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Local adaptive variation in a highly migratory fish: The smooth hammerhead shark *Sphyrna zygaena*

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ABSTRACT

Populations of highly mobile species that undertake long distance migrations are typically considered to be panmictic. Nonetheless, mechanisms related to behavior or local environmental conditions promote genetic isolation in the absence of physical barriers. Highly migratory shark species exhibit varying levels of fidelity to specific regions, shaping the genetic architecture of different populations and resulting in geographically based genetic variation with potential adaptive value. An understanding of the genetic variation of highly migratory species is needed to develop effective conservation strategies. This study aimed to assess the neutral and adaptive variation of the smooth hammerhead shark (*Sphyrna zygaena*) in the northern Mexican Pacific (NMP) via single nucleotide polymorphisms (SNPs). We analyzed 1480 SNPs in 92 individuals from four geographic regions in the NMP, of which 1469 SNPs were neutral loci (n-SNP), and 11 were putatively under selection (o-SNP) using four genoma scan methods. Genetic diversity was geographically similar among regions ($Ho = 0.275$). The neutral variation showed panmixia (n-SNPs; $F_{ST} = 0.0012$, $p = 0.44$), which may be associated with the high dispersal capacity of *S. zygaena*. A pattern of adaptive variation between individuals from the Gulf of California and Pacific coast was revealed using o-SNPs F_{ST}-based methods (24 oSNPs; $F_{ST} = 0.061$, $p < 0.001$), which may be promoted by individual preferences based on physiological limitations. The estimated effective population size (*Ne*) of *S. zygaena* was 1390 individuals, which is theoretically optimal for the population to persist over time.

1. Introduction

Assessing isolation mechanisms in populations of marine species with high dispersal potential is often complex, as broad geographic areas must be considered [1,2]. In pelagic shark species, many isolation mechanisms (e.g., site fidelity, residency, and philopatry) influence the structure of populations in the absence of physical barriers [3,4]. If sharks of the same species reside in isolation in restricted geographic areas for long enough, then small-scale population structure is likely to ensure [4]. In these cases, shark home ranges will vary in size and distribution based on the species or ontogenetic stage of the individuals in the population [5]. Nonetheless, site fidelity (i.e., the return of individuals to an area in which they have previously resided after long-distance movements) may not necessarily contribute to population structure; however, if site fidelity is related to reproduction (e.g., mating and parturition), then reproductive isolation will develop [3,4,6]. Natal or regional philopatry occurs when breeders preferentially return to their places of birth or birth regions, respectively [4].

The high dispersal potential of certain marine species generally suggests a limit to their potential for local adaptation [7–9]. However, the results of recent seascape genomics studies suggest that local adaptation can be maintained in the presence of gene flow [10,11]. Nonetheless, if persistent environmental heterogeneity restricts migration, then different preferences for different reproductive habitats linked to environmental variables may influence local adaptation [12]. Local adaptations are a type of genetic variation that must be conserved to improve species survival; thus, management and conservation strategies for exploited shark species must take into consideration how natural selection operates within large and genetically homogenous marine populations [13].

In recent decades, the development of genomic techniques permitting the evaluation of thousands of loci throughout the genome in both

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random sites and coding regions (e.g., exons in nuclear genes) has improved understanding of local adaptation in wild species [14]. The identification of outlier loci (i.e., loci that are more divergent than expected by genetic drift) has made it possible to detect genotypes and evaluate adaptation within populations [15–18]. This approach has allowed the detection of cryptic genetic structure in response to local selection in marine species that show low genetic differentiation based on neutral loci [19]. Furthermore, these cryptic patterns of differentiation that reflect local adaptation are particularly important for the conservation of exploited species, especially those vulnerable to overfishing.

Fisheries genetics examines patterns in the short- and long-term to enhance our understanding of the mechanisms that shape the distribution and abundance of commercial species, whereas classical fisheries scientific approaches typically focus on short term factors (e.g., size structure, size at maturity, and growth rates) [13,20]. To this end, the goal of fisheries genetics is to understand the dynamics and resilience of exploited populations. In exploited shark species, technical and analytical advances based on different molecular markers have altered our understanding of their evolution. Thus, the management of at-risk species can be improved by employing these approaches to elucidate broad scenarios and provide novel insights into population structure and adaptation.

An example of this approach is the case of the bonnethead shark (*Sphyrna tiburo*) from the southeastern the United States and Gulf of Mexico. *Sphyrna tiburo* seasonally migrates offshore and across latitudes and exhibits site fidelity to specific estuaries [21–23]. The population genetic structure of this species was confirmed by female philopatry to nursery areas and the presence of male-mediated gene flow along the northeastern coast of the Gulf of Mexico, which was apparent in mtDNA, microsatellite loci, and neutral single nucleotide polymorphism (SNP) data [24–26]. In particular, outlier SNP data reflected latitudinal selection and indicated that this selection was strong enough to outweigh the homogenizing pressure of male migration [24]. From this example, it is apparent that female philopatry may act to maintain the genetic diversity present in specific locations, whereas male-mediated gene flow may promote adaptive variation across the landscape, thus facilitating species persistence at local and regional scales [24].

The smooth hammerhead (*Sphyrna zygaena*) is a semi-oceanic cosmopolitan species with few records in the open ocean [27,28]. Compared to those of other members of the Sphyrnidae family, the latitudinal distribution (60 °N to 55 °S) of *S. zygaena* is broad, although this species is found mainly near the continental shelf [27]. *Sphyrna zygaena* is commercially important and fished with a wide variety of fishing gears in artisanal and industrial fisheries worldwide [27–30]. The international trade of *S. zygaena* is regulated, because it is listed as "Vulnerable" on the Red List of the International Union for Conservation of Nature (IUCN) [31] and included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In addition, population assessments of *S. zygaena* in the Gulf of California (GC) and Mexican Pacific have classified this species as Vulnerable due to its low catch abundance in recent decades [32–36].

By assessing the mechanisms that promote genetic isolation and local adaptation in shark species, it is possible to identified populations that are vulnerable to fishing pressure. To this end, the GC provides an interesting opportunity to study *S. zygaena*. The Baja California peninsula constitutes an important geographical barrier, resulting in dissimilar habitats between the GC and Pacific Ocean [37]. Many studies have indicated that environmental differences between the Pacific coast of the Baja California peninsula (PC) and GC influence genetic differentiation, giving rise to elasmobranch diversification and speciation [12, 38–40].

In this study, we assessed the population genomic structure of *S. zygaena* in the northern Mexican Pacific (NMP). Neutral and adaptive loci were identified and evaluated in individuals caught by the local artisanal fisheries. Due to the high migration potential of *S. zygaena*, we expected that no neutral genetic differences (neutral loci) would be present among regions in the NMP. However, given the environmental differences between the GC and PC, we hypothesized that we would detect local adaptive traits (outlier loci) in the genome. Our results further our understanding of the genomic variation of *S. zygaena*, which may help elucidate connectivity and spatial patterns and facilitate the development of appropriate management strategies.

2. Materials and methods

2.1. Sampling and DNA extraction

A total of 115 *S. zygaena* individuals were sampled between 2014 and 2017 from four regions in the NMP: the western coast of the Baja California peninsula (WCBC), the central region of the Gulf of California (CGC), the entrance to the Gulf of California (EGC), and Socorro Island (SI; Appendix A; Table A1). Muscle tissue samples were preserved in dimethyl sulfoxide (DMSO) solution (20% DMSO, saturated NaCl, and EDTA) or non-denatured ethanol (96%). Genomic DNA (gDNA) was extracted with a commercial G-Spin Total DNA extraction kit (Intron Biotechnology, Seoul, Korea), following the protocols of the manufacturer. All extractions were standardized to a final gDNA concentration of 100 ng/μL before library preparation.

2.2. SNP genotyping and the discovery of outlier SNPs (o-SNPs)

Libraries were prepared with nextera-tagmented reductively-amplified DNA (Nextera), which consists of DNA fragmentation with Nextera reagent (Illumina, Inc) following by ligation of short adapter sequences (9 bp) in 3' fragment ends [41]. The libraries were sequenced in a single-end run in an Illumina HiSeq 4000 DNA sequencer (San Diego, USA) with a read length of 150 bp (SNPsaurus, Eugene, USA). The dDocent pipeline [41] was used for *de novo* assembly, mapping, SNP calling, and genotyping with optimum values of K1 = 5 (number of times a sequence must occur within an individual to be included in the reference), K2 = 6 (number of individuals containing a sequence for it to be included in the reference), and c = 0.8 (similarity value to optimize the reference). To mitigate high levels of duplicates and repeats in large genomes, the RefOpt.sh script in the contig assembly was used. The initial data set contained 885,357 variants in 219,750 reads; contigs with less than five reads per individual and loci genotyped in <75% of the individuals were eliminated (additional methods are described in Appendix B). The following criteria were used to filter the data: presence in 97.5% of the individuals in the data set, minor allele frequency (MAF) > 5% in all data sets, and the presence of Hardy-Weinberg equilibrium (Appendix B; Table B1).

Four methods were used to identify loci putatively under selection (o-SNP). The first consisted of a Bayesian approach based on the locus-population specific F_{ST} coefficient [42] in Bayescan v. 2.1 [43]. This analysis included 20 pilot runs with 5000 iterations with a burn-in of 50, 000 steps, a sample size of 5,000, and a thinning factor of 10. The second method consisted of the hierarchical island model and coalescent simulations to obtain the p-values and *F*-statistics for each specific locus, which were determined at the observed levels of heterozygosity in

Table 1
Summary of the genetic diversity of *Sphyrna zygaena* from the northern Mexican Pacific (NMP). Localities: west coast of the Baja California peninsula (WCBC), Socorro Island (SI), central Gulf of California (CGC), and entrance of the Gulf of California (EGC). H_e: expected heterozygosity; H_o: observed heterozygosity.

Region	*N*	*He* ± *sd*	*Ho* ± *sd*
Global	92	0.275 ± 0.176	0.251 ± 0.164
WCBC	29	0.282 ± 0.176	0.241 ± 0.161
CGC	22	0.292 ± 0.178	0.284 ± 0.185
EGC	30	0.280 ± 0.179	0.256 ± 0.174
SI	11	0.321 ± 0.176	0.316 ± 0.197

Arlequin v. 3.5.0 e [44]. The third method employed was PCAdapt, a principal component analyses which detects outliers within genotyped individuals through individual F_{ST} coefficients using the package *pcadapt* v 4.3.2 in R [45,46]. Finally, to identify associations between SNPs and environmental variables, we performed a redundancy analysis (RDA). This method, implemented in the package *vegan* v 2.5.2 [47,48], assess the effect of environmental parameters on the observed genetic variation; to identify associations among SNPs and environmental variables. A stepwise per mutational ordination method was used to carry out the optimal model with high-adjusted R^2.

To conduct the RDA, we constructed a database with the data extracted from two satellite sensors: OceanWatch from NOAA, and NASA Ocean Color, using monthly and annual averages (4 km); to obtain the data for each pixel according to the individual geographic coordinates the data was processed in SeaDAS v8.4.o [49]. We selected environmental variables based on heterogeneity among regions and influence in the distribution of other Carcharhiniformes ([50]; Appendix C; Table C1). Variables were scaled and a multicollinearity test was applied, in the case of correlations above 0.6 only one environmental parameter was kept (Appendix C; Figure C1).

We first used all loci to calculate heterozygosity. Then, all neutral SNPs (n-SNPs) were used to estimate the genetic structure of the population and the effective population size (*Ne*). Finally, outlier SNPs (o-SNPs) were used to test for adaptive variation between the GC and PC. Putative outlier loci were blasted to elucidate their possible function using the Nucleotide BLAST tool from GenBank, filtering for Chondrichthyes and fish.

2.3. Genetic diversity and structure

Expected (*He*) and observed (*Ho*) heterozygosities were calculated for each location with the '*hierfstat*' package in R to estimate genetic diversity [51,52]. F_{ST} was calculated separately for n-SNP and o-SNP loci using the '*hierfstat*' package in R [53]. Genetic structure was evaluated using the Bayesian aggregation with FastSTRUCTURE [54]. In this analysis, the optimum *K* value was assessed with values between 1 and 5 and an a priori logistic distribution, which is more effective in populations with low signals of genetic structure. Additionally, a discriminant analysis of principal components (DAPC) was conducted with n-SNP and o-SNP data using the '*Adegenet*' and '*factoextra*' packages in R [55,56]. Group membership was defined by regions. In the case of o-SNP data, clustering was defined according to the major geographic regions (PC and GC).

2.4. Effective population size (Ne)

To estimate the effective population size (*Ne*), we used n-SNPs with the linkage disequilibrium method [57] and the square of the Burrows [58] correlation coefficient between pairs of loci in NeEstimator v. 2.1 [59]. We removed alleles with MAF values of 0.05 reported as the *Pcrit* value. The confidence intervals were estimated with the JackKnife method [60], which reduces the potential bias associated with confidence intervals [57].

3. Results

3.1. Summary statistics from filtered SNPs

After filtering, 1480 SNPs were retained from 92 individuals (Appendix B; Table B1). From this database, using four methods were identified the follow o-SNP: 2 for Bayescan, 24 for Arlequin, 127 for PCAdapt, and 19 for RDA (Appendix C; Figure C2 and C3). To strengthen the robustness of our outlier analysis, we prioritized outliers detected by at least two methods, reducing the total number while enhancing confidence through multi-method validation (11 o-SNP).

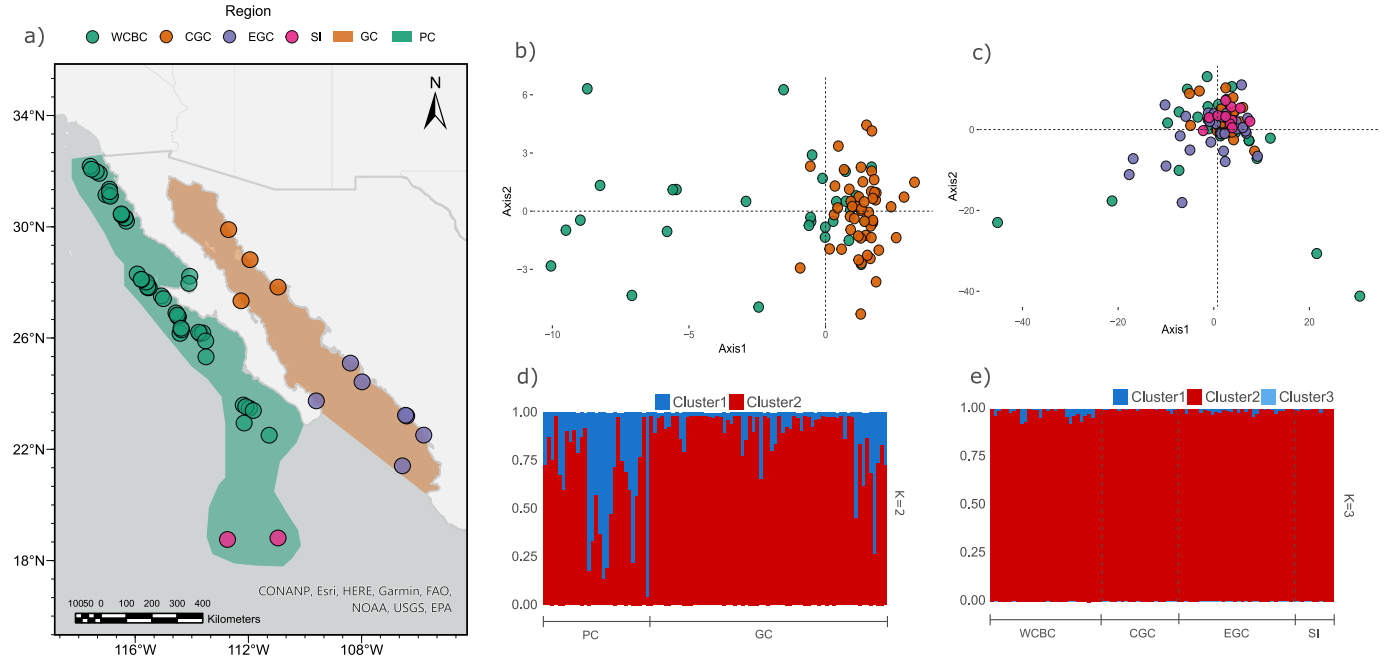

Fig. 1. a) Sampling locations of *Sphyrna zygaena* from the northern Mexican Pacific (NMP) and Gulf of California (GC). Pacific coast (PC, green shaded region) sampling locations: the western coast of the Baja California peninsula (WCBC, green dots) and Socorro Island (SI, pink dots). Gulf of California (orange shaded region) sampling locations: central region of the GC (CGC, orange dots) and the entrance to the GC (EGC, purple dots). Population genetic structure of *S. zygaena* from the NMP evaluated with **b)** discriminant analyses of principal components with o-SNPs (loci putatively under selection) and 24 loci, **c)** discriminant analyses of principal components using n-SNPs (neutral loci) with 1456 loci, **d)** Bayesian clustering analyses (K = 2) by major geographic region, and **e)** n-SNPs (K = 3) by region. All clusters are displayed in the grape chart. The signal of Cluster 3 is shown at the bottom.

3.2. Genetic diversity and neutral structure

The genetic diversity values were similar between regions, with a mean *Ho* value of 0.275 ± 0.176. The SI region showed the greatest expected heterozygosity (*Ho* = 0.316), while WCBC showed the lowest (*Ho* = 0.241; Table 1). No pattern of genetic structure emerged from the analysis of 1469 n-SNPs ($F_{ST} = 0.0012$, $p = 0.44$), and the DACP results did not show clear geographic groupings (Fig. 1c). Although the Bayesian cluster analysis indicated the possible existence of three genetic components, all regions were dominated by a single genetic component (Fig. 1e). Consequently, after pooling all samples, the *Ne* was estimated to be 1391 (*Pcrit* = 0.05, CI = 428.6 - ∞).

3.3. Adaptive genetic structure

The genetic structure pattern of the 11 o-SNPs indicated low differentiation between PC and GC ($F_{ST} = 0.021$, $p = 0.03$). The DAPC analysis and Structure among regions using 11 retained o-SNPs did not show a pattern of local adaptation (K = 1, Appendix C; Figure C4). To control uncertainty, a general linear model using logistic regression was used to link the identified outliers to environmental characteristics (Appendix C; Table C2); however, there is no evident correlation between environmental variables and o-SNPs. To further explore the environmental drivers of regional differences, we performed a standard PCA solely on the environmental data. This analysis revealed significant heterogeneity between the PC and GC, with two principal components explaining 56.45 % of the variance (Appendix C; Figure C5).

Based on the 11o-SNPs analysis, we consider using those with one approach, of which two methods are based on F_{ST} (Bayescan and Arlequin; 24 o-SNPs). These approaches have shown to be a combination to reduce type I and II error rates [16,61,62]. Some authors suggest that the SNP-environment association approach may be more sensitive to variations in allele frequencies and that it might be difficult to capture the adequate environmental factors [63,64]. When comparing both approaches, the two loci were identified in common: dDocent_Contig_17536, dDocent_Contig_31244; in this case, we used all o-SNP with both approaches. The genetic structure pattern of the 24 o-SNPs indicated major differentiation between PC and GC ($F_{ST} = 0.061$, $p < 0.001$). The DAPC results showed individual segregation along the first dimension, which explained 15 % of the variance. Furthermore, individuals from the PC were considerably more genetically dispersed than those from the GC (Fig. 1b). In addition, pairwise comparisons of F_{ST} values were significant among regions except between CGC and EGC (Table 2). The Bayesian clustering analysis showed that two genetic components maximized marginal probability. Sharks from the PC exhibited 66.6 % identity to the blue component, while the GC sharks exhibited 77.7 % identity to the red component (Fig. 1d).

Despite the discrepancies in the o-SNPs results among different methods, 24 o-SNPs were grouped independently to explore the adaptive genetic pattern present, with the remaining SNPs considered purely neutral. Blast analysis was performed with sequences containing o-SNPs, of which 12 resulted in hits with DNA regions annotated as regulatory elements (e.g., Hox genes and Zinc-finger proteins) and immune response proteins (e.g., MHC) in sharks or bonefish (Appendix C; Table C3). The remaining sequences did not produce significant hits.

Table 2
Pairwise values of the fixation index (F_{ST}) with outlier single nucleotide polymorphisms (o-SNPs) from the northern Mexican Pacific (NMP). F_{ST} values appear below the diagonal; p-values after Bonferroni correction appear above the diagonal. Significant values are shown in bold. Localities: west coast of the Baja California peninsula (WCBC), Socorro Island (SI), central Gulf of California (CGC), and the entrance to the Gulf of California (EGC).

	WCBC	CGC	EGC	SI
WCBC	–	0.001	0.0003	0.006
CGC	**0.078**	–	0.355	0.001
EGC	**0.067**	0.003	–	0.012
SI	**0.075**	**0.096**	**0.066**	–

4. Discussion

4.1. Genetic diversity and Ne

The heterozygosity values reported in this study ($H_O = 0.275$) were similar to those that have been reported for other Carcharhiniformes, such as *Carcharhinus amblyrhyncos* (H_O = 0.278; [65]), and higher compared to that reported for *Carcharhinus galapagensis* (H_O = 0.188–0.193; [66]. Furthermore, the level of genetic diversity fell within the known range for SNPs in other marine species [67–71].

One of the biological characteristics affecting the genetic diversity levels of a population is the mating systems of its members [72]. Polyandry can promote multiple paternity and has been identified in many elasmobranch species (reviewed in Refs. [73,74]). Generally, multiple paternity increases genetic diversity; however, male fertilization bias can reduce parental allele frequencies [72]. In the GC, polyandry and a male fertilization bias have been reported for *S. zygaena* [75], which may affect the genetic diversity of the population in this zone [76].

The *Ne* values reported in this study constitute the first estimate for *S. zygaena* in the NMP (*Ne* = 1391). However, given that the upper confidence interval was infinite, a higher sampling effort will like to increase accuracy. As such, we report an *Ne* value of at least 428 individuals for the entire NMP, which represents the lower limit of the confidence interval. This result may be considered low compared with those from similar studies in different geographic areas, such as those with *C. galapagensis* in the eastern (*Ne* = 758) and western (*Ne* = 3421) Pacific [66], whereas it is intermediate when compared with the *Ne* value reported for the Galapagos Islands (*Ne* = 171–205; [77]). In the congeneric *S. tiburo*, *Ne* values in the Atlantic vary among populations that are relatively close to one another [25]. For example, the *Ne* value of the southern Gulf of Mexico is high (2,119), whereas those from the southeastern Atlantic and western Florida coasts are an order of magnitud smaller (167 and 102, respectively) [25]. Considering the life history of each species, *S. zygaena* exhibits the greatest migration potential among oceanic basins, and thus the effects of genetic drift may be smaller compared to those of species with reproductively isolated populations, such as *C. galapagensis* [77], *Mustelus mustelus* [78], *Negaprion brevirostris* [79] and *S. tiburo* [25].

In the eastern Pacific, the *Ne* of *Sphyrna lewini* was estimated using microsatellite loci and varied from 226 to 604 individuals, which is substantially smaller than the ancestral range (mtDNA; *Ne* = 34,994–43,551) indicating a decrease in population size over time [80]. Despite the similarities in life histories between *S. lewini* and *S. zygaena*, their demographic and catch records differ. In the NMP, *S. lewini* catches have been larger than those of *S. zygaena* in recent decades [81], which agrees with the recently estimated *Ne* values.

On the other hand, the *Ne* value of *S. zygaena* from South Africa is much higher than that of the population from the NMP. Indeed, the *Ne* of the South African population, which was also obtained with microsatellite loci, is 6783 individuals [82,83]. Catch records from South Africa indicate that *S. zygaena* is one of the three most frequently caught sharks (total annual catch <10 metric tons) [84,85]. Nevertheless, there is no evidence of population decline in some regions (e.g., KwaZulu-Natal, South Africa), which could also explain the high *Ne* estimate. However, those *Ne* estimates may be biased given that some loci were in linkage disequilibrium and heterozygosity deficits were detected.

4.2. Panmictic population in the northern Mexican Pacific

According to the neutral genetic variation observed in this study, the *S. zygaena* population in the NMP appears to be panmictic, which may be mainly due to the limited geographic scale of the study. Previous studies

have established worldwide mitochondrial genetic differentiation [86]. In the South Pacific, *S. zygaena* individuals from South America and Australia/New Zealand, which are separated by more than 14,000 km, are genetically different [87]. In the eastern Pacific, latitudinal genetic differentiation has also been found between sharks from the northern hemisphere (i.e., the Mexican Pacific) and those from Ecuador and the southern hemisphere (i.e., Chile), separated by more than 4500 km [88]. In the south Atlantic, strong genetic structure exists between the western and eastern regions (>6000 km) [86]. This suggests that the dispersal capacity of *S. zygaena* adults may promote homogeneity among nearby regions, such as in the NMP (>1000 km), but not at larger scales.

The genetic structure pattern observed in *S. zygaena* juveniles shows differences at regional scales [83,89,90]. In South Africa, smooth hammerhead shark juveniles from the warm temperate southern coast have shown different genetic structure than those from the subtropical eastern coast, which is separated by the Agulhas bioregion (~260 km) [83,89,90]. In the NMP, genetic differentiation has been reported between regions in the GC (~800 km) [91]. These patterns indicate that juveniles often remain where they are born (i.e., in coastal habitats) for some time before moving to adult habitats [4]. Broadly, the genetic differences among nursery areas may be associated with the reproductive behaviors of adult females (e.g., philopatry), which foster reproductive isolation among groups, as can be observed in *S. tiburo* [24,26], *Negaprion brevirostris* [6], *Carcharodon carcharias* [92–94], *S. lewini* [95], and *Isurus oxyrhincus* [2].

A major concern in population genetics is sample size, with bigger sample sizes increasing the probability of capturing the true diversity of a population. To this end, the use of high-throughput SNP genotyping increases this probability by broadly scanning the genome through thousands of loci [96]. In this study, although both juveniles and adults were analyzed; it was not possible to conduct an analysis by either sex or developmental stage due to the insufficient sample size for each unit of analysis (Appendix C; Table C4). Nonetheless, the sample size for our study did allow for an evaluation of neutral and adaptive variation in the species. A previous study evaluating the mitochondrial genetic structure of *S. zygaena* among juveniles from different nursery areas showed significant genetic structure among potential nursery areas [91]. When taken together with the n-SNPs results of this study, these results strongly suggest that female philopatry is at work [4]. The absence of genetic structure in neutral SNPs that are bi-parentally inherited is consistent with the hypothesis that male dispersion is the main driver mediating gene flow, as has been observed in other elasmobranch species [24,65,66,97–100].

4.3. Adaptive genetic variation

In this study, we employed genome scan approaches to identify potential regions under natural selection in a non-model marine organism. This presents a challenge, as appropriate analytical methods for such species are still under development [70]. While we did not find a genome-environment association in our data, several factors might explain this outcome. Firstly, the complex nature of the marine environment requires specific spatial-temporal sampling strategies [64]. In this study, samples were collected across different years, necessitating the use of environmental data from varied time windows. This introduced substantial heterogeneity into the environmental data, potentially hiding local adaptive patterns (Appendix C; Figure C5). Secondly, some genome-environment associations can be spurious, meaning that no real association between o-SNPs and environmental variables is present [64]. Therefore, our results must be regarded as suggestive. While the identified outlier loci may not represent genes under selection, they warrant further investigation to explore potential adaptive variation [16].

According to the BLAST analyses performed on sequences with o-SNPs, these SNPs are related to immune system genes (*MHC* and *MIP3*) and antero-posterior development genes in vertebrates (*HOXB*, *HOXD*, and *Zic1*; Table S3) [92]. The immune system is highly polymorphic due to the selective pressure exerted by pathogens on their hosts [101]. Chondrichthyans are known to exhibit complex, adaptive immune systems with memories that are highly specific and capable of detecting and engaging pathogens in the long-term [102–105]. Indeed, chondrichthyan immune systems exhibit plastic features that permit rapid changes in response to pathogens, with immune system genes being under strong selective pressure [106,107]. *MHC* genes are polygenic and highly polymorphic in vertebrates and are subject to balancing selection with rapid variation, which is consistent with the existence of adaptive differentiation between PC and GC [108–110]. However, additional functional genomics studies are needed to clarify the mechanisms that promote variation among shark populations [111,112].

Some features of immune responses in marine organisms depend on changes in environmental conditions, particularly those related to temperature [113,114]. Although we did not find relationships among outlier loci and temperature, and salinity, these abiotic factors can trigger physiological stress in marine organisms, which may affect dispersal [115,116]. It is difficult to determine which abiotic factor may be driving genetic differentiation or adaptation in marine environments because they rarely act independently [116]. Moreover, abiotic factors may not be the main drivers of reproductive isolation, although they can promote habitat preferences, which can influence how natural selection acts on certain loci [117].

Oceanographic heterogeneity between the GC and PC has been suggested to exert selective pressure on some species, leading to ecological adaptations regardless of the migratory capacity [12,118]. The emergence of the Baja California peninsula, which was formed ~1–2 mya, created a physical barrier that contributed to the physicochemical differences between the PC and GC [119]. The GC is a long basin (~1200 km) [120] with a highly dynamic transition zone at its entrance (large salinity and temperature fluctuations) [121]. Although the GC shows latitudinal variation in water temperature, sea surface temperature is generally higher than in the PC [120,122]. In contrast, the PC is influenced by the California Current composed of cold, subarctic water and exhibits a shallow oxygen minimum zone, which is currently undergoing expansion due to ocean warming [117,121,123]. The PC also exhibits coastal upwelling, which results in pH fluctuations that influence the distributions of benthic functional groups, crabs, bivalves, and carnivores [124]. Sharks, unlike teleosts, are osmoconformers, meaning that their blood plasma shows similar osmolarity to that of seawater [125]. Thus, ocean acidification may represent a particularly problematic challenge for shark species to overcome [119]. Indeed, ocean acidification has been suggested to reduce the effectiveness of prey detection and attack behavior in sharks [122].

In addition to ocean acidification, thermal differences may produce barriers that limit the dispersion of elasmobranchs across regions [119], which may favor the persistence of particular genotypes that confer adaptive advantages. In the case of *S. zygaena*, temperature likely plays a main role in determining dispersal. In South Africa, seasonal distribution patterns are associated with cool superficial sea temperatures, with the largest *S. zygaena* catches recorded in winter and spring, which may reflect prey availability and habitat use [90,126]. This zone is characterized by a remarkable temperature gradient that ecologically subdivides the area into marine bioregions [127,128]. As such, thermal heterogeneity may be a potential barrier to dispersal, resulting in partial reproductive isolation in the South African populations [129].

Previous studies have shown similar genomic structure patterns among elasmobranchs, with either low or null neutral structure but clear adaptive structure [24,66,77,130]. For example, *S. tiburo* in the Gulf of Mexico and western Atlantic showed latitudinal adaptive genetic variation on the eastern and western coasts of Florida as revealed by o-SNP data [24]. This pattern was correlated with significant latitudinal differences in both the growth rate and size at maturity among sharks from the region. Therefore, low dispersal rates may be sufficient to remove evidence of population differentiation at neutral loci but not at locally

selected adaptive loci [131,132]. The genomic structure patterns in *S. zygaena* further support the role of heterogeneous marine habitats in shaping the ecological and evolutionary divergence of shark species [24,66,77,130]. Nevertheless, we are aware of the limitations of our analyses. Additional efforts is required to increase sample sizes of both organisms and genes throughout the distribution range of the smooth hammerhead shark to capture the local adaptation signal associated with environmental variation at different geographic scales.

4.4. Implications for conservation

Safeguarding the genetic diversity of populations is the focus of conservation genetics [15], as the longevity of a species depends on its genetic diversity in the presence of changing environmental conditions. Currently, *S. zygaena* is subject to international regulations regarding its export, as it appears in CITES Appendix II and islisted as "Vulnerable" by the IUCN. Therefore, an increase in fishing pressure is likely to have negative consequences for this species, which may be reflected in reduced genetic diversity and *Ne*. The coastal shark fishery of the Mexican Pacific is the sixth largest fishery in Mexico, including both industrial and artisanal fisheries [133]. In the NMP, *S. zygaena* is among the 10 most commonly caught shark species [134], although with historically low catch volumes [34]. Nonetheless, it should be noted that the misidentification of hammerhead sharks species has made it difficult to estimate historical catch volumes in many regions of the Mexican Pacific [134].

According to this study, organisms of *S. zygaena* inhabiting the NMP should be considered a single management unit. Although this species shows a highly migratory potential, its reported geographical area does not reflect its genetic structure across the eastern Pacific. Nonetheless, the selection signal in the NMP provides new insights for the management and conservation of *S. zygaena* along the Mexican Pacific coast, an important zone for shark fisheries. In this sense, recent studies have indicated that fisheries erode genetic variation causing changes in life history traits due to imposed selection intensity within a short time frame for trait heritability [133]. Fishery pressure can affect the presence of species in specific areas, including the Gulf of California. Indeed, in the 1960s, the GC harbored hammerhead shark species that have likely been extirpated (e.g. *S. tiburo* and *S. media*) [135]. It is difficult to demonstrate that a single factor, such as fishing, modifies genetic architecture, even more so when combined with the effects of climate change [136].

Female philopatry within regions must be considered [91]. As has been observed with other highly migratory sharks, *S. zygaena* uses nursery areas that increase the survival of their young [3]. Thus, breeding and nursery areas must be defined carefully, with management plans considering females and juvenile aggregation areas as potential refuge sites needed to maintain adult populations [4]. In the NMP, multiple nursery areas have been proposed [34], yet only four of these are recognized and protected by Mexican legislation [137]. Furthermore, juveniles predominate catches in the Mexican Pacific and should be considered a priority for future conservation efforts [34]. To this end, acoustic tracking studies are needed to determine the time periods in which juveniles are present within nursery areas to evaluate their vulnerability to fishing gears [138], as recruitment may be negatively affected by extraction of juvenile *S. zygaena* by artisanal fisheries [139–141].

In conclusion, protecting adaptive variation is crucial for preserving the genetic resources of *S. zygaena* and other exploited shark species, thus increasing their chance of survival in the face of environmental change [67,142]. Both PC and GC are environmentally distinct, in parameters such as temperature, depth, salinity, dissolved oxygen, and turbidity. These important environmental factors influence shark distributions [143–148] and their immune system responses [113,114], which may be partially responsible for the potential differences in adaptive variation between the PC and GC populations [149–152]. The GC provides important coastal nursery grounds and refuge areas for elasmobranchs [153–157] including *S. zygaena* [91], while also being an important fishing zone [35,36,81,158]. Thus, *S. zygaena* juveniles in the GC are likely to be more vulnerable than those of the PC and should be prioritized in future conservation efforts.

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CRediT authorship contribution statement

Daniela G. Félix-López: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Axayácatl Rocha-Olivares:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition. **Nancy C. Saavedra-Sotelo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

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Appendix A

Table A1
Sample size by dataset. Regions: west coast of the Baja California peninsula (WCBC), Socorro Island (SI), central region of the Gulf of California (CGC), and the entrance to the Gulf of California (EGC). Major geographic regions: Pacific coast (PC) and Gulf of California (GC).

Dataset	Region	Sample size
SNP-n	WCBC	29
	SI	11
	EGC	30
	CGC	22
SNP-o	PC	40
	GC	52

Appendix B

De novo assembly

We first constructed a phylogenetic tree in RaxML to determine the relationships among samples (Stamatakis, 2014). Then, we demultiplex the samples by removing the barcodes and renaming them with the correct ID for further analyses with BBduk and BBMap (Bbtools) (https://sourceforge.net/projects/bbmap/) using *cycle.sh* bash.

Afterwards, we used the dDocent pipeline pipeline (Puritz et al., 2014) *de novo* assembly by creating an environment in Python, using Anaconda to install all necessary repositories. To demultiplex the samples, we created an environment in Python to successfully run and select the power of the analysis.

As the first step, we ran the conventional filtering of dDocent using the SE option. Then, we optimized and selected the optimum values of K1 (the number of times a sequence must occur within an individual to be included in reference), K2 (number of individuals containing a sequence to be included in reference), and c (similarity value to optimize reference). We used *RefOpt.sh* with some modifications to call Trimmomatic during the runs for optimization.

Mapping and SNP calling

After the reference assembly was completed, we proceeded to filter for mapping and SNP calling. For this, we used VCFtools for filtering (Danecek et al., 2011) and vcfR (Knaus & Grünwald, 2017) for choosing the threshold values for the quality score, coverage, missing data, and minor alleles as follows:

1. Loci were removed that had a minor allele count <3 for the Genotype call rate & minimum minor allele count and all genotypes less than 50%.
2. Filtered loci with genotype call rates <0.6.
3. Removed loci with minor allele frequencies <0.01 and mean minimum depths (across all individuals) < 5.
4. Removed loci with more than 80% missing data (allowing only 20% missing data) and kept individuals that were at least 75% genotyped.
5. Filtered loci with minor allele frequencies <0.02 and mean minimum depths (across all individuals) and compared the number of loci pre/post-filtering.
6. Removed individuals with more than 65% missing data.
7. Ratios of reference/alternate alleles, quality/depth, and mapping quality. We filtered contig SNPs for which the allele balance was <0.2 and >0.8.
8. We calculated the average depth and standard deviation and recalculate depth for the remaining sites and compared the distribution of mean per site with excessively high depth, and INDELs were removed from data set.
9. Excess heterozygosity was addressed by removing loci with significant deviations from Hardy-Weinberg equilibrium (*hew* of 0.001 of threshold in VCFtools). To remove this, we used the bash *remove_loci_from_vcf.sh*.
10. We set final cut-off for minor allele frequency of 0.025 and set final cut-off for genotype call rate >90%, and sites with mean minimum depth <15 were removed.

Haplotyping

After the filtering with VCF, it is expected to have loci that contain multiple SNPs because SNPs on the same contig can be assumed to be linked and will introduce bias into data analysis if retained. To fix this, we constricted the SNPs considering just the first as a true call. Haplotyping is an efficient method to filter paralogs and account for physical linkage (Willis et al., 2017) to link SNPs into haplotypes, turning contigs with multiple SNPs into a single locus. Based on this, we haplotyped all the SNPs and checked the summary of haplotyping stats using the perl file rad_haplotyper.pl (https://github.com/chollenbeck/rad_haplotyper/blob/master/rad_haplotyper.pl). As a final step, we converted our inputs into a genepop file for further analysis.

Table B1
Description of filtering data, where the loci are represented before and after filtering as well as individuals.

Filtering description	Loci		Individuals	
	Before filtering	After filtering	Before filtering	After filtering
Filter loci with quality score <20	885,357	546,626	115	115
Genotype call rate & minimum minor allele count	546,626	175,012	115	115
Code loci with less than 3 reads per locus per individuals as missing and remove flagged loci	175,012	108,256	115	115
Filter loci with genotype call rate <0.6	108,256	79,571	115	115
Removing individuals with missing data more than 90%	79,571	79,571	115	104
Remove loci with minor allele frequency <0.01 and mean minimum depth (across all individuals) < 5	79,571	70,405	104	104
Remove loci with genotype call rate <0.8	70,405	31,301	104	104
Remove individuals with >75% missing data	31,301	31,301	104	102
Minimum allele frequency 0.02 and minimum mean depth 10	31,301	18,863	102	102
Exclude sites with 85% of missing data	18,863	13,537	102	102
Removing individuals >65% missing data	13,537	13,537	102	100
Check ratios of reference/alternate alleles, quality/depth, and mapping quality	13,537	9480	100	100
Recalculate site depth for the remaining sites	9480	8913	100	100
Comparing distribution of mean per site with excessively high depth	9480	7792	100	100
Remove indels	8953	8422	100	100
Remove loci that have multiple significant SNPs	8422	8110	100	100
Remove single significant SNPs	8110	8056	100	100
Minor allele frequency	8056	5917	100	100
Missing data: Cut-off final for genotype call rate to >90%	5917	3899	100	100
Set final cut-off for allowable missing data per individual to < 50%	3899	3899	96	100
Hardy-Weinberg Equilibrium	3899	3795	96	96
Haplotyping and converting file and removing repeated individuals	3789	1625	96	92

Appendix C

Table C1
Environmental variables used in the RDA.

Name	Environmental parameters
LONG	Longitude
LAT	Latitude
SSTM	Sea surface temperature monthly mean (SST -°C-)
SSTY	Sea surface temperature annual mean (SST -°C-)
SSSM	Salinity monthly mean (g L^{-1})
SSSY	Salinity annual mean (g L^{-1})
CHLOY	Chlorophyll annual mean (mg m^{-3})
CHLOM	Chlorophyll monthly mean (mg m^{-3})
Uwind	Eastward wind daily mean (m s^{-1})
Vwind	Northward wind daily mean (m s^{-1})
PAR	Photosynthetically active radiation monthly mean (einstein m^{-2} day^{-1})

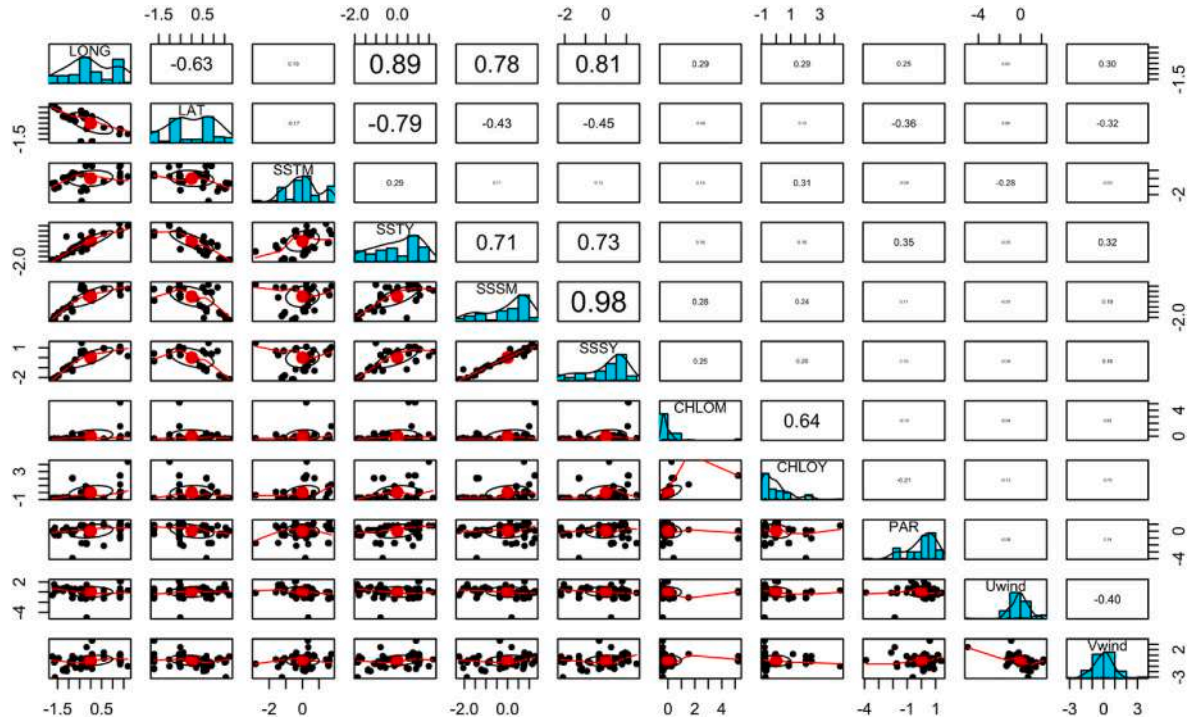

Fig
ure C1Matrix of correlations of environmental parameters: Longitude (LONG), latitude (LAT), sea surface temperature monthly (SSTM), sea surface temperature annual (SSTY), sea surface salinity monthly (SSSM), sea surface salinity annual (SSSY), total chlorophyll monthly (CHLOM), total chlorophyll annual (CHLOY), photosynthetically active radiation monthly (PAR), eastward wind daily (Uwind), and northward wind daily (Vwind).

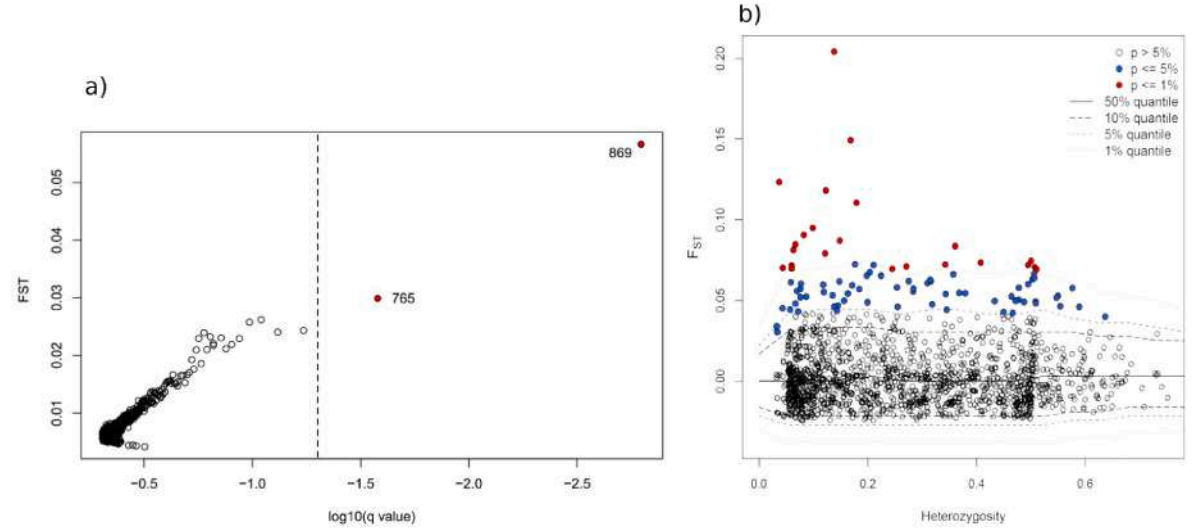

Fig. C2. Identification of outlier simple nucleotide polymorphisms (o-SNPs; red dots) from F_{ST}-based methods. A) 869 and 765 o-SNPs identified by the multinomial-Dirichlet model in Bayescan. B) o-SNPs identified by the hierarchical island model in Arlequin.

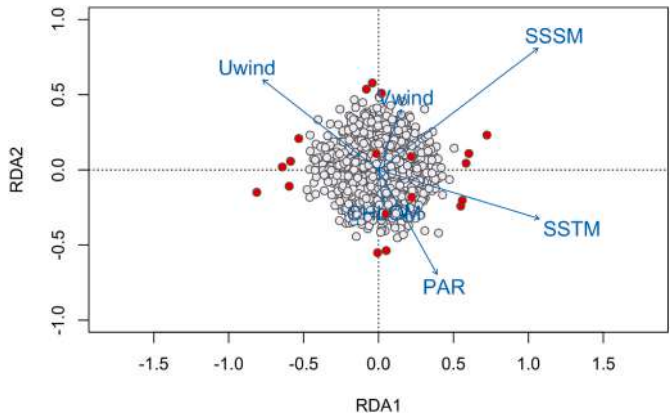

Fig. C3. Redundancy analysis. The red dots represent the o-SNP detected while white dots the neutral.

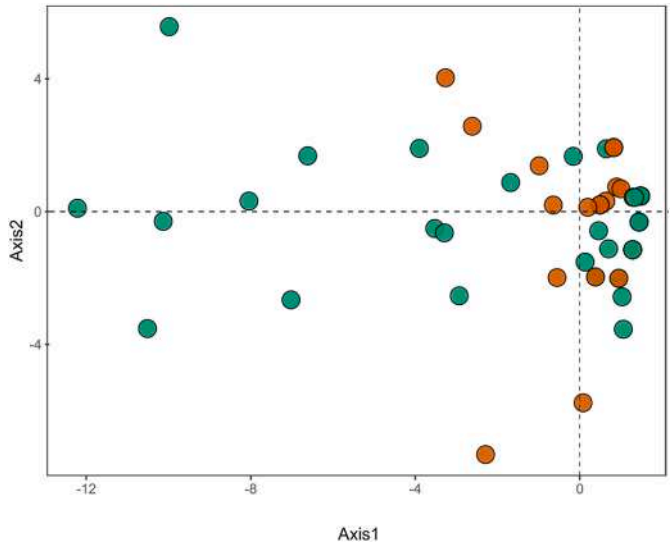

Fig. C4. Discriminant analyses of principal components using o-SNPs (neutral loci) with 11 retained outliers loci by different method from the northern Mexican Pacific (NMP) and Gulf of California (GC, orange dots). Pacific coast (PC, green dots).

Table C2
Comparative results of outlier SNP detection between BayeScan, Arlequin, RDA, and PCAdapt. In the analysis detection column, we show the programs that detect each locus as an outlier. The environmental variable corresponds to the parameter identified.

Analysis detection	Locus	Descripción	Variables	p-value
BayeScan Arlequin	dDocent_Contig_17536	*Salarias fasciatus* genome assembly, chromosome: 15	–	–
Arlequin PCAdapt BayeScan	dDocent_Contig_31244	Triakis scyllium tsIgH gene for immunoglobulin heavy chain-like protein, complete cds	Uwind	0.00791
Arlequin PCAdapt	dDocent_Contig_19293	–	–	–
RDA PCAdapt	dDocent_Contig_5723	*Scyliorhinus canicula* chromosome 26	SSSM	0.00646
RDA PCAdapt	dDocent_Contig_7185	*Scyliorhinus canicula* chromosome 27	–	–
RDA PCAdapt	dDocent_Contig_5539	No significant similarity found	–	–
RDA PCAdapt	dDocent_Contig_136834	*Scyliorhinus canicula* chromosome 31	–	–
RDA PCAdapt	dDocent_Contig_7933	*Scyliorhinus canicula* chromosome 22	–	–
RDA PCAdapt	dDocent_Contig_2425	*Scyliorhinus canicula* chromosome X	SSTM	0.0129
RDA PCAdapt	dDocent_Contig_6092	No significant similarity found	–	–
RDA PCAdapt	dDocent_Contig_42495	No significant similarity found	–	–

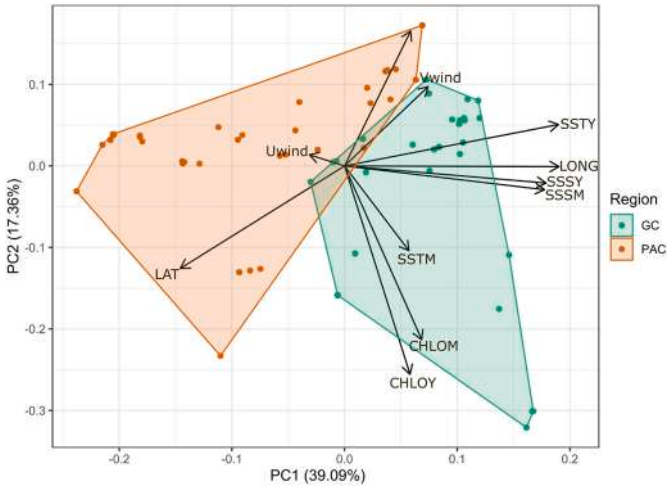

Fig. C5. PCA of the environmental parameters showing the heterogeneity between the Gulf of California (GC, green dots) and the Pacific coast (PAC, orange dots). Arrows represent environmental parameters, PAR: photosynthetically active radiation, CHLOM: chlorophyll monthly average, SSTM: sea surface temperature monthly average, SSSM: sea surface salinity, Uwind: eastward wind, Vwind: northward wind.

Table C3
BLAST results. Abbreviations: IP, Identity percentage; Hit, start and final match at sequence; E-value, the expected value of the number of expected matches in the GenBank database.

Locus	Description	E-value	IP	Hit		NCBI access number
				star	final	
dDocent_Contig_3253	Triakis scyllium DS-3 gene for MHC class II beta chain like protein, partial cds, isolate: N0	2.00E-17	92.86	2341	2410	LC009543.1
	Scyliorhinus canicula chromosome 27	2.00E-13	94.74	23791208	23791264	LR744056.1
dDocent_Contig_6010	*Scyliorhinus canicula* chromosome 30	8.00E-17	85.42	1873174	1873269	LR744059.1
dDocent_Contig_2585	PREDICTED: *Pristis pectinata* zic family member 1 (odd-paired homolog, Drosophila) (zic1), mRNA	2.00E-68	99.33	1276	1425	XM_052017215.1
	PREDICTED: Chiloscyllium plagiosum zinc finger protein ZIC 1 (LOC122556177), mRNA	3.00E-65	98	1660	1809	XM_043702697.1
	PREDICTED: *Hemiscyllium ocellatum* zinc finger protein ZIC 1 (LOC132821421), mRNA	7.00E-62	96.67	687	836	XM_060834005.1
dDocent_Contig_8311	*Scyliorhinus canicula* chromosome 20	4.00E-20	88.3	40177740	40177833	LR744049.1
	Raja brachyura genome assembly, chromosome: 15	0.022	100	49540139	49540166	OY740795.1
dDocent_Contig_15352	*Scyliorhinus canicula* chromosome 27	5.00E-24	88.07	21378914	21379019	LR744056.1
	PREDICTED: *Hemiscyllium ocellatum* LIM and calponin homology domains-containing protein 1-like (LOC132815543), transcript variant X11, mRNA	8.00E-22	86.24	5410	5517	XM_060824585.1
	PREDICTED: *Hemiscyllium ocellatum* LIM and calponin homology domains-containing protein 1-like (LOC132815543), transcript variant X10, mRNA	8.00E-22	86.24	5434	5541	XM_060824575.1
dDocent_Contig_5344	–					
dDocent_Contig_98371	*Scyliorhinus canicula* chromosome X	1.00E-34	87.14	12332236	12332375	LR744057.1
	Scyliorhinus canicula chromosome 23	3.00E-31	85.42	24694218	24694360	LR744052.1
	Scyliorhinus canicula chromosome 20	3.00E-31	85.82	74071254	74071393	LR744049.1
dDocent_Contig_2447	*Scyliorhinus canicula* chromosome 22	1.00E-24	88.68	27243749	27243852	LR744051.1
	PREDICTED: Rhincodon typus aldehyde dehydrogenase, dimeric NADP-preferring-like (LOC109928755), transcript variant X2, mRNA	6.00E-23	83.85	1802	1929	XM_048612698.1
dDocent_Contig_8984	–					
dDocent_Contig_4406	*Scyliorhinus canicula* chromosome 29	8.00E-17	89.74	14601444	14601521	LR744058.1
	Scyliorhinus canicula chromosome 20	5.00E-14	87.95	81343970	81344052	LR744049.1
	Scyliorhinus canicula chromosome X	6.00E-13	93.22	17931229	17931287	LR744057.1
dDocent_Contig_31244	Triakis scyllium tsIgH gene for immunoglobulin heavy chain-like protein, complete cds	1.00E-14	86.75	7937	8019	LC760724.1
	PREDICTED: Rhincodon typus Fc receptor-like protein 2 (LOC109929819), mRNA	3.00E-06	91.49	3020	3066	XM_048621008.1

(*continued on next page*)

Table C3 (*continued*)

Locus	Description	E-value	IP	Hit		NCBI access number
				star	final	
dDocent_Contig_13399	–					
dDocent_Contig_164545	*Scyliorhinus canicula* chromosome 26	5.00E-09	90.91	17097914	17097968	LR744055.1
	PREDICTED: Chiloscyllium plagiosum transcription factor CP2-like 1 (tfcp2l1), transcript variant X2, mRNA	1.00E-05	90	4029	4077	XM_043694202.1
	Raja brachyura genome assembly, chromosome: 25	1.00E-04	97.22	39752589	39752623	OY740805.1
dDocent_Contig_3636	PREDICTED: Stegostoma tigrinum C–C motif chemokine 19-like (LOC125451192), mRNA	1.00E-15	85.42	1271	1365	XM_048528032.2
	PREDICTED: Stegostoma tigrinum retinol dehydrogenase 7-like (LOC125454197), transcript variant X2, mRNA	2.00E-13	83	2463	2561	XM_048534718.2
	PREDICTED: Stegostoma tigrinum retinol dehydrogenase 7-like (LOC125454197), transcript variant X1, mRNA	2.00E-13	83	2537	2635	XM_048534717.2
dDocent_Contig_19293	–					
dDocent_Contig_3899	–					
dDocent_Contig_3786	–					
dDocent_Contig_17536	Thysanoteuthis rhombus genome assembly, chromosome: 14	4.00E-05	100	21299818	21299850	OY735211.1
	Thysanoteuthis rhombus genome assembly, chromosome: 43	5.00E-04	97.06	12195198	12195231	OY735240.1
dDocent_Contig_8138	*Scyliorhinus canicula* chromosome 23	0.022	84.91	16220682	16220733	LR744052.1
dDocent_Contig_18203	Triakis scyllium tsIgH gene for immunoglobulin heavy chain-like protein, complete cds	4.00E-15	90.41	14236	14308	LC760724.1
	Scyliorhinus canicula chromosome 23	8.00E-12	97.92	6069116	6069163	LR744052.1
	Scyliorhinus canicula chromosome 20	3.00E-11	86.84	73414275	73414347	LR744049.1
dDocent_Contig_5496	–					
dDocent_Contig_5345	*Scyliorhinus canicula* chromosome 23	3.00E-30	84.31	8351201	8351353	LR744052.1
	Scyliorhinus canicula chromosome 21	2.00E-22	88.12	36837807	36837907	LR744050.1
dDocent_Contig_19072	–					
dDocent_Contig_8719	–					

Table C4
Sample size per ontogenic stage per region

Region	Juvenile	Adults
WCBC	12	16
CGC	12	10
EGC	14	13
SI	7	6

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