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Regional (south-eastern Pacific Ocean) population genetics and global phylogeography of two endangered highly migratory pelagic sharks, the blue shark *Prionace glauca* and shortfin mako *Isurus oxyrinchus*

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Abstract

1. The blue shark *Prionace glauca* and the shortfin mako *Isurus oxyrinchus* are two large and highly migratory sharks inhabiting temperate and tropical waters worldwide that are heavily targeted by artisanal and industrial fisheries. The International Union for Nature Conservation classifies the blue shark and shortfin mako as 'Near Threatened' and 'Vulnerable', respectively, in the Nature Red List of Threatened Species v. 2019-2.
2. This study examined the population genetics of the shortfin mako and blue sharks at a regional (south-eastern Pacific Ocean) and global scale. The null hypothesis of no genetic discontinuities among ocean basins and/or between hemispheres was tested using two mitochondrial markers suitable for population genetics inference in these species: the non-coding control region and the protein-coding gene cytochrome c oxidase I in *I. oxyrinchus*, and the control region and cytochrome b in *P. glauca*.
3. Spatial genetic analyses suggested a single and two genetic clusters co-occurring along the south-eastern Pacific Ocean in the shortfin mako and blue shark, respectively. Phylogeographic analyses, migration estimates, haplotype networks and AMOVAs demonstrated that the two species exhibit an overall pattern of high genetic connectivity among hemispheres and across ocean basins with a signature of shallow genetic structuring worldwide.
4. This study has generated valuable information for the management and conservation of heavily exploited sharks and highlights the need for additional inclusive research programmes assessing inter-regional genomic discontinuities using more statistically powerful genetic markers to determine with precision population genetic discontinuities (if any) in these and other highly migratory sharks.

KEYWORDS

conservation biology, elasmobranchs, fishery management, population genetics, sharks

1 | INTRODUCTION

A considerable number of shark species are experiencing major biological impacts, including dire population declines, due to intense harvesting worldwide by artisanal and/or industrial fisheries, some of them unregulated and/or illegal (Heithaus et al., 2010; Queiroz et al., 2019). Sharks that are targeted or caught as by-catch by fisheries also exhibit a set of life history traits, including slow growth rate, low fecundity and late reproductive maturity that makes them particularly vulnerable to overexploitation (Musick et al., 2000; Reynolds, Jennings & Dulvy, 2001). Therefore, a general understanding of shark biology and ecology, including population delimitation and stock structure, is crucial to improve their conservation and fisheries management strategies, especially in the South Pacific Ocean where this knowledge is lacking or available only for a limited number of species (González et al., 2021).

During recent decades, genetic studies have proved most useful to identify genetically dissimilar populations and discriminate among fished stocks in sharks as well as other highly migratory large marine vertebrates (Nielsen & Beaumont, 2009; Dudgeon et al., 2012; González et al., 2021). Genetic approaches have also improved our knowledge of the population connectivity, migration rates, and the extent of philopatric behaviour in determining observed population genetic discontinuities. Overall, genetic tools have broadened our understanding of contemporary and historical processes driving shark population genetic structure and population size (Keeney et al., 2005; Duncan et al., 2006; Portnoy et al., 2014). The focus of this study is on improving our understanding of the population genetics of two highly migratory and large pelagic sharks that are currently experiencing environmental issues and that are in need of genetic resources that can guide conservation strategies and fisheries management.

The blue shark, *Prionace glauca*, is a highly migratory pelagic species distributed in temperate and tropical waters worldwide (Nakano & Stevens, 2008). *Prionace glauca* is one of the most abundant sharks in the ocean except polar waters, and it is probably the most exploited species worldwide (Camhi et al., 1998; but see Leone et al., 2017). The blue shark can cover distances between 1,000 and 10,000 km, including east–west and north–south trans-oceanic movements, during its lifetime (Kohler et al., 2002) and is known to exhibit complex behaviours and spatial segregation according to size, sex and reproductive status (Nakano & Stevens, 2008; Ferreira, 2013). This species is currently categorized worldwide as 'Near Threatened' in the IUCN Red List (Stevens, 2009). According to the International Commission for the Conservation of Atlantic Tunas (ICCAT), the North Atlantic stock is unlikely to be overfished at present (ICCAT, 2015). However, the Mediterranean population has undergone a 90% decline over three generations, primarily due to overfishing (Ferretti et al., 2008), and is currently categorized as 'Critically Endangered' (Sims et al., 2016). Several long-term tagging studies have revealed extensive movements of blue sharks on the western coast of the North Atlantic as well as eastward trans-Atlantic migrations (Kohler, Casey & Turner, 1998; Kohler et al., 2002; Vandeperre et al., 2014). The population structure and dynamics of *P. glauca* is still not completely understood and has become a controversial topic. A genetic study, using a short fragment of the mitochondrial *cytochrome oxidase b* (*cob*) gene, detected weak or null genetic differentiation among blue sharks captured from various locations in the Indo-Pacific Ocean (Taguchi et al., 2015). A second study that relied on nuclear and mitochondrial markers evidenced genetic heterogeneity among nursery grounds from the Atlantic Ocean (Portugal and Azores) and those from South Africa (Ferreira, 2013). However, a most recent genetic study showed the lack of spatio-temporal genetic differentiation in juvenile specimens collected from the same nursery areas using the same genetic markers (Veríssimo et al., 2017). Lastly, based on the mitochondrial *cob* and control region (CR) genetic markers, Leone et al. (2017) detected genetic differentiation between blue sharks from the Mediterranean Sea and the north-eastern Atlantic Ocean. Leone et al. (2017) noted that their samples included both juvenile and adult individuals, which could imply that the reported genetic differences could be explained by a combination of reproductive relatedness (i.e. presence of geographically delimited nursery grounds) together with a lack of or minimal adult population connectivity. Overall, the accumulated information suggests a putatively complex yet unresolved phylogeographic structure in *P. glauca*. Importantly, genetic information is lacking for populations of *P. glauca* inhabiting the Southern Hemisphere, especially for the south-east Pacific Ocean (SEP).

The shortfin mako, *Isurus oxyrinchus*, is also a highly migratory shark with a global distribution in tropical and temperate seas. It represents an important by-catch in the swordfish industrial long-line fishery as well as in drift-net fisheries in various countries (Compagno, 2001; Catarci & Fao, 2004). *Isurus oxyrinchus* exhibits moderate growth rates of ~20–30 cm per year during the first 2 years (Wells et al., 2013), late reproductive maturity (Semba, Aoki & Yokawa, 2011) and small litter size (4–16 individuals per reproductive event), which make them particularly susceptible to overfishing (Cailliet et al., 1983; Stevens, 1983; Mollet et al., 2000). Tagging studies have documented movements of more than 1,000 km over short periods (Casey & Kohler, 1992). This vagility coupled with their widespread distribution make shortfin mako sharks susceptible to unregulated fishing on the high seas (Cailliet et al., 2009). In February 2007, the shortfin mako moved up the IUCN's red list from 'Near Threatened' to 'Vulnerable'; and in August 2019, it was listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Sellheim, 2020). Studies on the population genetic structure of *I. oxyrhynchus* are uncommon and

are mostly restricted to reports from international scientific committees (e.g. Michaud et al., 2011; Taguchi et al., 2015). Early studies using fragment analysis of the mitochondrial DNA (mtDNA) indicated that the shortfin mako population inhabiting the North Atlantic was genetically different from that in the South Atlantic and Pacific oceans (Heist, Musick & Graves, 1996). A second study carried out using a limited number of nuclear DNA markers (i.e. four simple sequence repeats (SSRs)) detected low levels of genetic differentiation between the two aforementioned ocean basins (Schrey & Heist, 2003). Lastly, a technical report that used a fragment of the mitochondrial genome (i.e. CR), showed strong genetic differentiation between shortfin mako populations from the North Atlantic and Pacific oceans, the North and South Pacific Ocean, and the south-west and south-east Pacific Ocean (Michaud et al., 2011). This report suggested the existence of at least three stocks of *I. oxyrinchus* in the Pacific Ocean (Michaud et al., 2011).

Ultimately, the great majority of the studies focusing on the population genetics of blue and shortfin mako sharks have focused on the Atlantic Ocean. Genetic information for shark populations in the South Pacific is deficient, particularly for the SEP. Genetic information for blue and mako sharks inhabiting the SEP is crucial to the implementation of fishery regulations that ensure shark conservation regionally and worldwide sustainability. In this study, the regional genetic population structure in the SEP and global phylogeography of the sharks *P. glauca* and *I. oxyrinchus* is described. Specifically, it explored: (i) the possible co-occurrence of more than a single genetic population or deme in the SEP; and (ii) tested for the existence of genetic discontinuities among populations from several locales in the Pacific and Atlantic oceans in each hemisphere. For this purpose, two mitochondrial markers were used: the non-coding CR and the protein-coding gene cytochrome c oxidase I (*cox1*) in *I. oxyrinchus* and the CR and *cob* in *P. glauca*. The aforementioned markers have been successfully used in previous studies focusing on the population genetics of these and other shark species in different geographic regions (Kitamura & Matsunaga, 2010; Michaud et al., 2011; Leone et al., 2017; Veríssimo et al., 2017). Thus, the sequences obtained in this study were combined with those from previous studies for the same species (available in NCBI's GenBank database – Michaud et al., 2011; Ferreira, 2013; Taguchi et al., 2015; Leone et al., 2017; Veríssimo et al., 2017) in an attempt to achieve a more precise picture of the population genetics of the blue and shortfin mako sharks worldwide. Taking into account that the two species of shark are highly migratory, relatively high levels of gene flow across extensive oceanic regions in the two hemispheres were predicted.

2 | METHODS

2.1 | Collection and tissue sampling in sharks from the SEP

A total of 128 and 132 specimens of *P. glauca* and *I. oxyrinchus*, respectively, were captured by artisanal fishermen using either longline or gillnets targeting the swordfish *X. gladius* between January 2016 and December 2017 in the SEP. Specimens of *P. glauca* were captured between 18°47′S and 40°07′S, 70°38′W and 81°17′W while specimens of *I. oxyrinchus* were captured between 18°44′S and 38°53′S, 70°41′W and 87°28′W (Figure 1). Immediately after capture, each shark was geo-referenced using an onboard satellite GPS (precision = 12 m), sized (total length, measured from the tip of the nose to the end of the tail) and sexed (presence or absence of claspers in males and females, respectively). Next, a small muscle sample (~1 cm^3) was removed from the dorsal side of each specimen and immediately preserved in 40-mL flasks containing 95% ethanol. Preserved samples were transported to the laboratory at Universidad de Antofagasta, Antofagasta, Chile for Sanger sequencing.

2.2 | DNA extraction, amplification and sequencing

Total DNA was extracted from shark tissue samples using the E.Z.N.A.® Tissue DNA Kit (OmegA Bio-tek, Inc., USA) following the manufacturer's instructions. The quality and quantity of the isolated DNA from each sample was determined with a Biospec-nano spectrophotometer (Shimadzu). Then, each DNA sample was diluted in ultrapure water to 50 ng μL^{-1} for polymerase chain reaction (PCR) amplification. In the two shark species, the control region (CR) fragment was amplified using the forward primer CR-blues-F (5′-AAA CAC ATC AGG GGA AGG AG-3′) and the reverse primer CR-blues-R (5′-CAT CTT AGC ATC TTC AGT GCC-3′) (Leone et al., 2017). In *I. oxyrinchus*, the *cox1* gene fragment was amplified using the forward primer VF2 (5′-TGTA AAA CGA CGG CCA GTCAAC CAA CCA CAA AGA CAT TGG CAC-3′) and reverse primer FishR2 (5′-CAG GAA ACA GCT ATG ACA CTT CAG GGT GAC CGA AGA ATC AGA A-3′) (Ward et al., 2005). In *P. glauca*, a *cob* gene fragment was amplified using the forward primer PgCbL (CTA AAG CAG CAT AAT AAG GAG AAG G) and reverse primer CBH (TCT TCG ACT TAC AAG GCC GA) (Taguchi et al., 2015).

Standard PCR mixtures had a final volume of 35 μL including: 0.125 U μL^{-1} Taq polymerase (GoTaq® G2, Promega), 5 μL of 5 × PCR buffer, 4 μL magnesium chloride (25 mM), 1.5 μL bovine serum albumin (10 mg mL^{-1}), 0.5 μL of deoxynucleotide triphosphate (10 mM), 1 μL 10 pM each primer and 2.5 μL template DNA. PCR amplifications for the two genes were performed in a Boeco Ecogermany M-240R thermal cycler under the following conditions: (i) for the CR fragment, initial denaturation at 94°C for 120 s, followed by 35 cycles at 94°C for 30 s, 60°C for 30 s, 72°C for 30 s and a final extension at 72°C for 5 min; (ii) for the *cox1* gene fragment, initial denaturation at 95°C for 120 s, followed by 35 cycles at 95°C for 30 s, 54°C for 30 s, 72°C for 60 s, followed by chain extension at 72°C for 10 min; (iii) for the *cob* gene, initial denaturation at 94°C for 2 min, followed by 30 cycles of amplification (94°C for 1 min, 55°C for 1 min, 72°C for 2 min) and a final chain extension for 7 min at 72°C (adapted from Taguchi et al., 2015). PCR products were visualized in an agarose gel 1% and sent to Macrogen (Seoul, Korea;

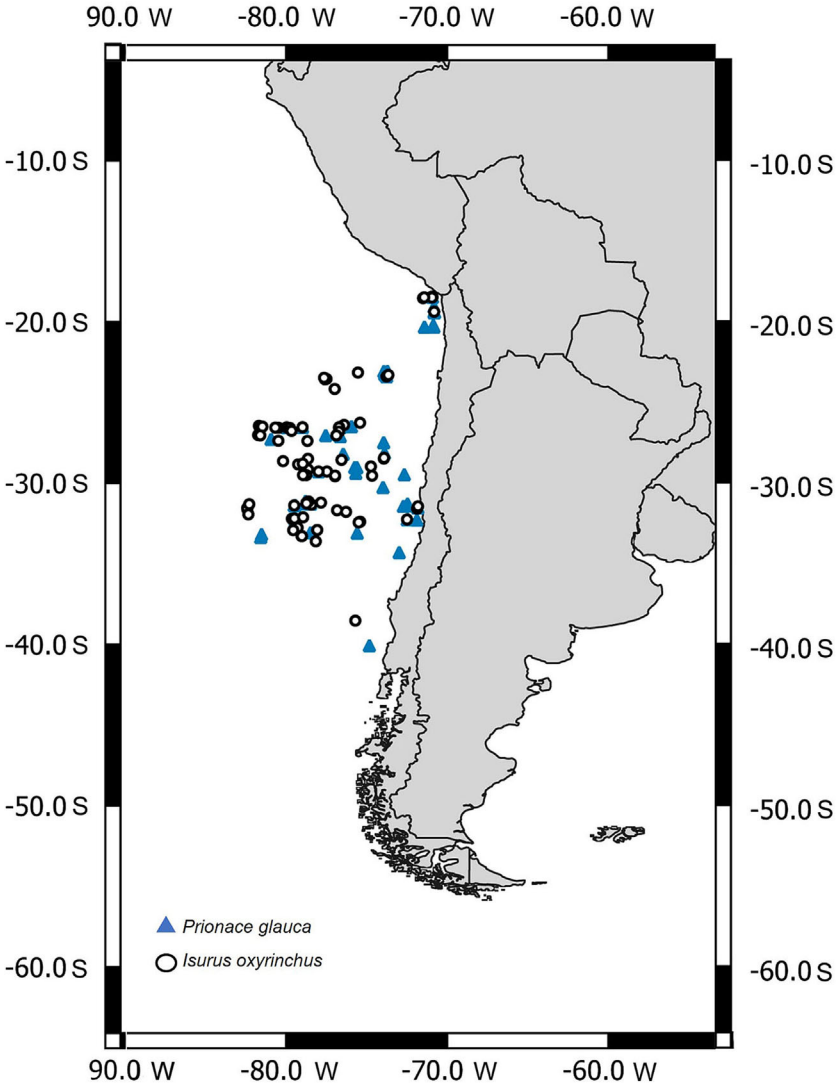

FIGURE 1 Regional map showing sampling stations where specimens of *Prionace glauca* (triangles) and *Isurus oxyrinchus* (circles) were captured during this study.

http://www.macrogen.com) for purification and sequencing of both DNA forward and reverse strands. Sequences were edited and contigs were assembled using ProSeq 2.9 beta (Filatov, 2002). All haplotype sequences obtained during this study were deposited in GenBank under the following accession numbers: OR243971-OR244016, OR261110-OR261237, and OR267010-OR267088.

2.3 | Population genetics of *P. glauca* and *I. oxyrinchus* in the SEP coast

These analyses were conducted only with the sequences obtained during the present study (*P. glauca*: 79 for CR and 72 *cob*; *I. oxyrhynchus*: 128 CR and 46 *cox1*). The software Arlequin 3.5 (Excoffier & Lischer, 2010) was used to assess the molecular diversity of the two shark species in the SEP. The standard diversity indices calculated were: number of polymorphic sites *S*, number of haplotypes *H*, haplotype diversity *Hd* (Nei, 1987) and nucleotide diversity π (Nei, 1987). Then, for each studied mitochondrial marker (*cox1*, CR, *cob*), the most likely number of genetic clusters k present in the SEP, as well as the spatial distribution of these populations across the sampled area, was inferred using the program GENELAND v.4.0.2 (Guillot, Mortier & Estoup, 2005). GENELAND implements a Bayesian Markov chain Monte Carlo (MCMC) clustering algorithm that identifies genetic discontinuities while taking into account the spatial distribution of the sampled individuals. For this analysis, a spatial model was selected and ran using the geo-reference (latitude and longitude) and genetic information (nucleotide sequences for each gene) obtained for each individual during sampling. A mixture model and correlated allele frequencies were used following guidelines in Falush, Stephens & Pritchard (2003) with the following parameters: K from 1 to 5 (which is equivalent to the number of sampling locations surveyed in this study), 1 × 10e6 MCMC iterations and a thinning interval of 1,000. The MCMC was run using a burn-in of 200 iterations to obtain posterior probabilities for each sampled individual belonging to any detected population.

2.4 | Global scale population genetics of *P. glauca* and *I. oxyrinchus*

Estimation of genetic diversity indices at a global scale for each shark species was conducted using the totality of the sequences available in GenBank plus those obtained during this study (total sequences in *P. glauca*: 688 for *cob* and 554 for CR; *I. oxyrhynchus*: 193 for *cox1* and 850 for CR). Immediately before the calculation of genetic diversity indices, multiple sequence alignments for each molecular marker (*cox1*, *cob* or CR) were conducted using the software MAFFT v.7 (Katoh, Rozewicki, & Yamada, 2019) using the default parameters in the Cypress Science Gateway (Miller, Pfeiffer, & Schwartz, 2011).

2.4.1 | Population genetic analyses for *P. glauca* and *I. oxyrinchus*

The software Arlequin 3.5 (Excoffier & Lischer, 2010) was used to assess the molecular diversity of each shark species worldwide and per geographic region (see below). The standard diversity indices calculated were: number of polymorphic sites *S*, number of haplotypes *H*, haplotype diversity *Hd* (Nei, 1987) and nucleotide diversity π (Nei, 1987). Also, analyses of molecular variance (AMOVAs) were conducted for each mitochondrial region and for each shark species. Samples were grouped per geographic locality and also per ocean basin and hemispheres (Figure 2). For *P. glauca*, the totality of the sequences obtained during this study plus those retrieved from GenBank of *cob* (744 bp) were analysed according the following geographic regions: Mediterranean (MED, $n = 160$); north-east Atlantic (NEA, $n = 47$); north-east Pacific (NEP, $n = 79$); north-west Pacific (NWP, $n = 92$); north-central Pacific (NCP, $n = 64$); south-west Pacific (SWP, $n = 23$); Indian Ocean (IO, $n = 53$); and SEP ($n = 170$). For CR, sequences (730 bp length) were grouped according to the following regions: MED ($n = 131$), NEA ($n = 200$), South-east Atlantic-SEA ($n = 72$), south-west Atlantic (SWA, $n = 72$); and SEP ($n = 79$). In addition, a second AMOVA using the *cob* marker was used to compare the following groups: MED + NEA, NEP + NWP + NCP, IO and SWP + SEP. Similarly, a third AMOVA using the CR marker was used to compare three groups: MED + NEA, SEP and SEA + SWA. Pairwise genetic differentiations between regions were estimated using the fixation index (FST) statistic after 10,000 permutations and values associated with probabilities were obtained through an exact test, after 100,000 MCMC and 1,000 dememorization steps.

For *I. oxyrinchus*, the *cox1* sequences (598 bp) were analysed according to the following five geographic regions (Figure 2): NWP ($n = 28$), MED ($n = 23$), north Indian Ocean (NIO, $n = 63$), SWA ($n = 23$) and SEP ($n = 56$). For the CR marker, sequences (659 bp length) were analysed according to the following nine regions: NEA ($n = 70$); NWP ($n = 43$); NEP ($n = 105$); NCP ($n = 48$); NIO ($n = 99$); south Indian Ocean (SIO; $n = 45$); SWP ($n = 149$); SEP ($n = 199$); and SEA ($n = 92$). In addition, another AMOVA (using the CR sequences) was performed to compare the following four groups defining regions per ocean basin and hemisphere: NEA + SEA, NWP + NEP + NCP,

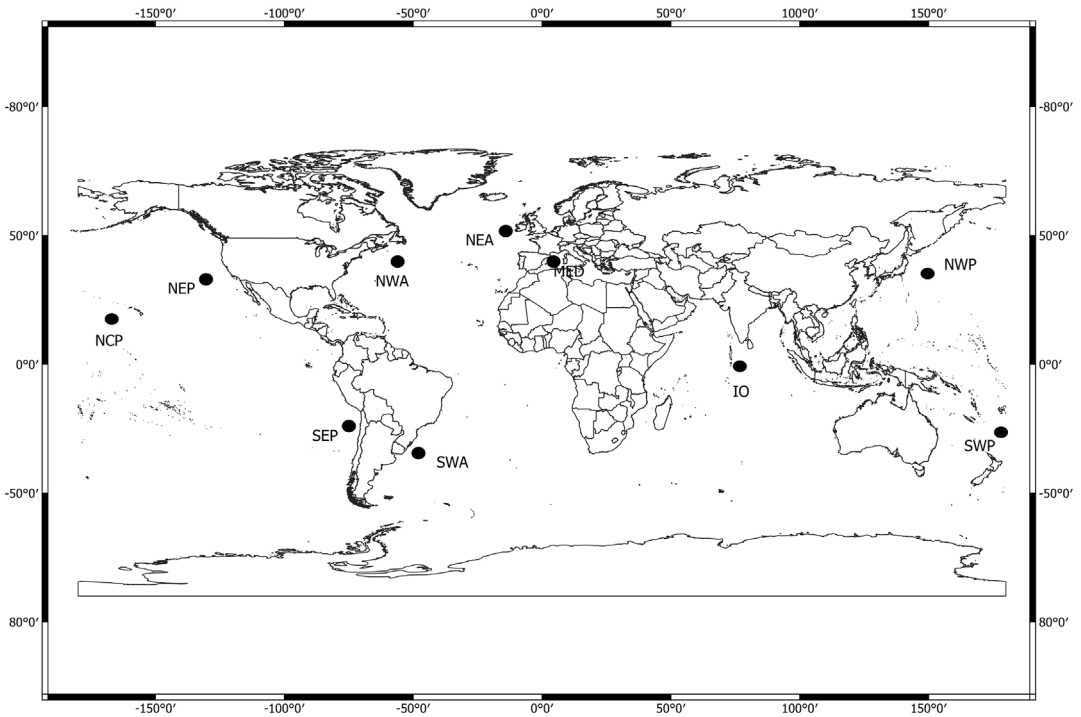

FIGURE 2 Global map showing geographic areas where specimens/sequences of blue and mako sharks were retrieved. IO, Indian Ocean (NIO, northern Indian Ocean; SIO, south Indian Ocean); MED, Mediterranean; NCP, north-central Pacific; NEA, north-east Atlantic; NEP, north-east Pacific; NWP, north-west Pacific; SEA, south-east Atlantic; SEP, south-east Pacific; SWA, south-west Atlantic; SWP, south-west Pacific.

NIO + SIO and SWP + SEP. Lastly, one AMOVA (using Cox1 sequences) was used to compare the following regions: NWP + SEP + SWP, NIO and MED + SWA. The AMOVAs were performed using distance-based matrices, and the statistical significance of each AMOVA was established with 10,000 permutations, using pairwise differences, in the software Arlequin 3.5 (Excoffier & Lischer, 2010). Pairwise genetic differentiations between regions were estimated using the FST statistic after 10,000 permutations and values associated with probabilities were obtained through an exact test, after 100,000 MCMC and 1,000 dememorization steps.

For each mitochondrial fragment, estimations of gene flow (Nm), the effective number of migrants exchanged between population per generation, *sensu* Wright (1969) among geographical regions were calculated using the software Arlequin 3.5 (Excoffier & Lischer, 2010).

Lastly, genealogical relationships in *P. glauca* (for both *cob* and CR) and *I. oxyrhynchus* (*cox1* and CR) were explored using all sequences from the different geographic regions using haplotype networks, which were constructed for each marker and species in HaploViewer (http://www.cibiv.at/greg/haploviewer/) based on neighbour-joining distances previously calculated in the software Mega v.6 (Tamura et al., 2013).

3 | RESULTS

3.1 | *Prionace glauca*

Of a total of 119 blue sharks captured in the SEP (Chile), 79 were successfully sequenced for CR and 72 for *cob*. The total length (of sequenced specimens) varied between 104 and 254 cm (X ± SD = 157.62 ± 38.60). Only 17 (21.5%) out of the 79 specimens captured were adults. For both mature and immature sharks, the sex ratios (males/females) were 0.45 and 0.55, respectively. Sequences of the CR fragment obtained in this study (n = 79 of 735 bp) had 18 polymorphic sites that defined a total of 33 haplotypes with Hd = 0.9231 ± 0.018 and π = 0.0044 ± 0.0025. In turn, for the *cob* fragment (n = 72 of 678 bp), 19 polymorphic sites were detected defining 20 haplotypes with Hd = 0.7696 ± 0.042 and π = 0.0019 ± 0.0013 (Table 1).

The spatial structure analysis performed separately for each mitochondrial fragment in the software GENELAND detected two genetic clusters co-occurring in the SEP; one genetic cluster exhibited greater distribution probabilities associated to northern and coastal latitudes (20°–25°S) whereas a second group was distributed westward between 30° and 40° S (Figure 3). For the CR, a total of 30 (38%) individuals were assigned to cluster 1 and 49 (62%) individuals to cluster 2 while for *cob*, 53 individuals were assigned to cluster 1 and 18 individuals to cluster 2. These individuals were assigned to one or other of the two genetic clusters with either a relatively moderate (p = 0.6) or high probability (p > 0.6). However, other 25 (CR) and 25 (*cob*) individuals were assigned to genetic clusters with relatively low probabilities (p = 0.51–0.59). Although only 16 adult *P. glauca* were sampled, most of CR (13 of 16) and *cob* (100%) sequences were assigned to population 1 while only 26% CR and 67% *cob* sequences of juveniles were assigned to population 1.

In the global phylogeographic analysis, CR sequences showed similar patterns for Hd and π values among geographical regions (Table 2). In turn, *cob* sequences exhibited highly variable Hd and π values among geographic regions, with the highest Hd and π recorded for sequences from MED and NEA and lowest Hd and π observed in the SWP, NEP, IO and NCP (Table 2).

The two AMOVAs used to test for genetic structure among each one of the different geographical regions compared (MED, NEA, SEA, SWP and SEP) revealed mean values of overall FST equal to 0.14 (CR; Table 3) and 0.13 (*cob*; Table 4). Importantly, in the two AMOVAs, molecular variation was much greater within than among populations (CR: 86.0 vs 13.75% and *cob*: 87.16 vs 12.84%, respectively). Still, this comparatively small variability among populations was significant (p < 0.0001 for each CR and *cob* test) and denoted low (shallow) but significant genetic structure in the blue shark across hemispheres and ocean basins (Table 3c,d). FST pairwise comparisons based on the CR demonstrated significant genetic differences among the most dissimilar geographical regions (MED, NEA, SEA, SWA and SEP), except between NEA and SEA (Table 3b). By contrast, FST pairwise comparisons based on the *cob* marker showed that blue sharks from the MED and NEA were not genetically dissimilar but differed from all other geographical regions. Blue sharks from the NEP did not differ with any other regions from Pacific and Indian oceans (NWP, NCP, SWP, SEP and IO; Table 4b), while blue sharks from the SEP were not genetically different from those in the NEP, SWP and IO, but there were significant genetic differences with those from NWP (Table 4b). The comparisons between the regions grouped per ocean basin and hemisphere based on *cob* showed significant genetic differentiation between hemispheres in the Pacific Ocean (Table 4c,d) but the IO region was not genetically different than those in more northern (NEP + NWP + NCP) and southern (SWP + SEP) regions.

Migration estimates indicated considerable gene flow between contiguous oceanic basins within hemispheres as well as between hemispheres (CR: NEA – SEA, Nm = 30.17; SWP – NEA, Nm = 16.48; SWP – SEA, Nm = 8.66; *cob*: NEP – NWP – NCP,

TABLE 1 Summary of the genetic diversity for *Prionace glauca* (PG) and *Isurus oxyrinchus* (IO) according to the cytochrome b (*cob*), cytochrome c oxidase I (*cox1*) and control region (CR) sequences from this study.

Spp.	Gene	N	*S*	*H*	*Hd*	*Hd* SD	π	π SD
PG	CR	79	18	33	0.9231	0.0179	0.004375	0.002530
	cob	72	19	20	0.7696	0.0423	0.001913	0.001343
IO	CR	128	24	27	0.7756	0.0362	0.003932	0.002316
	cox1	46	18	16	0.9246	0.0158	0.006867	0.003854

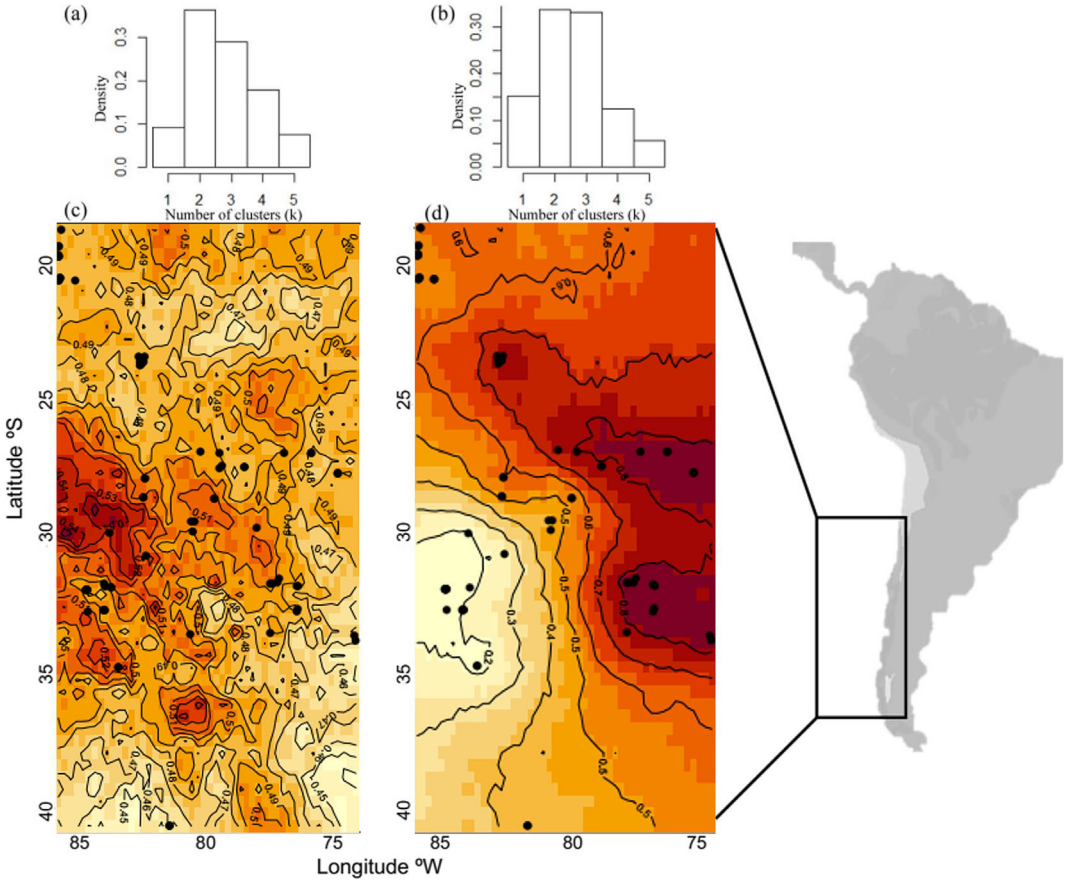

FIGURE 3 Spatial genetic analyses of blue shark *Prionace glauca* on the south-east Pacific coast. (a, b) Bayesian clustering analyses used to infer the number of genetic clusters k using the (a) control region (CR) and (b) cytochrome b (*cob*) mtDNA markers. (c, d) Posterior probability isoclines denoting the extent of genetic landscapes inferred in GENELAND using the (c) CR and (d) *cob* gene fragments. Black dots represent localities analysed in this study and regions with the greatest probability of inclusion are indicated using white, whereas diminishing probabilities of inclusion are proportional to the depth of colour (increasingly darker red colours).

Gene	Region	N	*S*	*H*	*Hd*	*Hd* SD	*π*	*π* SD
CR	MED	131	19	38	0.9026	0.0172	0.003803	0.002242
	NEA	200	28	48	0.9046	0.0121	0.004740	0.002689
	SEA	72	13	21	0.9002	0.0174	0.004373	0.002535
	SWA	72	22	35	0.9628	0.0093	0.004812	0.002748
	SEP	79	18	33	0.9231	0.0179	0.004375	0.002530
	Total	554	45	130	0.9223	0.0062	0.004611	0.002618
cob	MED	160	6	9	0.6391	0.0256	0.001089	0.000872
	NEA	47	13	11	0.7114	0.0472	0.001701	0.001211
	NEP	79	8	9	0.2379	0.0641	0.000371	0.000449
	NWP	92	12	11	0.3328	0.0633	0.000544	0.000562
	PNC	64	5	6	0.2584	0.0705	0.000365	0.000446
	SWP	23	2	3	0.1700	0.1025	0.000234	0.000357
	IO	53	6	7	0.2482	0.0786	0.000353	0.000439
	SEP	170	23	23	0.4305	0.0485	0.000700	0.000654
	Total	688	44	42	0.4816	0.0229	0.000814	0.000717

TABLE 2 Summary of the genetic diversity for *Prionace glauca* according to the cytochrome b (*cob*) and control region (CR) mitochondrial DNA regions for all databases (sequences from this study and from GenBank).

TABLE 3 Results of analysis of molecular variance for *Prionace glauca* among regions (a) and regions grouped per ocean basin and hemisphere (c) using control region fragment based on distance matrix methods, (b, d) pairwise distance comparisons based on distance matrix (below diagonal) and migration estimates (top diagonal).

a) Source of variation	d.f.	Variation (%)	*F*	*p*
Among populations	4	13.75		
Within populations	549	86.25	0.1375	<0.0001
Total	553			

b) Population	MED	NEA	SWA	SEA	SEP
MED = 131	0	2.112	2.524	1.258	6.72
NEA = 200	0.1913*	0	16.489	30.174	2.517
SWA = 72	0.1653*	0.0294*	0	8.662	5.583
SEA = 72	0.2859*	0.0163	0.0545*	0	1.573
SEP = 79	0.0692*	0.1656*	0.0821*	0.2411*	0

c) Source of variation	d.f.	Variation (%)	*F*	*p*
Among populations	2	7.14		
Within populations	551	92.86	0.0714	<0.0001
Total	553			

d) Population	MED + NEA	SEP	SEA + SWA
MED + NEA	0		
SEP	0.081*	0	
SEA+SWA	0.044*	0.151*	0

Note: The significance of the fixation index values was assessed via 1,000 permutations.
Bonferroni corrected at $p < 0.05$ (p-values <0.005).

Nm > 103.16; NEP – SWP, Nm = 50.9; NEP – SEP, Nm = 266.87; NEP – IO, Nm = 153.4).

The haplotype network constructed with the *cob* sequences ($n = 688$) demonstrated the existence of a single common haplotype widely distributed among all regions; and a second haplotype distributed only in the MED, NEA and NCP. The most common *cob* haplotype is surrounded by 12 unique haplotypes from the SEP, and other less frequent haplotypes shared among various studied regions (Figure 4). The network based on the CR marker ($n = 554$) showed higher diversity of haplotypes, with some shared haplotypes frequent in the MED, SEP and SEA, other shared haplotypes present in the NEA, SEA and SWA, and a high number of unique haplotypes (Figure 5).

3.2 | *Isurus oxyrinchus*

A total of 132 mako sharks were captured in the SEP (Chile), and 128 were successfully sequenced for CR but only 46 were sequenced for Cox1. Their total length varied between 63 and 289 cm (X ± SD = 138.86 ± 32.25). Only a single specimen was an adult. Sex ratio (males/females including immature and mature sharks) was 1:1.

Sequences of the CR marker obtained in this study ($n = 128$, each 711 bp long after alignment) had 24 polymorphic sites that defined a total of 27 haplotypes with Hd = 0.775 ± 0.036 and $\pi = 0.004 \pm 0.002$. For the *cox1* marker ($n = 46$ of 614 bp), 18 polymorphic sites were detected defining 16 haplotypes with *Hd* = 0.924 ± 0.015 and $\pi = 0.006 \pm 0.003$ (Table 1). The spatial structure analysis performed separately for each mitochondrial marker in the software GENELAND detected only a single genetic cluster occurring in the SEP.

In the global phylogeographic analysis, CR sequences ($n = 850$) showed *Hd* and π similar among geographical regions inhabiting the Northern Hemisphere. In the Southern Hemisphere, only *Hd* and π values from the SEA were similar to those in populations from the Northern Hemisphere. *Hd* and π values were lower in the SWP and SEP. However, the lowest *Hd* and π were recorded in sequences from NIO (Table 5). In turn, *cox1* sequences ($n = 202$) exhibited high *Hd* and π in the NWP, SWP and SEP compared to low *Hd* and π values recorded in the NIO (Table 5).

The AMOVAs used to test for genetic structure among each one of the different geographical regions compared (CR: NEA, NWP, NEP, NCP, NIO, SIO, SWP, SEP and SEA; *cox1*: MED, NIO, SWA, SEP and SWP) revealed mean values of overall FST equal to 0.06 (CR) and 0.15 (*cox1*; Tables 6 and 7). Importantly, in the AMOVAs, molecular variation was much greater within than among populations. The AMOVA grouping regions confirmed a significant genetic structure in the shortfin mako across hemispheres and ocean basins (Table 6c,d). FST pairwise comparisons based on the CR and *cox1* gene markers demonstrated significant genetic differences among most of the different geographical regions compared (Tables 6 and 7). For instance, only sharks from the NEP, NWP, NCP and SEP were not

TABLE 4 Results of analysis of molecular variance (AMOVA) for *Prionace glauca* among regions (a) and regions grouped per ocean basin and hemisphere (c) using the cytochrome b gene based on distance matrix methods and (b, d) pairwise distance comparisons based on distance matrix (below diagonal) and migration estimates (top diagonal).

a) Source of variation		d.f.		Variation (%)		F		p
Among populations		7		12.84				
Within populations		680		87.16		0.12838		<0.0001
Total		687						
b) Population	**MED**	**NEA**	**NEP**	**NWP**	**NCP**	**SWP**	**IO**	**SEP**
MED = 160	0	25.501	2.429	2.461	2.723	3.044	2.720	2.462
NEA = 47	0.0192	0	1.316	1.401	1.501	2.006	1.543	1.373
NEP = 79	0.1707*	0.2751*	0	−103.16	−289.51	−50.90	−153.40	266.87
NWP = 92	0.1688*	0.2629*	−0.0048	0	−90.752	−410.33	230.98	55.806
NCP = 64	0.1550*	0.2498*	−0.0017	−0.0055	0	34.294	367.14	47.028
SWP = 23	0.1410*	0.1994*	−0.0099	−0.0012	0.0143	0	−31.364	−35.514
IO = 53	0.1552*	0.2446*	−0.0032	0.0021	0.0013	−0.0016	0	233.14
SEP = 170	0.1688*	0.2668*	0.0018	0.0088*	0.0105	−0.0142	0.0021	0
c) Source of variation		**d.f.**		**Variation**		**F**		**p**
Among populations		3		14.56				
Within populations		684		85.44		0.14		<0.0001
Total		687						
d) Population		**MED + NEA**		**NEP + NWP + NCP**		**IO**		**SWP + SEP**
MED + NEA		0						
NEP + NWP + NCP		0.2028*		0				
IO		0.1557*		0.0010		0		
SWP + SEP		0.1806*		0.0108*		0.0022		0

Note: The significance of the fixation index values was assessed via 1,000 permutations.
*Bonferroni corrected at $p < 0.05$ (p-values <0.0018).

genetically different from each other when the comparisons were based on the CR (Table 6b). In turn, pairwise comparisons based on the *cox1* protein-coding gene fragment indicate that sharks from the MED were genetically different from all other geographic regions ($p < 0.05$). In turn, the NWP does not differ from other regions, except the MED. The NIO differs genetically only from the SEP. The SWA and SWP do not differ from each other, while mako sharks from the SEP are genetically different to those inhabiting the NIO and SWA (Table 7b). The comparisons among grouped regions, however, showed genetic differentiation among ocean basins (NWP + SEP + SWP, NIO and MED + SWA), probably due to marked genetic differences shown for the *cox1* sequences of MED.

Migration estimates indicated considerable gene flow between contiguous oceanic basins within an hemisphere as well as between hemispheres (CR: NWP – NEP – PNC, Nm > 107.19; SWP – NWP – NEP – NCP – NIO – SEP, Nm > 13.05; SEA – SWP, Nm = 27,57).

The haplotype network analysis constructed with the *cox1* marker ($n = 202$; Table 5) indicated the presence of a single dominant haplotype that was very frequent in the NIO and other haplogroups not well defined from a geographic standpoint. One of these haplogroups consisted mostly of haplotypes from the SEP that also included 10 unique haplotypes plus haplotypes shared with the NWP, NIO, SWA and other uncommon haplotypes from the MED (Figure 6). A second haplogroup was composed mostly of haplotypes present in the SEP, NWP, NIO, SWA and MED. In this latter haplogroup, four haplotypes were unique to the SEP. The haplotype network based on the CR marker exhibited a dominant haplotype, frequent in the NIO, SWP and SEP, and with lower frequency, present in the NCP, NEP, NWP, NEA and SEA. This dominant CR haplotype was surrounded by haplotypes more frequently found in the NEA, NEP, SWP and SEP, but also, at lower frequency, in the NIO (Figure 7).

4 | DISCUSSION

Population delimitation is crucial to improve conservation and fisheries management strategies in marine systems, especially in highly migratory sharks such as the blue shark *P. glauca* and the shortfin mako *I. oxyrinchus*, whose population structures were, until now, unknown in the South-east Pacific Ocean (González et al., 2021). This study explored, for the first time, the population genetics of these sharks at two geographical scales (regional and global) using two genetic markers well suited for phylogeographic inference.

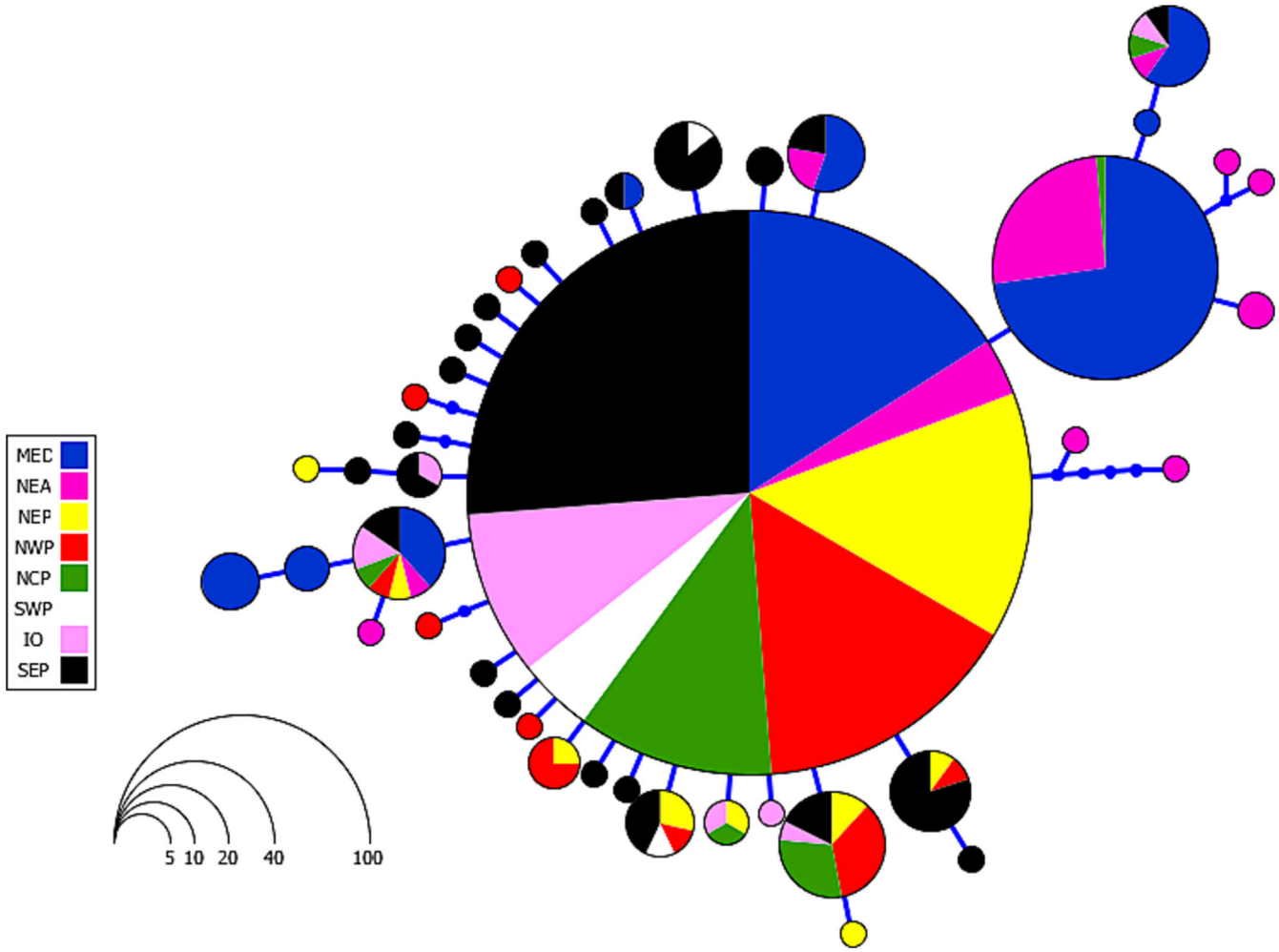

FIGURE 4 Neighbour-joining haplotype network estimated using cytochrome b (*cob*) sequences in blue shark *Prionace glauca*. Each point separating two circles indicates a single substitution. The area of each circle corresponds to the number of haplotypes it represents. The colour of each circle represents the location where the haplotype was found.

At a regional scale, a spatial genetic analysis (GENELAND) detected two blue shark genetic clusters co-occurring along the SEP coast while a single cluster was detected for the mako shark. At a global scale, AMOVAs, migration estimates and haplotype networks indicate that the two species exhibit an overall pattern of high population connectivity among contiguous ocean basins and between hemispheres with a signature of shallow (matrilineal) genetic structuring worldwide.

4.1 | Blue shark *Prionace glauca*

The blue shark *P. glauca* is one of the most abundant epipelagic sharks in the ocean from 60°N to 50°S (Compagno, 1984; Leone et al., 2017; Bailleul et al., 2018). However, information about its genetic structure is rare in the Southern Hemisphere, and genetic information was missing, until now, for the SEP (Ferreira, 2013; Veríssimo et al., 2017). It is known that blue shark mating, pupping and nursery sites occur in the Atlantic (Vandeperre et al., 2014; Veríssimo et al., 2017), MED (Megalofonou, Damalas & De Metrio, 2009) and North Pacific (Carrera-Fernández, Galván-Magaña & Ceballos-Vázquez, 2010). Limited data also suggest the existence of pupping and nursery areas in the SEP (approximately at 27°S – Bustamante & Bennett, 2013). The existence of regional pupping and nursery grounds coupled with philopatric behaviour (Vandeperre et al., 2014) is expected to drive genetic differentiation, at least at large spatial scales, in the blue shark. Interestingly, no consensus has been reached so far regarding the existence, or not, of large-scale spatial genetic structure in this species (see Leone et al., 2017; Bailleul et al., 2018). Using mtDNA (CR and *cob*), Leone et al. (2017) detected a statistically significant genetic break between MED and NEA blue shark populations. This break (although shallow) is also evident in the current analyses (i.e. using AMOVAs conducted with both the CR and *cob* markers) which also demonstrate genetic structuring in blue shark populations across a large spatial scale. It is, however, important to emphasize that the observed genetic differentiation between hemispheres and across

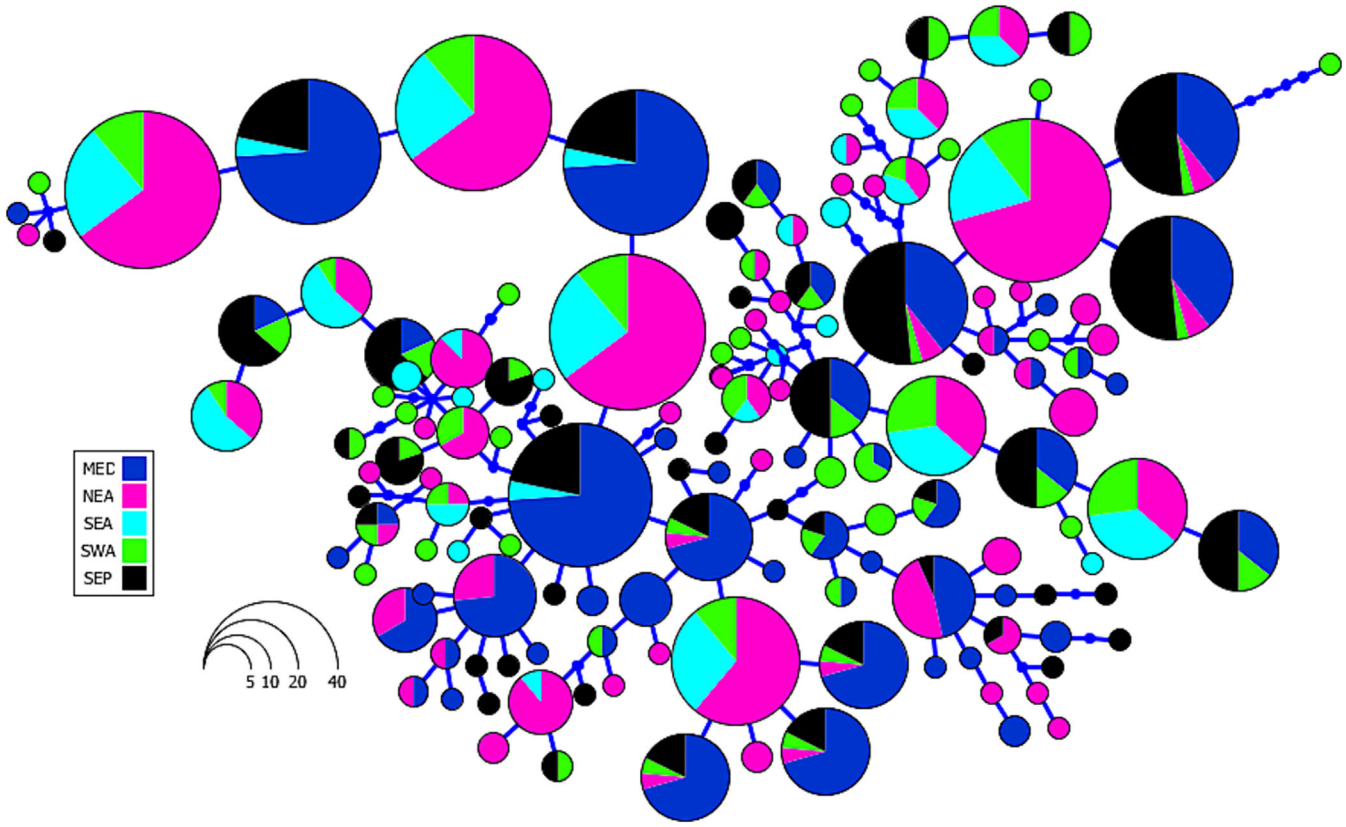

FIGURE 5 Neighbour-joining haplotype network estimated using control region sequences in blue shark *Prionace glauca*. Each point separating two circles indicates a single substitution. The area of each circle corresponds to the number of haplotypes it represents. The colour of each circle represents the location where the haplotype was found.

TABLE 5 Summary of the genetic diversity for *Isurus oxyrinchus* according to the cytochrome c oxidase I (*cox1*) and control region (CR) mitochondrial DNA regions for all databases (sequences from this study and from GenBank).

	Region	N	*S*	*H*	*Hd*	*Hd* SD	*π*	*π* SD
CR	NEA	70	14	13	0.801	0.0202	0.003756	0.002277
	NWP	43	14	9	0.8018	0.0391	0.004463	0.002648
	NEP	105	19	19	0.8711	0.0200	0.005002	0.002872
	NCP	48	15	11	0.8564	0.0294	0.005381	0.003091
	NIO	99	15	19	0.6252	0.0563	0.002800	0.001796
	SIO	45	13	8	0.7364	0.0423	0.003372	0.002104
	SWP	149	20	18	0.7968	0.0269	0.004046	0.002400
	SEP	199	24	25	0.7343	0.0305	0.003451	0.002106
	SEA	92	16	16	0.8239	0.0249	0.003630	0.002207
	Total	850	36	74	0.8073	0.0114	0.004075	0.002401
cox1	NWP	28	22	16	0.9444	0.0231	0.008724	0.004843
	MED	23	20	9	0.8261	0.0656	0.007429	0.004239
	NIO	63	21	15	0.7081	0.0593	0.005953	0.003400
	SWA	23	72	12	0.9051	0.0414	0.014983	0.007990
	SEP	56	21	20	0.9286	0.0150	0.007096	0.003963
	SWP	9	22	9	1.0	0.0524	0.013564	0.007890
	Total	202	104	52	0.9225	0.0118	0.009199	0.004916

ocean basins in this species is shallow considering that the two AMOVAs detected a pattern of molecular variation that was much greater within than among populations (CR: 94.27 vs 5.73% and *cox1*: 85.47 vs 14.53%, respectively). Indeed, the aforementioned analyses coupled with the information obtained from haplotype networks and migration estimates clearly indicate an overall background scenario

TABLE 6 Results of analysis of (a) molecular variance for *Isurus oxyrinchus* among regions (a) and regions grouped per ocean basin and hemisphere (c) using control region fragment based on distance matrix methods and (b, d) pairwise distance comparisons based on distance matrix (below diagonal) and migration estimates (top diagonal).

a) Source of variation	d.f.	Variation (%)	*F*	*p*
Among populations	8	5.73		
Within populations	841	94.27	0.05727	<0.0001
Total	849			

b) Population	NEA	NWP	NEP	NCP	NIO	SIO	SWP	SEP	SEA
NEA = 70	0	2.234	2.915	2.872	1.690	5.465	4.667	2.295	9.342
NWP = 43	0.1828*	0	187.46	−107.10	9.231	3.614	18.282	18.389	6.392
NEP = 105	0.1463*	0.00266	0	−117.05	11.031	5.494	41.658	21.871	8.589
NCP = 48	0.1482*	−0.0046	−0.0042	0	6.741	4.556	20.033	10.199	7.428
NIO = 99	0.2282*	0.0513*	0.0433*	0.0690*	0	2.886	13.057	37.465	6.601
SIO = 45	0.0838*	0.1215*	0.083*	0.0988*	0.1476*	0	8.650	4.486	14.456
SWP = 149	0.0967*	0.0266*	0.0118*	0.0243	0.0368*	0.0546*	0	27.574	30.986
SEP = 199	0.1788*	0.0264	0.0223*	0.0467*	0.0131	0.1002*	0.0178*	0	9.0822
SEA = 92	0.0508*	0.0725*	0.0550*	0.0630*	0.0704*	0.0334*	0.0158	0.0521*	0

c) Source of variation	d.f.	Variation (%)	*F*	*p*
Among populations	3	4.56		
Within populations	846	95.44	0.045	<0.0001
Total	849			

d) Population	NEA + SEA	NWP + NEP + NCP	NIO + SIO	SWP + SEP
NEA + SEA	0			
NWP + NEP + NCP	0.0922*	0		
NIO + SIO	0.0720*	0.0390*	0	
SWP + SEP	0.0700*	0.0194*	0.0105*	0

Note: The significance of the fixation index values was assessed via 1,000 permutations.
*$p < 0.05$ with Bonferroni correction (p-values <0.0014).

depicting strong connectivity among hemispheres and ocean basins (plus the mentioned signature of moderate to low population differentiation worldwide). These results partially agree with those of Bailleul et al. (2018), who using one mtDNA marker (*cob*) and nine microsatellites (SSRs) detected signatures of genetic bottlenecks in a sample of >200 blue sharks but nearly complete genetic homogeneity in blue sharks from the east Atlantic Ocean (Vigo, Spain and Azores islands), the MED (Gulf of Lion including Grau du Roi and Corsica from France, Malta and Greece) and the Pacific Ocean (Hawaii, Australia and New Zealand). The same authors, however, suggested that their results should be interpreted with caution due to limited sample size in some regions (i.e. only 9, 27 and 11 individuals were sampled, respectively, in Hawaii, New Zealand and Australia) and the existence of dissimilar demographic histories among geographic regions that might obscure signature of genetic differentiation across large spatial scales (Bailleul et al., 2018).

At a regional scale, the software GENELAND detected two genetic groups co-occurring along the SEP: one genetic cluster was distributed in northern and coastal latitudes (20°–25°S) whereas a second group was distributed westwards between 30° and 40° S. The existence of two genetic clusters in the SEP has been observed before in the porbeagle shark *Lamna nasus* (Gonzalez et al., 2021). The current results, however, also should be interpreted with caution given that ~31% of the individuals (using both CR and *cob* markers) were assigned to genetic clusters with relatively low probabilities ($p = 0.51–0.59$). Despite assignment probabilities, it is interesting that adults of *P. glauca* (13 out of 16 CR sequences and 100% *cob* sequences) were assigned to population 1 while only 26% CR and 67% *cob* sequences of the juveniles were assigned to population 1. This result could suggest the existence of at least two nursery grounds along the SEP, with adults restricted to offshore areas within this geographical region. We argue in favour of additional population genetic studies over a wider geographic area in the SEP as well as larger sample sizes (including adults and juveniles) and different molecular markers (i.e. single nucleotide polymorphisms retrieved from reduced-representation genome sequencing strategies) to confirm the existence of putative genetically dissimilar populations of blue sharks in the SEP and beyond. Such information is most needed to improve the fishery management of the species in the region (i.e. Chile, Peru, Ecuador) taking into account the current absence of coordination among the aforementioned countries currently exploiting this species.

TABLE 7 Results of analysis of (a) molecular variance for *Isurus oxyrinchus* among regions using the cytochrome c oxidase I gene based on distance matrix methods and (b, d) pairwise distance comparisons based on distance matrix (below diagonal) and migration estimates (top diagonal).

a) Source of variation	d.f.	Variation (%)	*F*	*p*
Among populations	5	14.53		
Within populations	196	85.47	0.14527	<0.0001
Total	201			

b) Population	NWP	MED	NIO	SWA	SEP	SWP
NWP = 28	0	1.675	7.616	17.544	14.098	74.462
MED = 23	0.2298*	0	1.1980	1.861	0.845	2.859
NIO = 63	0.0616	0.2943*	0	38.870	2.238	4.116
SWA = 23	0.0277	0.2117*	0.0127	0	3.846	22.186
SEP = 56	0.0342	0.3715*	0.1825*	0.1150*	0	5.280
SWP = 9	0.0066	0.1488	0.1083	0.0220	0.0865	0

c) Source of variation	d.f.	Variation (%)	*F*	*p*
Among populations	2	10.27		
Within populations	199	89.73	0.102	<0.0001
Total	201			

d) Population	NWP + SEP + SWP	NIO	MED + SWA
NWP + SEP + SWP	0		
NIO	0.1157*	0	
MED + SWA	0.1169*	0.05922*	0

Note: The significance of the fixation index values was assessed via 1,000 permutations.
*$p < 0.05$ with Bonferroni corrected *p*-values (<0.003).

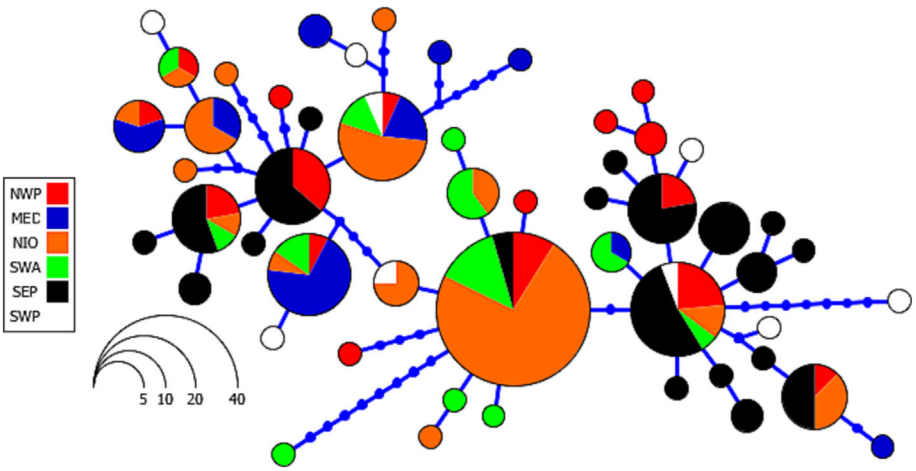

FIGURE 6 Neighbour-joining haplotype network estimated using cytochrome c oxidase I (*cox1*) sequences in shortfin mako *Isurus oxyrinchus*. Each point separating two circles indicates a single substitution. The area of each circle corresponds to the number of haplotypes it represents. The colour of each circle represents the location where the haplotype was found.

4.2 | Shortfin mako *Isurus oxyrinchus*

The shortfin mako is a large pelagic and highly migratory shark widespread in oceanic and coastal waters (Compagno, 1984). However, there was no genetic information for this species within the SEP and biological information is scarce (Acuña et al., 2001; Cerna & Licandeo, 2009). At a global scale, previous studies using either a fragment of the mitochondrial genome CR or restriction fragment length polymorphisms found evidence of strong genetic differentiation between shortfin mako populations from the North Atlantic and Pacific Ocean, the North Pacific and South Pacific oceans and between the SWP and SEP, and suggested the presence of at least three shortfin mako stocks in the Pacific Ocean. The same analyses suggested gene flow among populations in the Pacific and Atlantic oceans through the Indian Ocean (Michaud et al., 2011). Schrey & Heist (2003), however, detected low levels of genetic differentiation among these same geographic areas using nuclear markers (four SSRs). Most recently, Corrigan et al. (2018) sampled shortfin mako from six regions across the Southern Hemisphere (Indo-Pacific, Eastern Australia, New Zealand and South Africa), and,

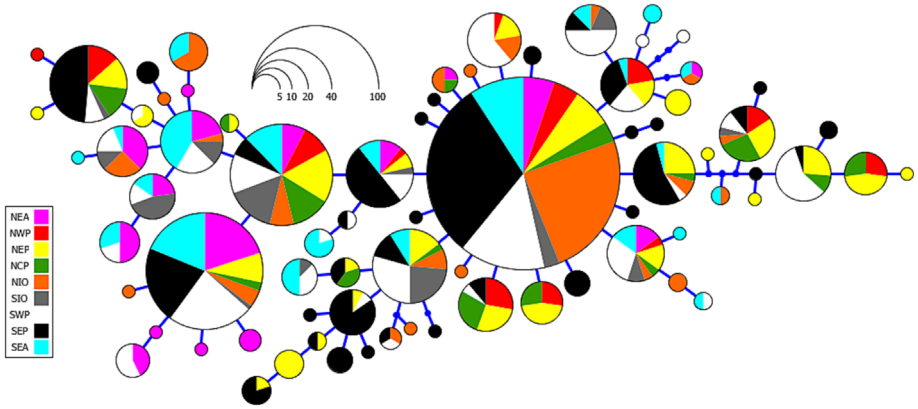

FIGURE 7 Neighbour-joining haplotype network estimated using control region sequences in shortfin mako *Isurus oxyrinchus*. Each point separating two circles indicates a single substitution. The area of each circle corresponds to the number of haplotypes it represents. The colour of each circle represents the location where the haplotype was found.

based on two different types of genetic markers, suggested that the shortfin mako constitutes a globally panmictic population (information from SSRs) but with a matrilineal genetic sub-structure across hemispheres (information from the CR fragment). The current results are in agreement with the aforementioned and other previous studies using mitochondrial markers (Heist, Musick & Graves, 1996; Michaud et al., 2011): analyses support the previously reported matrilineal genetic structuring in this species worldwide although it is noted that AMOVAs and migration estimates indicate high levels of connectivity among hemispheres and ocean basins.

Importantly, the two mtDNA markers used in this study provided somewhat dissimilar patterns of genetic connectivity in the shortfin mako (and to a certain extent, in the blue shark). Specifically, the AMOVA based on the CR marker indicated that only sharks from the NEP, NWP and PCN were not genetically dissimilar from each other while the AMOVA based on the *cox1* gene showed that the NWP does not differ from other studied geographic regions (except the MED where shortfin mako are genetically different from all other geographic regions). Furthermore, the AMOVA based on the CR showed that sharks from the SEP were genetically different from other compared geographical regions while the AMOVA based on the *cox1* gene did not show any genetic dissimilarity between the SEP and NWP. It should be noted that the genetic differences are shallow given the overall low FST value estimated for the two studied species based on two different mtDNA markers. Second, the differences among mtDNA markers used in this study are not necessarily unexpected: the non-coding CR is likely to experience greater mutation rates compared to the functionally constrained protein-coding gene *cox1* (Avise, 2000). Thus, *cox1* (and maybe other protein coding genes) might fail to detect actual genetic differentiation among populations that can be revealed by interrogation of the CR. Despite the observed differences between markers, it is likely that soft physical and/or biological geographic barriers might be driving, at least to some minimal degree, shallow genetic differentiation among ocean basins in the shortfin mako, even though this species exhibits an impressively high mobility and analysis shows a high background level of connectivity.

The mechanisms favouring connectivity among hemispheres and ocean basins are not completely understood in sharks, including the shortfin mako. Nonetheless, cold water corridors might provide opportunities for large spatial scale movements (i.e. between contiguous ocean basins in each hemisphere and between hemispheres within ocean basins) in the shortfin mako and other shark species. For instance, in the Pacific Ocean, the Humboldt Current (off northern Chile and Peru) generates a 'tongue' of relatively cool surface waters that extends thousands of kilometres offshore, providing opportunities for trans-equatorial movements and connectivity across hemispheres in the Pacific for populations of shortfin mako, and other migratory species (Heist, Musick & Graves, 1996; Sepúlveda & González, 2017). Satellite-tagging studies worldwide (e.g. Abascal et al., 2011; Corrigan et al., 2018) over long time periods are needed to improve the understanding of migratory routes and connections among populations in sharks, including the shortfin and blue sharks.

The pattern of (shallow) genetic differentiation at a global scale observed herein for the shortfin mako (and blue shark) has been recorded before in other sharks with a widespread distribution, and genetic differentiation among ocean basins (or hemispheres) has been suggested to be driven by tropical biogeographic breaks in coastal (e.g. *Sphyrna lewini*, Chapman, Pinhal & Shivji, 2009; *Carcharhinus leucas*, Karl et al., 2011), semi-oceanic (*Carcharhinus signatus*, Domingues et al., 2019) and pelagic species (*Carcharhinus falciformis*, Clarke et al., 2015). The shallow but rather complex genetic patterns detected for the shortfin mako worldwide is consistent with this species' behavioural attributes. For instance, satellite telemetry has shown that shortfin mako from Indian, Atlantic and West Pacific regions are highly migratory and that some individuals migrate long-distances, although other sharks exhibit fidelity to relatively small geographical areas for extended time periods (Corrigan et al., 2018). Similarly, Abascal et al. (2011) analysed the movements of the shortfin mako in the SEP using pop-up satellite archival tags and did not find obvious patterns in their horizontal trajectories, with the exception of an inshore trend around the start of the austral winter when some individuals remained in the upper water column while others reached about 800 m depth, a behaviour that could be associated to their feeding habits (Rosas-Luis et al., 2016). Extensive horizontal and vertical migrations in the water column might contribute towards genetic mixing among shortfin mako from different geographical areas.

Lastly, in the shortfin mako, there was lower genetic diversity in the South Pacific (both SWP and SEP) and Indian Ocean (NIO and SIO) compared with the Northern Hemisphere, suggesting possible bottlenecks and/or founder events in the South Pacific. The latter could have occurred during glacial periods, as suggested before for other large migratory sharks (Bolaño-Martínez et al., 2019; González et al., 2021; but see Pimm et al., 1989).

5 | CONCLUSIONS

We have explored the regional and worldwide population genetics of two large Endangered or Near Threatened and highly migratory sharks, heavily targeted by artisanal and industrial fisheries, and we have shown that they exhibit an overall pattern of high population connectivity among hemispheres and across ocean basins with a signature of shallow matrilineal genetic structuring worldwide. The observed population genetic pattern suggests that other markers with more statistical power (than mtDNA) to detect genetic dissimilarities (e.g. genome-wide single nucleotide polymorphisms) among populations might be able to reveal genetic discontinuities between contiguous (and more distant) ocean basins within hemispheres as well as between hemispheres. We argue in favour of the aforementioned studies while focusing, in parallel, on the sampling of neonates, juveniles and mature females to evaluate metapopulation genetic connectivity and philopatry in the two species (see Tillett et al., 2012; Portnoy et al., 2015; Bernard et al., 2016; Biais et al., 2017; González et al., 2021). The two studied sharks are under intense fishing pressure from artisanal and industrial fleets worldwide and some local populations are in decline due to overfishing (i.e. the blue shark in the Mediterranean – Ferretti et al., 2008; Rigby et al., 2019). From 2019, *I. oxyrinchus* has been listed in Appendix II of CITES that currently imposes limitations on the international trade in products derived from and specimens of this shark species, and promotes conservation programmes between countries (Sellheim, 2020). The information generated during this and future studies can help guide conservation and fisheries management in the two studied species while practical conservation and management measures are required immediately, and should include reduced fishing effort, fishing gear restrictions to avoid accidental captures in fisheries not targeting sharks, and spatio-temporal fisheries closures. Furthermore, it is essential to improve our knowledge about the location of nursery grounds and growth rates in specific areas across the geographic range of these two species. A sampling of neonates, juveniles and mature females needs to be prioritized to evaluate genetic connectivity among populations (Bernard et al., 2016; Biais et al., 2017; González et al., 2021). Such information will help to implement genetic monitoring programmes of stocks in the South Pacific (and south Hemisphere). Importantly, these measures need to be coordinated among countries targeting these vulnerable sharks taking into account that efficient fishery management at both regional and global scales can only be achieved with international collaboration and inclusive research strategies (Hoyle et al., 2017). In the SEP, a monitoring programme is being developed that includes tagging, records of captures and pregnant females, trophic ecology and onboard scientific observer to record catches by sex and size of sharks along the geographical range associated to fishery activity.

AUTHOR CONTRIBUTIONS

M. Teresa González: Conceptualization; investigation; writing—original draft; methodology; validation; visualization; formal analysis; writing—review and editing; data curation; supervision; resources; project administration. **Natalia V. Leiva**: Investigation; methodology; validation; visualization; writing—review and editing; formal analysis; data curation. **Patricia M. Zárate**: Conceptualization; investigation; writing—original draft; methodology; validation; visualization; writing—review and editing; project administration; formal analysis; data curation; supervision; resources. **J. Antonio Baeza**: Conceptualization; investigation; writing—original draft; methodology; writing—review and editing; visualization; validation; project administration; formal analysis; data curation; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

None of the authors have conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Genbank at https://www.ncbi.nlm.nih.gov/genbank/.

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