CHAPTER FOUR

Conservation genetics of elasmobranchs of the Mexican Pacific Coast, trends and perspectives

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Abstract

One of the most critical threats to biodiversity is the high extinction rate driven by human activities. Reducing extinction rates requires the implementation of conservation programmes based on robust scientific data. Elasmobranchs are important ecological components of the ocean, and several species sustain substantial economic activities. Unfortunately, elasmobranchs are one of the most threatened and understudied animal taxa. The Mexican Pacific Coast (MPC) is a region with high elasmobranch diversity and is the seat of major elasmobranch fisheries. But it is also a developing region with several conservation and management challenges which require national and international attention. Here, we review the conservation genetics

Advances in Marine Biology, Volume 83
ISSN 0065-2881
https://doi.org/10.1016/bs.amb.2019.08.002

literature of elasmobranchs from the MPC. We present a synthesis of the works using samples from the region and emphasize the main gaps and biases in these data. In addition, we discuss the benefits and challenges of generating genomic information to improve the management and conservation of an elasmobranch biodiversity hotspot in a developing country. We found 47 elasmobranch genetic articles that cover <30% of the elasmobranch diversity in the region. These studies mainly used mitochondrial DNA sequences to analyse the genetic structure of commercially important and abundant species of the order Carcharhiniformes. Some of these papers also assessed mating systems, demographic parameters, and taxonomic uncertainties, all of which are important topics for efficient management decisions. In terms of conservation genetics, elasmobranchs from the MPC remain understudied. However, high-throughput sequencing technologies have increased the power and accessibility of genomic tools, even in developing countries such as Mexico. The tools described here provide information relevant for biodiversity conservation. Therefore, we strongly suggest that investment in genomic research will assist implementation of efficient management strategies. In time, this will reduce the extinction risk of the unique elasmobranch biodiversity from the MPC.

1. Background

Biological extinctions are natural phenomena, and five mass extinctions have occurred before human existence. However, the current rate of diversity loss is higher than pre-human rates (Ceballos et al., 2017). This is considered one of the most critical threats to ecosystem health and services and consequently to human well-being (Ceballos et al., 2017; Young et al., 2016). Several species and innumerable populations of animals are already extinct as direct or indirect consequence of human actions, while many more are being driven to extinction (Ceballos et al., 2015; Young et al., 2016). Reducing anthropogenic defaunation rates requires the implementation of conservation and management programmes based on robust scientific data about the taxonomy, ecology and conservation status of the global fauna. However, our understanding of the basic biology of most animal species is inadequate. Moreover, the existing information is both taxonomically (Donaldson et al., 2016) and geographically biased (Beheregaray, 2008; Meijaard et al., 2015). These biases are particularly true for sharks and rays. Despite the fact that several elasmobranchs are large, charismatic and economically important, the taxonomic group is underrepresented in the scientific literature (Domingues et al., 2018; Dulvy et al., 2014; Heupel and Simpfendorfer, 2010; McClenachan et al., 2012; IUCN). This lack of information about elasmobranchs is more evident in developing nations

(Bester-van der Merwe and Gledhill, 2015; Dulvy et al., 2014; Reis et al., 2016; White and Kyne, 2010), where elasmobranch diversity is relatively high (see chapter "Biodiversity and Conservation of sharks in Pacific Mexico" by Saldaña Ruiz et al. this volume; Stein et al., 2018) and is coupled with greater fishery pressures and management challenges (Davidson et al., 2016; Dulvy et al., 2017; Kyne et al., 2012; Worm et al., 2013; Worm and Branch, 2012).

Despite this lack of information, elasmobranchs have been and remain of particular interest to conservation researchers. They have a unique evolutionary history, with long-term high diversity due to several radiations spanning the last ~400 million years (Compagno, 1990; Stein et al., 2018). The group has sophisticated morphological, ecological and behavioural adaptive specializations, which have allowed colonization of several freshwater and almost all marine habitats (Compagno, 1990). As predators, elasmobranchs have important roles as connectors throughout food webs, across habitats and ecosystems (see chapter "Shark ecology, the role of the apex predator and current conservation status" by Galván-Magaña et al. this volume; Wetherbee and Cortés, 2004), where they export and import energy and nutrients between different level of the trophic webs, or between different ecosystems. They can also be key in shaping community and ecosystem structures, and changes in their abundance could have strong ecological effects, especially in the marine realm (Bond et al., 2019; Bornatowski et al., 2018; Grubbs et al., 2016; Stevens et al., 2000). Historically, elasmobranchs have been an important income and food resource for humans (Applegate et al., 1993; Rick et al., 2002), and in the last decades we have witnessed the major expansion of shark and ray fisheries at a global scale (Dent and Clarke, 2015; see chapter "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). More recently, wild elasmobranch sighting tourism has also increased around the word. This activity has the potential to generate increased economic, conservation and social benefits (Mieras et al., 2017). However, this industry is underdeveloped and focuses on few species, leaving fisheries as the main economic importance of elasmobranchs (see chapter "The economy of shark conservation: The role of ecotourism and citizen science" by Cisneros-Montemayor of volume 84; Plata Zepeda et al., 2018). Unfortunately, many elasmobranchs show extreme life histories, including late maturity, long gestation periods and low fecundity, making them intrinsically susceptible to overexploitation (Dulvy et al., 2017). Hence, numerous elasmobranch populations have diminished due to overfishing (see chapter "Biodiversity and Conservation of sharks in Pacific Mexico" by Saldaña Ruiz

et al. this volume; Camhi et al., 2009; Dulvy et al., 2017; Oliver et al., 2015; see chapter "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). In fact, around 31% of elasmobranch species are threatened with the risk of extinction, making them globally one of the most threatened animal taxa (Dulvy et al., 2014; IUCN).

The intrinsically limited accessibility of marine habitats makes problematic the collection of direct biological observations for marine animals, an issue which is emphasized in highly mobile and low-density species such as elasmobranchs. Molecular approaches provide a unique tool to solve these problems. With relatively few small tissue samples collected from live or dead animals, we can extract genomic data and obtain biological information that might be unreachable by other means (Frankham et al., 2010). From individual relationships (parentage or relatedness) and population demography (migration, population size, demographic history, population structure and mating systems), to phylogenetic relationships (taxonomic status) and evolutionary processes (adaptation, introgression, responses to climatic change), the potential information generated by genomic methods is fundamental to the development of efficient conservation plans (Allendorf et al., 2010; Frankham et al., 2010; Primmer, 2009). The use of genetic data to assist conservation and management has been so important in recent decades that conservation genetics has emerged as a new research discipline (Frankham et al., 2010). This discipline integrates evolutionary genetic theory and molecular tool technologies with the main goal of preventing population extirpations and consequent species extinctions, therefore preserving the ecological and evolutionary processes in which these biological entities are involved (Frankham et al., 2010; Hedrick and Miller, 1992). The increasing use of and advances in conservation genetic approaches have been reflected by better conservation management of some elasmobranch species in the last decade (Dudgeon et al., 2012; Larson et al., 2017). Despite the potential benefits of genetic information on shark and ray conservation, genetic data is absent for most elasmobranch species. Furthermore, most conservation efforts currently do not consider existing studies (Domingues et al., 2018; Ovenden et al., 2015). For example, <20% of elasmobranch species in Mexico haven been investigated in terms of genetic/genomics analyses, and the current elasmobranch fisheries management law (NOM-29-PESC-2006; DOF 2018) does not include any reference to these investigations.

To date, some reviews have described the approaches and findings of elasmobranch conservation genetics (Domingues et al., 2018; Dudgeon et al., 2012; Larson et al., 2017), however, none of them have focussed

on Mexican elasmobranch fauna. Mexico is recognized as an elasmobranch biodiversity hotspot, a major source of elasmobranch products and a priority region for the conservation of sharks and rays (Dulvy et al., 2017; Stein et al., 2018). This is particularly true for the Mexican Pacific Coast (MPC), where ~120 species of sharks and rays have been identified (Ehemann et al., 2018) and over 5000 tonnes of elasmobranch catches are reported every year (see chapters "Biodiversity and Conservation of sharks in Pacific Mexico" by Saldaña Ruiz et al. this volume; "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). Here, we provide a long-needed review of elasmobranch genetic conservation from the MPC based on literature available previous to February 2019. This review has three broad objectives: First, we attempt to present a numerical synthesis of the work done with samples from the MPC, including species, markers, geographic area, and main research questions. Second, we emphasize the strong taxonomic, geographic and institutional bias in conservation genetic research, which, although not exclusive to the MPC, is highly evident in the region. Third, we highlight the enormous gap in elasmobranch conservation genetics of the MPC and discuss the benefits and challenges of generating genomic information to assist with the management and conservation of an elasmobranch biodiversity hotspot in a developing country. We expect the review will promote collaborative research efforts intended to reduce bias and fill gaps in elasmobranch conservation genetic research from the region.

2. Studies to date

For this review we compiled a database by searching in Web of Science and Google Scholar using the terms 'genetics', 'genomics', 'elasmobranch', 'shark', 'ray', 'Pacific', and 'Mexico' in the title, abstract and keywords section of all articles published before February 2019. From there, we scanned all results and selected papers where samples from MPC were used. This resulted in a list of 47 scientific papers on which we base our review.

2.1 Markers

The use of molecular methods in elasmobranchs from the MPC has followed the development of the field at the global scale. This chapter is by no means an exhaustive review of conservation genetics methodologies used in elasmobranchs, since other recently published reviews have described them extensively (Dudgeon et al., 2012; Larson et al., 2017).

Rather, we discuss these approaches as they have been specifically applied in the MPC, as well as their context within the broader research.

Allozyme markers dominated genetic studies of sharks around the world during the 1980s and 90s (Dudgeon et al., 2012). However, this was not the case in the MPC. Only a single study, and the first published example of shark genetic research in the MPC, used allozymes to distinguish between species of thresher sharks (Eitner, 1995). The later development of polymerase chain reaction (PCR) technology facilitated the use of specific regions from both the nuclear and the mitochondrial genomes in genetic research. Due to the ease of isolation and its relatively low mutational rate, mitochondrial DNA (mtDNA) markers were extensively used in MPC elasmobranch research. Particularly in phylogeographic and population structure analyses either with sequences (Félix-López et al., 2019; Kitamura et al., 1996) or restriction fragment length polymorphisms (RFLP's; Grijalva-Chon et al., 2002). Meanwhile, the use of nuclear markers has allowed for higher resolution analyses and the exploration of more recent evolutionary and ecological forces. These range from contemporary connectivity between populations to individual relatedness. Research using amplification of nuclear fragments included one sequence-based (Castillo-Páez et al., 2017), two RFLP-based (Pérez Jiménez et al., 2005; Pérez-Jiménez et al., 2013) and several microsatellite-based (Bernard et al., 2018; Byrne and Avise, 2012; Schultz et al., 2008; see Table 1) studies. Additionally, an unpublished work used amplified fragment length polymorphism (AFLPs; Sandoval-Castillo and Beheregaray, 2019). It should be noted that a combination of both nuclear and mitochondrial markers can allow the integration of contemporary and historical perspectives, providing greater power for interpretation of evolutionary and ecological patterns. However, <30% of the listed studies incorporate both types of markers (Table 1).

The most recent advances in sequencing technologies are now allowing massive sequence data production at a very affordable cost, even for non-model species (Luikart et al., 2019). This has shifted genetic analysis in two main ways. First, there has been a shift from the use of only a few markers per study, to the use of thousands of markers distributed genome-wide, to the use of entire genomes (Attard et al., 2018) which have changed radically the possibilities of genomic analyses. Second, there has been a shift from the use of only putatively neutral markers to the exploration of adaptive genetic variation (Sandoval-Castillo et al., 2018). This transition has been slow within the study of elasmobranchs but has been demonstrated in at least three studies from the MPC, including the use of the whole mitochondrial

Table 1 Genetic studies in elasmobranchs from the Mexican Pacific Coast.

Family	Species	Genetic markers	Locality within the Mexican Pacific Coast	Geographic extension	mtDNA diversity	nDNA diversity	Citation
Alopidea	*Alopias pelagicus*	mtDNA(COI)	Mexican TNP	Pacific Ocean	h = 0.59 π = 0.10		Cardeñosa et al. (2014)
	Alopias spp.	13 Allozymes	Mexican TNP	Northeast Pacific			Eitner (1995)
	Alopias spp.	mtDNA(CR)	Mexican TNP	Global			Trejo (2005)
Carcharhinidae	*Carcharhinus brachyurus*	mtDNA(CR)	Baja California Peninsula	Global	h = 0.76 π = 1.60		Benavides et al. (2011)
	Carcharhinus falciformis	mtDNA(CR)	Mexican Pacific Coast	Pacific Ocean	h = 0.48 π = 0.09		Galván-Tirado et al. (2013)
	Carcharhinus falciformis	mtDNA(CR)	Mexican Pacific Coast	Global	h = 0.93 π = 0.61		Clarke et al. (2015)
	Carcharhinus galapagensis	SNPs	Revillagigedo Islands	Interoceanic	h = 0.69 π = 3.08	He = 0.21	Pazmiño et al. (2018)
	Carcharhinus galapagensis *Carcharhinus obscurus*	mtDNA(ND2) 900 exons	Gulf of California Revillagigedo Islands	Mexican Pacific Coast	h = 0.89 π = 0.5		Corrigan et al. (2017)
	Carcharhinus leucas	mtDNA(CR/Ctb)	Mexican TEP	Interoceanic			Kitamura et al. (1996)
	Carcharhinus limbatus	mtDNA(CR)	Gulf of California	Global	h = 0.84 π = 0.41		Keeney and Heist (2006)
	Carcharodon carcharias	mtDNA(CR)	Guadalupe Island	Pacific Ocean	h = 0.79 π = 0.31		Jorgensen et al. (2009)
	Negaprion brevirostris	mtDNA(CR)/9 Mst	Mexican TNP	Global	h = 0.78 π = 0.58	Ho = 0.73 He = 0.81	Schultz et al. (2008)
	Prionace glauca	14 Mst	Baja California Peninsula	Pacific Ocean		Ho = 0.62 He = 0.60	King et al. (2015)

Continued

Table 1 Genetic studies in elasmobranchs from the Mexican Pacific Coast.—cont'd

Family	Species	Genetic markers	Locality within the Mexican Pacific Coast	Geographic extension	mtDNA diversity	nDNA diversity	Citation
Gymnuridae	*Gymnura marmorata Gymnura crebripunctata*	mtDNA (Ctb)	Mexican TNP	Mexican TNP			Smith et al. (2009)
Hexanchidae	*Hexanchus griseus*	mtDNA(CR/Ctb/16S)	Mexican TNP	Global	$h = 0.83$ $\pi = 0.10$		Vella and Vella (2017)
Lamnidae	*Carcharodon carcharias*	mtDNA(CR)	Guadalupe Island	Global	$h = 1$ $\pi = 0.04$		Gubili et al. (2012)
	Carcharodon carcharias	MtDAN(CR)	Mexican TNP	Interoceanic	$h = 0.77$ $\pi = 0.18$		Oñate-González et al. (2015)
	Carcharodon carcharias	mtDNA(Genome)	Baja California Peninsula	Baja California Peninsula	$h = 0.73$ $\pi = 0.13$		Díaz-Jaimes et al. (2016)
	Carcharodon carcharias	10 Mst	Guadalupe Island	Pacific Ocean		$He = 0.58$	Bernard et al. (2018)
Megachasmidae	*Megachasma pelagios*	mtDNA(Cox1)/1 Mst	Baja California Peninsula	Pacific Ocean	$h = 0.33$ $\pi = 0.06$		Liu et al. (2018)
Myliobatidae	*Rhinoptera steindachneri*	mtDNA(ND2)	Mexican TNP	Mexican TNP	h-0.54 $\pi = 5.30$		Sandoval-Castillo and Rocha-Olivares (2011)
	Mobulidae	mtDNA(Whole Genome) 1000 exons	Mexican TNP	Global			White et al. (2017)
Pristidae	*Pristis pectinata Pristis pristis*	eDNA	Mexican TEP	Mexican TEP			Bonfil (Personal communication)

Rhincodontidae	*Rhincodon typus*	mtDNA(CR)	Gulf of California	Interoceanic	h = 0.96 π = 0.61		Castro et al. (2007)
	Rhincodon typus	mtDNA(CR)	Gulf of California	Gulf of California	h = 0.90 π = 0.50		Ramírez-Macías et al. (2007)
	Rhincodon typus	8 Mst	Gulf of California	Global		Ho = 0.66 He = 0.69	Schmidt et al. (2009)
	Rhincodon typus	mtDNA(CR)/14 Mst	Gulf of California	Global	h = 0.92 π = 1.2	Ho = 0.64 He = 0.60	Vignaud et al. (2014)
Rhinobatidae	*Pseudobatus productus*	RFLP	Mexican TNP	Mexican TNP	h = 0.77 π = 1.19		Sandoval-Castillo et al. (2004)
	Zapteryx exasperata	mtDNA(ND2/CR/CAT)	Mexican TNP	Mexican TNP	h = 0.76, 0.39,0.84 π = 0.13, 0.07, 0.11		Castillo-Páez et al. (2013)
	Zapteryx exasperata *Zapteryx xyster*	mtDNA(ND2, CR, CR) nDNA (RAG1)	Mexican Pacific Coast	Mexican Pacific Coast			Castillo-Páez et al. (2017)
	Pseudobatus productus	mtDNA(CR/ND2) 500 AFLP	Mexican TNP	Mexican TNP			Sandoval-Castillo and Beheregaray (2019)
Sphyrnidae	*Sphyrna lewini*	mtDNA(CR)	Mexican TNP	Global	h = −0.51 π = 0.09		Duncan et al. (2006)
	Sphyrna lewini	mtDNA(CR)/15 Mst	Mexican TNP	Northeast Pacific	h = 0.53 π = 0.11	Ho = 0.77 He = 0.79	Nance et al. (2011)
	Sphyrna lewini	mtDNA(CR)/5 Mst	Mexican Pacific Coast	Mexican Pacific Coast	h = 0.49 π = 1.10		Castillo-Olguín et al. (2012)
	Sphyrna lewini	6 Mst	Baja California Peninsula	Global		Ho = 0.70 He = 0.75	Daly-Engel et al. (2012)
	Sphyrna zygaena	mtDNA (CR)	Mexican TNP	Mexican TNP			Félix-López et al. (2019)

Continued

Table 1 Genetic studies in elasmobranchs from the Mexican Pacific Coast.—cont'd

Family	Species	Genetic markers	Locality within the Mexican Pacific Coast	Geographic extension	mtDNA diversity	nDNA diversity	Citation
Squatinidae	*Squatina californica*	RFLP	Gulf of California	Gulf of California	h = 0.14 π = 0.08		Grijalva-Chon et al. (2002)
	Squatina spp.	mtDNA(COI/16S)	Mexican TNP	Global			Stelbrink et al. (2010)
	Squatina californica	mtDNA(CR)	Mexican TNP	Mexican TNP	h = 0.97 π = 1.3		Ramírez-Amaro et al. (2017)
Triakidae	*Mustelus albipinnis*	RFLP/ITS1	Mexican TNP	Mexican TNP			Pérez Jiménez et al. (2005)
	Mustelus californicus	4 Mst	Gulf of California	Gulf of California			Tarula-Marin and Saavedra-Sotelo (2019)
	Mustelus henlei	4 Mst	Baja California Peninsula	Baja California Peninsula			Byrne and Avise (2012)
	Mustelus henlei	4 Mst	Mexican Pacific Coast	Northeast Pacific			Chabot and Haggin (2014)
	Mustelus henlei	mtDNA(CR)/6 Mst	Mexican TNP	Northeast Pacific	h = 0.77 π = 0.40	Ho = 0.45 He = 0.56	Chabot et al. (2015)
	Mustelus henlei	mtDNA(CR)/6 Mst	Mexican TNP	Mexican TNP	h = 0.84 π = 0.33	Ho = 0.71 He = 0.68	Sandoval-Castillo and Beheregaray (2015)
	Mustelus spp	RFLP/ITS2	Mexican TNP	Mexican TNP			Pérez-Jiménez et al. (2013)
	Ttriakis semifasciata	mtDNA (CR)/5 Mst	Baja California Peninsula	Northeast Pacific		Ho = 0.80 He = 0.81	Barker et al. (2015)
Urolophidae	*Urobatis halleri*	7Mst	Mexican TNP	Northeast Pacific		He = 0.88	Plank et al. (2010)

AFLP = amplified fragment length polymorphisms; CO1 = cytochrome oxidase 1; CR = control region; Ctb = cytochrome *b*; eDNA = environmental DNA; ITS1 = Internal transcribed spacer 1; Mst = microsatellites; mtDNA = mitochondrial DNA; NCR = non-coding region; nDNA = nuclear DNA; ND2 = NADH-dehydrogenase 2; RAG1 = recombination activating gene 1; RFLP = restriction fragment length polymorphisms; SNP = single nucleotide polymorphisms; WG = whole genome; 16S = 16S ribosomal RNA; TNP = Temperate Northern Pacific; TEP = Tropical Eastern Pacific; h = haplotype diversity; π = nucleotide diversity; Ho = observed heterozygosity; He = expected heterozygosity.

genome (Corrigan et al., 2017), hundreds of exons (White et al., 2017) and thousands of single nucleotide polymorphisms (SNPs) (Pazmiño et al., 2018). Not only do these changes improve resolution for delimitations of taxonomic units, but they also allow the development of management plans that consider adaptive potential under scenarios of future climatic change.

2.2 Applications

As elasmobranch conservation genetics is a relatively young area of research, we briefly review how molecular methods have been applied to studies of sharks and rays from the MPC. We discuss applications ranging from the broad taxonomic to the intraspecific level, and their relevance for elasmobranch conservation.

2.2.1 Taxonomic delimitation and species identification

Accurate species identification is fundamental for the implementation of efficient management and conservation plans. Often, morphology is the easiest approach for species identification. However, there are many circumstances where genetic techniques are more efficient, including the identification of morphologically cryptic species, as well as morphologically different life stages, body parts or hybrids.

Morphologically similar or cryptic elasmobranch lineages have been identified in the MPC using genetic approaches. The single study in this region to use allozymes suggested the existence of a cryptic lineage (lineages that are morphologically impossible or extremely difficult to delimit) of the thresher shark Alopias (Eitner, 1995). While thresher shark samples collected from the Pacific Coast of the Baja California Peninsula were morphologically similar to *A. superciliosus*, they were found to be genetically more similar to *A. vulpinus*. Similarly, cryptic allopatric lineages separated by the Baja California Peninsula were described first in the shovelnose guitarfish *Pseudobatus productus* (Sandoval-Castillo et al., 2004) and then in the Pacific cownose ray *Rhinoptera steindachneri* (Sandoval-Castillo and Rocha-Olivares, 2011). In both cases, high genetic distance ($F_{ST} > 0.5$) between two mitochondrial lineages suggested the existence of cryptic species. Other cryptic lineages have been found in samples of the banded guitarfish from the North and South MPC (Castillo-Páez et al., 2017). In this group, the morphological plasticity of the northern lineages partially overlaps with that of the southern lineages and suggests that morphologically diagnostic characteristics of already described lineages are uninformative.

Later works suggest the existence of disparate evolutionary units (populations that are historically isolated and likely to have distinct evolutionary potential) in the pelagic thresher shark *A. pelagicus* from the North Pacific (Cardeñosa et al., 2014), in the great white shark *Carcharodon carcharias* from the Pacific Ocean (Oñate-González et al., 2015) and in the shovelnose guitarfish from the Gulf of California (Sandoval-Castillo and Beheregaray, 2019). In these examples, additional phenotypic and genetic studies are needed to determine the taxonomic status of the cryptic lineages. However, all examples clearly show cryptic evolutionary significant units that would have likely remained unnoticed without the use of genetic approaches. To date, the only compelling genetic evidence that resulted in the description of a new species in the MPC is the work by Pérez Jiménez et al. (2005) and Pérez-Jiménez et al. (2013) They combined RFLPs of nuclear genes with morphological and reproductive data to describe a new species of smooth-hound shark, *Mustelus albipinnis*. While such outcomes have been so far limited, all studies revealing cryptic lineages are important for identifying underestimated biodiversity, and for attributing the correct life history, ecological and demographic traits for improved management of either cryptic species or populations.

Delineation of taxonomic groups is impractical if they cannot be empirically identified. Globally, there are several examples of the use of genetic barcodes on shark body parts and processed fisheries products to identify individuals to the level of species, population or geographic region of origin (Hanner et al., 2016; Rodrigues-Filho et al., 2012; Ward et al., 2008). This approach has proved to be an excellent tool in the management and conservation of elasmobranchs, in two main ways. First, in the international trade of elasmobranch products, visual identification of species is practically impossible. Whole bodies of organisms are not typically available, and, when they are, the necessary taxonomic skills of border protection authorities may be lacking. The use of genetic barcodes has allowed the otherwise impossible identification of international trades of elasmobranch species controlled under the Convention of International Trade in Endangered Species. These include species found in the MPC such as hammerheads sharks *Sphyrna* spp. (Abercrombie et al., 2005), the basking shark *Cetorhinus maximus* (Magnussen et al., 2007) and manta rays *Mobula* spp. (Steinke et al., 2017).

From a more local perspective, correct species identification of catch and by-catch is essential for defining the species composition of fisheries and the delineation and assessment of fishery stocks. However, one of the biggest problems in the management and monitoring of elasmobranch fisheries is

the lack of species-specific data on catch and landings (Dulvy et al., 2014; see chapter "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). This problem is highlighted in developing countries like Mexico, where fisheries and management officers, who directly implement the management policies, have limited legal, economic and educational resources necessary to enforce the identification of target or by-catch species on board. For example, in several parts of the MPC, most species of the genus *Carcharhinus* are reported as one species (Sandoval-Castillo personal communication). Worse, juveniles of this genus are reported as 'cazon' together with species from a different family with very different life history and demographic characteristics (Triakidae) and thus with different conservation management priorities. Affordable and efficient genetic assays for elasmobranch species identification have been developed using species-specific primers on a multiplex Polymerase Chain Reaction (PCR), some of which can differentiate and assign samples to up to 21 species (Caballero et al., 2012; Hanner et al., 2016; Rodrigues-Filho et al., 2012). These are rapid, low-cost techniques that require minimum technology, and as such they are suitable for use in developing countries where both economic and technological resources are limited. Unfortunately, none of these techniques have been applied in the MPC, but recent efforts to implement them have been conducted in the Baja California Peninsula (Flores-Ramirez personal communication, 2019). Their routine application in the monitoring of elasmobranch fisheries would provide baseline information necessary for improved management and conservation decisions in the region.

2.2.2 Geographic patterns of genetic structure

Exploring the spatial patterns of genetic differentiation within lineages is important for identifying appropriate management units within a geographic jurisdiction (Ovenden et al., 2015). It is also imperative to identify and understand the historical and contemporary processes which create and maintain global biodiversity (Beheregaray, 2008; Ovenden et al., 2015; Rodríguez-Correa et al., 2017). This is vital for effective management of exploited species. Due to the relatively high mobility of most species, it may be anticipated that elasmobranchs would show low genetic differentiation within species' geographic distributions. However, several studies have shown that elasmobranchs vary widely in levels of genetic subdivision, depending on taxonomic group and spatial scale (Dudgeon et al., 2012; Larson et al., 2017). These range from low genetic differentiation between

ocean basins in large pelagic species (e.g. Bernard et al., 2018; Jorgensen et al., 2009; King et al., 2015), to strong genetic subdivision at narrow regional scales in small coastal species (e.g. Castillo-Páez et al., 2017; Lewallen et al., 2007; Sandoval-Castillo and Beheregaray, 2015; Sandoval-Castillo et al., 2004). Another general pattern in population studies of elasmobranchs is that nuclear markers tend to show greater genetic connectivity, while mitochondrial markers tend to show stronger genetic differentiation due in part to differential evolutionary mutation rates, inheritance and selection for variability. Since mtDNA is matrilineally inherited while nuclear DNA (nDNA) is both maternally and paternally inherited, the frequently greater genetic divergences in mtDNA is suggestive of a general sex-biased dispersal in elasmobranches. This has been associated with stronger female philopatry and a higher male migratory potential (Dudgeon et al., 2012; Feldheim et al., 2014; Portnoy and Heist, 2012). However, these patterns are not inexorable; even codistributed and closely related species can have very different dispersal patterns (Corrigan et al., 2015a; Phillips et al., 2017).

At present, population structure studies represent the vast majority of the genetic literature from the MPC (see Table 1). Many of these works are at global, interoceanic or oceanic scales, where a few samples from one or two localities on the MPC are included, of relatively large pelagic species. But there are also several papers of a regional scale (Northeast Pacific; NEP), national scale (MPC) or subregional scale (Mexican Northern Temperate Pacific; MNTP; Mexican Tropical Easter Pacific; MTEP), focussed on the genetic populations of mainly coastal epibenthic species and some coastal pelagic species.

2.2.2.1 Global and interoceanic:

At the largest geographic scale, sharks from the Carcharhinidae family dominate research in the MPC, perhaps because many of these species are commercially important and relatively abundant worldwide. Few papers show interoceanic or even global connectivity when using nuclear markers. For example, using eight microsatellites, Schmidt et al. (2009) reported a single population of the whale shark *Rhincodon typus* at global scale. However, when using the mtDNA control region, Vignaud et al. (2014) found a significant differentiation between the Atlantic and Indo-Pacific populations. Similarly, the scalloped hammerhead *Sphyrna lewini* shows mtDNA genetic structure, while nuclear markers show connectivity across the Indian and Pacific Oceans (Daly-Engel et al., 2012; Duncan et al., 2006). These results highlight the importance of incorporating both nuclear and mitochondrial

information, to disentangle not just sex-biased, but also demographic and time scale dependent ecological processes which are relevant to the genetic structure of elasmobranchs.

2.2.2.2 The Pacific Ocean:

Three other species show extensive connectivity within the Pacific Ocean, even when using mtDNA; the silky shark *Carcharhinus falciformis* (Clarke et al., 2015; Galván-Tirado et al., 2013), blue shark *Prionace glauca* (King et al., 2015) and megamouth shark *Megachasma pelagios* (Liu et al., 2018). Moreover, the blue shark and the megamouth shark show no apparent division between Atlantic and Pacific Oceans with either mitochondrial or nuclear data (Liu et al., 2018; Veríssimo et al., 2017). However, a lack of genetic structure can be found in two very different demographic scenarios: one with relatively small populations with very high demographic connectivity, and the other with very large but demographically independent populations (Gagnaire et al., 2015). The blue shark is perhaps the most abundant pelagic shark (Compagno et al., 2005), and modelling data have suggested that the lack of genetic differentiation in this species is due to large population size rather than high demographic connectivity (Bailleul et al., 2018). Conversely, the megamouth shark is rarely observed (Compagno et al., 2005), and the low genetic diversity of the species is suggestive of a small population size (Liu et al., 2018). The observed lack of genetic differentiation across ocean basis is therefore most likely due to high connectivity in the megamouth shark. Distinguishing between these two possible scenarios is important for determining patterns of evolutionary resilience due to local adaptation (Allendorf et al., 2010) that should be considered in any long-term management plan.

Most of the population studies show genetic breaks at oceanic level, especially between the Western and Eastern Pacific. The open Pacific Ocean appears to be an effective biogeographic barrier, even for relatively large and highly mobile species such as the great white shark *Carcharodon carcharias* (Bernard et al., 2018; Jorgensen et al., 2009; Oñate-González et al., 2015), the Galapagos shark *Carcharhinus galapagensis* (Pazmiño et al., 2018), and the pelagic thresher shark *Alopias pelagicus* (Cardeñosa et al., 2014). These species show moderate but significant genetic differentiation between Mexico and the Southwest Pacific, a pattern consistent among studies using mtDNA (Cardeñosa et al., 2014; Oñate-González et al., 2015; Vella and Vella, 2017), microsatellites (Bernard et al., 2018; Cardeñosa et al., 2014) and SNPs (Pazmiño et al., 2018). Ambient temperature directly affects the physiological

processes of any organism, including elasmobranchs (Gervais et al., 2018; Pouca et al., 2019). At the same time, the thermal environment influences the biological interactions experienced by these organisms, from parasitism (Dallarés et al., 2017) to competition and predation (Yates et al., 2015). Indeed, temperature gradients have been considered important biogeographic barriers, limiting not just the distribution of species (Aguilar et al., 2019; Goodman et al., 2019), but also the gene flow between populations (Sandoval-Castillo et al., 2018). Warm equatorial waters are also considered an important biogeographic barrier for several marine species, including some sharks (Chabot and Allen, 2009). Genetic differentiation between the MPC and South American Pacific coast has so far been suggested only in the copper shark *Carcharhinus brachyurus* (Benavides et al., 2011). However, there is not more comparative analysis with samples from both regions, highlighting the need for more collaborative work between North and South American researchers.

2.2.2.3 Mexican Pacific region:

When reviewing the works at a more regional scale, most species studied at this geographic level are benthic or epibenthic species. The most frequent pattern is the 'allopatric' isolation between the Gulf of California (GC) and the Pacific Coast of the Baja California Peninsula (PBC), which have been reported in the shovelnose guitarfish *Pseudobatos productus* (Sandoval-Castillo et al., 2004); the California butterfly ray *Gymnura marmorata* (Smith et al., 2009); the cownose ray *Rhinoptera steindachneri* (Sandoval-Castillo and Rocha-Olivares, 2011); the banded guitarfish *Zapterix exasperate* (Castillo-Páez et al., 2013); and the California angel shark *Squatina californica* (Ramírez-Amaro et al., 2017). The congruent pattern among these species highlight the importance of the Baja California Peninsula as a biogeographic barrier and the need to consider different evolutionary units for the management of these species.

Two species of sharks form the family Triakidae show genetic separation between North Santa Barbara (California) and the PBC and the GC. These are the leopard shark *Triakis semifasciata* (Barker et al., 2015) and the brown smooth-hound shark *Mustelus henlei* (Chabot et al., 2015). Barker et al. (2015) also report a small differentiation between Mexico and Southern California, but the number of samples used was very small, which can bias the level of genetic differentiation estimated. These sharks have relatively higher mobility than benthic rays from the family Urotrygonidae, however the round stingray *Urobatis halleri* shows genetic homogeneity from the GC

to the Southern California coast (Plank et al., 2010). More interestingly, both the round stingray and the brown smooth-hound shark have high connectivity over 2500 km, but also both species show genetic differentiation between Santa Catalina Island and the California Coast (~40 km distance). Both studies suggested that currents and bathymetry play fundamental roles in this separation, stressing the importance of oceanographic conditions to the population structure of elasmobranchs. Unfortunately, most of the works at national scale are based on samples from the PBC and the GC, while the MTEP is significantly less explored. Few comparative papers with coastal species show an interesting separation between tropical and temperate lineages. Separation occurs at a population level in the scalloped hammerhead shark *S. lewini* (Castillo-Olguín et al., 2012) and at a phylogenetic level in the bedded guitarfish *Zapteryx* spp. (Castillo-Páez et al., 2017). This supports the imperative of developing more extensive research around the MTEP.

2.2.2.4 Finer scale:

Finally, there are a few works at a finer geographic scale (<100 km among several sampling sites), with two patterns arising from these studies. First, the species studies show clear isolation by geographic distance, suggesting that the mobility of costal elasmobranchs is more limited than previously believed. For example, Sandoval-Castillo and Beheregaray (2015) reported high connectivity in the smooth-hound shark from the Northern PBC to the Upper GC (>2000 km). However, they also found low genetic differentiation correlated with geographic distance, and that this correlation is stronger in females than in males. The authors suggest the management of the species should consider a metapopulation with subpopulations and migratory corridors that should be preserved in order to reduce the extirpation or even extinction of the heavily exploited species. Isolation by distance was also found in a more pelagic species, the smooth hammerhead *Sphyrna zygaena*, with adult females and juveniles showing a stronger spatial autocorrelation (Félix-López et al., 2019). These highlight the need for studies that use high-resolution geographic sampling to understand migration patterns relevant for the management of coastal species.

Second, high geographic resolution combined with oceanographic data could allow testing of the adaptive effects of oceanographic factors on the genetic structure of elasmobranchs. More recently, Sandoval-Castillo and Beheregaray (2019) have shown isolation by ecological distance (genetic and environmental distances are directly correlated, independent of

geographic distance, Shafer and Wolf, 2013) in one species within the GC. In this region, the shovelnose guitarfish *Pseudobatos productus* has lower genetic connectivity, and, differences in temperature and bathymetry are correlated with the genetic differentiation between three subpopulations. The geographic distribution of each of these three subpopulations overlap with three biogeographic regions previously defined based on the complex oceanography of the GC (Ortega et al., 2010). The authors suggest that these populations are independent management units with demographic differences potentially associated with local adaptations. This should be considered in the management plan for the species, and perhaps, the same pattern could be present in other commercially important species in the region.

2.2.3 Demography

The significant population declines and increasing extinction risks over several species of sharks and rays around the world have become a major concern for conservation biologists in the last decade (Dulvy et al., 2014, 2017; Worm et al., 2013). The genetic diversity loss associated with population declines could lead to excessive genetic drift and inbreeding depression. Potentially severe consequences include compromised evolutionary persistence and resilience of species to environmental changes (Frankham, 2015). Genetic studies aiming to elucidate demographic parameters such as connectivity, population size, and genetic diversity are essential for identifying the risks associated with population size declines (Allendorf et al., 2013), and consequently for the management and conservation of elasmobranchs.

Several works in the MPC have used genetic diversity as a rough estimate of population size, however very few have used coalescent or linkage disequilibrium analyses which are better able to infer genetic signals of demographic events. Regardless, a common pattern in the MPC is the effect of the last glacial maximum. For example, Ramírez-Macías et al. (2007) suggested that whale sharks in the GC have passed through a recent population expansion, based only on high haplotype diversity but low nucleotide diversity of sequences in the mitochondrial control region. Coalescent analyses support the idea of a moderately large global population (Castro et al., 2007; Schmidt et al., 2009) with a recent demographic expansion (Vignaud et al., 2014). Sandoval-Castillo and Beheregaray (2015) report a geographic expansion from the GC to the PBC, possibly associated with the function of the GC as refuge during the last glacial maximum. Using a couple of coalescent

approaches King et al. (2015) report historical and contemporary small effective population size on the blue shark from the Pacific Ocean. This is an unexpected result for a pelagic shark with high abundance, vagility, and fecundity that comprises a single breeding unit across a wide geographic range in the North Pacific Ocean. However, the authors attribute the low effective population size (Ne), to a population bottleneck during the last glacial maximum and posterior geographic expansion during the actual interglacial period. On the other hand, the scalloped hammerhead in the Eastern Pacific shows evidence of a population bottleneck related with geographic expansion and population subdivisions during the Holocene (Castillo-Olguín et al., 2012; Nance et al., 2011). Meanwhile, the pelagic silky shark has a historically stable population in the NEP, but shows local demographic expansions possibly associated with the onset of warmer currents following the last glacial maximum (Galván-Tirado et al., 2013). Finally, the smooth hammerhead in the North Mexican Pacific has experienced a recent population expansion from a bottleneck which occurred during the Late Pleistocene (Félix-López et al., 2019).

Most of these studies have estimated historical Ne based on coalescent theory and mtDNA sequence. Although the demographic history of a population can determine the relative consequences of modern population declines (van der Valk et al., 2019), contemporary Ne reflects current genetic health and can approximate recent numbers of breeding individuals (Frankham et al., 2010). Contemporary Ne is more relevant for the conservation and management of existing populations. Using genetic data to estimate contemporary abundance relies on the genetic signal associated with inbreeding to calculate Ne, and the equivalence between Ne and abundance (e.g. census size or Nc). This equivalence depends largely on several life history characteristics, which may be difficult to obtain (Ovenden et al., 2016). While no consistent relationships exist across taxa, larger species with long-lived individuals, low fecundity, late maturity and high survivorship of adults more often than not show Ne/Nc ratios approaching one (Dudgeon and Ovenden, 2015; Portnoy et al., 2008) facilitating the demographic interpretation of genetically estimated Ne. These are life history characteristics of most elasmobranchs, making Ne a promising method for assessing trends in population sizes important for the management of sharks and rays (Dudgeon and Ovenden, 2015). As such, an increase in studies estimating and monitoring contemporary Ne in elasmobranch populations should be helpful for improving management decisions in the MPC.

2.2.4 Reproductive strategies

Different reproductive strategies result in different recruitment efficiencies. In the long-term, this can influence population stability and evolutionary resilience to population declines (Lowerre-Barbieri et al., 2017). Thus, knowledge of reproductive strategies is important for implementing management plans, including recovery plans for elasmobranch populations depleted by human activity. Unfortunately, direct observation of the reproductive biology of elasmobranchs is difficult due to their biological characteristics (Compagno et al., 2005; Portnoy and Heist, 2012). Currently, a wide variety of molecular approaches can be used to provide information about the reproductive biology of elasmobranchs, with several examples around the world (Portnoy and Heist, 2012), including a few within the NEP (Larson et al., 2017).

Two main reproductive strategies have been explored in elasmobranchs using genetic data, with the first being female philopatry to mating or nursery areas. The occurrence of this behaviour has been shaped by selective pressures associated with juvenile survival and generational recruitment, and therefore has a significant impact on species resilience (Portnoy and Heist, 2012). The study of genetic female philopatry in elasmobranchs originally emerged because it was the easiest explanation for incongruences in genetic structure between nuclear and mitochondrial markers (Dudgeon et al., 2012). However, the idea was later supported by more complex analyses including comparative analyses between females and males (Sandoval-Castillo and Beheregaray, 2015), and relatedness analyses combined with parental analyses (Feldheim et al., 2014).

In the MPC, several papers studying the population structure of different elasmobranch species have suggested some level of female philopatry, even in species with remarkably different dispersal potentials. Most of these findings have been based solely on the presence of mitochondrial genetic structure (e.g. Castillo-Olguín et al., 2012; Félix-López et al., 2019; Ramírez-Amaro et al., 2017; Sandoval-Castillo and Rocha-Olivares, 2011; Sandoval-Castillo et al., 2004) or the discrepancy between signals of mitochondrial and nuclear differentiation (Castillo-Páez et al., 2017; Daly-Engel et al., 2012). However, these results could also be explained by the intrinsic evolutionary characteristics of mtDNA (Avise et al., 1987). As such, more ad hoc statistical analyses and sampling designs are required to estimate the effect of sex-biased dispersal on the observed population structure (Dudgeon et al., 2012; Portnoy and Heist, 2012). One exception in the MPC is the work by Sandoval-Castillo and Beheregaray (2015), who integrated high geographic

resolution sampling and individual-level genetic analysis to determine effective dispersal on the smooth hound shark. The authors used the relatively lower effective dispersal of females compared with males to infer female philopatry. Although these approaches still can confuse between philopatry (actively selecting a site) and limited home range (limited mobility), the authors combine genetic seascape analyses and the presence of mating and nursery aggregation in the GC to support their hypothesis. Perhaps the best proof of philopatry in any shark from the MPC is the work by Jorgensen et al. (2009). In this paper, genetic data was combined with satellite tag data to demonstrate that both sexes preferentially return to a small subset of available coastal sites. However, molecular tools can be powerful enough to be used as permanent identification tools in long-term mark and recapture experiments. If sample size is large enough, kinship and parentage analysis can discriminate as to whether female philopatry occurs in a few individuals or in a whole population (Feldheim et al., 2014; Veríssimo et al., 2017), providing more valuable and reliable information relevant to the management of elasmobranchs.

The second main reproductive strategy that has been analysed with molecular data is polygamy, or more specifically polyandry (multiple mating by females). It is important to determine the prevalence of polyandry, because it can change the effective population size and genetic diversity of a population, with significant demographic consequences (Byrne and Avise, 2012; Karl, 2008). However, due to inherent logistical difficulties, polyandry has been directly observed in few species of elasmobranchs (Pratt and Carrier, 2001; Snelson et al., 2009). Molecular techniques have allowed assessment of the frequency of polyandry by calculating the multiple paternity levels in litters. In fact, polyandry detected using genetic approaches has been reported in over 20 species of elasmobranch (Boomer et al., 2013; Corrigan et al., 2015b; Fitzpatrick et al., 2012; Rossouw et al., 2016) including a few from the NEP (Larson et al., 2017). However, the occurrence and prevalence of multiple paternities in elasmobranchs varies between species, populations, individuals and even reproductive seasons. Polyandry in samples from the MPC has been reported just in the brown smooth-hound shark. Analysing 14 litters and their respective mothers collected from the PBC, Byrne and Avise (2012) report one of the highest occurrence of multiple paternity of any shark (93%). However, depending of the year of collection, only a 0–40% incidence of multiple paternity was observed in 18 litters of the same species collected from California (Chabot and Haggin, 2014). Moreover, Tarula-Marin and Saavedra-Sotelo (2019)

determined that genetic monogamy is prevalent in the young grey smoothhound shark, a very closely related species. It was previously suggested that the differences in polyandry frequency depend on factors such as mother's size, individual behaviour, home rage, philopatric tendencies, population size and post copulatory mechanisms (Boomer et al., 2013; Byrne and Avise, 2012; Chabot and Haggin, 2014; Green et al., 2017; Larson et al., 2011; Lyons et al., 2017). But more comparative analyses (between populations, reproductive seasons and species) are necessary to not just understand these differences in frequency, but also understand why polyandry is present in elasmobranchs.

Intuitively, polyandry has multiple benefits; it can increase fertilization success, counteract inbreeding issues, elevate the genetic diversity of the offspring and therefore relative fitness, and it can increase the effective population size (see Byrne and Avise, 2012; Green et al., 2017). However, the few studies comparing genetically polyandrous against monogamous litters of sharks did not find evidence of higher fertilization success (Portnoy et al., 2007), nor an increase in survival rate or genetic diversity of offspring (Dibattista et al., 2008). Moreover, instead of increasing Ne, polyandry can reduce it when the parental contribution per litter is highly skewed and variable (Karl, 2008). This is the case in most empirical data for elasmobranchs (Chabot and Haggin, 2014; Green et al., 2017; Larson et al., 2011; Rossouw et al., 2016). These apparent contradictions have given support to the convenience polyandry theory, which suggests that females increase receptivity to mating when the relative costs of resistance overcome the cost of mating (Boulton et al., 2018). More empirical testing is needed to rule out other possible evolutionary benefits of polyandry. However, understanding the reasons for polyandry and its demographic effects in elasmobranchs is fundamental to implementing appropriate fisheries management plans, and currently there are few efforts towards the evaluation of mating systems in rays and sharks from the MPC (Saavedra-Sotelo personal communication, 2019).

2.3 Taxonomic and geographic bias

We found 47 scientific research articles on elasmobranch genetics using samples from the MPC (Table 1). Below, we describe a few of the most notable patterns regarding the nature of this work. Temporally, a clear exponential growth in genetic research occurs in the last decade, when >69% of the works were produced. This follows the same pattern of increase across

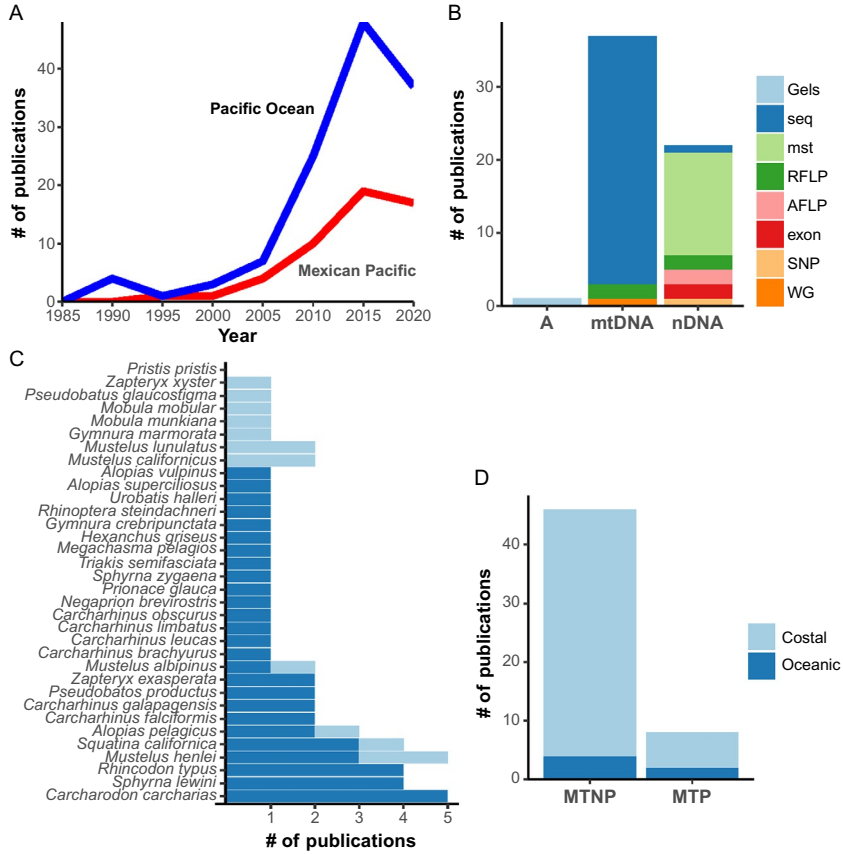

Fig. 1 Genetic studies in elasmobranchs from the Mexican Pacific Coast (A) Number of publications per year: from 1985 to 2019. (B) Nuber of publications per marker and method: A = allozymes; mtDNA = mitochondrial DNA; nDNA = nuclear DNA; seq = sequences; mst = microsatellites; RFLP = restriction fragment length polymorphisms; SNP = single nucleotide polymorphisms; WG = whole genome. (C) Number of publications per species: light blue = phylogenetic studies with no intraspecific information; dark blue- = intraspecific studies. (D) Number of publications per region: MTNP = Mexican Temperate Northern Pacific, MTEP = Mexican Tropical Eastern Pacific.

the entire Pacific Ocean, but at a smaller scale (Fig. 1A). The works are dominated by analysis of mtDNA sequences, followed by microsatellites (Fig. 1B); unfortunately, few papers combine the power of bi-parental and matrilineal markers (26%). The dominance of mtDNA sequences is similar to that observed at a global level for phylogeographic analyses >10 years ago (Beheregaray, 2008). In the MPC, this dominance is still present and reflects the limited availability of economic and technological resources in the region.

More concerning is that half of the genetic research using samples from the MPC includes null or minimal participation of local researchers (Table 1). We strongly believe that investment in the development of new and support of existent local skills (Mexican molecular ecologists and elasmobranch biologists), and international collaborations would catalyse the production of genomic research in the region. In time, this will improve our ability to implement efficient management plans for elasmobranchs at a local, international and perhaps even global scale.

The genetic research in the MPC is also taxonomically biased; in the 47 works reported here, 35 species from 14 families were analysed, representing <30% of the species diversity in the MPC (Ehemann et al., 2018). If we remove the species that were analysed with only a few samples for systematic studies (light grey in Fig. 1C), and from where we cannot obtain intraspecific inferences, this number decreased to 27 species, representing just over 22% of the elasmobranch fauna in the region. The family Carcharhinidae dominates the representation with eight species, followed by sharks from the family Triakidae with seven species (Table 1 Fig. 1C). This is expected, since both families are highly diverse and contain commercially important and abundant species in the MPC, especially from the genera *Carcharhinus* and *Mustelus* (see chapter "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). However, per species, the analyses have a different bias. While most species are the main subject of one study, only 13 species were analysed in two or more studies (Table 1 Fig. 1C). More interestingly, there are three species that were the focus in more than three studies with intraspecific analyses, the white shark *Carcharodon carcharias,* the whale shark *Rhincodon typus* and the scalloped hammerhead shark *Sphyrna lewini* (Fig. 1C). These are arguably three of the most charismatic elasmobranchs in the world. However, no studies exist for the largetooth sawfish *Pristis pristis* or the smalltooth sawfish *Plebejus acmon* (but see Section 3), the most critically endangered species (CITES 2019) in the region (Ehemann et al., 2018). The same is true for the Cortez skate *Beringraja cortezensis*, a species endemic to the GC with a very narrow distribution and uncertain conservation status (Last et al., 2016). These patterns reflect a strong bias for large charismatic and/or commercially important species in the field, as occurs in other types of conservation research (McClenachan et al., 2012). We do not promote a reduction in research for charismatic or economically important species; rather, we draw attention to the fact that conservation genetic research has either completely ignored or only

partially analysed around 90% of the elasmobranch fauna in the region. In fact, although all these genetic studies focus on economically important species, no genetic data exist for the other 30 species caught as target or by-catch in the region (CONAPESCA-INP, 2004; see chapter "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki volume 84). We believe that to move from the current overexploitation and high extinction risk to a long-term sustainable management of MPC elasmobranch fauna, genetic research should have a taxonomically broader focus This will require a considerable investment in basic and applied national research, from both local and international entities (e.g. FAO, CONACYT), in addition to the implementation of national and international collaborations. We especially recommend fomenting the use of new sequencing technologies which facilitate the application of traditional and modern genetic approaches, mainly by dropping the cost per sample per locus, decreasing the number of samples necessary for efficient analysis (e.g. Gaughran et al., 2018), and reducing the logistic difficulties implicated with elasmobranch sampling (see Section 3).

Another notable pattern was a geographic bias. First, there are more studies in coastal areas than oceanic regions (Table 1; Fig. 1D). There were just two oceanic sampling sites; the Revillagigedo Archipelago is 390 km southwest from Baja California Peninsula and is considered a hotspot of elasmobranch diversity (Sandoval-Castillo unpublished data), while Guadalupe Island is 260 km offshore of Baja California and is an important aggregation for white sharks (Jorgensen et al., 2009). This bias was expected due to the considerable logistic difficulties implicated in sampling from oceanic areas. But more concerning is the second geographic bias, the difference between the northern and southern MPC. The MPC includes two marine biogeographic realms, the Temperate Northern Pacific (TNP) and the Tropical Eastern Pacific (TEP). Both realms have relatively high elasmobranch diversity (Carrillo-Briceño et al., 2018; Ehemann et al., 2018), supporting important fisheries and tourism activities (see chapters "The economy of shark conservation: The role of ecotourism and citizen science" by Cisneros-Montemayor of volume 84; "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). However, the number of genetic works using samples from the TEP is much smaller than those using samples from the TNP (Table 1; Fig. 1D). The southwest of Mexico has the lowest social and technological development in the country, which restricts the scientific productivity in

the Mexican TEP (Díaz-Gómez et al., 2018). But also, the geographic closeness of the Mexican TNP with USA has promoted the elasmobranch research in the region and this is reflected by the number of papers by or in collaboration with American institutions (Table 1). The TEP is an important biogeographic region with high diversity of elasmobranchs (Carrillo-Briceño et al., 2018) and it is evident than the different oceanographic conditions between the TNP and the TEP can separate populations of the same species (Castillo-Olguín et al., 2012) or sister species (Castillo-Páez et al., 2017). Thus, expanding elasmobranch research to the Mexican TEP is imperative not just for delimiting variation among stock, but also for understanding the evolutionary and ecological processes that maintain and produce elasmobranch diversity. With genetic knowledge expanding and sequence technology costs decreasing, conservation genetic/genomic research in the MPC should more easily cover more species and localities, and therefore improve the development of efficient management plans.

3. Future Work

In the last decade, high-throughput sequencing technologies (HST) have facilitated genomic research of non-model species. This has made it possible to genotype hundreds of individuals at thousands of loci. It has also allowed the study of variation in gene expression and epigenetic variation without the need for a reference genome. Even whole-genome analysis is now feasible for non-model organisms (Luikart et al., 2019; Primmer, 2009). Large, genome-wide datasets have drastically changed conservation genetics research, reducing its relative cost, expanding the questions it can address, and boosting its power and accuracy (Primmer, 2009). However, these technological advantages have not yet been widely exploited in the MPC, and in fact have not yet been extensively used in elasmobranch research at a global level (but see Corrigan et al., 2017; Pazmiño et al., 2018). Although HST have a lot of potential, we describe below what we believe could be the most relevant applications for conservation biology of sharks and rays in the MPC.

3.1 Forensic genomics

Since DNA barcoding can efficiently discriminate between species and even populations of elasmobranchs (Hanner et al., 2016; Rodrigues-Filho et al., 2012; Ward et al., 2008), the approach can be used to help to trace fishery products (including fins and meat) and identify illegal trade of protected

species or populations. Conventionally, these approaches use one or two loci sequences (normally the mitochondrial COI and the nuclear ITS2 genes) obtained through PCR amplification from individual specimen genomic DNA (Ward et al., 2008). However, this approach has several challenges. For instance, it requires high concentrations of the DNA template (100–500 ng), and PCR can coamplify pseudogenes (imperfect paralogous copies of a gene) or intracellular endosymbiotic genomes (bacterial, fungal or viral), which can produce spurious variations (Smith et al., 2012). Additionally, intra-individual variability can be present (e.g. heteroplasmy; two or more different organelle genomes in the same individual), and the same genotype can sometimes be detected in sister species due to the presence of foreign DNA (introgressive hybridization) or very recent divergence (incomplete lineage sorting) (Parmentier et al., 2013; Ward et al., 2008). Any of these occurrences can lead to ambiguous or false identification when traditional DNA barcode methods are used. High-throughput sequencing can help to overcome some of these limitations, because millions of sequences from thousands of DNA templates can be generated in parallel. This reduces the required quantity of original DNA template (5–20 ng), allowing analysis of degraded or very small tissue samples (e.g. Sigsgaard et al., 2017). It also facilitates the generation of multiple barcodes for several individuals simultaneously, making the process faster and cheaper (Shokralla et al., 2015). But perhaps most importantly, the analysis of larger numbers of loci can help to identify pseudogenes, endosymbiotic genes, gene introgression, and apparent incomplete lineage sorting (Coissac et al., 2016; Shokralla et al., 2015). This will also increase power to discriminate not just species but also populations or even individuals. This can improve traceability of fishery products including the identification of illegal trades or catch, a key requisite for the better management of elasmobranchs stocks.

3.2 Environmental DNA (eDNA)

Most of the research described in this review was done using opportunistic sampling from the by-products of commercial fisheries catches. However, active sampling was used for the two most studied species, the whale shark and the white sharks (Oñate-González et al., 2015; Ramírez-Macías et al., 2007). These protocols involve a spear or a dart with a core modified to take biopsies from free-ranging animals tracked by boat, or sometimes approached by divers. These methods usually require special permits that are not always easy to obtain. For these reasons, active sampling is logistically

difficult, expensive and time consuming. Moreover, this sampling can inflict high levels of stress and physical damage to the sampled animals. Fortunately, organisms leave traces of DNA in their environment via faeces, saliva, urine, blood, and skin cells. Environmental DNA (eDNA) is usually degraded and found in low concentrations, making it extremely difficult to recover any signal with traditional genetic methods (Rees et al., 2014). The massive amount of sequence data obtained from HST has made it possible to recover DNA data directly from environmental samples (Shokralla et al., 2012). The use of eDNA removes the need to capture, injure or even observe the target species, making genetic surveys easier, cheaper and faster. In the MPC, this approach can be used in elusive, rare or critically endangered species for simple presence/absence surveys, such as that currently being done in largetooth and smalltooth sawfish (*Pristis pristis* and *P. pectinata*) from the Mexican TEP (Bonfil et al. unpublished data). Recent papers have also shown that eDNA has the potential for population level analyses, such as the estimation of abundance and genetic diversity of shark aggregations (Lafferty et al., 2018; Sigsgaard et al., 2016). This information will help to identify possible aggregation sites, seasonal movements, and perhaps evaluate fisheries interactions; all of which are essential information for better protection, monitoring, and recovery plans of elasmobranch species in the MPC.

3.3 Seascape genomics

Seascape genomics is a relatively new research field, which integrates geographic environmental and genomic variation in marine systems to understand the effects of environmental factors on microevolutionary process such as migration, genetic drift and selection (Balkenhol et al., 2019; Riginos et al., 2016). High-throughput sequencing technologies have increased the power of seascape genomics to resolve genetic structure at very fine geographic scales and taxonomic levels. Analysing thousands of markers provides greater resolution of demographic parameters (e.g. migration rates), and facilitates the identification of candidate adaptive loci (Grummer et al., 2019; Riginos et al., 2016). This information can enable identification of cryptic population boundaries associated with breaks in genetic flow due to adaptive divergences, which could be key for the future adaptability of fisheries resources (Grummer et al., 2019; Riginos et al., 2016). Seascape genetic analysis has so far been used to describe cryptic lineages of elasmobranchs from the GC (Sandoval-Castillo and Beheregaray 2019). In the same study, the authors also identify environmental factors driving major adaptive

divergences, as well as the oceanographic barriers limiting connectivity between lineages. This information can be integrated with future climate models to predict the effect of environmental change on the evolutionary potential of the species, as has been done in other taxa (e.g. Razgour et al., 2019). We suggest that the power of seascape genomics can be further applied to not just to elucidate species distributions and geographic population structure in the MPC, but also to clarify the relative role of oceanographic factors influencing microevolutionary processes in the region. As such, it will be useful for determining elasmobranchs' evolutionary potential to respond to fisheries pressure and climatic change.

3.4 Demographic analysis

The use of HST to produce genome-wide or even whole-genome data will revolutionize the application of genetics to estimate demographic parameters, including effective population size (historical and contemporary) and inbreeding. Inbreeding increases homozygosity, which can cause inbreeding depression (reduced fitness of inbred individuals; Frankham, 2015). Genomic data can directly measure patterns of homozygosity across the genome, providing more precise estimates of individual inbreeding. Moreover, the use of thousands of genetic variations mapped to relative positions in the genome has allowed implementation of new approaches. For example, with whole-genome sequences we can detect runs of homozygosity (ROH), which are long tracts of homozygosity in an individual produced by identical haplotypes inherited from each parent. ROH can be used to estimate inbreeding with very high precision, and also identify inbreeding depression by testing for associations between the presence of ROH and individual fitness traits (Luikart et al., 2019). Even when fitness data are not available, evolutionary constraints can serve as an approximation of genotypic fitness (see van der Valk et al., 2019). This can be applied in elasmobranches to not just estimate inbreeding depression, but also to develop genetic rescue programmes for populations with extremely low evolutionary potential.

As previously mentioned, contemporary Ne is a very important parameter for conservation genetics, and its calculation has always been challenging. However, the use of genomic data has improved the accuracy, precision, and efficiency compared to previous genetic approaches for estimates of contemporary Ne (Larson et al., 2014; Nunziata and Weisrock, 2018). In addition, several methods for demographic history reconstruction, such as approximate Bayesian computation (ABC; Cornuet et al., 2008) or

diffusion approximations for demographic inference (∂a∂i; Gutenkunst et al., 2009), show drastically improved statistical power when used with genomic data, even with few individual samples (~5–15). In fact, historical patterns of Ne can be inferred with the whole-genome sequence of a single individual using pairwise sequential Markovian coalescence (PSMC; Li and Durbin, 2011). Genomic data have been used to estimate Ne in two species of sharks from the Pacific Ocean (Pazmiño et al., 2017; Reid-Anderson et al., 2019). However, they have never been used in MPC populations, despite the importance of estimating Ne and its fluctuations for assessing extinction risk. This knowledge will improve conservation management of endangered species and will help to prioritize efforts in a region with very limited resources for conservation.

3.5 Gene expression and epigenetics

High-throughput sequencing technologies can be used to sequence all the messenger RNA within a tissue (RNAseq) in order to analyse the expressed fraction of the genome (transcriptome; Wang et al., 2009). This data can be applied de novo (without any genome reference) to any species to capture functional genomic variation, making it a very useful tool for conservation biology. A population comparative transcriptomic approach can help to identify genes responsive to environmental stresses, and at the same time identify genes and gene pathways that are candidates for local adaptation (Brauer et al., 2017; Sandoval-Castillo et al., 2019). This can improve understanding of genetic activity related to habitat fragmentation and environmental change. As gene expression can vary without any molecular change in the genome (phenotypic plasticity), it can also provide a completely different view of the evolutionary effects of small population sizes (Brauer et al., 2017) and acclimation potential (Healy and Schulte, 2018). There are a few studies that used RNAseq to characterize the transcriptome of shark species (Chana-Munoz et al., 2017; Goshima et al., 2016; Machado et al., 2018; Onimaru et al., 2018; Richards et al., 2013). Although these works are important resources for future research, there is only one study that exploited the potential of comparative transcriptomic analyses in elasmobranchs (Lighten et al., 2016; see below).

Some changes in expression can be transgenerational, and therefore even more relevant for conservation. Heritable variations in ecologically important phenotypic traits can occur in the absence of DNA sequence variation via epigenetic modifications of the genome, including DNA methylations

and histone modifications (Goldberg et al., 2007). These modifications are expected to appear at a much faster rate than genetic mutation, potentially allowing organisms to adapt to different habitats or respond to climatic change, even in populations with depleted genetic variation and apparently low evolutionary potential. For example, Lighten et al. (2016) showed differential expression between two populations of winter skate *Leucoraja ocellata*. The authors demonstrated that these differences have an epigenetic basis (the differences in expression are correlated with differences in methylation in the genome) and suggested that they have allowed the rapid adaptation of one population to warmer waters. Although it is still unclear as to how far epigenetic adaptations could help to ameliorate population decline, epigenetics is likely to be an important research topic in conservation genomics for elasmobranchs.

3.6 Genomic of fisheries

The MPC is a hotspot of elasmobranch biodiversity (Ehemann et al., 2018) but is also one of the most important regions in the world for elasmobranch fisheries (see chapter "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). There are at least 65 species of sharks and rays that are caught, either as target species or by-catch (CONAPESCA-INP, 2004; see chapter "Fisheries interactions and the challenges of both targeted and non-targeted take in shark conservation" by Sosa-Nishizaki of volume 84). However, the genetic data reported here covers just over 50% of these species; moreover, the existing information has not been implemented into any management plan in the region. Considering the global increase in pressure on marine resources, a failure to incorporate genetic information into future management and conservation of elasmobranches from the MPC puts this biodiversity at high risk. Based on the information presented in this review, we suggest focusing genetic efforts in four fundamental areas:

Species identification: Develop forensic genomics protocols that allow identification of species and population of origin of fisheries products (meat and fins). This would reduce inherent uncertainty of landing data and would also help to identify illegal trade of protected species.

Fisheries stock delimitation: Identify the number of genetic stock and management units of elasmobranches in the MPC to estimate appropriate demographic parameters. This will allow the development of species- and even stock-specific sustainable exploitation plans.

Abundance: Calculate modern Ne and migration rates, which are necessary to determine demographic parameters. This will allow us to estimate not just the abundance of a species, but also its harvesting rate and demographic resilience.

Evolutionary response: Develop long-term seascape genomic, comparative expression and genomic diversity studies, which are necessary to understand the evolutionary response of stocks, populations and species to fisheries pressure and climatic change. This information is necessary to estimate evolutionary potential.

These four suggestions will enable the identification of extinction risk, and the implementation of efficient management strategies a regional and global scale.

4. Conclusion

The last decade has borne witness to unprecedented growth in conservation genetic research of MPC elasmobranchs, however the field remains understudied and has enormous potential for further development. The genetic tools described here demonstrate the potential to provide information extremely relevant for conservation, and which is unlikely to be obtained by other methods. This should be enough to justify increased investment in genomic research in the region. With HST costs decreasing, genomic applications are now more accessible (see Glenn, 2011, with updates from Glen, 2016 NGS Field Guide: Overview http://www.molecularecologist.com/2016/03/2016-ngs-field-guide-preview/), even to developing areas such as the MPC. In addition, the analysis of thousands of independent markers also reduces the number of samples required to archive high-precision genetic estimates (Gaughran et al., 2018; Li and Durbin, 2011; Willing et al., 2012), and some methods (e.g. eDNA) even avoid the logistic complications intrinsic to sampling elasmobranches, potentially reducing cost even further (Lafferty et al., 2018; Sigsgaard et al., 2016). The implementation of genomic methods will not just increase our power, precision and accuracy for acquiring conservation-related information: it could also change our perspectives regarding the evolutionary potential of small populations, the use of genetic rescue as a conservation tool and the importance of gene expression plasticity in wild populations. This information will be critical for implementing efficient management plans for elasmobranch populations in the face of climatic change, habitat degradation and overexploitation.

However, conservation genomics can be highly technical, making the understanding and communication of basic concepts challenging. Therefore, developing communication strategies that maximize the appropriate uptake of research outcomes by fishery managers and politicians is a fundamental priority. This will enable the translation of genomic data into applicable conservation and management plans. In summary, we encourage investment in genomic research, and the development of conservation geneticists who are not only able to produce genomic results, but also correctly interpret and translate them in plain terms. This will increase our chances of implementing efficient management and conservation strategies that will reduce the extinction risk of the unique elasmobranch biodiversity in the MPC.

Acknowledgements

We would like to thank Shawn Larson and Chris Chabot for the valuable comments on an early version. We would especially like to thank Luciano Beheregaray, Katie Gates and Nancy Saavedra-Sotelo for their ideas and contributions which improved the manuscript.

References

Abercrombie, D.L., Clarke, S.C., Shivji, M.S., 2005. Global-scale genetic identification of hammerhead sharks: application to assessment of the international fin trade and law enforcement. Conserv. Genet. 6, 775–788.

Aguilar, L.A., Matthews, S.A., Ayre, D.J., Minchinton, T.E., 2019. Modelling the differences between El Niño and La Niña years and planktonic larval duration on dispersal across the southeast Australian biogeographic barrier. Geo Geogr. Environ. 6, e00074.

Allendorf, F.W., Hohenlohe, P.A., Luikart, G., 2010. Genomics and the future of conservation genetics. Nat. Rev. Genet. 11, 697.

Allendorf, F., Luikart, G., Aitken, S., 2013. Conservation and the Genetics of Populations. Wiley, Blackwell, Oxford.

Applegate, S.P., Soltelo-Macías, F., Espinosa-Arrubarrena, L., 1993. An overview of Mexican shark fisheries, with suggestions for shark conservation in Mexico. In: Conservation Biology of Sharks. 115, NOAA Technical Report NMFS, pp. 31–37.

Attard, C.R., Beheregaray, L.B., Sandoval-Castillo, J., Jenner, K.C.S., Gill, P.C., Jenner, M.-N.M., Morrice, M.G., Möller, L.M., 2018. From conservation genetics to conservation genomics: a genome-wide assessment of blue whales (*Balaenoptera musculus*) in Australian feeding aggregations. R. Soc. Open Sci. 5, 170925.

Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A., Saunders, N.C., 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annu. Rev. Ecol. Syst. 18, 489–522.

Bailleul, D., Mackenzie, A., Sacchi, O., Poisson, F., Bierne, N., Arnaud-Haond, S., 2018. Large-scale genetic panmixia in the blue shark (*Prionace glauca*): A single worldwide population, or a genetic lag-time effect of the "grey zone" of differentiation? Evol. Appl. 11, 614–630.

Balkenhol, N., Dudaniec, R.Y., Krutovsky, K.V., Johnson, J.S., Cairns, D.M., Segelbacher, G., Selkoe, K.A., von der Heyden, S., Wang, I.J., Selmoni, O., Joost, S., 2019. Landscape genomics: understanding relationships between environmental heterogeneity and genomic

characteristics of populations. In: Rajora, O.P. (Ed.), Population Genomics: Concepts, Approaches and Applications. Spring, pp. 261–322.
Barker, A.M., Nosal, A.P., Lewallen, E.A., Burton, R.S., 2015. Genetic structure of leopard shark (*Triakis semifasciata*) populations along the Pacific coast of North America. J. Exp. Mar. Biol. Ecol. 472, 151–157.
Beheregaray, L.B., 2008. Twenty years of phylogeography: the state of the field and the challenges for the Southern Hemisphere. Mol. Ecol. 17, 3754–3774. https://doi.org/10.1111/j.1365-294X.2008.03857.x.
Benavides, M.T., Feldheim, K.A., Duffy, C.A., Wintner, S., Braccini, J.M., Boomer, J., Huveneers, C., Rogers, P., Mangel, J.C., Alfaro-Shigueto, J., 2011. Phylogeography of the copper shark (*Carcharhinus brachyurus*) in the southern hemisphere: implications for the conservation of a coastal apex predator. Mar. Freshwater Res. 62, 861–869.
Bernard, A.M., Richards, V.P., Stanhope, M.J., Shivji, M.S., 2018. Transcriptome-derived microsatellites demonstrate strong genetic differentiation in Pacific White Sharks. J. Hered. 109, 771–779.
Bester-van der Merwe, A.E., Gledhill, K.S., 2015. Molecular species identification and population genetics of chondrichthyans in South Africa: current challenges, priorities and progress. Afr. Zool. 50, 205–217.
Bond, M., Valentin-Albanese, J., Babcock, E.A., Heithaus, M., Grubbs, R., Cerrato, R., Peterson, B., Pikitch, E., Chapman, D., 2019. Top predators induce habitat shifts in prey within marine protected areas. Oecologia 190, 375–385.
Boomer, J.J., Harcourt, R.G., Francis, M.P., Walker, T.I., Braccini, J.M., Stow, A.J., 2013. Frequency of multiple paternity in gummy shark, *Mustelus antarcticus*, and rig, *Mustelus lenticulatus*, and the implications of mate encounter rate, postcopulatory influences, and reproductive mode. J. Hered. 104, 371–379. https://doi.org/10.1093/jhered/est010.
Bornatowski, H., Angelini, R., Coll, M., Barreto, R.R., Amorim, A.F., 2018. Ecological role and historical trends of large pelagic predators in a subtropical marine ecosystem of the South Atlantic. Rev. Fish Biol. Fish. 28, 241–259.
Boulton, R.A., Zuk, M., Shuker, D.M., 2018. An inconvenient truth: the unconsidered benefits of convenience polyandry. Trends Ecol. Evol. 33, 904–915. https://doi.org/10.1016/j.tree.2018.10.002.
Brauer, C.J., Unmack, P.J., Beheregaray, L.B., 2017. Comparative ecological transcriptomics and the contribution of gene expression to the evolutionary potential of a threatened fish. Mol. Ecol. 26, 6841–6856. https://doi.org/10.1111/mec.14432.
Byrne, R.J., Avise, J.C., 2012. Genetic mating system of the brown smoothhound shark (*Mustelus henlei*), including a literature review of multiple paternity in other elasmobranch species. Mar. Biol. 159, 749–756.
Caballero, S., Cardenosa, D., Soler, G., Hyde, J., 2012. Application of multiplex PCR approaches for shark molecular identification: feasibility and applications for fisheries management and conservation in the Eastern Tropical Pacific. Mol. Ecol. Resour. 12, 233–237.
Camhi, M.D., Valenti, S., Fordham, S., Fowler, S., Gibson, C., 2009. The Conservation Status of Pelagic Sharks and Rays: Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop. IUCN Species Survival Commission Shark Specialist Group, Newbury, UKx+ 78p.
Cardeñosa, D., Hyde, J., Caballero, S., 2014. Genetic diversity and population structure of the pelagic thresher shark (Alopias pelagicus) in the Pacific Ocean: evidence for two evolutionarily significant units. PLoS One 9, e110193.
Carrillo-Briceño, J.D., Carrillo, J.D., Aguilera, O.A., Sanchez-Villagra, M.R., 2018. Shark and ray diversity in the Tropical America (Neotropics)—an examination of environmental and historical factors affecting diversity. PeerJ 6, e5313. https://doi.org/10.7717/peerj.5313.

Castillo-Olguín, E., Uribe-Alcocer, M., Díaz-Jaimes, P., 2012. Assessment of the population genetic structure of Sphyrna lewini to identify conservation units in the Mexican Pacific. Cienc. Mar. 38, 635–652.

Castillo-Páez, A., Sosa-Nishizaki, O., Sandoval-Castillo, J., Galván-Magaña, F., Blanco-Parra, M.-D.-P., Rocha-Olivares, A., 2013. Strong population structure and shallow mitochondrial phylogeny in the banded guitarfish, *Zapteryx exasperata* (Jordan y Gilbert, 1880), from the northern Mexican Pacific. J. Hered. 105, 91–100.

Castillo-Páez, A., Sandoval-Castillo, J., Corro-Espinosa, D., Tovar-Ávila, J., Blanco-Parra, M.-D.-P., Saavedra-Sotelo, N.C., Sosa-Nishizaki, O., Galván-Magaña, F., Rocha-Olivares, A., 2017. Cutting through the Gordian knot: unravelling morphological, molecular, and biogeographical patterns in the genus *Zapteryx* (guitarfish) from the Mexican Pacific. ICES J. Mar. Sci. 74, 1630–1638.

Castro, A., Stewart, B., Wilson, S., Hueter, R., Meekan, M., Motta, P., Bowen, B., Karl, S., 2007. Population genetic structure of Earth's largest fish, the whale shark (*Rhincodon typus*). Mol. Ecol. 16, 5183–5192.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Sci. Adv. 1, e1400253.

Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc. Natl. Acad. Sci. 114, E6089–E6096.

Chabot, C., Allen, L., 2009. Global population structure of the tope (*Galeorhinus galeus*) inferred by mitochondrial control region sequence data. Mol. Ecol. 18, 545–552.

Chabot, C.L., Haggin, B.M., 2014. Frequency of multiple paternity varies between two populations of brown smoothhound shark, *Mustelus henlei*. Mar. Biol. 161, 797–804. https://doi.org/10.1007/s00227-013-2378-2.

Chabot, C.L., Espinoza, M., Mascareñas-Osorio, I., Rocha-Olivares, A., 2015. The effect of biogeographic and phylogeographic barriers on gene flow in the brown smoothhound shark, *Mustelus henlei*, in the northeastern Pacific. Ecol. Evol. 5, 1585–1600.

Chana-Munoz, A., Jendroszek, A., Sønnichsen, M., Kristiansen, R., Jensen, J.K., Andreasen, P.A., Bendixen, C., Panitz, F., 2017. Multi-tissue RNA-seq and transcriptome characterisation of the spiny dogfish shark (*Squalus acanthias*) provides a molecular tool for biological research and reveals new genes involved in osmoregulation. PLoS One 12, e0182756. https://doi.org/10.1371/journal.pone.0182756.

Clarke, C.R., Karl, S.A., Horn, R.L., Bernard, A.M., Lea, J.S., Hazin, F.H., Prodöhl, P.A., Shivji, M.S., 2015. Global mitochondrial DNA phylogeography and population structure of the silky shark, *Carcharhinus falciformis*. Mar. Biol. 162, 945–955.

Coissac, E., Hollingsworth, P.M., Lavergne, S., Taberlet, P., 2016. From barcodes to genomes: extending the concept of DNA barcoding. Mol. Ecol. 25, 1423–1428. https://doi.org/10.1111/mec.13549.

Compagno, L.J., 1990. Alternative life-history styles of cartilaginous fishes in time and space. Environ. Biol. Fishes 28, 33–75.

Compagno, L., Dando, M., Fowler, S., 2005. Sharks of the World. Princeton Field Guides. Princeton University Press Princeton, New Jersey.

CONAPESCA-INP, 2004. Plan de acción nacional para el manejo y conservación de tiburones, rayas y especies afines en México. Comisión Nacional de Acuacultura y Pesca e Instituto Nacional de la Pesca.

Cornuet, J.-M., Santos, F., Beaumont, M.A., Robert, C.P., Marin, J.-M., Balding, D.J., Guillemaud, T., Estoup, A., 2008. Inferring population history with DIY ABC: a user-friendly approach to approximate Bayesian computation. Bioinformatics 24, 2713–2719. https://doi.org/10.1093/bioinformatics/btn514.

Corrigan, S., Huveneers, C., Stow, A., Beheregaray, L.B., 2015a. A multilocus comparative study of dispersal in three codistributed demersal sharks from eastern Australia. Can. J. Fish. Aquat. Sci. 73, 406–415.

Corrigan, S., Kacev, D., Werry, J., 2015b. A case of genetic polyandry in the shortfin mako *Isurus oxyrinchus*. J. Fish Biol. 87, 794–798. https://doi.org/10.1111/jfb.12743.

Corrigan, S., Delser, P.M., Eddy, C., Duffy, C., Yang, L., Li, C., Bazinet, A.L., Mona, S., Naylor, G.J., 2017. Historical introgression drives pervasive mitochondrial admixture between two species of pelagic sharks. Mol. Phylogen. Evol. 110, 122–126.

Dallarés, S., Pérez-del-Olmo, A., Montero, F.E., Carrassón, M., 2017. Composition and seasonal dynamics of the parasite communities of Scyliorhinus canicula (L., 1758) and Galeus melastomus Rafinesque, 1810 (Elasmobranchii) from the NW Mediterranean Sea in relation to host biology and ecological features. Hydrobiologia 799, 275–291.

Daly-Engel, T.S., Seraphin, K.D., Holland, K.N., Coffey, J.P., Nance, H.A., Toonen, R.J., Bowen, B.W., 2012. Global phylogeography with mixed-marker analysis reveals male-mediated dispersal in the endangered scalloped hammerhead shark (*Sphyrna lewini*). PLoS One 7, e29986.

Davidson, L.N., Krawchuk, M.A., Dulvy, N.K., 2016. Why have global shark and ray landings declined: improved management or overfishing? Fish Fish. 17, 438–458.

Dent, F., Clarke, S., 2015. State of the Global Market for Shark Products. FAO Fisheries and Aquaculture Technical Paper: I, *No. 590*, FAO.

Díaz-Gómez, E., Castro-del Ángel, C.A., Santamaría-Hernández, E., Flores-Montiel, D.M., 2018. Indice Nacional de Cienccia. Tecnologia e Innovacion. CAIINNO.

Díaz-Jaimes, P., Reeb, C., Sosa-Nizhisaki, O., O'Sullivan, J.B., 2016. Assessing genetic variation in juvenile white sharks using teeth collected from landfills in Baja California. México. Conserv. Genet. Resour. 8, 431–434. https://doi.org/10.1007/s12686-016-0589-9.

Dibattista, J.D., Feldheim, K.A., Gruber, S.H., Hendry, A.P., 2008. Are indirect genetic benefits associated with polyandry? Testing predictions in a natural population of lemon sharks. Mol. Ecol. 17, 783–795. https://doi.org/10.1111/j.1365-294X.2007.03623.x.

Domingues, R.R., Hilsdorf, A.W.S., Gadig, O.B.F., 2018. The importance of considering genetic diversity in shark and ray conservation policies. Conserv. Genet. 19, 501–525.

Donaldson, M.R., Burnett, N.J., Braun, D.C., Suski, C.D., Hinch, S.G., Cooke, S.J., Kerr, J.T., 2016. Taxonomic bias and international biodiversity conservation research. FACETS 1, 105–113. https://doi.org/10.1139/facets-2016-0011.

Dudgeon, C.L., Ovenden, J.R., 2015. The relationship between abundance and genetic effective population size in elasmobranchs: an example from the globally threatened zebra shark *Stegostoma fasciatum* within its protected range. Conserv. Genet. 16, 1443–1454. https://doi.org/10.1007/s10592-015-0752-y.

Dudgeon, C., Blower, D., Broderick, D., Giles, J., Holmes, B., Kashiwagi, T., Krück, N., Morgan, J., Tillett, B., Ovenden, J., 2012. A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. J. Fish Biol. 80, 1789–1843.

Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., 2014. Extinction risk and conservation of the world's sharks and rays. eLIFE 3, e00590.

Dulvy, N.K., Simpfendorfer, C.A., Davidson, L.N., Fordham, S.V., Bräutigam, A., Sant, G., Welch, D.J., 2017. Challenges and priorities in shark and ray conservation. Curr. Biol. 27, R565–R572.

Duncan, K., Martin, A., Bowen, B., De Couet, H., 2006. Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). Mol. Ecol. 15, 2239–2251.

Ehemann, N.R., del Valle González-González, L., Chollet-Villalpando, J.G., De La Cruz-Agüero, J., 2018. Updated checklist of the extant Chondrichthyes within the Exclusive Economic Zone of Mexico. ZooKeys 774, 17.

Eitner, B.J., 1995. Systematics of the genus *Alopias* (Lamniformes: Alopiidae) with evidence for the existence of an unrecognized species. Copeia 1995, 562–571.
Feldheim, K.A., Gruber, S.H., DiBattista, J.D., Babcock, E.A., Kessel, S.T., Hendry, A.P., Pikitch, E.K., Ashley, M.V., Chapman, D.D., 2014. Two decades of genetic profiling yields first evidence of natal philopatry and long-term fidelity to parturition sites in sharks. Mol. Ecol. 23, 110–117.
Félix-López, D.G., Bolaño-Martinez, N., Díaz-Jaimes, P., Oñate-González, E.C., Ramírez-Pérez, J.S., García-Rodríguez, E., Corro-Espinosa, D., Osuna-Soto, J.E., Saavedra-Sotelo, N.C., 2019. Possible female philopatry of the smooth hammerhead shark, *Sphyrna zygaena*, revealed by genetic structure patterns. J. Fish Biol. 94, 671–679.
Fitzpatrick, J.L., Kempster, R.M., Daly-Engel, T.S., Collin, S.P., Evans, J.P., 2012. Assessing the potential for post-copulatory sexual selection in elasmobranchs. J. Fish Biol. 80, 1141–1158. https://doi.org/10.1111/j.1095-8649.2012.03256.x.
Frankham, R., 2015. Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Mol. Ecol. 24, 2610–2618.
Frankham, R., Briscoe, D.A., Ballou, J.D., 2010. Introduction to Conservation Genetics. Cambridge University Press.
Gagnaire, P.A., Broquet, T., Aurelle, D., Viard, F., Souissi, A., Bonhomme, F., Arnaud-Haond, S., Bierne, N., 2015. Using neutral, selected, and hitchhiker loci to assess connectivity of marine populations in the genomic era. Evol. Appl. 8, 769–786.
Galván-Tirado, C., Díaz-Jaimes, P., García-de León, F.J., Galván-Magaña, F., Uribe-Alcocer, M., 2013. Historical demography and genetic differentiation inferred from the mitochondrial DNA of the silky shark (*Carcharhinus falciformis*) in the Pacific Ocean. Fish. Res. 147, 36–46.
Gaughran, S.J., Quinzin, M.C., Miller, J.M., Garrick, R.C., Edwards, D.L., Russello, M.A., Poulakakis, N., Ciofi, C., Beheregaray, L.B., Caccone, A., 2018. Theory, practice, and conservation in the age of genomics: the Galápagos giant tortoise as a case study. Evol. Appl. 11, 1084–1093.
Gervais, C.R., Nay, T.J., Renshaw, G., Johansen, J.L., Steffensen, J.F., Rummer, J.L., 2018. Too hot to handle? Using movement to alleviate effects of elevated temperatures in a benthic elasmobranch, Hemiscyllium ocellatum. Mar. Biol. 165, 162.
Glenn, T.C., 2011. Field guide to next-generation DNA sequencers. Mol. Ecol. Resour. 11, 759–769.
Goldberg, A.D., Allis, C.D., Bernstein, E., 2007. Epigenetics: a landscape takes shape. Cell 128, 635–638. https://doi.org/10.1016/j.cell.2007.02.006.
Goodman, M.C., Hannah, S.M., Ruttenberg, B.I., 2019. The relationship between geographic range extent, sea surface temperature and adult traits in coastal temperate fishes. J. Biogeogr. 46, 1438–1450.
Goshima, M., Sekiguchi, R., Matsushita, M., Nonaka, M., 2016. The complement system of elasmobranches revealed by liver transcriptome analysis of a hammerhead shark, *Sphyrna zygaena*. Dev. Comp. Immunol. 61, 13–24. https://doi.org/10.1016/j.dci.2016.03.009.
Green, M.E., Appleyard, S.A., White, W., Tracey, S., Ovenden, J., 2017. Variability in multiple paternity rates for grey reef sharks (*Carcharhinus amblyrhynchos*) and scalloped hammerheads (*Sphyrna lewini*). Sci. Rep. 7, 1528. https://doi.org/10.1038/s41598-017-01416-w.
Grijalva-Chon, J., Kaichi, A., Numachi, K., 2002. Homogeneidad genética en tiburón angelito (*Squatina californica*) del Golfo de California, evidencia por análisis PCR–RFLP de la región control del ADN mitocondrial. Cienc. Mar 17, 37–42.
Grubbs, R.D., Carlson, J.K., Romine, J.G., Curtis, T.H., McElroy, W.D., McCandless, C.T., Cotton, C.F., Musick, J.A., 2016. Critical assessment and ramifications of a purported marine trophic cascade. Sci. Rep. 6, 20970.

Grummer, J., Beheregaray, L.B., Bernatchez, L., Hand, B., Luikart, G., Narum, S., Taylor, E., 2019. Aquatic landscape genomics and environmental effects on genetic variation. Trends Ecol. Evol. 34, 641–654.

Gubili, C., Duffy, C., Cliff, G., Wintner, S., Shivji, M., Chapman, D., Bruce, B., Martin, A., Sims, D., 2012. Application of molecular genetics for conservation of the white shark, Carcharodon carcharias, L. 1758. In: Domeier, M. (Ed.), Global Perspectives on the Biology and Life History of the White Shark. CRC, pp. 357–380.

Gutenkunst, R.N., Hernandez, R.D., Williamson, S.H., Bustamante, C.D., 2009. Inferring the joint demographic history of multiple populations from multidimensional SNP frequency data. PLoS Genet. 5, e1000695. https://doi.org/10.1371/journal.pgen.1000695.

Hanner, R.H., Naaum, A.M., Shivji, M.S., 2016. Conclusion: DNA-based authentication of shark products and implications for conservation and management. In: Naaum, A.M., Hanner, R. (Eds.), Seafood Authenticity and Traceability. Elsevier, pp. 171–179.

Healy, T.M., Schulte, P.M., 2018. Conserved patterns of alternative splicing in response to cold acclimation in fish. bioRxiv 1, 429704.

Hedrick, P.W., Miller, P.S., 1992. Conservation genetics: techniques and fundamentals. Ecol. Appl. 2, 30–46.

Heupel, M., Simpfendorfer, C., 2010. Science or slaughter: need for lethal sampling of sharks. Conserv. Biol. 24, 1212–1218.

Jorgensen, S.J., Reeb, C.A., Chapple, T.K., Anderson, S., Perle, C., Van Sommeran, S.R., Fritz-Cope, C., Brown, A.C., Klimley, A.P., Block, B.A., 2009. Philopatry and migration of Pacific white sharks. Proc. R. Soc. Lond. Ser. B: Biol. Sci. 277, 679–688.

Karl, S.A., 2008. The effect of multiple paternity on the genetically effective size of a population. Mol. Ecol. 17, 3973–3977. https://doi.org/10.1111/j.1365-294X.2008.03902.x.

Keeney, D.B., Heist, E.J., 2006. Worldwide phylogeography of the blacktip shark (*Carcharhinus limbatus*) inferred from mitochondrial DNA reveals isolation of western Atlantic populations coupled with recent Pacific dispersal. Mol. Ecol. 15, 3669–3679. https://doi.org/10.1111/j.1365-294X.2006.03036.x.

King, J., Wetklo, M., Supernault, J., Taguchi, M., Yokawa, K., Sosa-Nishizaki, O., Withler, R., 2015. Genetic analysis of stock structure of blue shark (*Prionace glauca*) in the north Pacific ocean. Fish. Res. 172, 181–189.

Kitamura, T., Takemura, A., Watabe, S., Taniuchi, T., Shimizu, M., 1996. Mitochondrial DNA analysis for the cytochrome b gene and D-loop region from the bull shark *Carcharhinus leucas*. Fish. Sci. 62, 21–27.

Kyne, P.M., Carlson, J.K., Ebert, D.A., Fordham, S.V., Bizzarro, J.J., Graham, R.T., Kulka, D.W., Tewes, E.E., Harrison, L.R., Dulvy, N.K., 2012. The Conservation Status of North American, Central American, and Caribbean Chondrichthyans. IUCN Species Survival Commission Shark Specialist Group Vancouver, BC.

Lafferty, K.D., Benesh, K.C., Mahon, A.R., Jerde, C.L., Lowe, C.G., 2018. Detecting southern California's white sharks with environmental DNA. Front. Mar. Sci. 5, 1–6.

Larson, S., Christiansen, J., Griffing, D., Ashe, J., Lowry, D., Andrews, K., 2011. Relatedness and polyandry of sixgill sharks, *Hexanchus griseus*, in an urban estuary. Conserv. Genet. 12, 679–690. https://doi.org/10.1007/s10592-010-0174-9.

Larson, W.A., Seeb, L.W., Everett, M.V., Waples, R.K., Templin, W.D., Seeb, J.E., 2014. Genotyping by sequencing resolves shallow population structure to inform conservation of Chinook salmon (*Oncorhynchus tshawytscha*). Evol. Appl. 7, 355–369. https://doi.org/10.1111/eva.12128.

Larson, S.E., Daly-Engel, T.S., Phillips, N.M., 2017. Review of current conservation genetic analyses of Northeast Pacific sharks. Adv. Mar. Biol. 77, 79–110. Elsevier.

Last, P.R., White, W.T., Carvalho, M., Seret, B., Stehmann, M., Naylor, G.J., Marshall, L., 2016. Rays of the World. CSIRO.

Lewallen, E.A., Anderson, T.W., Bohonak, A.J., 2007. Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. Mar. Biol. 152, 599–609.

Li, H., Durbin, R., 2011. Inference of human population history from individual whole-genome sequences. Nature 475, 493. https://doi.org/10.1038/nature10231.

Lighten, J., Incarnato, D., Ward, B.J., van Oosterhout, C., Bradbury, I., Hanson, M., Bentzen, P., 2016. Adaptive phenotypic response to climate enabled by epigenetics in a K-strategy species, the fish Leucoraja ocellata (Rajidae). R. Soc. Open Sci. 3, 160299. https://doi.org/10.1098/rsos.160299.

Liu, S.Y.V., Joung, S.J., Yu, C.-J., Hsu, H.-H., Tsai, W.-P., Liu, K.M., 2018. Genetic diversity and connectivity of the megamouth shark (*Megachasma pelagios*). PeerJ 6, e4432.

Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catalán, I.A., Muhling, B., Erisman, B., Cadrin, S.X., Alós, J., Ospina-Alvarez, A., Stachura, M.M., Tringali, M.D., Burnsed, S.W., Paris, C.B., 2017. Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish Fish. 18, 285–312. https://doi.org/10.1111/faf.12180.

Luikart, G., Kardos, M., Hand, B.K., Rajora, B.K., Aitken, S.N., Hohenlohe, P.A., 2019. Population genomics: advancing understanding of nature. In: Rajora, O.P. (Ed.), Population Genomics: Concepts, Approaches and Applications. Springer, pp. 3–82.

Lyons, K., Chabot, C.L., Mull, C.G., Paterson Holder, C.N., Lowe, C.G., 2017. Who's my daddy? Considerations for the influence of sexual selection on multiple paternity in elasmobranch mating systems. Ecol. Evol. 7, 5603–5612.

Machado, A.M., Almeida, T., Mucientes, G., Esteves, P.J., Verissimo, A., Castro, L.F.C., 2018. De novo assembly of the kidney and spleen transcriptomes of the cosmopolitan blue shark, *Prionace glauca*. Mar. Genom. 37, 50–53. https://doi.org/10.1016/j.margen.2017.11.009.

Magnussen, J.E., Pikitch, E.K., Clarke, S., Nicholson, C., Hoelzel, A.R., Shivji, M.S., 2007. Genetic tracking of basking shark products in international trade. Anim. Conserv. 10, 199–207.

McClenachan, L., Cooper, A.B., Carpenter, K.E., Dulvy, N.K., 2012. Extinction risk and bottlenecks in the conservation of charismatic marine species. Conserv. Lett. 5, 73–80.

Meijaard, E., Cardillo, M., Meijaard, E.M., Possingham, H.P., 2015. Geographic bias in citation rates of conservation research. Conserv. Biol. 29, 920–925.

Mieras, P.A., Harvey-Clark, C., Bear, M., Hodgin, G., Hodgin, B., 2017. The economy of shark conservation in the Northeast Pacific: the role of ecotourism and citizen science. Adv. Mar. Biol. 78, 121–153. Elsevier.

Nance, H.A., Klimley, P., Galván-Magaña, F., Martínez-Ortíz, J., Marko, P.B., 2011. Demographic processes underlying subtle patterns of population structure in the scalloped hammerhead shark, *Sphyrna lewini*. PLoS One 6, e21459.

Nunziata, S.O., Weisrock, D.W., 2018. Estimation of contemporary effective population size and population declines using RAD sequence data. Heredity 120, 196–207. https://doi.org/10.1038/s41437-017-0037-y.

Oliver, S., Braccini, M., Newman, S.J., Harvey, E.S., 2015. Global patterns in the bycatch of sharks and rays. Mar. Policy 54, 86–97.

Oñate-González, E.C., Rocha-Olivares, A., Saavedra-Sotelo, N.C., Sosa-Nishizaki, O., 2015. Mitochondrial genetic structure and matrilineal origin of white sharks, *Carcharodon carcharias*, in the Northeastern Pacific: implications for their conservation. J. Hered. 106, 347–354.

Onimaru, K., Tatsumi, K., Shibagaki, K., Kuraku, S., 2018. A de novo transcriptome assembly of the zebra bullhead shark, Heterodontus zebra. Sci. Data 5, 180197. https://doi.org/10.1038/sdata.2018.197.

Ortega, E., Álvarez-Borrego, S., Arriaga, S., Renner, M., Bridge, E., 2010. Physical, chemical, and biological oceanography of the Gulf of California. In: Brusca, R. (Ed.), The Gulf of California: Biodiversity and Conservation. University of Arizona Press, Tucson. University of Arizona, pp. 24–48.

Ovenden, J.R., Berry, O., Welch, D.J., Buckworth, R.C., Dichmont, C.M., 2015. Ocean's eleven: a critical evaluation of the role of population, evolutionary and molecular genetics in the management of wild fisheries. Fish Fish. 16, 125–159.

Ovenden, J.R., Leigh, G.M., Blower, D.C., Jones, A.T., Moore, A., Bustamante, C., Buckworth, R.C., Bennett, M.B., Dudgeon, C.L., 2016. Can estimates of genetic effective population size contribute to fisheries stock assessments? J. Fish Biol. 89, 2505–2518. https://doi.org/10.1111/jfb.13129.

Parmentier, I., Duminil, J., Kuzmina, M., Philippe, M., Thomas, D.W., Kenfack, D., Chuyong, G.B., Cruaud, C., Hardy, O.J., 2013. How effective are DNA barcodes in the identification of african rainforest trees? PLoS One 8, e54921. https://doi.org/10.1371/journal.pone.0054921.

Pazmiño, D.A., Maes, G.E., Simpfendorfer, C.A., Salinas-de-León, P., van Herwerden, L., 2017. Genome-wide SNPs reveal low effective population size within confined management units of the highly vagile Galapagos shark (*Carcharhinus galapagensis*). Conserv. Genet. 18, 1151–1163. https://doi.org/10.1007/s10592-017-0967-1.

Pazmiño, D.A., Maes, G.E., Green, M.E., Simpfendorfer, C.A., Hoyos-Padilla, E.M., Duffy, C.J., Meyer, C.G., Kerwath, S.E., Salinas-de-León, P., van Herwerden, L., 2018. Strong trans-Pacific break and local conservation units in the Galapagos shark (*Carcharhinus galapagensis*) revealed by genome-wide cytonuclear markers. Heredity 120, 407.

Pérez Jiménez, J.C., Nishizaki, O.S., Castillo Geniz, J.L., Buth, D., 2005. A New Eastern North Pacific smoothhound shark (Genus *Mustelus*, Family Triakidae) from the Gulf of California. Copeia 2005, 834–845. https://doi.org/10.1643/0045-8511(2005)005[0834:ANENPS]2.0.CO;2.

Pérez-Jiménez, J., Rocha-Olivares, A., Sosa-Nishizaki, O., 2013. Morphological and molecular differentiation of smooth-hound sharks (Genus *Mustelus*, Family Triakidae) from the Gulf of California. J. Appl. Ichthyol. 29, 268–270.

Phillips, N.M., Chaplin, J.A., Peverell, S.C., Morgan, D.L., 2017. Contrasting population structures of three Pristis sawfishes with different patterns of habitat use. Mar. Freshwat. Res. 68, 452–460.

Plank, S., Lowe, C., Feldheim, K., Wilson Jr., R., Brusslan, J., 2010. Population genetic structure of the round stingray *Urobatis halleri* (Elasmobranchii: Rajiformes) in southern California and the Gulf of California. J. Fish Biol. 77, 329–340.

Plata Zepeda, Y.M., Ramírez Romero, P., Sosa-Rodríguez, F.S., 2018. Economic assessment of tourism based on shark-seeing and diving as a more profitable activity than commercial fishing. In: Leal Filho, W., Pociovălișteanu, D., Borges de Brito, P., Borges de Lima, I. (Eds.), Towards a Sustainable Bioeconomy: Principles, Challenges and Perspectives. Springer, pp. 205–230.

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

Portnoy, D.S., Piercy, A.N., Musick, J.A., Burgess, G.H., Graves, J.E., 2007. Genetic polyandry and sexual conflict in the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic and Gulf of Mexico. Mol. Ecol. 16, 187–197. https://doi.org/10.1111/j.1365-294X.2006.03138.x.

Portnoy, D.S., McDowell, J.R., McCandless, C.T., Musick, J.A., Graves, J.E., 2008. Effective size closely approximates the census size in the heavily exploited western Atlantic population of the sandbar shark, *Carcharhinus plumbeus*. Conserv. Genet. 10, 1697. https://doi.org/10.1007/s10592-008-9771-2.

Pouca, C.V., Gervais, C., Reed, J., Michard, J., Brown, C., 2019. Quantity discrimination in Port Jackson sharks incubated under elevated temperatures. Behav. Ecol. Sociobiol. 73, 93.

Pratt, H.L., Carrier, J.C., 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, Ginglymostoma cirratum. In: Tricas, T.C., Gruber, S.H. (Eds.),

The Behavior and Sensory Biology of Elasmobranch Fishes: An Anthology in Memory of Donald Richard Nelson. Springer Netherlands, Dordrecht, pp. 157–188.
Primmer, C.R., 2009. From conservation genetics to conservation genomics. Ann. N. Y. Acad. Sci. 1162, 357–368.
Ramírez-Amaro, S., Ramírez-Macías, D., Vázquez-Juárez, R., Flores-Ramírez, S., Galván-Magaña, F., Gutiérrez-Rivera, J.N., 2017. Population structure of the Pacific angel shark (*Squatina californica*) along the northwestern coast of Mexico based on the mitochondrial DNA control region. Cienc. Mar. 43, 69–80.
Ramírez-Macías, D., Vázquez-Juárez, R., Galván-Magaña, F., Munguía-Vega, A., 2007. Variations of the mitochondrial control region sequence in whale sharks (*Rhincodon typus*) from the Gulf of California. Mexico. Fish. Res. 84, 87–95.
Razgour, O., Forester, B., Taggart, J.B., Bekaert, M., Juste, J., Ibáñez, C., Puechmaille, S.J., Novella-Fernandez, R., Alberdi, A., Manel, S., 2019. Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. Proc. Natl. Acad. Sci. 116, 10418–10423.
Rees, H.C., Maddison, B.C., Middleditch, D.J., Patmore, J.R.M., Gough, K.C., 2014. REVIEW: the detection of aquatic animal species using environmental DNA—a review of eDNA as a survey tool in ecology. J. Appl. Ecol. 51, 1450–1459. https://doi.org/10.1111/1365-2664.12306.
Reid-Anderson, S., Bilgmann, K., Stow, A., 2019. Effective population size of the critically endangered east Australian grey nurse shark *Carcharias taurus*. Mar. Ecol. Prog. Ser. 610, 137–148.
Reis, R., Albert, J., Di Dario, F., Mincarone, M., Petry, P., Rocha, L., 2016. Fish biodiversity and conservation in South America. J. Fish Biol. 89, 12–47.
Richards, V.P., Suzuki, H., Stanhope, M.J., Shivji, M.S., 2013. Characterization of the heart transcriptome of the white shark (Carcharodon carcharias). BMC Genomics 14, 697.
Rick, T.C., Erlandson, J.M., Glassow, M.A., Moss, M.L., 2002. Evaluating the economic significance of sharks, skates, and rays (Elasmobranchs) in prehistoric economies. J. Archaeol. Sci. 29, 111–122.
Riginos, C., Crandall, E.D., Liggins, L., Bongaerts, P., Treml, E.A., 2016. Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. Curr. Zool. 62, 581–601. https://doi.org/10.1093/cz/zow067.
Rodrigues-Filho, L.F., Pinhal, D., Sodré, D., Vallinoto, M., 2012. Shark DNA forensics: applications and impacts on genetic diversity. In: Caliskan, M. (Ed.), Analysis of Genetic Variation in Animals. InTech, pp. 269–286.
Rodríguez-Correa, H., González-Rodríguez, A., Oyama, K., 2017. Perspectivas de la Ecología molecular en un país megadiverso. Rev. Mex. Biodivers. 88, 3–13.
Rossouw, C., Wintner, S.P., Bester-Van Der Merwe, A.E., 2016. Assessing multiple paternity in three commercially exploited shark species: *Mustelus mustelus, Carcharhinus obscurus* and *Sphyrna lewini*. J. Fish Biol. 89, 1125–1141. https://doi.org/10.1111/jfb.12996.
Sandoval-Castillo, J., Beheregaray, L.B., 2015. Metapopulation structure informs conservation management in a heavily exploited coastal shark (*Mustelus henlei*). Mar. Ecol. Prog. Ser. 533, 191–203.
Sandoval-Castillo, J., Beheregaray, L.B., 2019. Oceanographic heterogeneity drives ecological radiation in elasmobranchs. J. Biogeogr.
Sandoval-Castillo, J., Rocha-Olivares, A., 2011. Deep mitochondrial divergence in Baja California populations of an aquilopelagic elasmobranch: the golden cownose ray. J. Hered. 102, 269–274.
Sandoval-Castillo, J., Rocha-Olivares, A., Villavicencio-Garayzar, C., Balart, E., 2004. Cryptic isolation of Gulf of California shovelnose guitarfish evidenced by mitochondrial DNA. Mar. Biol. 145, 983–988.

Sandoval-Castillo, J., Robinson, N.A., Hart, A.M., Strain, L.W., Beheregaray, L.B., 2018. Seascape genomics reveals adaptive divergence in a connected and commercially important mollusc, the greenlip abalone (*Haliotis laevigata*), along a longitudinal environmental gradient. Mol. Ecol. 27, 1603–1620.

Sandoval-Castillo, J., Gates, K., Brauer, C., Unmack, P., Bernatchez, L., Beheregaray, L.B., 2019. Gene Expression Responses to Heat Stress to Future Climate in Australian Rainbowfishes. Clim. Change. in preparation.

Schmidt, J.V., Schmidt, C.L., Ozer, F., Ernst, R.E., Feldheim, K.A., Ashley, M.V., Levine, M., 2009. Low genetic differentiation across three major ocean populations of the whale shark, *Rhincodon typus*. PloS one 4, e4988.

Schultz, J., Feldheim, K., Gruber, S., Ashley, M., McGovern, T., Bowen, B., 2008. Global phylogeography and seascape genetics of the lemon sharks (genus *Negaprion*). Mol. Ecol. 17, 5336–5348.

Shafer, A.B., Wolf, J.B., 2013. Widespread evidence for incipient ecological speciation: a meta-analysis of isolation-by-ecology. Ecol. Lett. 16, 940–950.

Shokralla, S., Spall, J.L., Gibson, J.F., Hajibabaei, M., 2012. Next-generation sequencing technologies for environmental DNA research. Mol. Ecol. 21, 1794–1805. https://doi.org/10.1111/j.1365-294X.2012.05538.x.

Shokralla, S., Hellberg, R.S., Handy, S.M., King, I., Hajibabaei, M., 2015. A DNA mini-barcoding system for authentication of processed fish products. Sci. Rep. 5, 15894. https://doi.org/10.1038/srep15894.

Sigsgaard, E.E., Nielsen, I.B., Bach, S.S., Lorenzen, E.D., Robinson, D.P., Knudsen, S.W., Pedersen, M.W., Jaidah, M.A., Orlando, L., Willerslev, E., Møller, P.R., Thomsen, P.F., 2016. Population characteristics of a large whale shark aggregation inferred from seawater environmental DNA. Nat. Ecol. Evol. 1, 0004. https://doi.org/10.1038/s41559-016-0004.

Sigsgaard, E.E., Nielsen, I.B., Carl, H., Krag, M.A., Knudsen, S.W., Xing, Y., Holm-Hansen, T.H., Møller, P.R., Thomsen, P.F., 2017. Seawater environmental DNA reflects seasonality of a coastal fish community. Mar. Biol. 164, 128. https://doi.org/10.1007/s00227-017-3147-4.

Smith, W., Bizzarro, J., Richards, V.P., Nielsen, J., Márquez-Flarías, F., Shivji, M.S., 2009. Morphometric convergence and molecular divergence: the taxonomic status and evolutionary history of *Gymnura crebripunctata* and *Gymnura marmorata* in the eastern Pacific Ocean. J. Fish Biol. 75, 761–783.

Smith, M.A., Bertrand, C., Crosby, K., Eveleigh, E.S., Fernandez-Triana, J., Fisher, B.L., Gibbs, J., Hajibabaei, M., Hallwachs, W., Hind, K., Hrcek, J., Huang, D.-W., Janda, M., Janzen, D.H., Li, Y., Miller, S.E., Packer, L., Quicke, D., Ratnasingham, S., Rodriguez, J., Rougerie, R., Shaw, M.R., Sheffield, C., Stahlhut, J.K., Steinke, D., Whitfield, J., Wood, M., Zhou, X., 2012. Wolbachia and DNA barcoding insects: patterns, potential, and problems. PLoS One 7, e36514. https://doi.org/10.1371/journal.pone.0036514.

Snelson, F.F., Roman, B.L., Burgess, G.H., 2009. The reproductive biology of pelagic elasmobranchs. In: Pitcher, T.J., Camhi, M.D., Pikitch, E.K., Babcock, E.A. (Eds.), Sharks of the Open Ocean. Blackwell, pp. 24–53.

Stein, R.W., Mull, C.G., Kuhn, T.S., Aschliman, N.C., Davidson, L.N., Joy, J.B., Smith, G.J., Dulvy, N.K., Mooers, A.O., 2018. Global priorities for conserving the evolutionary history of sharks, rays and chimaeras. Nat. Ecol. Evol. 2, 288.

Steinke, D., Bernard, A.M., Horn, R.L., Hilton, P., Hanner, R., Shivji, M.S., 2017. DNA analysis of traded shark fins and mobulid gill plates reveals a high proportion of species of conservation concern. Sci. Rep. 7, 9505.

Stelbrink, B., von Rintelen, T., Cliff, G., Kriwet, J., 2010. Molecular systematics and global phylogeography of angel sharks (genus *Squatina*). Mol. Phylogen. Evol. 54, 395–404. https://doi.org/10.1016/j.ympev.2009.07.029.

Stevens, J., Bonfil, R., Dulvy, N., Walker, P., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. 57, 476–494.

Tarula-Marin, O., Saavedra-Sotelo, N.C., 2019. First record of mating system of the gray smooth-hound shark (*Mustelus californicus*) in the Gulf of California: genetic monogamy in young females. J. Mar. Biol. Assoc. U.K. in review.

Trejo, T., 2005. Global phylogeography ofthresher sharks (*Alopias spp.*) inferred from mitochondrial DNA control region sequences M.Sc. Thesis, Marine Science, California State University.

van der Valk, T., Díez-del-Molino, D., Marques-Bonet, T., Guschanski, K., Dalén, L., 2019. Historical genomes reveal the genomic consequences of recent population decline in Eastern gorillas. Curr. Biol. 29, 165–170.e166. https://doi.org/10.1016/j.cub.2018.11.055.

Vella, N., Vella, A., 2017. Population genetics of the deep-sea bluntnose sixgill shark, *Hexanchus griseus*, revealing spatial genetic heterogeneity. Mar. Genom. 36, 25–32. https://doi.org/10.1016/j.margen.2017.05.012.

Veríssimo, A., Sampaio, Í., McDowell, J.R., Alexandrino, P., Mucientes, G., Queiroz, N., da Silva, C., Jones, C.S., Noble, L.R., 2017. World without borders—genetic population structure of a highly migratory marine predator, the blue shark (*Prionace glauca*). Ecol. Evol. 7, 4768–4781.

Vignaud, T.M., Maynard, J.A., Leblois, R., Meekan, M.G., Vázquez-Juárez, R., Ramírez-Macías, D., Pierce, S.J., Rowat, D., Berumen, M.L., Beeravolu, C., 2014. Genetic structure of populations of whale sharks among ocean basins and evidence for their historic rise and recent decline. Mol. Ecol. 23, 2590–2601.

Wang, Z., Gerstein, M., Snyder, M., 2009. RNA-Seq: a revolutionary tool for transcriptomics. Nat. Rev. Genet. 10, 57. https://doi.org/10.1038/nrg2484.

Ward, R.D., Holmes, B.H., White, W.T., Last, P.R., 2008. DNA barcoding Australasian chondrichthyans: results and potential uses in conservation. Mar. Freshwat. Res. 59, 57–71.

Wetherbee, B.M., Cortés, E., 2004. Food consumption and feeding habits. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Biology of Sharks and Their Relatives. CRC, pp. 225–246.

White, W., Kyne, P., 2010. The status of chondrichthyan conservation in the Indo-Australasian region. J. Fish Biol. 76, 2090–2117.

White, W.T., Corrigan, S., Yang, L., Henderson, A.C., Bazinet, A.L., Swofford, D.L., Naylor, G.J., 2017. Phylogeny of the manta and devilrays (Chondrichthyes: mobulidae), with an updated taxonomic arrangement for the family. Zool. J. Linn. Soc. 182, 50–75.

Willing, E.-M., Dreyer, C., Van Oosterhout, C., 2012. Estimates of genetic differentiation measured by FST do not necessarily require large sample sizes when using many SNP markers. PloS one 7, e42649.

Worm, B., Branch, T.A., 2012. The future of fish. Trends Ecol. Evol. 27, 594–599.

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C.A., Chapman, D., Heithaus, M.R., Kessel, S.T., Gruber, S.H., 2013. Global catches, exploitation rates, and rebuilding options for sharks. Mar. Policy 40, 194–204.

Yates, P.M., Heupel, M.R., Tobin, A.J., Simpfendorfer, C.A., 2015. Spatio-temporal occurrence patterns of young sharks in tropical coastal waters. Estuar. Coasts 38, 2019–2030.

Young, H.S., McCauley, D.J., Galetti, M., Dirzo, R., 2016. Patterns, causes, and consequences of anthropocene defaunation. Annu. Rev. Ecol. Evol. Syst. 47, 333–358.