ORIGINAL RESEARCH

Connectivity and genetic diversity patterns of a small demersal shark species, *Mustelus lunulatus* (Carcharhiniformes: Triakidae), in Pacific Panama

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ABSTRACT. Commonly known as the sicklefin smooth-hound shark due to its characteristic molariform teeth, *Mustelus lunulatus*, is one of the main shark species targeted by fisheries along the Pacific coast of Panama. It is distributed from southern California to Ecuador, including Malpelo Island in Colombia. The species inhabits benthic zones on the continental shelf and nearshore coastal waters of the Pacific. This study evaluated the genetic diversity, population structure and connectivity of *M. lunulatus* using COI mitochondrial. Tissue samples were collected from three major Pacific Gulf systems of Panama: Gulf of Chiriqui, Gulf of Montijo, and Gulf of Panama. Genetic analysis revealed differences among regions. Among the analyzed areas, Gulf of Montijo exhibited the highest haplotypic diversity (Hd = 0.83) with a moderately negative Tajima's D value (D = -0.42436), suggesting a population with signs of expansion and lower fishing pressure. On the other hand, Gulf of Chiriqui showed reduced haplotypic diversity (Hd = 0.42) and positive Tajima's D (D = 0.33350), consistent with a population under demographic contraction of intense targeted fishing. Gulf of Panama showed intermediate levels of haplotypic diversity (Hd = 0.79), and a strongly negative Tajima's D (D = -1.52793). The observed genetic structuring and different levels of genetic diversity across study sites underscore the importance of incorporating genetic data into sustainable fisheries and management. These findings support the delineation of region-specific conservation strategies to ensure the long-term sustainability of *M. lunulatus* populations in Panama's Pacific coastal ecosystems, especially at the Gulf of Montijo.

Key words: Genetic diversity, fisheries, *Mustelus lunulatus*, mtDNA, Tropical Eastern Pacific.

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Patrones de conectividad y diversidad genética de una pequeña especie de tiburón demersal, *Mustelus lunulatus* (Carcharhiniformes: Triakidae), en el Pacífico de Panamá

RESUMEN. Comúnmente conocido como Mamon de orilla debido a sus característicos dientes molariformes, el *Mustelus lunulatus* es una de las principales especies de tiburones capturadas por las pesquerías a lo largo de la costa pacífica de Panamá. Se distribuye desde el sur de California hasta Ecuador, incluyendo la Isla Malpelo en Colombia. La especie habita en zonas bentónicas de la plataforma continental y en aguas costeras cercanas a la costa del Pacífico. Este estudio evaluó la diversidad genética, la estructura poblacional y la conectividad de *M. lunulatus* utilizando el gen mitocondrial COI. Se recogieron muestras de tejido de los tres principales sistemas del Pacífico de Panamá: el Golfo de Chiriquí, el Golfo de Montijo y el Golfo de Panamá. El análisis genético reveló diferencias entre las regiones. Entre las áreas analizadas, el Golfo de Montijo mostró la mayor diversidad haplotípica (Hd = 0,83) con un valor de D de Tajima moderadamente negativo (D = -0,42436), lo que sugiere una población con signos de expansión y menor presión pesquera que otras áreas. Por otro lado, el Golfo de Chiriquí mostró una diversidad haplotípica reducida

(Hd = 0,42) y un valor D de Tajima positivo (D = 0,33350), lo que concuerda con una población en contracción demográfica debido a la intensa pesca dirigida. El Golfo de Panamá por su parte mostró niveles intermedios de diversidad haplotípica (Hd = 0,79) y un valor D de Tajima fuertemente negativo (D = -1,52793). La estructuración genética observada y los diferentes niveles de diversidad genética en los distintos lugares de estudio subrayan la importancia de incorporar los datos genéticos en la gestión pesquera. Estos hallazgos respaldan la delineación de estrategias de conservación específicas para cada región con el fin de garantizar la sostenibilidad y gestión adecuada de las poblaciones de *M. lunulatus* en los ecosistemas costeros del Pacífico de Panamá, especialmente en el Golfo de Montijo.

Palabras clave: Diversidad genética, pesquerías, *Mustelus lunulatus*, ADN mitocondrial, Pacífico tropical oriental.

INTRODUCTION

Elasmobranchs are characterized by a slow growth rate, late maturity, low fecundity and low reproductive potential, which limits their ability to maintain an optimal population size and recover from fishing and other selection forces (Stevens et al. 2000; Cailliet et al. 2005; Musick 2005). Some species are important top predators in the ecosystems playing an important role in energy transfer and ecosystem balance (Ceccarelli and Ayling 2010; Bornatowski et al. 2014). Sharks can regulate populations and community structure through different direct (e.g. predation) and indirect (e.g. competition and interference) mechanisms. Thus, they contribute to maintenance and stability of marine and estuarine food webs (Stevens et al. 2000; Bornatowski et al. 2014). Shark species are exploited around the world by industrial, artisanal, traditional and sport fisheries. They are one of the most threatened fish groups worldwide, mainly by fishery impact (Kitchell et al. 2002; Roff et al. 2018). Therefore, a considerable decline in their populations has been observed on a global scale, mainly due to overfishing, pollution and habitat degradation (Stevens et al. 2000; Kitchell et al. 2002; Roff et al. 2018).

Declines in shark populations cause changes that affect not only species survival, but also the distribution and abundance of their prey and trophic dynamics (Stevens et al. 2000; Bornatowski et al. 2014). Species of *Mustelus* spp. Linck, 1790, belong to the family Triakidae. Among Triakidae, the genus is represented by 25 species worldwide distributed in tropical, temperate and cold seas, from shallow to moderate depths (200 m) (Heemstra 1997). In Panama, all Triakidae species are members of the genus *Mustelus* spp. represented by three species in the Pacific: *M. lunulatus*, *M. henlei,* and *M. dorsalis* (Robertson and Allen 2015). Taxonomy and systematics of the genus *Mustelus* spp. are complicated due to the lack of morphological information and reduced variation among species that made it difficult to determine species boundaries (Heemstra 1997; López et al. 2006). This long-standing confusion over classification and taxonomic ID of *Mustelus* spp. has impacted negatively on the number of biological, ecological and fishery studies on this genus (López et al. 2006; Farrell et al. 2009). In addition, the lack of species-specific biological and fisheries data regarding *Mustelus* spp. hinders the development of effective management and conservation strategies at local, subregional and regional level (Marino et al. 2014) .

At present, general knowledge of species belonging to the genus *Mustelus* spp. is scarce, being one of the most problematic elasmobranch genera with respect to taxonomy and systematics (López et al. 2006; Boomer et al. 2012; Naylor et al. 2012). The morphological similarity among *Mustelus* species, as well as the great variability of morphometric and meristic characters, has made difficult their accurate taxonomic identification (Giresi et al. 2013). This species is distributed from southern California to Ecuador, including Malpelo Island in Colombia (Compagno 1984). It inhabits the bottoms of the continental shelf and shallow coastal waters at a

depth of 0-200 m. It is a viviparous a placentate species with an elongated, slender body and oval horizontal eyes, molariform and asymmetrical teeth with cusp reduced to a low point, cusps absent, except in young sharks, condition of buccopharyngeal denticles unknown, strongly falcate ventral caudal lobe in adults, uniform gray or gray-brown color above, light below, without white or black spots or dark bars. Its diet is based on crustaceans, mollusks, and small fish, which is enabled by jaw musculature features and specialized low cuspid clenched teeth that easily crush hard-shelled preys (Gómez et al. 2003; Jardas et al. 2007). *Mustelus* species are commercialized for human consumption and reach a maximum length of up to 175 cm (Navia et al. 2006; Briones-Mendoza et al. 2018; Justo 2022). Furthermore, this species has a fecundity of 6 to 19 offspring per litter (Martínez-Ortíz and Garcia-Dominguez 2013). *Mustelus lunulatus* reproduces annually in the northern Gulf of California females reproduce annually, with a gestation period of approximately 11 months and maturation for females and males at 103 and 91 cm of total length (TL), respectively (Pérez-Jiménez and Sosa-Nishizaki 2010). Species of this genus are the most important sharks in the landings of the artisanal fishery in Panama (Rodríguez-Arriati 2021). For these reasons, it is necessary to identify critical habitats (breeding sites, feeding or migratory routes), as well as characterize the demographic and reproductive patterns of these species to improve management and conservation strategies (Dulvy et al. 2014).

Population genetics provides practical tools for conservation management and understanding the evolution of shark species (Domingues et al. 2018). In this sense, the evaluation of genetic structure in overexploited populations is a very important tool to define conservation units and management strategies (Dudgeon et al. 2012). The exploitation of resources in marine environments can have a high impact on the genetic diversity of populations, by modifying their structure, general population dynamics, reducing fecundity and effective population size (Díaz-Ferguson et al. 2010; Díaz-Ferguson 2012). These techniques have been useful for providing information on demographic patterns relevant to conservation, for example, defining population units, identifying historical and contemporary connectivity patterns between populations, kinship relationships, reproductive behavior, and genetic diversity estimates (Nance et al. 2011; Domingues et al. 2018).

Anthropogenic pressures affecting sharks are diverse and significant, and their impact is felt at multiple levels within marine ecosystems. One of the most critical factors is overfishing, which includes both intentional target fisheries and bycatches. According to the International Union for Conservation of Nature (IUCN), 'about 30% of shark and ray species are threatened' due to these practices becoming illegal, unreported and undocumented fishing (IUCN 2024). Overfishing not only diminishes shark populations, also alters the balance of marine ecosystems. Another important pressure is habitat fragmentation and degradation. The Food and Agriculture Organization of the United Nations (FAO) notes that 'the loss of habitats such as coral reefs and seagrasses affects the species that depend on them' (FAO 2020). Degradation of these critical environments can reduce the availability of shelter and food for sharks, contributing to their decline (Ferretti et al. 2010).

Finally, illegal trade in sharks and their products, especially shark finning, is one of the most urgent threats (Cardeñosa et al. 2022). The international shark fin trade has been identified as a major driver of population decline worldwide (Clarke et al. 2007; Worm et al. 2013). This trade not only contributes to overexploitation but also feeds a chain of illegal activities that endanger the survival of these species. These anthropogenic pressures can in turn cause changes in genetic diversity patterns, reducing the genetic pool and compromising the adaptive value of these species (DiBattista 2008). In Panama, genetic studies in shark species are reduced to a handful of species, *Negaprion brevirostris*, *Sphyrna lewini*, *Rhincodon*

typus and *Triaenodon obesus* (Guzmán et al. 2021; Elizondo-Sancho et al. 2022; Díaz-Ferguson et al. 2026; Díaz-Ferguson and Guzmán in preparation).

Despite the IUCN assessment, *Mustelus* spp. was included as a species with insufficient data, and some species like *M. fasciatus* and *M. schmitti*, were considered critically endangered and threaten, respectively (Rosa and Gadig 2010; IUCN 2024). Results from this research constitutes the first genetic characterization of *M. lunulatus* in the main fishery areas of the Pacific Panama. The information obtained will allow scientists and managers to understand the dynamics of fisheries selection and other selective factors in the genetic structure of this commercially important shark species, providing key formation for its management and conservation.

MATERIALS AND METHODS

Sample collection

This study was conducted in the Pacific of Panama, focusing on three important fishing areas: the Gulf of Chiriqui, which is located in the southwestern region of the Republic of Panama and extends from Punta Burica (8° 2′ 39″ N-82° 52′ 153″ W) on the Western site of Chiriqui province to Punta Mariato (7° 12′ 534″ N-80° 53′ 178″ W) to the Eastern site of Veraguas province. The area includes insular and marine coastal zones of Coiba National Park, Gulf of Chiriqui Marine National Park, David Mangroves Marine Reserve, and the largest wetland of the country, the Gulf of Montijo, located between (7° 35′ 45″ to 7° 50′ 45″) north latitude and (80° 58′ 45″ to 81° 13′ 30″) west longitude in the Pacific Ocean of Panama (Maté 2005). This is one of the main marine-estuarine coastal systems of the Panama Pacific and is essential part of Panama's Marine Protected Areas System under the Ramsar site category. The Gulf of Montijo is also part of the Buffer Zone of Coiba National Park. The Gulf of Panama, located at 8° 44.138' N and 79° 15.955′ W, has an area of 27,175 km^2 (ANAM 2004). This area is considered the largest fishery area of the Republic of Panama, characterized by conspicuous oceanographic conditions, i.e. upwelling conditions from January to March, supporting anchoveta and arenque fisheries (D'Croz and O'Dea 2007; Crawford et al. 2023) (Figure 1).

Samples were collected during 2021 and 2022. A total of 33 tissue samples from fishing ports and fishing areas were collected by capturing live organisms. Fishing ports were Puerto Mutis (Gulf of Montijo), Puerto Remedios (Gulf of Chiriqui), and Puerto Vacamonte (Gulf of Panama). To take the samples, a small piece of tissue preserved in 70% alcohol was cut from the dorsal fin or trunk, since in some cases animals came without fins or head. These were only taken in the Gulf of Chiriqui, leaving from Puerto Remedios and La Barqueta beach, using a pelagic longline for tissue collection. Ten individual longlines were used, 38 fathoms long with 10.3 cm, C-type hooks with various pieces of fish as bait. Sampling time was 30 to 50 min. When a shark was detected on the long line, the boat was positioned over the site, taking care not to waste time in the maneuver. The longline was raised, and the shark was carefully released. External FD-94-Bar Anchor type tags (Floy Tag) were placed using an applicator in the center of the first dorsal fin (to know that the shark's tissue has already been taken). Tissue samples were collected by making a small tissue cut from the posterior margin of the first dorsal fin. Samples were collected with scissors and forceps that had been previously disinfected with ethanol 70%. Tissue samples were placed in 1.5 ml tubes filled with ethanol 70%. All samples were labeled with their respective coding. All collected animals were returned to the water, ensuring that the shark's reaction was observed before release (Llerena et al. 2012).

DNA extraction, quantification and quality

A small piece of muscle tissue or fin was tak-

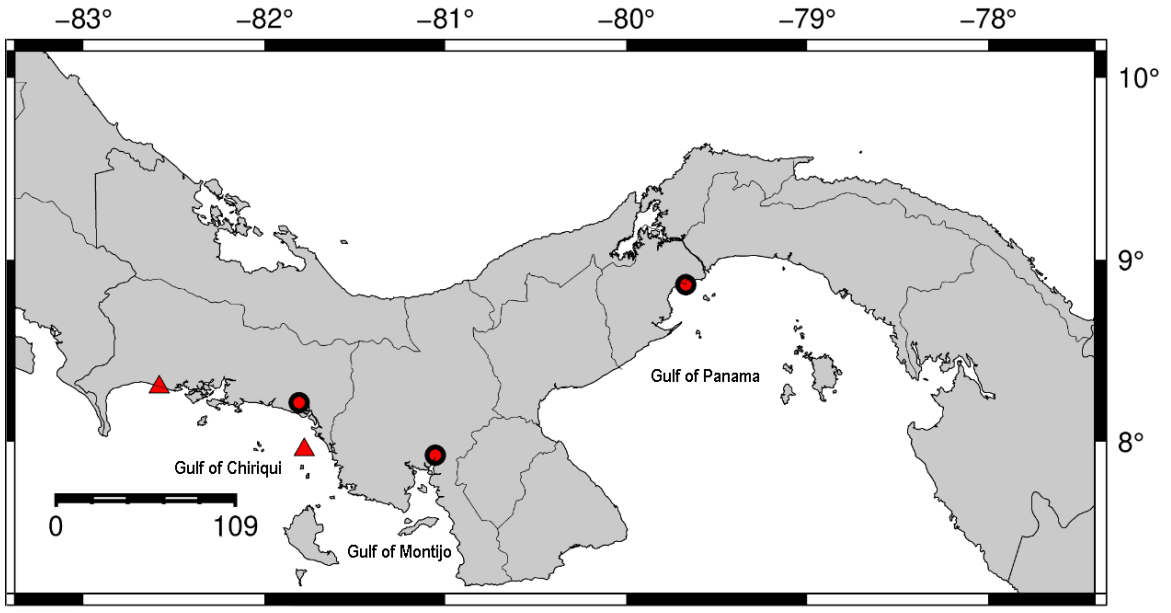

Figure 1. Map of study areas of the Pacific Panama. Circles indicate fishing ports and triangles indicate fishing areas in Open Ocean or near the coast.

en and preserved in a 1.5 ml tube at 70% ethanol. The DNA from tissues was extracted using the DNeasy® Blood and Tissue DNA extraction kit (QIAGEN). After extraction, DNA was stored in 1.5 ml tubes at -20 °C. The quality and concentration of the DNA was determined using the NanodropTM 2000 spectrophotometer (Thermo Scientific).

DNA amplification

A 650 bp fragment in the Mitochondrial Cytochrome oxidase I (COI) gene region was amplified by Polymerase Chain Reaction (PCR) using the FishF1 (Forward) and FishR1 (Reverse) primers designed by with the following sequences: Forward primer FishF1 5'-TCAACCAACCACAAAGACATTGGCAC-3' Reverse primer FishR1 5'-TAGACTTCTGGG TGGCCAAAGAATCA-3' (Ward et al., 2005). The following reagents were used in the PCR reaction: 12.5 µL of Taq PCR from the Kit (QIAGEN), 1 µL of FisF1 Forward primer, 1 uL of Reverse primer, 6.5 µL of DNase- and RNase-free water and 4 µL of DNA. PCR was performed on a 2,720 Thermal Cycler (Applied Biosystems) under the following conditions: initial denaturation was carried out for 1 min at 95 °C, followed by 5 cycles of denaturation at 95 °C for 30 s, hybridization at 50 °C for 40 s and extension at 72 °C for 1 min. This was followed by 35 cycles of denaturation at 95 °C for 30 s, hybridization at 55 °C for 40 s and extension at 72 °C for 1 min. Amplification was terminated by an extension step at 72 °C for 5 min, in which the PCR product was kept at a temperature of 4 °C until visualization on agarose with the electrophoresis a PCR products were visualized with an agarose gel electrophoresis (QA-Agarose /MP Biomedicals) diluted in 1× TBE buffer then stained with a drop of RedTM Dropper Bottle Gel (Orelup SSP®), to verify the presence of amplified DNA, along with a 100 bp Gelpilot molecular weight marker (QIAGEN) which indicated the size of the amplified DNA fragment. The gel was then run at 70 v for 35 min. Subsequently, PCR products were visualized under UV light to confirm amplification.

DNA alignment

Sequences obtained from the mitochondrial COI gene fragment were edited and aligned using the ClustalW algorithm in Sequencher® version 5.4.6 DNA sequence analysis software.

Genetic diversity and structure

The DNASP 6 program (Librado and Rozas 2009) was used to calculate genetic diversity indices for each population, such as the number of polymorphic sites (Ns), haplotypic diversity (Hd), nucleotide diversity (π), and total number of haplotypes (H), as well as the number of migrants per generation (Nm), net genetic distance between populations (Da), and nearest-neighbor statistic (Snn).

Phylogeography and historical demography

The visualization of genetic differentiation and distances between populations was performed using a Neighbor-Joining (NJ) Dendrogram (Figure 2). This NJ dendrogram was visualized in the Geneious Prime program (Geneious Prime 2022). In addition, a haplotype network was performed to see the distribution of haplotypes by population with the program PopART (Leigh and Bryant 2015). To measure the effect of demographic changes or population demographic history based on DNA sequences, neutrality was assessed using Tajima's D and Fu and Li's D* statistics (Fu and Li 1993; Tajima1989).This index allows investigating deviations from neutrality, as well as population balance, expansion or contraction (Díaz-Ferguson 2012).

RESULTS

A total of 33 sequences of COI gene segment (cytochrome oxidase I) were obtained for genetic analysis. Subsequently, sequences were aligned, their ends were trimmed and edited to obtain fragments of 619 bp. Fragments showed a variable region located between 240 and 527 bp and generated 10 haplotypes. Amplified samples were analyzed and compared with reference sequences in Genbank. Accession numbers were generated for each sequence and haplotype in GenBank (Table 1).

Genetic diversity indices were calculated for each locality (Table 2). The highest haplotype diversity (Hd) was observed in the Gulf of Montijo (Hd = 0.836) and the Gulf of Panama (Hd = 0.791), while the Gulf of Chiriqui exhibited lower haplotype diversity (Hd = 0.429). Nucleotide diversity (π) was also highest in the Gulf of Montijo (π = 0.0227) compared to the Gulf of Panama (π = 0.0032) and the Gulf of Chiriqui (π = 0.0008). Tajima's D values were not statistically significant for any of the studied populations ($p > 0.05$). Nevertheless, negative values were observed in the Gulf of Montijo (D = -0.424) and the Gulf of Panama (D = -1.528), while a positive value was found in the Gulf of Chiriqui (D = 0.334), suggesting slight differences in allele frequency distributions among sites. Similarly, Fu and Li's D* tests yielded the following values: Gulf of Montijo (D* = -0.038), Gulf of Chiriqui (D* = 0.887), Gulf of Panama (D* = -1.811), and all localities together (D* = -1.552). All results were not statistically significant ($p > 0.05$), indicating no strong deviation from neutrality.

Pairwise genetic differentiation between populations is shown in (Table 3). Higher Nm values were observed between Chiriqui and Panama (2.27) and Chiriqui and Montijo (2.36), indicating moderate gene flow. The lowest Da was observed between Chiriqui and Panama (0.00034), while the highest occurred between Panama and Montijo (0.00166). The Nm estimate between Panama and Montijo was negative (-53.93), likely due to low genetic variation and small sample size, which can produce negative values in Nm calculations. This does not indicate negative migration but reflects limited genetic exchange. The Snn values ranged from 0.098 to 0.578, with higher values suggesting stronger

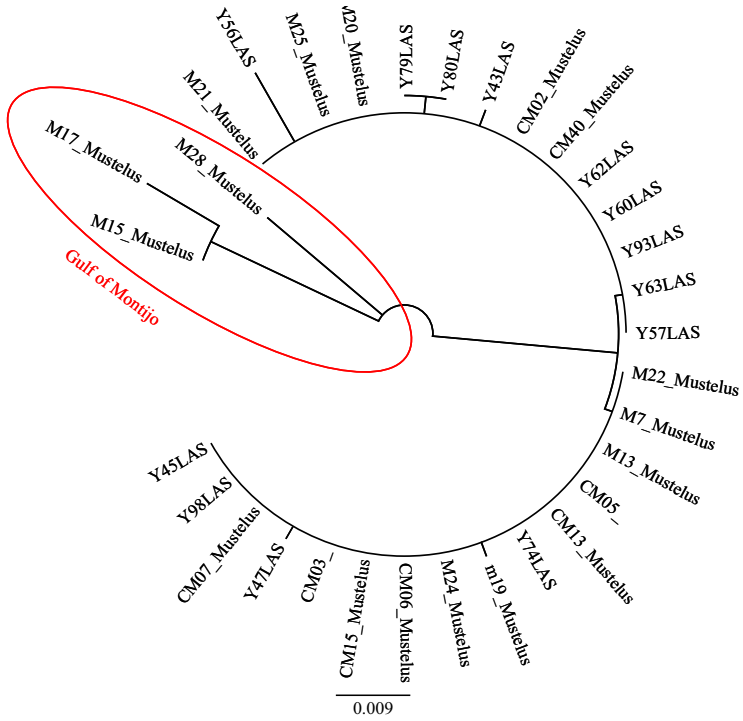

Figure 2. Neighbor-Joining (NJ) dendrogram of genetic distances of individuals from the different localities of *Mustelus lunulatus*. M: Gulf of Montijo, CM: Gulf of Chiriqui, and Y: Gulf of Panama.

Table 1. Total number of haplotypes by Gulf area and assigned GenBank accession number.

Sample location	N	Total number of haplotypes per location	GenBank accession number
Gulf of Montijo (GM)	11	6	OP889220
Gulf of Chiriqui (GC)	8	2	OP889218
			OP889219
Gulf of Panama (GP)	14	6	OP889221
			OP889222
			OP889223
			OP889224

genetic differentiation, particularly between Panama and Montijo.

A total of 10 haplotypes were observed from 33 *M. lunulatus* sequences (Figure 3). Haplotype 2 was the most frequent and was present in all localities. Haplotypes 6, 3 and 4 were derived from haplotype 2 and were exclusive to the Gulf of Montijo. Haplotype 1 was also present at all three localities. The haplotype network showed a black circle, corresponding to an unsampled haplotype. The Gulf of Montijo locality had the highest number of unique haplotypes.

Table 2. Genetic diversity indices based on the sequences of a segment of the mitochondrial cytochrome oxidase subunit I (COI) gene. N = number of samples, H = number of haplotypes, π = nucleotide diversity, Hd = haplotype diversity, S = polymorphic sites.

Location	N	H	Hd	π	S	Tajima's	Fu and Li's D*
Gulf of Montijo (GM)	11	6	0.83636	0.02268	39	-0.42436	-0.038
Gulf of Chiriqui (GCH)	8	2	0.42857	0.00080	1	0.33350	0.887
Gulf of Panama (GP)	14	6	0.79121	0.00319	9	-1.52793	-1.811
All localities together	33	10	0.74621	0.00993	46	-1.98340	-1.552

*Fu and Li (1993).

Table 3. Pairwise genetic differentiation between populations. gene flow (Nm), net divergence (Da), and nearest-neighbor statistic (Snn).

Comparison	Nm	Da	Snn
Gulf Chiriqui/Gulf Panama	2.27	0.00034	0.09800
Gulf Chiriqui/Gulf Montijo	2.36	0.00158	0.50112
Gulf Panama/Gulf Montijo	-53.93	0.00166	0.57833

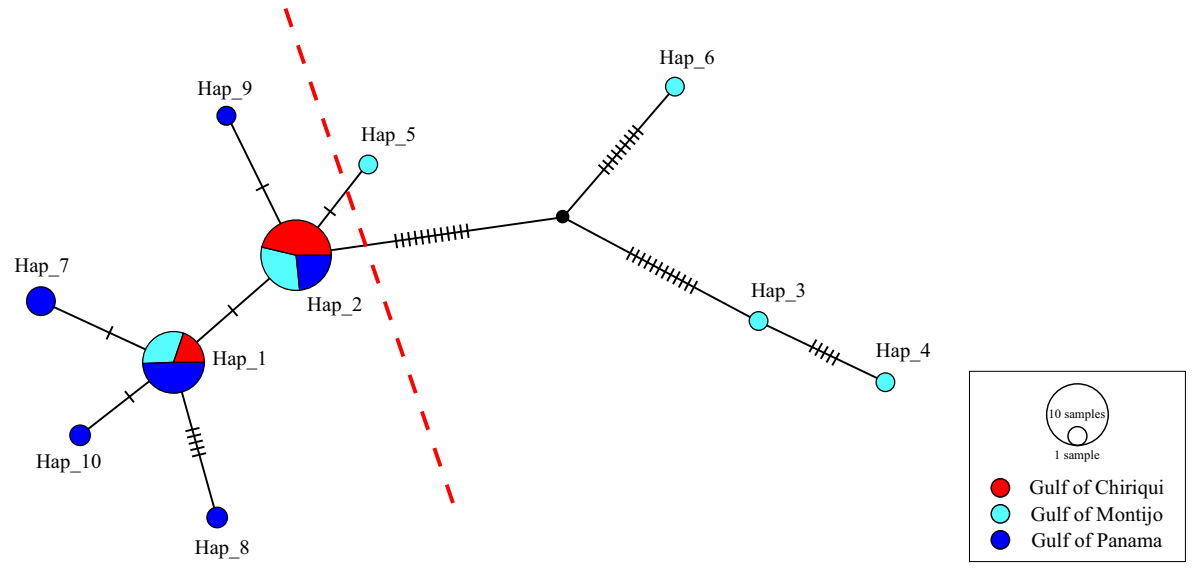

Figure 3. Haplotype network showing the genealogical relationships between sequences (individuals) of *Mustelus lunulatus*. Each circle represents a haplotype, and the size represents the relative frequency of each haplotype. Colors represent the sampled localities: Gulf of Chiriqui (red), Gulf of Montijo (light blue) and Gulf of Panama (blue). Dash lines show separation of unique haplotypes from Gulf of Montijo (light blue circle) and their relationship with Gulf of Chiriqui most common haplotype (red circle).

DISCUSSION

Genetic diversity, demographic history and fishery

Genetic studies in shark and ray populations are reduced in general, and absent for some species (Barbato et al. 2025). This is the first research to focus on the genetic structure, diversity and connectivity of a demersal shark population considered among the most captured shark species from Panamanian fisheries. Genetic data is essential for the establishment of realistic populations models including population limits, connectivity patterns and potential conservation units (Díaz-Ferguson et al. 2010, 2023). This information allows scientists and managers to establish effective management and conservation strategies.

Genetic diversity was calculated from 33 *M. lunulatus* sequences, which revealed 10 distinct haplotypes. The overall haplotype diversity (Hd = 0.746) is comparable to values reported in other species. For instance, *M. henlei* exhibited high haplotype diversity (Hd = 0.840) but low nucleotide diversity ($\pi = 0.0033$), a pattern typically associated with species that have experienced demographic stability or recent population expansion from a common ancestor (Sandoval-Castillo and Beheregaray 2015). In contrast, *Triaenodon obesus* showed more moderate values (Hd = 0.550 ± 0.025; $\pi = 0.00213$), suggesting lower mitochondrial variation at the regional scale, possibly due to limited connectivity or differing demographic history (Whitney et al. 2011). Meanwhile, this pattern is mirrored in mitochondrial markers, with *M. punctulatus* showing very low variability (Hd = 0.16 - 0.31 and $\pi = 0.0003$-0.001), while *M. mustelus* exhibits higher haplotype diversity (Hd = 0.52-0.54 and $\pi = 0.001$), consistent with broader demographic connectivity and population structure. Overall, the genetic diversity observed in *M. lunulatus* falls within the range reported for other coastal elasmobranchs. As expected, demersal coastal populations, which generally have smaller effective population sizes than pelagic migratory species, tend to show lower genetic diversity and larger population sizes (Karl et al. 2011; Domingues et al. 2018). Additionally, species of the genus *Mustelus* are known to exhibit female philopatry, which could limit gene flow and contribute to population structuring (Ramírez-Amaro et al. 2018) . This study covered the three major gulf systems of Pacific Panama, encompassing approximately 1,700 km of coastal area. Among them, the Gulf of Chiriqui, an area under intense fishing pressure, showed the lowest genetic diversity (Hd = 0.42857; $\pi = 0.00080$), with only two haplotypes identified among eight individuals. Positive Tajima's D value (D = 0.33350) in this zone suggests a potential signal of population contraction or balancing selection, consistent with reports of high capture rates in this region (Smith 1994).

In contrast, the Gulf of Montijo, despite its smaller geographic area, presented the highest genetic diversity among the three regions (Hd = 0.83636; $\pi = 0.02268$; 6 haplotypes out of 11 individuals) and a negative Tajima's D value (-0.42436), although not strongly significant, may indicate a recent population expansion. Moreover, haplotype network analysis revealed that Montijo harbors the highest number of unique haplotypes (3, 4, and 6), all derived from the central and most common haplotype (haplotype 2), which was present across all three localities. This suggests that Gulf of Montijo is potentially a nursery and spawning area due to its estuarine and physiographic features and therefore acts as a source population and genetic pool for connected areas (Guzmán et al. 2020).

The Gulf of Panama exhibited intermediate haplotype richness (6 haplotypes out of 14 individuals), moderate haplotype diversity (Hd = 0.79121), but very low nucleotide diversity ($\pi = 0.00319$). The strongly negative Tajima's D (-1.52793) is indicative of a recent population expansion, possibly following a bottleneck event. This pattern matches the ecological dynamics of the region, where upwelling processes support high productivity and may

facilitate recruitment of demersal species (Kottillil et al. 2023; Smith 1994). For example, pelagic and migratory species such as the whale shark (*R. typus*) and hammerhead sharks (*Sphyrna lewini*) often show higher haplotype and nucleotide diversity due to their wide-ranging movements and transoceanic connectivity, which promote gene flow between populations (Karl et al. 2011; Alghozali et al. 2019). In contrast, small coastal species like *M. lunulatus*, which have more restricted home ranges and limited dispersal capabilities, exhibit lower genetic diversity levels, reflecting more isolated and potentially vulnerable populations (Ramírez-Amaro et al. 2018; Guzmán et al. 2021).

Genetic connectivity

Results of the genetic connectivity of this study indicate a moderate level of genetic connectivity between populations of *M. lunulatus* in the Gulf of Chiriqui and the Gulf of Montijo (Nm = 2.36, Snn = 0.50112), suggesting some degree of population structuring, though not complete isolation. This contrasts slightly with findings that reported high connectivity between the Gulf of Chiriqui and the Gulf of Montijo for species such as *Scomberomorus sierra*, *Caranx caninus*, and *Lutjanus guttatus*, supporting the existence of a single stock in that region for species with highly dispersal potential (Díaz-Ferguson et al. 2023) The presence of haplotype 2 in all localities suggests historical genetic connectivity between populations. Similarly, the presence of haplotype 1 in all three localities supports this interpretation and may be related to their geographic proximity. However, although some haplotypes are unique to Montijo, these haplotypic relationships are not sufficient to indicate a clear genetic structure between populations.

Genetic connectivity is the main feedback mechanism of biodiversity in marine animals. Either by local movements, migration or through dispersal, connectivity has been recognized as a key mechanism influencing population structure and genetic differentiation in fishes and sharks (Veríssimo et al. 2010; Díaz-Ferguson 2012). In this regard, differences in the population structure between pelagic and demersal coastal species have been suggested. Population genetic studies conducted mainly in large pelagic shark species reveal genetic homogeneity at large spatial scales, for example in basking sharks (*Cetorhinus maximus*) as well as in whale sharks (*R. typus*) (Hoelzel et al. 2006; Guzmán et al. 2021). The differences may be attributed to species-specific ecological and behavioral traits, including larval dispersal capacity, reproductive strategies, and habitat preferences. Additionally, local oceanographic conditions may influence connectivity patterns differently among species, even within the same geographic area. This pattern is often attributed to their high dispersal potential, which facilitates gene flow across ocean basins, and to their typically large effective population sizes, which reduce the effects of genetic drift and promote genetic uniformity across wide geographic ranges. In contrast, species with a smaller displacement range, such as small demersal shark species usually have a complex population structure and connectivity patterns are usually associated to life history features, habitat preferences and site fidelity (Dudgeon et al. 2012; Portnoy and Heist 2012; Chapman et al. 2015). For example, populations of *Mustelus* spp. are often connected through a series of tiered populations (Boomer et al. 2012). Additionally, genetic studies conducted on other small coastal shark populations with limited viability showed high genetic differentiation of populations across ocean basins due to environmental barriers (nurse shark *Ginglymostoma cirratum*) (Karl et al. 2012). Also, small coastal species along continuous continental coasts showed clear genetic differentiation in species like the leopard shark *Triakis semifasciata* (Lewallen et al. 2007).

In contrast to our results, Pereyra et al. (2010) reported low nucleotide diversity ($\pi = 0.0015$) and haplotype diversity ($h = 0.226$) in *M. schmitti*, along with significantly negative Tajima's D (-2.33; $p < 0.01$) and Fu's Fs (-13.28; $p < 0.01$), suggesting a recent population expansion. The absence of sig-

nificant neutrality test results in our study indicates a different demographic history for the studied populations, possibly reflecting demographic stability or moderate levels of gene flow. Genetic connectivity plays a critical role in shaping population structure and maintaining genetic diversity within and among marine species, particularly in coastal sharks where dispersal patterns and habitat preferences may influence gene flow dynamics.

In the Central Mediterranean Sea, similar findings have been reported for *Mustelus* species, where strong fishing pressure combined with limited dispersal capacity has resulted in reduced connectivity and the formation of distinct population structures. Specifically, at least two genetically distinct stocks have been identified in *M. mustelus* and *M. punctulatu*s (Barbato et al. 2025). These patterns are consistent with other demersal elasmobranchs, such as the brown dogfish (*M. henle*i) and the spiny dogfish (*Squalus acanthias)*, which also exhibit population-level genetic divergence due to restricted gene flow. Likewise, *M. antarcticus* has shown clear genetic differentiation among populations, further underscoring the limited connectivity in demersal sharks (Veríssimo et al. 2010; Petrolo et al. 2021). This genetic structuring reflects both the species' dispersal limitations and localized environmental pressures. The resulting genetic variation is essential for the long-term resilience of populations, as it supports adaptive potential in changing environments. However, such variation is not homogeneously distributed and often clusters into discrete groups of genetically similar individuals, emphasizing the need to incorporate genetic data into fisheries management, particularly for species vulnerable to overexploitation due to their life history traits.

Understanding the impact of fishing on shark species is crucial as it puts a lot of pressure on certain shark species, which can disproportionately affect those populations. Bycatch is also a key factor, as many sharks are accidentally caught in nets targeting other species, which can have a significant impact on their population.

CONCLUSIONS

This study represents the first effort to relate historical fishery data with genetic diversity, population structure, and historical demographic parameters of *M. lunulatus* in the Eastern Tropical Pacific. Overall, genetic diversity levels were moderate to high in some localities, particularly in the Gulf of Montijo, suggesting that this area may function as an important nursery or reproductive ground. Such areas may contribute disproportionately to the maintenance of regional genetic diversity and connectivity. Although the species exhibits life-history traits such as relatively short gestation periods and faster maturation compared to other elasmobranchs, which may confer some resilience to fishing pressure. Our results indicate that overexploitation may have negatively affected genetic diversity and effective population size at a microgeographic scale.

However, mitochondrial DNA reflects historical patterns of maternal inheritance and may not fully resolve contemporary population structure. Future studies incorporating additional nuclear markers, such as microsatellites or genome-wide SNPs, would provide higher resolution to better assess recent divergence and contemporary gene flow among sampled localities. The identification of potentially important areas such as the Gulf of Montijo highlights the need for effective protection of estuarine and coastal habitats, which may play a critical role in sustaining genetic diversity and long-term population viability of demersal sharks in Panama and along the Pacific coast of Central America.

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Author contributions

Sara C. Justo-Riverol: sampling collections; DNA extraction; analysis; writing. Edgardo E. Díaz-Ferguson: conceptualization; editing; writing; Proof Concept in marine genetics.

REFERENCES

Alghozali FA, Wijayanti DP, Sabdono A. 2019. Genetic diversity of scalloped hammerhead sharks (*Sphyrna lewini*) landed in muncar fishing port, Banyuwangi. Biodiversitas. 20 (4): 1154-1159. DOI: https://doi.org/10.13057/biodiv/d200430

[ANAM] Autoridad Nacional del Ambiente. 2004. Informe del estado del ambiente: GEO Panamá 2004. Balboa: ANAM. 175 p. https://bdigital.binal.ac.pa/bdp/informe%20del%20ambiente.pdf.

Barbato M, Bonanomi S, Borme D, Ćetković I, Colloca F, Di Lorenzo M, Marino IAM, Mazzoldi C, Pešić A, Sala A, et al. 2025. New findings into the genetic population structure of two commercially valuable and threatened sharks, *Mustelus mustelus* (Linnaeus, 1758) and *M. punctulatus* (Risso, 1827), allow refining management strategy in the Central Mediterranean Sea. Front Mar Sci. 12: 1520573. DOI: https://doi.org/10.3389/fmars.2025.1520573

Boomer JJ, Harcourt RG, Francis MP, Stow AJ. 2012. Genetic divergence, speciation and biogeography of *Mustelus* (sharks) in the central Indo-Pacific and Australasia. Mol Phylogenet Evol. 64: 697-703. DOI: https://doi.org/10.1016/j.ympev.2012.05.024

Bornatowski H, Navia AF, Braga RR, Abilhoa V, Corrêa MFM. 2014. Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. ICES J Mar Sci. 71 (7): 1586-1592. DOI: https://doi.org/10.1093/icesjms/fsu025

Briones-Mendoza J, Pincay-Espinoza JE, Palma-Chávez J, Romero-Caicedo A. 2018. Notas sobre la biología del tiburón mamona *Mustelus lunulatus* (Carcharhiniformes: Triakidae) en el Pacífico Central ecuatoriano. Rev Biol Mar Oceanogr. 53 (2): 279-284. DOI: https://doi.org/10.22370/rbmo.2018.53.2.1301

Cailliet GM, Musick JA, Simpfendorfer CA, Stevens JD. 2005. Ecology and life history characteristics of chondrichthyan fish. In: Fowler SL, Cavanagh RD, Camhi M, Burgess GH, Cailliet GM, Fordham SV, Simpfendorfer CA, Musick JA, editors. Sharks, rays and chimaeras: the status of the chondrichthyan fishes, status survey. Gland: IUCN/Shark Specialist Group. p. 12-18.

Cardeñosa D, Shea SK, Zhang H, Fischer GA, Simpfendorfer CA, Chapman DD. 2022. Two thirds of species in a global shark fin trade hub are threatened with extinction: conservation potential of international trade regulations for coastal sharks. Conserv Lett. 15: e12910. DOI: https://doi.org/10.1111/conl.12910

Ceccarelli D, Ayling T. 2010. Role, importance and vulnerability of top predators on the Great Barrier Reef - a review. Research Publication. 105. Townsville: Great Barrier Reef Marine Park Authority. 150 p.

Chapman DD, Feldheim KA, Papastamatiou YP, Hueter RE. 2015. There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. Annu Rev of Mar Sci. 7: 547-570. DOI: https://doi.org/10.1146/annurev-marine-010814-015730

Clarke SC, Milner-Gulland EJ, Bjørndal T. 2007. Social, economic, and regulatory drivers of the shark fin trade. Mar Resour Econ. 22 (3): 305-327.

Clarke TM, Espinoza M, Wehrtmann IS. 2014. Reproductive ecology of demersal elasmobranchs from a data-deficient fishery, Pacific of Costa Rica, Central America. Fish Res. 157: 96-105. DOI: https://doi.org/10.1016/j.fishres.2014.04.003

Compagno LJV. 1984. FAO species catalogue. Vol. 4. Sharks of the world. Part 2. Carcharhiniformes. FAO Fish Synop. 125: 251-633.

Crawford G, Mepstead M, Díaz-Ferguson E. 2023. Characterizing oceanographic conditions near Coiba Island and Pacific Panama using 20 years of satellite-based wind stress, SST and chlorophyll-*a* measurements. Mar Fish Sci. 37 (3): 391-411. DOI: https://doi.org/10.47193/mafis.37X2024010112

D'Croz L, O'Dea A. 2007. Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. Estuar Coast Shelf Sci. 73: 325-340. DOI: https://doi.org/10.1016/j.ecss.2007.01.013

Díaz-Ferguson E. 2012. Introducción a la ecología molecular marina: aplicaciones y perspectivas. 1st ed. Panama: Universal Books. 212 p.

Díaz-Ferguson E, Chial M, Gonzalez M, Muñoz E, Chen O, Dúran O, Vega A, Ramos Delgado C. 2023. Building a teleost fish traceability program based on genetic data from Pacific Panama fish markets. Animals. 13 (14): 2272. DOI: https://doi.org/10.3390/ani13142272

Díaz-Ferguson E, Haney R, Wares J, Silliman B. 2010. Population genetics of a trochid gastropod broadens picture of Caribbean Sea connectivity. PLoS ONE. 5: e12675. DOI: https://doi.org/10.1371/journal.pone.0012675

Díaz-Ferguson E, Justo-Riverol S, Barreiros P. 2026. Genetic and taxonomic data corroborates the first report of lemon sharks, *Negaprion brevirostris,* in estuarine waters of Coiba National Park, Panama. DOI: https://doi.org/10.21203/rs.3.rs-8183344/v1

Díaz-Ferguson E, Justo SC, Del Cid V, Posada J. 2023. Fishery and conservation implications of molecular characterization and traceability of ceviche samples from Pacific Panama. Mar Fish Sci. 37 (3): 379-390. DOI: https://doi.org/10.47193/mafis.37X2024010101

DiBattista JD. 2008. Patterns of genetic variation in anthropogenically impacted populations. Conserv Genet. 9: 141-156. DOI: https://doi.org/10.1007/s10592-007-9317-z

Domingues RR, Hilsdorf AWS, Gadig OBF. 2018. The importance of considering genetic diversity in shark and ray conservation policies. Conserv Genet. 19: 501-525. DOI: https://doi.org/10.1007/s10592-017-1038-3

Dudgeon CL, Blower DC, Broderick D, Giles JL, Holmes BJ, Kashiwagi T, Krück NC, Morgan JAT, Tillett BJ, Ovenden JR. 2012. A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. J Fish Biol. 80 (5): 1789-1843. DOI: https://doi.org/10.1111/j.1095-8649.2012.03265.x

Dulvy NK, Fowler SL, Musick JA, Cavanagh RD, Kyne PM, Harrison LR, Carlson JK, Davidson LNK, Fordham SV, Francis MP, et al. 2014. Extinction risk and conservation of the world's sharks and rays. Elife. 3: e00590. DOI: https://doi.org/10.7554/elife.00590

Elizondo-Sancho M, Rodríguez-Arriatti Y, Albertazzi FJ, Bonilla-Salazar A, Arauz-Naranjo D, Arauz R, Areano E, Avalos-Castillo CG, Brenes Ó, Chávez EJ, et al. 2022. Population structure and genetic connectivity of the scalloped hammerhead shark (*Sphyrna lewini*) across nursery grounds from the Eastern Tropical Pacific: implications for management and conservation. PLoS ONE. 17: e0264879. DOI: https://doi.org/10.1371/journal.pone.0264879

[FAO] Food and Agriculture Organization of the United Nations. 2020. The state of food and agriculture 2020. Overcoming water challenges in agriculture. Rome: FAO. 210 p. DOI:

https://doi.org/10.4060/cb1447en

Farrell ED, Clarke MW, Mariani S. 2009. A simple genetic identification method for Northeast Atlantic smoothhound sharks (*Mustelus* spp.). ICES J Mar Sci. 66 (3): 561-565. DOI: https://doi.org/10.1093/icesjms/fsn218

Feitosa LM, Martins APB, Giarrizzo T, Macedo W, Monteiro IL, Gemaque R, Nunes JLS, Gomes F, Schneider H, Sampaio I, Souza R, et al. 2018. DNA-based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot. Sci Rep. 8: 21683. DOI: https://doi.org/10.1038/s41598-018-21683-5

Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK. 2010. Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett. 13: 1055-1071. DOI: https://doi.org/10.1111/j.1461-0248.2010.01489.x

Fu YX, Li WH. 1993. Statistical tests of neutrality of mutations. Genetics. 133 (3): 693-709. DOI: https://doi.org/10.1093/genetics/133.3.693

Geneious Prime. 2022. Geneious Version 7.04. Biomatters. https://www.geneious.com/.

Giresi MM, Grubbs RD, Portnoy DS, Gold JR. 2013. A morphological key to distinguish among smooth-hound sharks (*Genus Mustelus*) in the Gulf of Mexico. Gulf and Caribb Res. 65: 143-146.

Gómez GO, Zapata LA, Franke R, Ramos GE. 2003. Hábitos alimentarios de *Mustelus lunulatus* y *M. henlei* (Pisces: Triakidae) colectados en el Parque Nacional Natural Gorgona, Pacífico colombiano. Bol Invest Mar Cost. 32: 219-229.

Guzmán HM, Beaver CE, Díaz-Ferguson E. 2021. Novel insights into the genetic population connectivity of transient whale sharks (*Rhincodon typus*) in Pacific Panama provide crucial data for conservation efforts. Front Mar Sci. 8: 744109. DOI: https://doi.org/10.3389/fmars.2021.744109

Guzmán HM, Cipriani R, Vega AJ, Morales-Saldaña JM. 2020. Fisheries and conservation assessment of sharks in Pacific Panama. Aquat Conserv Mar Freshwat Ecosyst. 30: 315-330. DOI: https://doi.org/10.1002/aqc.3245

Heemstra PC. 1997. A review of the smooth-hound sharks (Genus *Mustelus*, Family Triakidae) of the western Atlantic Ocean, with descriptions of two new species and a new subspecies. Bull Mar Sci. 60: 894-928.

Hoelzel AR, Shivji MS, Magnussen J, Francis MP. 2006. Low worldwide genetic diversity in the basking shark (*Cetorhinus maximus*). Biol Lett. 2 (4): 639-642. DOI: https://doi.org/10.1098/rsbl.2006.0513

[IUCN] International Union for Conservation of Nature. 2024. *Carcharhinus leucas*. Red List of Threatened Species. DOI: https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T39372A2910670.en

Jardas I, Šantić M, Nerlović V, Pallaoro A. 2007. Diet composition of blackspotted smoothhound, *Mustelus punctulatus* (Risso, 1826), in the eastern Adriatic Sea. J Appl Ichthyol. 23: 72-77. DOI: https://doi.org/10.1111/j.1439-0426.2006.00826.x

Justo S. 2022. Estructura y variabilidad genética de tiburones del género *Mustelus* spp. en el golfo de Chiriquí y Montijo como áreas de influencia del Parque Nacional Coiba [thesis]. Panamá: International Maritime University of Panama.

Karl SA, Castro ALF, Garla RC. 2012. Population genetics of the nurse shark (*Ginglymostoma cirratum*) in the western Atlantic. Mar Biol. 159: 489-498. DOI: https://doi.org/10.1007/s00227-011-1828-y

Karl SA, Castro ALF, Lopez JA, Charvet P, Burgess GH. 2011. Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred from mitochondrial and microsatellite DNA. Conserv Genet. 12: 371-382. DOI: https://doi.org/10.1007/s10592-010-0145-1

Kitchell JF, Essington TE, Boggs CH, Schindler DE, Walters CJ. 2002. The role of sharks and longline fisheries in a pelagic ecosystem of the Central Pacific. Ecosystems. 5: 202-216. DOI: https://doi.org/10.1007/s10021-001-0065-

5

Kottillil S, Rao C, Bowen BW, Shanker K. 2023. Phylogeography of sharks and rays: a global review based on life history traits and biogeographic partitions. PeerJ. 11: e15396. DOI: https://doi.org/10.7717/peerj.15396

Leigh J, Bryant D. 2015. PopART: Full-feature software for haplotype network construction. Methods Ecol Evol. 6 (9): 1110-1116. DOI: https://doi.org/10.1111/2041-210X.12410

Lewallen EA, Anderson TW, Bohonak AJ. 2007. Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. Mar Biol. 152: 599-609. DOI: https://doi.org/10.1007/s00227-007-0714-0

Librado P, Rozas J. 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. Bioinformatics. 25 (11): 1451-1452. DOI: https://doi.org/10.1093/bioinformatics/btp187

Llerena Y, Espinoza E, Peñaherrera C. 2012. Manual para el monitoreo y marcaje en tiburones juveniles de las zonas de manglar de la Reserva Marina de Galápagos. Puerto Ayora: Dirección del Parque Nacional Galápagos y Fundación Charles Darwin.

López JA, Ryburn JA, Fedrigo O, Naylor GJP. 2006. Phylogeny of sharks of the family Triakidae (Carcharhiniformes) and its implications for the evolution of carcharhiniform placental viviparity. Mol Phylogenet Evol. 40 (1): 50-60. DOI: https://doi.org/10.1016/j.ympev.2006.02.011

Marino IM, Riginella E, Cariani A, Tinti F, Farrell E, Mazzoldi C, Zane L. 2014. New molecular tools for the identification of 2 endangered smooth-hound sharks, *Mustelus mustelus* and *Mustelus punctulatus*. J Hered. 106 (1): 123-130. DOI: https://doi.org/10.1093/jhered/esu064

Martínez-Ortíz J, Garcia-Dominguez M. 2013. Guía de campo condrictios del Ecuador: quimeras, tiburones y rayas. Quito: Ministerio de Agricultura, Ganadería, Acuacultura y Pesca. 246 p.

Maté JL. 2005. Análisis de la situación de la pesca en los golfos de Chiriquí y Montijo. Panama: STRI and the Nature Conservancy. http://hdl.handle.net/10088/6679.

Musick JA. 2005. Introduction: management of sharks and their relatives (Elasmobranchii). In: Musick JA, Bonfil R, editors. Management techniques for elasmobranch fisheries. FAO Fish Tech Pap. 474. https://www.fao.org/4/a0212e/a0212e05.htm.

Nance HA, Klimley P, Galván-Magaña F, Martínez-Ortíz J, Marko PB. 2011. Demographic processes underlying subtle patterns of population structure in the scalloped hammerhead shark, *Sphyrna lewini*. PLoS ONE. 6: e21459. DOI: https://doi.org/10.1371/journal.pone.0021459

Navia AF, Giraldo A, Mejía-Falla PA. 2006. Notas sobre la biología y dieta del toyo vieja (*Mustelus lunulatus*) en la zona central de pesca del Pacífico colombiano. Invest Mar. 34 (2): 217-222. DOI: https://doi.org/10.4067/S0717-71782006000200024

Naylor GJP, Caira JN, Jensen K, Rosana KAM, White WT, Last PR. 2012. A DNA sequence-based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. Bull Am Mus Nat Hist. 367: 1-262. DOI: https://doi.org/10.1206/754.1

Pereyra S, García G, Miller P, Oviedo S, Domingo A. 2010. Low genetic diversity and population structure of the narrownose shark (*Mustelus schmitti*). Fish Res. 106: 468-473. DOI: https://doi.org/10.1016/j.fishres.2010.09.022

Pérez-Jiménez JC, Sosa-Nishizaki O. 2010. Determining reproductive parameters for population assessments of two smoothhounds (*Mustelus californicus* and *Mustelus lunulatus*) from the northern Gulf of California, Mexico. Bull Mar Sci. 86 (1): 3-13.

Petrolo E, Boomer J, O'Hare J, Bilgmann K, Stow A. 2021. Stock structure and effective

population size of the commercially exploited gummy shark *Mustelus antarcticus*. Mar Ecol Prog Ser. 678: 109-124.

Portnoy DS, Heist EJ. 2012. Molecular markers: progress and prospects for understanding reproductive ecology in elasmobranchs. J Fish Biol. 80: 2031-2054. DOI: https://doi.org/10.1111/j.1095-8649.2011.03206.x

Ramírez-Amaro S, Picornell A, Arenas M, Castro JA, Massutí E, Ramon MM, Terrasa B. 2018. Contrasting evolutionary patterns in populations of demersal sharks throughout the western Mediterranean. Mar Biol. 165: 3. DOI: https://doi.org/10.1007/s00227-017-3254-2

Robertson DR, Allen GR. 2015. Peces costeros del Pacífico Oriental Tropical: sistema de información en línea. Versión 2.0. Balboa: Smithsonian Tropical Research Institute. https://biogeodb.stri.si.edu/sftep/en/pages.

Rodríguez-Arriatti YN. 2021. Assessment of the artisanal shark fishery in the Pacific coast of Panama highlights a high proportion of immature and threatened species. Pan Am J Aquat Sci. 16 (2): 189-195.

Roff G, Brown CJ, Priest MA, Mumby PJ. 2018. Decline of coastal apex shark populations over the past half century. Commun Biol. 1: 223. DOI: https://doi.org/10.1038/s42003-018-0233-1

Rosa MR, Gadig OBF. 2010. Taxonomic comments and an identification key to species for the smooth-hound sharks genus *Mustelus* Link, 1790 (Chondrichthyes: Triakidae) from the western South Atlantic. Pan Am J Aquat Sci. 5: 401-413.

Sandoval-Castillo J, Beheregaray LB. 2015. Metapopulation structure informs conservation management in a heavily exploited coastal shark (*Carcharhinus obscurus*). Ecol Evol. 5 (22): 5427-5439. DOI: https://doi.org/10.1002/ece3.1792

Smith PJ. 1994. Genetic diversity of marine fisheries resources: possible impacts of fishing. FAO Fish Tech Pap. 344. 50 p.

Soto-López K, Ochoa-Báez RI, Tovar-Ávila J, Galván-Magaña F. 2018. Reproductive biology of the brown smooth-hound shark, *Mustelus henlei* (Chondrichthyes: Triakidae), off northwestern Mexico based on macroscopic and histological analyses. Cienc Mar. 44: 125-139. DOI: https://doi.org/10.7773/cm.v44i2.2805

Stevens JD, Bonfil R, Dulvy NK, Walker PA. 2000. The effects of fishing on sharks, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci. 57 (3): 476-494. DOI: https://doi.org/10.1006/jmsc.2000.0724

Tajima F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics. 123: 585-595.

Veríssimo A, McDowell JR, Graves JE. 2010. Global population structure of the spiny dogfish *Squalus acanthias*, a temperate shark with an antitropical distribution. Mol Ecol. 19: 1651-1662.

Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PDN. 2005. DNA barcoding Australia's fish species. Philos Trans R Soc Lond B Biol Sci. 360: 1847-1857. DOI: https://doi.org/10.1098/rstb.2005.1716

Whitney NM, Robbins WD, Schultz JK, Bowen BW, Holland KN. 2011. Oceanic dispersal in a sedentary reef shark (*Triaenodon obesus*): genetic evidence for extensive connectivity without a pelagic larval stage. J Biogeogr. 39 (6): 1144-1156. DOI: https://doi.org/10.1111/j.1365-2699.2011.02660.x

Worm B, Davis B, Kettemer L, Ward-Paige CA, Chapman D, Heithaus MR, Kessel ST, Gruber SH. 2013. Global catches, exploitation rates, and rebuilding options for sharks. Mar Policy. 40: 194-204. DOI: https://doi.org/10.1016/j.marpol.2012.12.034