impact on metapopulation structure. These results highlight the importance of protecting nursery areas and habitat connectivity for the conservation management of the species. Our study clarifies important biological aspects of the brown smooth-hound shark that have implications for the design of shark management policies and marine protected areas in the Gulf of California, an iconic marine ecosystem of global significance.

KEY WORDS: Marine connectivity · Philopatry · Seascape genetics · Elasmobranchs · Conservation genetics · Gulf of California

INTRODUCTION

The ecological importance of sharks in marine ecosystems is being increasingly recognized. Nevertheless, elasmobranchs are considered one of the most threatened biological groups due to expanding fisheries and degradation of coastal habitats worldwide (Dulvy & Forrest 2010, Ferretti et al. 2010). The implementation of shark management policies has been extremely difficult given the general absence of relevant biological information for most species (Musick et al. 2000, Herndon et al. 2010). In the absence of traditional life-history studies, inferences from genetic data can provide valuable information regarding an organism's natural history, particularly with respect to population connectivity, stock structure and metapopulation dynamics (Schwartz et al. 2007).

The identification of genetic discontinuities in marine habitats has been particularly challenging, as there are many highly mobile marine organisms distributed continuously over large spatial scales (Palumbi 2003, Reiss et al. 2009). Nevertheless, with advances in the type and amount of genetic data that can be amassed, as well as in the statistical methods to analyse them (Beaumont & Rannala 2004, Guillot et al. 2009, Davey et al. 2011), a growing number of sur-

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veys indicate that several marine species are structured into metapopulations at various geographic scales (Palumbi 2003, Hauser & Carvalho 2008, Pelc et al. 2009). For a long time, elasmobranchs were neglected in studies of both historical (Beheregaray 2008) and contemporary (Dudgeon et al. 2012) connectivity. Recently, several studies reported population structure at small geographic scales (100s of km) for coastal elasmobranchs that display wide distributions and high mobility. This structure has been attributed mainly to geophysical barriers (Sandoval-Castillo & Rocha-Olivares 2011, Portnoy et al. 2014) or, more frequently, to site fidelity (Mourier & Planes 2013, Vignaud et al. 2013, Feldheim et al. 2014, Ashe et al. 2015). It appears that a lack of congruence between dispersal potential and realized dispersal due to philopatry is not uncommon in coastal sharks; however, determining whether or not this is the case is important to inform management of highly exploited species (Worm et al. 2013, Dulvy et al. 2014).

The brown smooth-hound shark *Mustelus henlei* (Gill, 1863) is an epibenthic shark with a distribution from Oregon, USA, to the Gulf of California (GC), Mexico, and from Ecuador to north of Peru (Compagno 1984). This species is common in coastal waters from the intertidal zone to depths of 200 m (Ebert 2003). It is a placental viviparous shark with relatively early maturity (2 to 3 yr; Yudin & Cailliet 1990) and high fecundity (1 to 20 pups yr^{-1}; Pérez-Jiménez & Sosa-Nishizaki 2008). The maximum length reported is 100 cm (Yudin & Cailliet 1990). There is no information about the extent or direction of long-term migrations; however, one study in Tomales Bay (California) reported fine-scale movements with immigration in summer and emigration in winter, which suggests a degree of site fidelity (Campos et al. 2009). The distance travelled was on average 15.3 km d^{-1} (Campos et al. 2009), suggesting that *M. henlei* is capable of moving over vast distances over longer periods. Moreover, the presence of the species in the northern and southeastern Pacific (Compagno 1984) may be evidence for trans-equatorial migrations.

M. henlei has been commercially fished since the late 1980s, and today it is one of the most significant components of the large elasmobranch fishery along the Baja California peninsula (BCP) and the GC. This species represents ~30% of the annual coastal shark catch in the region, corresponding to around 5000 t and over 300 000 individuals (Pérez-Jiménez & Sosa-Nishizaki 2008, Bizzarro et al. 2009, Smith et al. 2009, INAPESCA 2010). Despite the heavy fishing pressure, there is no report of declining *M. henlei* stocks in Mexico. However, lack of evidence can be attributed to very limited species-specific catch statistics and absence of long-term monitoring of fishing activities and landings. Most landing statistics about Mexican elasmobranch fisheries are based on multispecies data, and systematic observations of the commercial activity are almost nonexistent; the few available historical data are probably grossly underestimated (Pérez-Jiménez & Sosa-Nishizaki 2008, Bizzarro et al. 2009, Smith et al. 2009, INAPESCA 2010). Moreover, the current Mexican legislation for elasmobranch fisheries, NOM-029-2006, lacks species-specific policies due to poor or nonexistent biological data for most species and populations. Although the life history of *M. henlei* is relatively well known in California (Ebert 2003), biological studies of this species are essentially absent in Mexico. Exceptions are a genetic analysis that shows high prevalence of multiple paternity in litters of *M. henlei* from the western coast of Baja California (Byrne & Avise 2012) and a study on reproductive biology in the upper region of the GC that suggests a distinct population of *M. henlei* compared to that found along the southwestern coast of the United States (Pérez-Jiménez & Sosa-Nishizaki 2008). Clarifying population structure is critical for the conservation management of exploited marine fishes because low but significant population differentiation can have major demographic and evolutionary consequences for the species (Palumbi 2003, Knutsen et al. 2011). Assessments of population structure and connectivity of *M. henlei* in Mexico are therefore a priority, to provide more realistic demographic parameters for the management of this heavily exploited shark.

The GC shows complex oceanographic and geological features and is well known for its exceptional biodiversity and conservation importance (Roberts et al. 2002, Sala et al. 2002, Enríquez-Andrade et al. 2005). Four well-delimited oceanographic regions are recognised (see Fig. 1; Lavín & Marinone 2003). The Upper Gulf (UG) has shallow waters (<100 m on average), high salinity (up to 40), large temperature variation (9 to 38°C) and large tidal ranges (>6 m). The Islands (IG) region has channels over 500 m deep and is characterized by strong tidal-mix upwellings that maintain high productivity and low temperatures (~11°C) throughout the year. The Lower Gulf (LG) has a series of geostrophic gyres affecting the circulation and thermodynamics of the area across all seasons. Finally, the region known as Open Gulf (OG) is similar to the LG but with fewer gyres and a greater influence of oceanic waters from the Pacific (Lavín & Marinone 2003). The Pacific coast of the BCP is divided into North Pacific (NP)

and South Pacific (SP) regions by an important biogeographic break around the mid BCP. This break is related to the convergence of currents with a dramatic temperature difference and the presence of semipermanent oceanographic eddies (Bernardi et al. 2003, Jacobs et al. 2004). We propose that these oceanographic conditions create environmental discontinuities, and perhaps physiological barriers, that could limit elasmobranch dispersal between bioregions, both within the Gulf of California and between the gulf and the Pacific coast.

The GC and the Pacific coast of the BCP in Mexico (GC-BCP) also shows a complex geological history that could have impacted the biogeography of its coastal marine fauna (e.g. Bernardi et al. 2003, Sandoval-Castillo & Rocha-Olivares 2011, Bernardi 2014). A transitory proto-gulf was formed ~12 million years ago (Mya) with the emergence of small islands and the detachment of a proto-peninsula from the mainland (Murphy & Aguirre-Leon 2002). Around 5.5 Mya, the permanent GC was formed, but it remained connected to the Pacific Ocean by channels between islands and the proto-peninsula. By the early Pleistocene (~2.8 Mya), emerging land and fluctuations in sea level closed the channels, joining the islands and the proto-peninsula to subsequently form the present-day BCP (Murphy & Aguirre-Leon 2002). The dynamic history of the area could have produced multiple events of population fragmentation and range expansion, potentially influencing the genetic architecture of both gulf and open coast elasmobranch populations (e.g. Sandoval-Castillo et al. 2004, Sandoval-Castillo & Rocha-Olivares 2011, Castillo-Páez et al. 2014).

In this study, we carried out phylogeographic and population genetic analyses to assess metapopulation structure and connectivity in *M. henlei* from the GC-BCP. Genetic data from samples collected across all bioregions of the GC-BCP were combined with information from oceanographic variables to assess the relative influence of historical biogeography and contemporary oceanography in metapopulation structure. The putatively high dispersal capacity predicted for *M. henlei* (Campos et al. 2009) and the known geomorphology of the GC-BCP suggest that *M. henlei* would be comprised of a panmictic population with a history of colonization associated with the late stages of formation of the GC. Our findings support the historical prediction, but from a contemporary perspective, they instead indicate significant metapopulation structure influenced by a combination of spatial distance between demes and female philopatric behaviour. Our study has implications for understanding factors that underpin population structure in a highly mobile and economically important coastal shark. It also contributes novel information for the design of shark management policies and marine protected areas in the Gulf of California, an iconic marine ecosystem of global significance.

METHODS

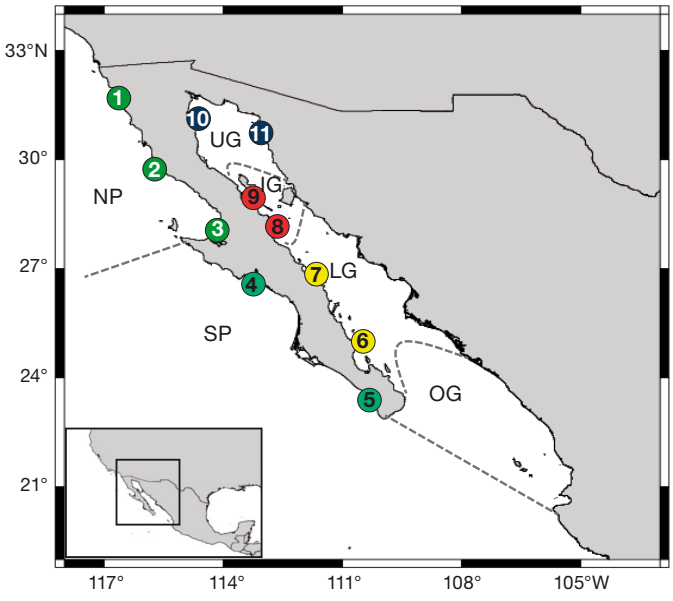
Sampling

Between March and July 2008, sampling was conducted at 11 localities around the BCP and the GC where commercial fishermen often land elasmobranchs. All samples were obtained from fishing trips conducted using bottom-set gillnets at 20 to 180 m deep and up to 75 km away from landing sites. The localities were selected to cover 3 bioregions in the gulf (UG, IG, LG) and 2 bioregions along the Pacific coast (NP and SP) (Fig. 1). Muscle tissue samples of 141 *Mustelus henlei* (82 females, 38 males and 21 unsexed) were collected and stored in ~95% ethanol. Samples of codistributed *M. californicus*, *M. lunulatus* and *M. albipinnus* were also collected from the UG and used to confirm the identification of *M. henlei* samples.

Genetic markers

We extracted genomic DNA using a salting out protocol (Sunnucks & Hale 1996). A ~600 bp fragment of the mitochondrial control region was amplified using conditions described in Sandoval-Castillo & Rocha-Olivares (2011). We designed primers (FPre200 5′-RYC YTT GGC TCC CAA AGC-3′ and RCR900 5′-GGG MGG RCK RKA AAT CTT GA-3′) using conserved elasmobranch sequences from GenBank (accession numbers AF106038, Y16067, NC003137, NC000890, EU528659.1). The PCR products were sequenced using primer FPhe200 and BigDye Terminator chemistry in an ABI 3730 automated sequencer (Applied Biosystems), and sequences were aligned using Sequencher 4.7 (Gene Codes Corporation).

We PCR-amplified 12 polymorphic *Mustelus* microsatellite markers based on conditions described in Boomer & Stow (2010). Scanned data were analysed to detect bins using GeneMapper 4.0 (Applied Biosystems). Micro-Checker 2.2.3 (Van Oosterhout et al. 2004) was used to assess scoring errors and null alleles in the amplified genotypes. Additionally, tests of locus independence and Hardy-Weinberg equilibrium were conducted using Genepop 4.0 (Rousset



		n
(NP)	**North Pacific**	**25**
(1)	Popotla	5
(2)	San Quintin	11
(3)	Laguna Manuela	9
(SP)	**South Pacific**	**23**
(4)	San Ignacio	10
(5)	Todos Santos	13
(LG)	Lower Gulf	24
(6)	La Paz	19
(7)	Mulege	5
(IG)	**Islands**	**30**
(8)	El Barril	15
(9)	Bahia de los Angeles	15
(UG)	**Upper Gulf**	**39**
(10)	San Felipe	20
(11)	Puerto Peñasco	19
Total		**141**

Fig. 1. Gulf of California and Baja California peninsula showing the 11 sampling sites for *Mustelus henlei*. Bioregions are separated by dashed lines. For the Pacific Ocean, bioregions include the North Pacific (NP, localities 1–3) and South Pacific (SP, localities 4 and 5), and for the Gulf of California, bioregions include the Lower Gulf (LG, localities 6 and 7), Islands (IG, localities 8 and 9), Upper Gulf (UG, localities 10 and 11) and Open Gulf (OG, not sampled)

2008) with a Bonferroni adjustment at 95% CI and 1000 randomisations. Six microsatellites (MaND5, MaWGT, Ma07B, MaWD7, Ma6B5 and MaD2X), amplified consistently, were polymorphic and did not show significant linkage disequilibrium between pairs of loci or deviations from Hardy-Weinberg equilibrium — these were the markers selected for subsequent analyses.

Data analysis

Historical analyses: population demography and migration

Historical migration among regions was estimated in Migrate-n 3.2.6 (Beerli & Palczewski 2010) for both the mtDNA and the microsatellite datasets. This software implements an expansion of coalescence theory which considers migration and uses a Bayesian algorithm to sample coalescent genealogies that best fit the given genetic data under a specific mutation model. We used the mutational model of Felsenstein (F84; Felsenstein & Churchill 1996) for mtDNA sequences and the Brownian motion model for microsatellite data. For both datasets, we ran 1 long chain, 3 replicates, 200 000 sampled genealogies, 100 sampling increments, burn-in of 1000 trees per chain and a static heating scheme of 4 temperatures (1, 1.5, 3 and 100). Since a calibrated molecular clock is not available for *Mustelus*, the demographic parameters were estimated considering mutation rates of $\mu = 4 \times 10^{-8}$ and 1×10^{-3} for mtDNA and microsatellites, respectively, which are commonly used in elasmobranchs (Duncan et al. 2006, Corrigan et al. 2008, Karl et al. 2011). To examine past population dynamics, we calculated Fu's F_S (Fu 1997) in Arlequin (Excoffier & Lischer 2010) and tested for significance using 1000 simulations. If population sizes have been stable, this statistic is expected to return values close to zero. Significantly negative or positive values of F_S are expected under population expansion or bottleneck scenarios, respectively. The distribution of pairwise differences among haplotypes (mismatch distribution) was also assessed in Arlequin as a way to test for historical demographic expansion. This was conducted using Harpending's raggedness index with 10 000 replicates.

Spatial population structure, contemporary migration and sex-biased dispersal

Levels of genetic differentiation among populations were estimated by calculating the pairwise fixation indices Φ_{ST} for mtDNA and F_{ST} for microsatellites. Hierarchical patterns of population structure were tested for both marker types using an analysis of molecular variance (AMOVA) in Arlequin. AMOVA divides the total variance into covariance components, in this case variance within sampling localities, among localities and among bioregions (NP, SP, LG, IG, UG). Localities were assigned to biogeographic regions according to

Lavín & Marinone (2003; see Fig. 1). Hierarchical fixation indexes were tested for significance using 1000 permutations.

To determine the geographic scale of genetic similarity across different distance classes, a spatial autocorrelation test was performed using the microsatellite data in Genalex 6.4 (Peakall & Smouse 2006). This estimates an autocorrelation coefficient (r) between all pairs of individuals whose geographical separation is in a specified distance class. By random permutation of genotypes, a null distribution of r-values is then generated under the assumption of no geographical structure. Finally, the statistical significance of each empirical r-value is tested against a null distribution (Smouse & Peakall 1999). Runs were conducted for all samples, as well as for females and males separately, using 10 000 permutations and 1000 bootstraps. Using the same program, an assignment-based test was performed to assess differences in dispersal between sexes, a pattern generally expected for elasmobranchs (Portnoy & Heist 2012). This method estimates an assignment index corrected (AIc) for the probability of an individual being born locally (Favre et al. 1997). Individuals with higher dispersal should show negative values, while those that are less dispersing will show positive values (e.g. Möller & Beheregaray 2004). Mean AIc values were compared between sexes and statistically assessed with a Mann-Whitney *U*-test.

Table 1. Sampling localities, bioregions and summary of mitochondrial and nuclear genetic diversity in *Mustelus henlei*. n: sample size; *H*: number of haplotypes; *h*: haplotype diversity; π: nucleotide diversity; H_O: heterozygosity observed; H_E: heterozygosity expected; *A*: mean number of alleles per locus

	Mitochondrial sequences				Microsatellites		
	n	*H*	*h*	π(%)	H_O	H_E	*A*
North Pacific	**25**	**10**	**0.647**	**0.22**	**0.680**	**0.691**	**6**
Popotla	5	1	0.000	0.00	0.730	0.700	3.7
San Quintin	11	6	0.800	0.27	0.682	0.672	4.7
Laguna Manuela	9	5	0.722	0.28	0.648	0.699	4.7
South Pacific	**23**	**7**	**0.708**	**0.20**	**0.754**	**0.713**	**5.7**
San Ignacio	10	6	0.778	0.27	0.700	0.657	4.0
Todos Santos	13	5	0.692	0.15	0.795	0.741	5.5
Lower Gulf	**24**	**12**	**0.888**	**0.36**	**0.696**	**0.683**	**5.1**
La Paz	19	12	0.918	0.40	0.694	0.690	5.0
Mulege	5	4	0.900	0.23	0.700	0.663	3.5
Islands	**30**	**11**	**0.881**	**0.39**	**0.683**	**0.643**	**4.8**
El Barril	15	9	0.914	0.41	0.678	0.679	4.7
Bahia de los Angeles	15	9	0.886	0.37	0.689	0.594	4.0
Upper Gulf	**39**	**8**	**0.823**	**0.31**	**0.738**	**0.679**	**5.7**
San Felipe	20	8	0.853	0.33	0.758	0.693	5.5
Puerto Peñasco	19	8	0.842	0.31	0.717	0.662	4.8
Total	**141**	**24**	**0.840**	**0.33**	**0.712**	**0.684**	**7.0**

Ecological versus spatial isolation

Isolation by geographical and/or ecological distances was tested using partial Mantel tests in IBWS 3.16 (Jensen et al. 2005). This nonparametric test assesses correlation among 3 distance matrices, in this case a genetic, a geographical and an ecological matrix. The genetic matrix was based on fixation indices (Φ_{ST} for mtDNA and F_{ST} for microsatellites) between localities. Geographical distances were estimated as the linear distances along the coastline between sampling localities based on Google Earth (5.1.2009). Finally, as ecological distances, we used the average annual data for the last 100 yr of 6 key oceanographic variables (surface temperature, salinity, oxygen, nutrients, chl *a* and bathymetry) obtained from the NOAA World Ocean Data Base (www.nodc.noaa.gov/OC5/WOD/pr_wod.html). Distances were calculated as the differences between sampling sites in the mean of these variables, predicted to potentially impact on the distribution and dispersal of coastal sharks.

RESULTS

Genetic diversity

A total of 24 mitochondrial haplotypes were resolved in *Mustelus henlei*, and these confirmed the identification of samples done in the field. The most common haplotype (32.6% of samples) was found at all localities, whereas the 3 most common haplotypes (63.1%) were found in all bioregions (Fig. 1). Overall, there was high haplotype diversity (0.840) but low nucleotide diversity (0.33%). Haplotype diversity varied widely across localities (0 to 0.918). Variability in the nuclear markers was also moderate to high, both in number of alleles per locus (5 to 10, mean = 7) and in observed heterozygosity (0.594 to 0.704, mean = 0.677). Nuclear and mtDNA diversities were generally higher in the GC than along the Pacific coast (Table 1).

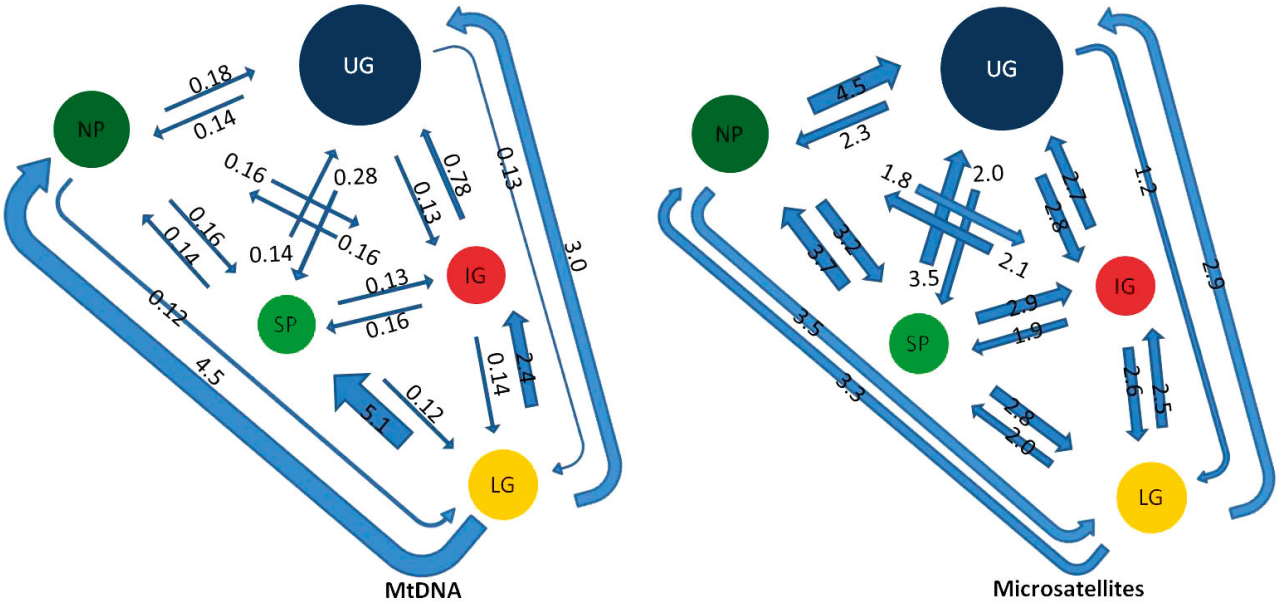


Fig. 2. Historical gene flow of *Mustelus henlei* between bioregions: North Pacific (NP), South Pacific (SP), Lower Gulf (LG), Islands (IG) and Upper Gulf (UG). Thickness of arrows is proportional to the effective number of migrants per generation (N_em) based on $N_em = \Theta M$ and $N_em = \Theta M/4$ from mitochondrial and microsatellite data, respectively, where Θ is the estimator for population size, and M is the estimator for gene flow. Size of the circles is proportional to Θ

Historical migration and demographic expansion

The coalescent-based estimates of the number of effective migrants per generation suggest that bioregions have been historically connected (Fig. 2). The magnitude of migration was considerably greater based on the nuclear compared to the mtDNA dataset, including comparisons between NP and UG bioregions, which are currently separated by more than 1500 km.

Fu's F_S statistics suggest demographic expansion, being negative for all bioregions and also when pooling samples from the 2 areas (i.e. GC and Pacific coast; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m533p191_supp.pdf). Mismatch distributions are consistent with these results, being unimodal for all bioregions and not statistically different from a sudden expansion model (see Fig. S1 in the Supplement). The time since population expansion in bioregions ranged from 0.7 to 2.4 Mya, with a slightly more recent estimate of expansion for the Pacific coast (Table S1).

Contemporary metapopulation structure

Relatively low but statistically significant population genetic differentiation was detected among localities in both mitochondrial (mean Φ_{ST} = 0.042, p = 0.04) and microsatellite (mean F_{ST} = 0.017, p < 0.0001) datasets. Pairwise comparisons between localities indicated nil to moderate values of differentiation based on mtDNA (Φ_{ST} = 0.0000 to 0.2399) and microsatellites (F_{ST} = 0.0000 to 0.0105). Values of fixation indices were generally higher between GC and Pacific coast localities than between localities within each coast (Table S2 in the Supplement), but there is no significant mtDNA or nuclear variation explained by the separation of the GC and Pacific coast (Φ_{ST} = 0.069, p = 0.06; F_{ST} = 0.006, p = 0.08) (Table S3). The AMOVAs revealed significant mtDNA variation among bioregions (Φ_{CT} = 0.066, p = 0.003) and nuclear variation among localities within bioregions (F_{SC} = 0.011, p = 0.025) (Table 2).

Isolation by geographical and environmental distances

Mantel tests showed significant correlations between genetic and geographical distances for both the mtDNA (p = 0.0001) and microsatellite (p = 0.003) datasets (Fig. S2 in the Supplement). Accordingly, for microsatellites, spatial autocorrelation analysis revealed significant positive autocorrelation (i.e. greater than random genetic similarity) among individuals sampled at the same locality (r = 0.011, p = 0.001) (Fig. 3A). The overall agreement between

Table 2. Hierarchical analysis of molecular variance (AMOVA) in *Mustelus henlei* based on microsatellites and mtDNA. AMOVA for 13 localities and 5 bioregions (North Pacific, South Pacific, Lower Gulf, Islands, Upper Gulf). Values in **bold** denote significant results ($p < 0.05$)

	Microsatellites % variation	Fixation index	p	mtDNA % variation	Fixation index	p
Among bioregions	0.6	F_{CT} = 0.006	0.1916	6.67	Φ_{CT} = **0.066**	**0.004**
Among localities	1.1	F_{SC} = **0.011**	**0.0254**	0	Φ_{SC} = 0.000	0.853
Within localities	98.3			95.79		
Total		F_{ST} = **0.017**	**<0.0001**		Φ_{ST} = **0.0420**	**0.028**

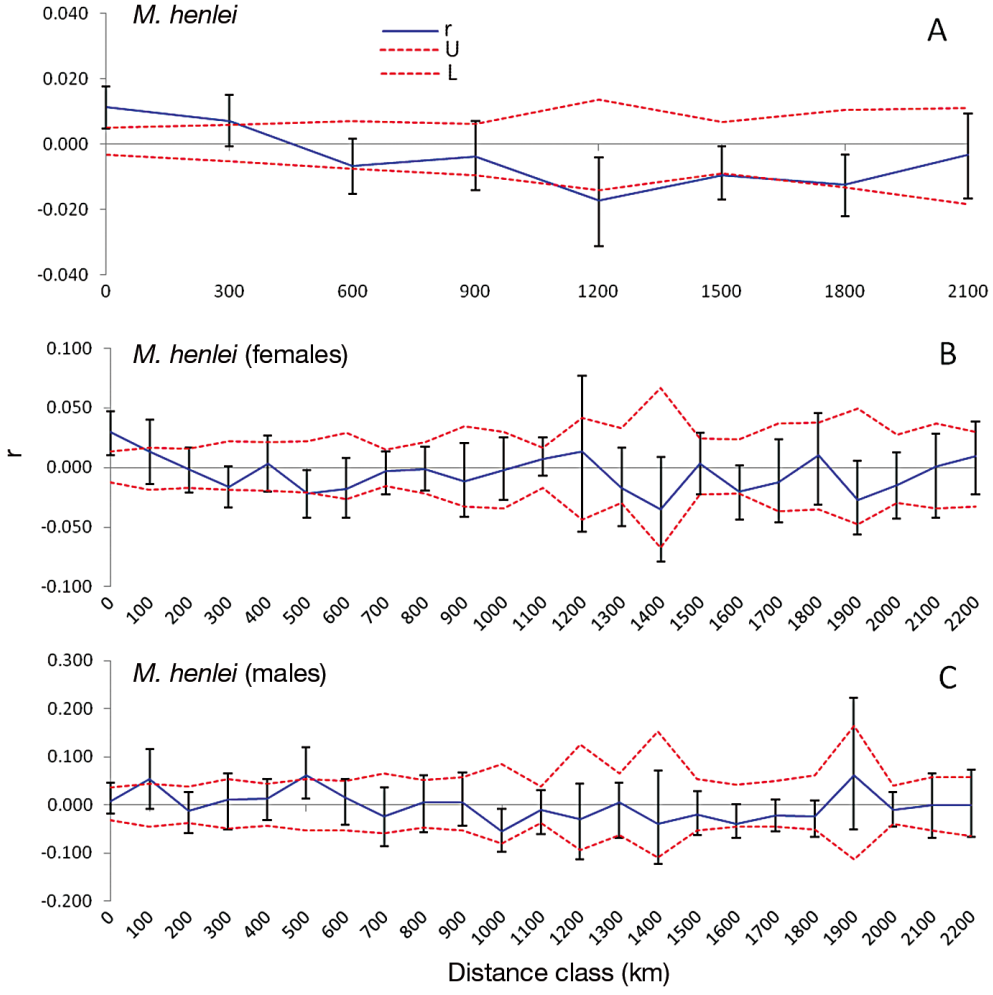


Fig. 3. Correlogram plots of the spatial autocorrelation coefficient r based on microsatellite data for *Mustelus henlei*. Upper (U) and lower (L) bounds at 95% confidence. (A) All samples; (B) females; (C) males

mitochondrial and nuclear datasets points to a biologically sound pattern of structure instead of statistical issues due to the relatively small number of microsatellite loci used. The analysis of ecological isolation showed that salinity, nutrient concentration and bathymetry might impact the genetic structure observed. However, none of these environmental variables were correlated with genetic structure after correcting for geographical distances (Table 3). These results suggest that the oceanographic factors considered in this study have little effect on the genetic structure of *M. henlei*, whereas geographical distance plays a more important role in influencing population isolation.

Table 3. Analysis of isolation by ecological and geographical distance in *Mustelus henlei* showing correlation values between genetic (mtDNA and microsatellites), geographical and environmental distance across all localities. The last 4 columns show correlation values for genetic and environmental distances after controlling for geographical distances. Values in **bold** denote significant correlations ($p < 0.05$)

	mtDNA		Microsatellites		Contr. for geogr. distance			
					mtDNA		Microsatellites	
	r	p	r	p	r	p	r	p
Geographical distance	0.669	**<0.001**	0.486	**0.003**				
Surface temperature	0.282	0.138	0.165	0.199	−0.328	0.997	−0.328	0.747
Salinity	0.641	**0.002**	0.423	**0.009**	−0.465	0.606	0.016	0.573
Oxygen saturation	0.091	0.312	0.145	0.437	0.097	0.217	0.097	0.404
Nutrients concentration	0.575	**0.007**	0.032	0.116	0.185	0.072	0.018	0.654
Chl *a* concentration	0.022	0.799	0.023	0.854	−0.316	0.953	−0.316	0.923
Bathymetry	0.453	**0.017**	0.236	0.063	−0.298	0.064	−0.298	0.078

Sex-biased dispersal

Our data support male-biased dispersal. Spatial autocorrelation correlograms were different for the 2 sexes. While females show positive significant correlation among individuals from the same locality (r = 0.03, p = 0.001) (Fig. 3B), correlation for males did not depart from the random distribution of genotypes (Fig. 3C). Moreover, mean AIc values were negative for males (−0.092) and positive for females (0.043), also suggesting male-biased dispersal, although this difference was not statistically significant ($Z = -0.722$, p = 0.470). The pattern of sex-biased dispersal inferred by individual-based analyses was also consistent with the population-level analyses described above, which consistently showed higher levels of gene flow based on biparentally inherited markers and greater population structure based on the maternally inherited mtDNA.

DISCUSSION

Our analyses support the hypothesis of a historically connected metapopulation of the brown smooth-hound *Mustelus henlei,* which is currently composed of partially isolated demes in different bioregions in the GC and the BCP. Despite the suggested high dispersal potential for *M. henlei*, our results strongly indicate a pattern of isolation by geographical distance among localities (particularly between the GC and the Pacific coast) and no evidence for structure associated with the complex environmental discontinuities of the region. We also show that females preferentially remain in their natal area and that dispersal in *M. henlei* is probably male-biased. Our results have important implications for conservation management programs of the heavily exploited *M. henlei* fishery of the GC and also for other coastal epibenthic sharks with presumably high dispersal potential and similar life histories.

Population history

The historical analyses of demography and migration consistently indicate that *M. henlei* expanded its range concomitantly with the formation of the GC, without experiencing vicariant subdivision in the study area. A strong signal of Pleistocene population expansion was recovered for the species based on mismatch analysis, a result supported by Fu's F_S statistics. We propose that the last stages of formation of the GC during the early Pleistocene (e.g. Murphy & Aguirre-Leon 2002) provided new habitat and opportunities for both demographic and range expansions. It is thought that the demography of several species of elasmobranchs around the world were influenced by Pleistocene glacial cycles (Chevolot et al. 2006, Duncan et al. 2006, Schultz et al. 2008, Corrigan & Beheregaray 2009). These past climatic changes are known to have caused significant alterations to marine ecosystems, including the creation of vast areas of new habitat (Hewitt 2000). The signal of spatial expansion together with more recent demographic growth along the Pacific coast (Table S1, Fig. S1 in the Supplement) supports the idea of colonisation events from the GC to the Pacific coast. This is consistent with suggestions that the last glacial cycling had weaker effects inside the GC, allowing it to function as a warm refuge for temperate species during glaciation periods and as a centre of origin during interglacial periods (Jacobs et al. 2004).

The BCP has been reported as an important biogeographic barrier for several species of fish, invertebrates, mammals (Bernardi et al. 2003, Jacobs et al. 2004) and elasmobranchs (Sandoval-Castillo et al. 2004, Sandoval-Castillo & Rocha-Olivares 2011, Castillo-Páez et al. 2014). Nonetheless, we found no significant differences between Pacific coast and GC samples of *M. henlei* (Table S3). In addition, the Migrate-n analysis detected strong gene flow between all regions, including those separated by the BCP and by over 1500 km of contemporary coastline.

Gene flow estimated using coalescent-based methods is strongly influenced by historical events (Kuhner 2009). Therefore, the high gene flow between Pacific coast and GC regions detected with Migrate-n likely reflects historical rather than contemporary connectivity. The historical connectivity is likely the fingerprint of events of recent colonization (~1 Mya), as suggested by the mismatch distribution analysis and summary statistics. Overall, *M. henlei* appears to be a recent colonizer in the GC-Pacific coast and shows no phylogeographic breaks related to the region's vicariant biogeographic history.

Contemporary metapopulation structure and sex-biased dispersal

Our results indicate that *M. henlei* shows low, but significant, levels of population genetic structure, with partially isolated demes found in different bioregions of the GC and the BCP. This contrasts with tag-based estimates of dispersal for *M. henlei* that suggest high migration potential, such as over 15 km d^{-1} (Campos et al. 2009). This distance is similar to the >1000 km in 3 mo reported for a related species, *M. lenticulatus*, in New Zealand (Francis 1988). Despite the presumably high dispersal potential of *Mustelus*, genetic structure over relatively short distances (<500 km) has been reported for *M. manazo* from Japan (Chen et al. 2001). We suggest that although *M. henlei* can disperse long distances, individuals return or preferentially use a few key areas for breeding, which results in fine-scale genetic structure.

A growing number of population genetic studies elsewhere have reported that environmental discontinuities, including those related to fine-scale oceanographic processes, provide better explanations for patterns of population structure in coastal species rather than biogeographic history (Galindo et al. 2006, Banks et al. 2007, Mendez et al. 2010). In the GC, studies have reported associations between the distribution of zooplankton (Brinton & Townsend 1980), phytoplankton (Round 1967) and bony fishes (Walker 1960, Riginos 2005, Peguero-Icaza et al. 2008) and the gulf's bioregions and their unique oceanographic patterns. Although the microsatellite and mtDNA datasets used here represent selectively neutral markers, substantial correlation between neutral genetic structure and environmental variation can be detected due to genetic hitchhiking or coupling (Vasemägi et al. 2005, Bierne et al. 2011). We statistically assessed this possibility with an analysis of ecological isolation that compares data from 7 oceanographic variables with information about population genetic structure (Table 3). None of the correlations were significant after correcting for geographical distances, suggesting a more important role of geography rather than oceanography as a driver of population structure in *M. henlei*.

The metapopulation structure reported in *M. henlei* was better explained by isolation by distance between demes, a conclusion statistically supported by Mantel tests for both nuclear and mtDNA datasets (Table 3) and by spatial autocorrelation analysis of individual multilocus genotypes (Fig. 3). Isolation by distance has been found in other coastal sharks, such as *Carcharinus melanopterus* (Vignaud et al. 2013), *Negaprion brevirostris* (Ashe et al. 2015), *Stegostoma fasciatum* (Dudgeon et al. 2009) and the closely related *Triakis semifasciata* from the Californian coast (Lewallen et al. 2007). To some degree, this pattern of spatial genetic structure can be attributed to female philopatric behaviour, whereas connectivity along the region appears mostly due to male dispersal. While *M. henlei* females showed greater than random genetic similarity among individuals sampled from the same locality, this was not observed for males. In addition, the mean AIc value was negative for males and positive for females, suggesting females as the philopatric sex, although this difference was not significant ($Z = -0.722$, $p = 0.470$). However, the latter could have been compromised by low power due to the smaller number of male samples (38 males compared to 82 females) and a weak sex-bias signal (Mossman & Waser 1999). Additional support for female philopatry comes from comparing levels of structure between mitochondrial and nuclear markers. If only modes of inheritance are taken into account (i.e. no differences in operational sex ratios and effective size of genomes considered), mitochondrial markers should show higher structure than nuclear markers under a scenario of male-mediated dispersal (Goudet et al. 2002, Prugnolle & de Meeus 2002). On average, mtDNA data revealed stronger differentiation in pairwise comparisons than microsatellites. Altogether, results from analyses of spatial autocorrelation, corrected assignment index and different signal between mitochondrial and nuclear markers support the proposal of male-biased dispersal in *M. henlei*.

Determining unequivocally that a shark species is philopatric requires enormous research (Hueter et al. 2005, Dudgeon et al. 2012). However, by combining fisheries data with our genetic findings, we show that the species has moderate philopatric behaviour, at least for the GC portion of its range. So far there has

been no long-term tagging or tracking data for *M. henlei*, but fisheries data in the GC show consistent inter-annual female aggregations (Pérez-Jiménez & Sosa-Nishizaki 2008) and the existence of nursery sites in the GC (Salomón-Aguilar et al. 2009). Philopatry has been reported for several species of marine organisms with high dispersal capabilities (FitzSimmons et al. 1997, Weimerskirch & Wilson 2000, Möller & Beheregaray 2004). In fact, for several species of sharks, local genetic structure has been associated with female philopatry to their natal area (Hueter et al. 2005, Portnoy & Heist 2012). Using genetic data to investigate philopatry can be negatively affected by sampling strategies (Dudgeon et al. 2012). Our sampling was conducted during the mating season of the species from March until June (Pérez-Jiménez & Sosa-Nishizaki 2008). As such, the identified genetic structure is better attributed to fidelity to breeding areas rather than to sampling biases.

Conservation implications for a highly exploited shark species

Our findings have direct implications for the design of conservation policies and the zoning of marine reserves that allow appropriate management for a heavily exploited shark. Despite the historical importance of the Mexican elasmobranch fishery around the world (FAO 2010), national regulations regarding elasmobranch management and conservation (e.g. NOM-29-PEC) were only recently implemented (2007). While this represents a significant improvement to shark management in Mexico, the legislation lacks species-specific guidelines and does not account for stock structure, geographic variation in population demography or connectivity patterns. This work shows evidence of moderate genetic structure in *M. henlei*, which could have important demographic and evolutionary impacts for this species (Palumbi 2003, Knutsen et al. 2011). We propose the existence of a minimum of 5 subpopulations of *M. henlei* that are associated to some extent with distinct bioregions (Lavín & Marinone 2003; Fig. 1). However, our results confirm some degree of connectivity between subpopulations, suggesting a functional metapopulation for the species. Because these subpopulations are not completely isolated, management implemented in one subpopulation could affect population dynamics in other areas. For example, heavy fishing pressures over one local population could create an artificial source-sink structure, with negative effects for the metapopulation (Crowder et al. 2000, Neubert 2003). Therefore, integrated management of the 5 subpopulations is necessary to prevent stock collapses that can lead to local extirpation with ecological and economic consequences, as has occurred elsewhere (Dulvy & Forrest 2010, Nadon et al. 2012).

Although there is no evidence of significant depletion of *M. henlei* populations, the most serious and continuous threat for this species in Mexico is the heavy commercial fishery (Pérez-Jiménez & Sosa-Nishizaki 2008, Bizzarro et al. 2009, Smith et al. 2009, INAPESCA 2010). In source–sink metapopulation dynamics, resiliency to fishing pressure differs between subpopulations. The effect of overexploitation in sink subpopulations may be mitigated by the input of immigrants from other subpopulations, but overexploitation in source subpopulations can cause rapid and catastrophic results for the metapopulation (Crowder et al. 2000, Neubert 2003). Our migration analysis shows that LG probably functions as a source population, whereas NP and UG operate as sink populations (Fig. 2). These results suggest that NP and UG could probably sustain larger fisheries than LG, but demographic studies are needed to determine the fishery capacity for each subpopulation.

Relatively low levels of philopatric behaviour, as reported here, might have substantial implications for shark conservation. Shark fidelity to specific nursery areas increases vulnerability to human impacts (Hueter et al. 2005, Heupel et al. 2007, Kinney & Simpfendorfer 2009). However, the presence of genetically differentiated subpopulations with recurrent habitat utilization for reproduction could also be an opportunity for affordable and efficient spatially based conservation measures, such as the establishment of marine protected areas (MPAs) around nursery areas (Bond et al. 2012, Knip et al. 2012). However, nursery areas are not stand-alone systems; they often depend on recruitment from other regions to maintain stable breeding populations (Kinney & Simpfendorfer 2009). Thus, management plans focusing only on protecting breeding sites will likely fail in maintaining viable *M. henlei* populations. Migrants have important demographic and ecological implications for a metapopulation (such as maintaining a stable effective population size and genetic variability; Frankham et al. 2011), and reduced levels of connectivity among wild populations increase their susceptibility to extinction due to habitat destruction, regional overfishing and climate change (Frankham et al. 2009). Therefore, the creation of marine reserves that protect the integrity of nursery areas and their connectivity is fundamental for the conservation of philopatric species, such as the likely philopatric *M. henlei*.

Unfortunately, most of the nursery grounds around the GC-BCP area are exposed to intensive fishing regimes and habitat destruction (Salomón-Aguilar et al. 2009), stressing the need for a system of MPAs in the region. The few existing MPAs in the GC were designed based on local diversity levels (i.e. species diversity). It has been suggested that the management of only 6 shark mating and nursery grounds would be enough to protect all shark species that reproduce in the GC (Salomón-Aguilar et al. 2009). However, a network of MPAs that considers breeding sites and patterns of connectivity between them would better protect ecological processes that maintain diversity on broader temporal and spatial scales (Lubchenco et al. 2003, Hooker et al. 2011, Pendoley et al. 2014). Our data suggest that a network of MPAs with at least 1 breeding area per bioregion, including migratory corridors between adjacent reserves, would increase its conservation potential not just for *M. henlei* but also for other mobile species using coastal areas.

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LITERATURE CITED

Ashe JL, Feldheim KA, Fields AT, Reyier EA and others (2015) Local population structure and context-dependent isolation by distance in a large coastal shark. Mar Ecol Prog Ser 520:203–216

Banks SC, Piggott MP, Williamson JE, Bové U, Holbrook NJ, Beheregaray LB (2007) Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. Ecology 88:3055–3064

Beaumont MA, Rannala B (2004) The Bayesian revolution in genetics. Nat Rev Genet 5:251–261

Beerli P, Palczewski M (2010) Unified framework to evaluate panmixia and migration direction among multiple sampling locations. Genetics 185:313–326

Beheregaray LB (2008) Twenty years of phylogeography: the state of the field and the challenges for the Southern Hemisphere. Mol Ecol 17:3754–3774

Bernardi G (2014) Baja California disjunctions and phylogeographic patterns in sympatric California blennies. Front Ecol Evol 2:53

Bernardi G, Findley L, Rocha-Olivares A (2003) Vicariance and dispersal across Baja California in disjunct marine fish populations. Evolution 57:1599–1609

Bierne N, Welch J, Loire E, Bonhomme F, David P (2011) The coupling hypothesis: why genome scans may fail to map local adaptation genes. Mol Ecol 20:2044–2072

Bizzarro JJ, Smith WD, Márquez-Farías JF, Tyminski J, Hueter RE (2009) Temporal variation in the artisanal elasmobranch fishery of Sonora, Mexico. Fish Res 97:103–117

Bond ME, Babcock EA, Pikitch EK, Abercrombie DL, Lamb NF, Chapman DD (2012) Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the Mesoamerican Barrier Reef. PLoS ONE 7:e32983

Boomer JJ, Stow AJ (2010) Rapid isolation of the first set of polymorphic microsatellite loci from the Australian gummy shark, *Mustelus antarcticus* and their utility across divergent shark taxa. Conserv Genet Resour 2: 393–395

Brinton E, Townsend AW (1980) Euphausiids in the Gulf of California — the 1957 cruises. Calif Coop Ocean Fish Investig Rep 21:211–236

Byrne RJ, Avise JC (2012) Genetic mating system of the brown smoothhound shark (*Mustelus henlei*), including a literature review of multiple paternity in other elasmobranch species. Mar Biol 159:749–756

Campos BR, Fish MA, Jones G, Riley RW and others (2009) Movements of brown smoothhounds, *Mustelus henlei*, in Tomales Bay, California. Environ Biol Fishes 85:3–13

Castillo-Páez A, Sosa-Nishizaki O, Sandoval-Castillo J, Galván-Magaña F, Rocha-Olivares A (2014) Strong population structure and shallow mitochondrial phylogeny in the banded guitarfish, *Zapteryx exasperata* (Jordan y Gilbert, 1880), from the northern Mexican Pacific. J Hered 105:91–100

Chen CT, Huang SY, Lee SC (2001) Genetic variation between populations of starspotted dogfish *Mustelus manazo* in central Japan and northern Taiwan. Fish Sci 67: 30–35

Chevolot M, Ellis JR, Hoarau G, Rijnsdorp AD, Stam WT, Olsen JL (2006) Population structure of the thornback ray (*Raja clavata* L.) in British waters. J Sea Res 56:305–316

Compagno LJV (1984) FAO species catalogue, Vol 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2—Carcharhiniformes. FAO Fish Synop 125:251–655

Corrigan S, Beheregaray LB (2009) A recent shark radiation: molecular phylogeny, biogeography and speciation of wobbegong sharks (family: Orectolobidae). Mol Phylogenet Evol 52:205–216

Corrigan S, Huveneers C, Schwartz TS, Harcourt RG, Beheregaray LB (2008) Genetic and reproductive evidence for two species of ornate wobbegong shark *Orectolobus* spp. on the Australian east coast. J Fish Biol 73: 1662–1675

Crowder LB, Lyman S, Figueira W, Priddy J (2000) Source-sink population dynamics and the problem of siting marine reserves. Bull Mar Sci 66:799–820

Davey JW, Hohenlohe PA, Etter PD, Boone JQ, Catchen JM, Blaxter ML (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. Nat Rev Genet 12:499–510

Dudgeon CL, Broderick D, Ovenden JR (2009) IUCN classification zones concord with, but underestimate, the population genetic structure of the zebra shark *Stegostoma fasciatum* in the Indo-West Pacific. Mol Ecol 18:248–261

Dudgeon CL, Blower DC, Broderick D, Giles JL and others (2012) A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. J Fish Biol 80:1789–1843

Dulvy NK, Forrest RE (2010) Life histories, population dynamics, and extinction risks in Chondrichthyans. In: Carrier JC, Musick JA, Heithaus MR (eds) Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, FL, p 639–679

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD and others (2014) Extinction risk and conservation of the world's sharks and rays. eLife 3:e00590

Duncan KM, Martin AP, Bowen BW, De Couet HG (2006) Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). Mol Ecol 15:2239–2251

Ebert DA (2003) Sharks, rays, and chimaeras of California. University of California Press, Berkeley, CA

Enríquez-Andrade R, Anaya-Reyna G, Barrera-Guevara JC, Carvajal-Moreno MÁ, Martínez-Delgado ME, Vaca-Rodríguez J, Valdés-Casillas C (2005) An analysis of critical areas for biodiversity conservation in the Gulf of California Region. Ocean Coast Manage 48:31–50

Excoffier L, Lischer HEL (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Resour 10: 564–567

FAO (Food and Agriculture Organization of the United Nations) (2010) The state of world fisheries and aquaculture 2010. Fisheries and Aquaculture Department, FAO, Rome

Favre L, Balloux F, Goudet J, Perrin N (1997) Female-biased dispersal in the monogamous mammal *Crocidura russula*: evidence from field data and microsatellite patterns. Proc R Soc B 264:127–132

Feldheim KA, Gruber SH, DiBattista JD, Babcock EA and others (2014) Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. Mol Ecol 23:110–117

Felsenstein J, Churchil GA (1996) A hidden Markov model approach to variation among sites in rate of evolution. Mol Biol Evol 13:93–104

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–1071

FitzSimmons NN, Limpus CJ, Norman JA, Goldizen AR, Miller JD, Moritz C (1997) Philopatry of male marine turtles inferred from mitochondrial DNA markers. Proc Natl Acad Sci USA 94:8912–8917

Francis MP (1988) Movement patterns of rig (*Mustelus lenticulatus*) tagged in southern New Zealand. N Z J Mar Freshw Res 22:259–272

Frankham R, Ballou JD, Briscoe DA (2009) Introduction to conservation genetics. Cambridge University Press, Cambridge

Frankham R, Ballou JD, Eldridge MD, Lacy RC, Ralls K, Dudash MR, Fenster CB (2011) Predicting the probability of outbreeding depression. Conserv Biol 25:465–475

Fu YX (1997) Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. Genetics 147:915–925

Galindo HM, Olson DB, Palumbi SR (2006) Seascape genetics: a coupled oceanographic-genetic model predicts population structure of Caribbean corals. Curr Biol 16: 1622–1626

Goudet J, Perrin N, Waser P (2002) Tests for sex-biased dispersal using bi-parentally inherited genetic markers. Mol Ecol 11:1103–1114

Guillot G, Leblois R, Coulon A, Frantz AC (2009) Statistical methods in spatial genetics. Mol Ecol 18:4734–4756

Hauser L, Carvalho GR (2008) Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. Fish Fish 9:333–362

Herndon A, Gallucci VF, DeMaster D, Burke W (2010) The case for an international commission for the conservation and management of sharks (ICCMS). Mar Policy 34: 1239–1248

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. Nature 405:907–913

Hooker SK, Cañadas A, Hyrenbach KD, Corrigan C, Polovina JJ, Reeves RR (2011) Making protected area networks effective for marine top predators. Endang Species Res 13:203–218

Hueter R, Heupel M, Heist E, Keeney D (2005) Evidence of philopatry in sharks and implications for the management of shark fisheries. J Northwest Atl Fish Sci 35:239–247

INAPESCA (Instituto Nacional de Pesca) (2010) Carta Nacional Pesquera. Diario Oficila de la Federacion, Secretaria de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación (SAGARPA), Mexico City

Jacobs DK, Haney TA, Louie KD (2004) Genes, diversity, and geologic process on the Pacific coast. Annu Rev Earth Planet Sci 32:601–652

Jensen JL, Bohonak AJ, Kelley ST (2005) Isolation by distance, web service. BMC Genet 6:13

Karl SA, Castro ALF, Lopez JA, Charvet P, Burgess GH (2011) Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred from mitochondrial and microsatellite DNA. Conserv Genet 12:371–382

Kinney MJ, Simpfendorfer CA (2009) Reassessing the value of nursery areas to shark conservation and management. Conserv Lett 2:53–60

Knip DM, Heupel MR, Simpfendorfer CA (2012) Evaluating marine protected areas for the conservation of tropical coastal sharks. Biol Conserv 148:200–209

Knutsen H, Olsen EM, Jorde PE, Espeland SH, Andr ÉC, Stenseth NC (2011) Are low but statistically significant levels of genetic differentiation in marine fishes 'biologically meaningful'? A case study of coastal Atlantic cod. Mol Ecol 20:768–783

Kuhner MK (2009) Coalescent genealogy samplers: windows into population history. Trends Ecol Evol 24:86–93

Lavín MF, Marinone SG (2003) An overview of the physical oceanography of the Gulf of California. In: Velasco-Fuentes OU, Sheinbaum J, Ochoa de la Torre JL (eds) Nonlinear processes in geophysical fluid dynamics. Kluwer Academic Publishers, Dordrecht

Lewallen EA, Anderson TW, Bohonak AJ (2007) Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. Mar Biol 152:599–609

Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves 1. Ecol Appl 13:3–7

Mendez M, Rosenbaum HC, Subramaniam A, Yackulic C, Bordino P (2010) Isolation by environmental distance in mobile marine species: molecular ecology of franciscana dolphins at their southern range. Mol Ecol 19:2212–2228

Möller LM, Beheregaray LB (2004) Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Mol Ecol 13:1607–1612

Mossman CA, Waser PM (1999) Genetic detection of sex-biased dispersal. Mol Ecol 8:1063–1067

Mourier J, Planes S (2013) Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. Mol Ecol 22:201–214

Murphy RW, Aguirre-Leon G (2002) Nonavian reptiles: origins and evolution. In: Case T, Cody M, Ezcurra E (eds) A new island biogeography in the Sea of Cortes. Oxford University Press, Oxford

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). Fisheries 25:9–13

Nadon MO, Baum JK, Williams ID, McPherson JM and others (2012) Re-creating missing population baselines for Pacific reef sharks. Conserv Biol 26:493–503

Neubert MG (2003) Marine reserves and optimal harvesting. Ecol Lett 6:843–849

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. Ecol Appl 13:146–158

Peakall ROD, Smouse PE (2006) GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295

Peguero-Icaza M, Sánchez-Velasco L, Lavín MF, Marinone SG (2008) Larval fish assemblages, environment and circulation in a semienclosed sea (Gulf of California, Mexico). Estuar Coast Shelf Sci 79:277–288

Pelc RA, Warner RR, Gaines SD (2009) Geographical patterns of genetic structure in marine species with contrasting life histories. J Biogeogr 36:1881–1890

Pendoley KL, Schofield G, Whittock PA, Ierodiaconou D, Hays GC (2014) Protected species use of a coastal marine migratory corridor connecting marine protected areas. Mar Biol 161:1455–1466

Pérez-Jiménez JC, Sosa-Nishizaki O (2008) Reproductive biology of the brown smoothhound shark *Mustelus henlei,* in the northern Gulf of California, México. J Fish Biol 73:782–792

Portnoy DS, Heist EJ (2012) Molecular markers: progress and prospects for understanding reproductive ecology in elasmobranchs. J Fish Biol 80:1120–1140

Portnoy DS, Hollenbeck CM, Belcher CN, Driggers WB and others (2014) Contemporary population structure and post-glacial genetic demography in a migratory marine species, the blacknose shark, *Carcharhinus acronotus.* Mol Ecol 23:5480–5495

Prugnolle F, de Meeus T (2002) Inferring sex-biased dispersal from population genetic tools: a review. Heredity 88: 161–165

Reiss H, Hoarau G, Dickey-Collas M, Wolff WJ (2009) Genetic population structure of marine fish: mismatch between biological and fisheries management units. Fish Fish 10:361–395

Riginos C (2005) Cryptic vicariance in Gulf of California fishes parallels vicariant patterns found in Baja California mammals and reptiles. Evolution 59:2678–2690

Roberts CM, McClean CJ, Veron JEN, Hawkins JP and others (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295:1280–1284

Round FE (1967) The phytoplankton of the Gulf of California. Part I. Its composition, distribution and contribution to the sediments. J Exp Mar Biol Ecol 1:76–97

Rousset F (2008) Genepop'007: a complete re-implementation of the genepop software for Windows and Linux. Mol Ecol Resour 8:103–106

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002) A general model for designing networks of marine reserves. Science 298:1991–1993

Salomón-Aguilar CA, Villavicencio-Garayzar CJ, Reyes-Bonilla H (2009) Shark breeding grounds and seasons in the Gulf of California: fishery management and conservation strategy. Cienc Mar 35:369–388

Sandoval-Castillo J, Rocha-Olivares A (2011) Deep mitochondrial divergence in Baja California populations of an aquilopelagic elasmobranch: the golden cownose ray. J Hered 102:269–274

Sandoval-Castillo J, Rocha-Olivares A, Villavicencio-Garayzar C, Balart E (2004) Cryptic isolation of Gulf of California shovelnose guitarfish evidenced by mitochondrial DNA. Mar Biol 145:983–988

Schultz JK, Feldheim KA, Gruber SH, Ashley MV, McGovern TM, Bowen BW (2008) Global phylogeography and seascape genetics of the lemon sharks (genus *Negaprion*). Mol Ecol 17:5336–5348

Schwartz MK, Luikart G, Waples RS (2007) Genetic monitoring as a promising tool for conservation and management. Trends Ecol Evol 22:25–33

Smith WD, Bizzarro JJ, Cailliet GM (2009) The artisanal elasmobranch fishery on the east coast of Baja California, Mexico: characteristics and management considerations. Cienc Mar 35:209–236

Smouse PE, Peakall R (1999) Spatial autocorrelation analysis of individual multiallele and multilocus genetic structure. Heredity 82:561–573

Sunnucks P, Hale DF (1996) Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus *Sitobion* (Hemiptera: Aphididae). Mol Biol Evol 13:510–524

Van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Vasemägi A, Nilsson J, Primmer CR (2005) Expressed sequence tag-linked microsatellites as a source of gene-associated polymorphisms for detecting signatures of divergent selection in Atlantic salmon (*Salmo salar* L.). Mol Biol Evol 22:1067–1076

Vignaud T, Clua E, Mourier J, Maynard J, Planes S (2013) Microsatellite analyses of blacktip reef sharks (*Carcharhinus melanopterus*) in a fragmented environment show structured clusters. PLoS ONE 8:e61067

Walker BW (1960) The distribution and affinities of the marine fish fauna of the Gulf of California. Syst Biol 9: 123–133

Weimerskirch H, Wilson RP (2000) Oceanic respite for wandering albatrosses. Nature 406:955–956

Worm B, Davis B, Kettemer L, Ward-Paige CA and others (2013) Global catches, exploitation rates, and rebuilding options for sharks. Mar Policy 40:194–204

Yudin KG, Cailliet GM (1990) Age and growth of the gray smoothhound, *Mustelus californicus*, and the brown smoothhound, *M. henlei*, sharks from central California. Copeia 191–204

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