



# The importance of considering genetic diversity in shark and ray conservation policies

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## Abstract

Many populations of elasmobranchs (sharks and rays) are experiencing severe declines due to the high demand for shark fins in Asia, the activities of unregulated fisheries, and increases in shark and ray catches. Recently, the effects of the decline in the populations of marine fish species on genetic diversity have drawn increasing attention; however, only a few studies have addressed the genetic diversity of shark and ray populations. Here, we report the results of a quantitative analysis of the genetic diversity of shark and ray species over the past 20 years and discuss the importance and utility of this genetic information for fisheries management and conservation policies. Furthermore, we suggest future actions important for minimizing the gaps in our current knowledge of the genetic diversity of shark and ray species and to minimize the information gap between genetic scientists and policymakers. We suggest that shark and ray fisheries management and conservation policies consider genetic diversity information, such as the management unit, effective population size ( $N_e$ ), haplotype and nucleotide diversity, observed heterozygosity, and allelic richness, because the long-term survival of a species is strongly dependent on the levels of genetic diversity within and between populations. In addition, sharks and rays are a group of particular interest for genetic conservation due to their remarkable life histories.

**Keywords** Conservation · Elasmobranch · Evolution · Fisheries management · Genetic variability · Molecular marker

## Introduction

Genetic data have aided conservation research and management by facilitating the detection of genetically distinct populations, the measurement of genetic connectivity and the identification of the risks associated with demographic change and inbreeding (Allendorf et al. 2013). A good example for which genetic information has been considered in fisheries management is the Pacific salmon (*Oncorhynchus* spp.), for which genetic data have influenced conservation

efforts associated with population restoration (Waples 1995). However, the effective application of genetic data to the management plans for several marine species, including sharks and rays, remains a challenge (Kenchington et al. 2003).

The effects of population-level declines are of major concern in conservation biology because small populations suffer from inbreeding and genetic drift. These effects lead to loss of genetic diversity, which has several potential consequences, such as compromising the ability of a population to evolve in order to cope with environmental changes and reducing its chances of long-term persistence (Frankham et al. 2002). Therefore, councils of evolutionary biologists and fisheries scientists are interested in elucidating the genetic patterns and demographic connectivity of different groups of individuals or populations as well as the distributions of genetic variation within and between populations (Waples and Gaggiotti 2006; Grant and Cheng 2012; Ovenden 2013).

Sharks and rays (including stingrays and skates) are groups of interest to conservationists due to their ecological importance in the marine environment and their current

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high levels of overexploitation (Dulvy et al. 2014). Currently, there are more than 1160 validly named species of elasmobranchs in the world (Weigmann 2016), representing a significant number of apex and mesopredators that occupy top positions in the food chain (Heithaus et al. 2008; Ferretti et al. 2010). However, despite their ecological importance, elasmobranchs are one of the most imperiled groups of marine species worldwide (Cortés 2002; Bräutigam et al. 2015) due to their life history characteristics, including late sexual maturity, lengthy pregnancy, low fertility, slow growth and long life span, making them particularly susceptible to anthropogenic pressures such as overfishing, environmental changes, and pollution (Seitz and Poulakis 2006; Dulvy et al. 2014). Indeed, these anthropogenic pressures can cause changes in genetic diversity through population reduction, thus compromising these species' ability to evolve (DiBattista 2008).

Currently, massive population-level declines and extinction risks due to overfishing over recent decades present significant threats to sharks and rays in all oceans (Ferretti et al. 2010; Worm et al. 2013; Dulvy et al. 2014). The main issues that jeopardize shark and ray species include the high demand for shark fins and gill plates in Asia, unregulated fisheries, bycatching, and increased shark fishing due to the collapse of other fisheries (Musick et al. 2000; Clarke et al. 2006; Herndon et al. 2010; Dulvy et al. 2014; McClenachan et al. 2016). According to a study by Worm et al. (2013), the global catch of sharks from reported and unreported landings, discards, and shark finning was estimated as approximately 100 million tons in 2010. Such fishing pressures are more challenging to elasmobranchs because of their high susceptibility relative to most teleosts and because sharks and rays require several decades to recover from overfishing (Stevens et al. 2000).

In general, fisheries management of shark and ray relies on a series of studies on the basic biology, life history, and population ecology of elasmobranchs (Simpfendorfer et al. 2011). However, the population genetic diversity of sharks and rays is generally neglected in fisheries management, and the possibility of change appears distant, as many international conservation efforts currently fail to acknowledge genetic variation (Laikre 2010; Ovenden et al. 2013). Therefore, the expansion of global population genetics studies describing the genetic diversity of shark and ray species worldwide is urgently needed in order to identify genetically distinct populations and to preserve genetic diversity. It is imperative to address the severe factors that jeopardize shark and ray populations.

Against this background, we conduct a critical review and discuss the importance of including genetic diversity data in shark and ray fisheries management plans and, consequently, in conservation policies. Specifically, we discuss the importance of sharks and rays within a conservation

genetics context, presenting the possible effects of fishing on their genetic diversity, and we address the current limitations and the need for an increase in genetic studies of this taxonomic group in order to assess genetic diversity across geographical ranges. In addition, we suggest future actions important to minimize the knowledge gap between shark and ray geneticists and the authors of conservation policies.

## What makes sharks and rays particularly interesting to conservation genetics?

In addition to their ecological importance, elasmobranchs are a group of particular interest to conservation geneticists—researchers who use genetic/genomic techniques to solve problems in conservation biology—due to the remarkable features of their life histories. These features include (i) the evolutionary uniqueness of elasmobranchs, (ii) their reproductive strategy, (iii) the effects of overfishing on evolution, (iv) their broad geographic distribution, and (v) the limited number of studies describing their genetic diversity.

### Evolutionary uniqueness

Sharks and rays compose a major lineage of evolutionarily unique vertebrates consisting of approximately 1160 living species; these species represent a small fraction (< 3.0%) of modern fish fauna (Nelson et al. 2016; Weigmann 2016). Compared with marine teleosts, sharks and rays present a low species richness (1160 shark and ray species versus 30,000 teleost species). In particular, some shark and ray orders contain only one family and few genera and species, such as Echinorhniiformes (1 genus, 2 species), Pristiophoriformes (2 genera, 7 species), and Heterodontiformes (9 species), and there are even several monotypic families, such as the shark families Mitsukurinidae, Cetorhinidae, Pseudocarchariidae, and Leptochariidae and the ray families Hypnidae, Hexatrygonidae, and Plesiobatidae (Ebert et al. 2013; Last et al. 2016). Furthermore, intrinsic factors, such as diversity of form and function as a means of successful evolutionary resilience, contribute to a lower historic extinction rate and a higher evolutionary adaptability for shark and ray species, allowing them to inhabit several marine and freshwater ecosystems (Ferretti et al. 2010; Ebert et al. 2013; Richards et al. 2013). In addition, over the past 455 million years, sharks have been able to survive mass extinctions that have left ocean waters with far fewer fish (Grogan et al. 2012). Such resilience suggests that sharks have unique genetic properties that support their adaptability and evolutionary success; therefore, their genetic properties must be preserved.

## Reproductive strategy

Shark and ray species exhibit a wide diversity of reproductive strategies, including multiple paternity, parthenogenesis, sperm storage, and philopatry, and these strategies can have considerable effects on genetic diversity (Chapman et al. 2004; Daly-Engel et al. 2010; Conrath and Musick 2012; Bernal et al. 2015). For example, multiple paternity has been documented in many shark and ray species (e.g., Chevolut et al. 2007; Daly-Engel et al. 2010; Byrne and Avise 2012), and whether multiple paternity assists in maintaining genetic diversity is a subject of debate (Zeh and Zeh 2003; Karl 2008). Theoretical studies argue that under natural conditions, an increase in multiple paternity will reduce effective population size ( $N_e$ ) and consequently the genetic diversity (Ramakrishnan et al. 2004). On the other hand, multiple matings and sperm storage events could increase the  $N_e$  after a bottleneck (Karl 2008). In addition, Byrne and Avise (2012) posited the “sperm storage” theory, in which females mating with multiple males promotes competition among the sperm, which might lead either to improved fertilization success or to better genes for their zygotes.

Parthenogenesis, or “virgin birth” (the production of offspring without fertilization by a male), has been documented in sharks and rays (e.g., Chapman et al. 2007; Portnoy et al. 2014a, b; Fields et al. 2015). Although it is difficult to estimate the possible effects on wild populations, this reproductive strategy can be advantageous because of its adaptive significance (Booth and Schuett 2011). In particular, at low population densities, when females undergo fertilization failure because of the difficulty in finding males, facultative parthenogenesis could have adaptive significance (Fields et al. 2015). On the other hand, due to elevated homozygosity, parthenogenesis is believed to increase inbreeding, reduce fitness, increase the likelihood of the fixation of deleterious alleles, and consequently increase the probability of extinction (Watts et al. 2006; Chapman et al. 2007; Booth and Schuett 2011). The first report of facultative parthenogenesis was just recently documented in wild populations of smalltooth sawfish (*Pristis pectinata*, Pristidae), with five individuals reportedly close to or in complete homozygosity (Fields et al. 2015).

Another important reproductive strategy that can affect genetic diversity is natal philopatry, which is defined by the return of a far-ranging individual to its exact birthplace (Chapman et al. 2015). For instance, sex-biased dispersion, such as male-biased dispersal and female philopatry to a coastal nursery has been documented for the great white shark (*Carcharodon carcharias*, Lamnidae; Pardini et al. 2001) and bonnethead (*Sphyrna tiburo*, Sphyrnidae; Portnoy et al. 2015). According to Portnoy et al. (2015), sex-biased dispersion can facilitate sorting of locally adaptive variation, with the dispersion of one sex facilitating the

movement of potentially adaptive variation among locations and environments.

## Effects of overfishing on the evolutionary process

Overfishing may impact evolutionary processes mainly by changing body size and by promoting early sexual maturity; additionally, overfishing affects bioeconomics and macroecological patterns (Belgrano and Fowler 2013; Heino et al. 2015). For sharks, only a few studies based exclusively on phenotypic traits have shown direct evidence of the influence of fisheries on evolution. Walker et al. (1998) reported changes in the growth rate of gummy sharks (*Mustelus antarcticus*, Triakidae) caused by length-selective fishing mortality. Furthermore, Clarke et al. (2013) reported that the median lengths of silky sharks (*Carcharhinus falciformis*, Carcharhinidae) and oceanic whitetip sharks (*Carcharhinus longimanus*, Carcharhinidae) decreased significantly in the Pacific Ocean between 1995 and 2010. Though these phenotypic changes may indicate an evolutionary response to overfishing, the possible genetic consequences are unknown. Recently, Gallagher et al. (2014) suggested that the ecological, behavioral, and physiological adaptations of hammerhead sharks (Sphyrnidae) that once promoted evolutionary success are now maladaptive under current levels and modes of exploitation. For example, the high agility that supports their prey capture strategy of burst swimming behavior also results in a high rate (60–80%) of at-vessel and post-release mortality (Gallagher et al. 2014). However, though no studies of direct fisheries-induced evolution of shark and ray species exist, the examples cited above suggest that evolutionary traits and unique adaptations can be affected by overexploitation.

## Broad geographic distribution

Many sharks and rays are widely distributed and highly mobile (e.g., the shortfin mako *Isurus oxyrinchus*, Lamnidae, and the pelagic stingray *Pteroplatytrygon violacea*, Dasyatidae), features that make it difficult to sample enough individuals from different locations to allow for the identification of discrete populations over the entire distribution of the species. For example, at least 150 shark species regularly migrate across national boundaries, and ¼ of threatened shark species have ranges that include at least 18 countries (Dulvy et al. 2014).

Unlike bony fishes and other marine organisms, shark and ray species do not have a planktonic larval stage with dispersal via ocean currents. Instead, their dispersal is mediated entirely by the active movement of adult individuals. In general, large migratory and oceanic species such as the blue shark (*Prionace glauca*, Carcharhinidae) tend to present more homogeneous populations (Taguchi et al. 2015),

whereas smaller, more coastal species, such as the spot-tail shark (*Carcharhinus sorrah*, Carcharhinidae), commonly exist in isolated populations (Giles et al. 2014). These coastal sharks and rays tend to experience more obstacles, such as marine barriers and oceanographic heterogeneity. Therefore, assessing the extant genetic diversity throughout their distribution is imperative to avoid local gene pool erosion. For example, the blue shark is likely the most wide-ranging species of shark and the most heavily fished shark species in the world, but only a few range-limited studies (e.g., Ovenden et al. 2009; King et al. 2015; Taguchi et al. 2015; Li et al. 2016) have attempted to describe the genetic structure and diversity of this species. These studies did not indicate any genetic differentiation in the Pacific and Indo-Pacific regions, a result that was attributed mainly to the blue shark's high agility. Nevertheless, the authors indicated the need for cooperative fisheries management among different countries, even though management programs do not have any genetic data available along the broad distribution of the blue shark. Consequently, there is a considerable gap to obtaining a holistic view of the population structure of this species. Moreover, it will not be possible to detect negative changes and reductions in genetic diversity unless the major distribution points of sharks and rays are studied.

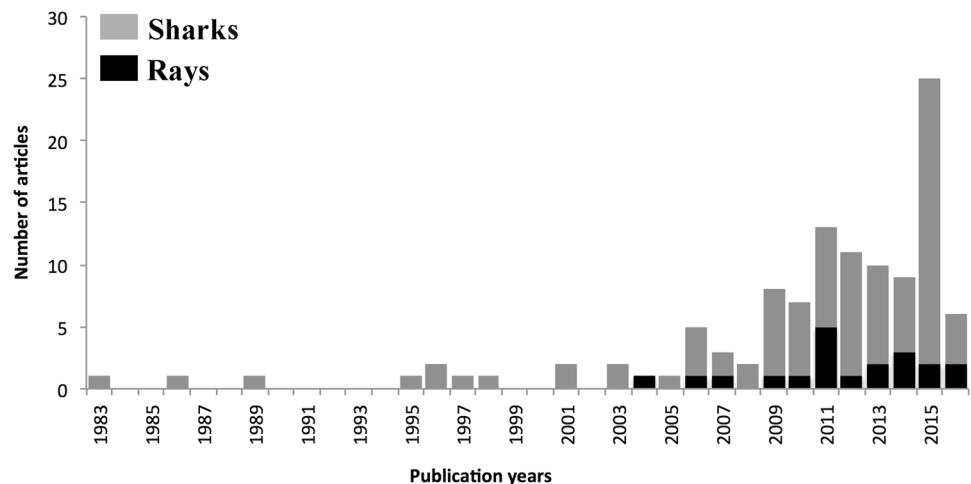
Although there are currently no global genetic population studies of the blue shark, a few widely distributed shark species, such as the scalloped hammerhead (*Sphyrna lewini*, Sphyrnidae), the whale shark (*Rhincodon typus*, Rhincodontidae), the sand tiger shark (*Carcharias taurus*, Odontaspidae), the sandbar shark (*Carcharhinus plumbeus*, Carcharhinidae), the dusky shark (*Carcharhinus obscurus*, Carcharhinidae), the copper shark (*Carcharhinus brachyurus*, Carcharhinidae) and the silky shark (*Carcharhinus falciformis*, Carcharhinidae), have been studied globally.

Although these studies are incipient and some of them report only limited genetic markers, they demonstrate that different populations of single shark species are genetically discrete entities worldwide that may have different levels of genetic diversity (Duncan et al. 2006; Castro et al. 2007; Ahonen et al. 2009; Portnoy et al. 2010; Benavides et al. 2011b; Clarke et al. 2015). Therefore, each discrete shark population should be managed separately to reduce the risk of depleting their genetic resources.

### Few studies describe the genetic diversity of sharks and rays

Despite an increase in the number of genetics studies in the last decade (Fig. 1), currently, only ~10% of shark and ray species have been investigated in terms of their population genetic structure, genetic diversity and demographic history. For example, no population genetics study performed to date has aimed at describing the genetic diversity and identifying the discrete populations along the distribution range of the pelagic stingray, a cosmopolitan species frequently caught as bycatch in pelagic longline fisheries around the world (Forselledo et al. 2008). The same is true for species with narrow geographic distributions and species that are critically endangered, such as the daggernose shark (*Isogomphodon oxyrinchus*, Carcharhinidae) (Lessa et al. 2016). Furthermore, the majority of studies represent the first genetic examination of a particular species (Dudgeon et al. 2012), although there are a few exceptions, such as studies in which some species, including the white shark and the scalloped hammerhead, are re-examined. The absence of genetic evaluations of many shark species complicates the transition from the current overexploitation and short- and long-term conservation.

**Fig. 1** Numbers of articles published between 1983 and 2016 that describe the genetic diversity of shark and ray species





## The effects of fishing on the genetic diversity of shark and ray populations

Despite the negative relationship between overexploited populations and genetic diversity, the use of genetics in the management plans of threatened species remains a challenge (Laikre 2010). The effects of population declines on marine fishes in terms of decreased genetic diversity have recently drawn attention. Many authors claim the need for an application of genetic diversity metrics in fisheries management plans because of the harmful consequences of inbreeding, the loss of genetic diversity, the loss of evolutionary potential and changes in population structures of species (Kenchington et al. 2003; Allendorf et al. 2008; Frankham 2010; Laikre et al. 2010b; Hoban et al. 2013a, b).

Studies have used historical and contemporary samples to address the question of how fisheries affect the genetic diversity (mtDNA and microsatellites) of fish and marine mammal stocks (Hauser et al. 2002; Pichler and Baker 2000). For example, the heterozygosity (microsatellites), number of alleles per locus, and  $N_e$  of the New Zealand snapper (*Pagrus auratus*, Sparidae) declined between 1950 and 1988 after the creation of a fishery for this population (Hauser et al. 2002). McCusker and Bentzen (2010) found a positive relationship between genetic diversity (mtDNA and microsatellites) and fish stock abundance. Meanwhile, Pinsky and Palumbi (2014) compiled data for 140 species of marine fishes across 11,049 loci and clearly showed a reduction in allelic richness in 9 overfished stocks among 12 genera and families. According to Allendorf et al. (2008), uncontrolled harvesting may lead to genetic impacts, such as the alteration of population subdivision, loss of genetic variation, and selective genetic changes. To date, no study has assessed the direct relationship between abundance and genetic diversity metrics (i.e., nucleotide and haplotype diversity, observed heterozygosity and allelic richness) in shark and ray species. Nevertheless, many species that are under intense fishing pressure have shown low values of genetic diversity, as indicated mainly by nucleotide diversity and observed heterozygosity (Table 1; Fig. 3). Although the low genetic diversity of shark and ray species is probably more associated with bottlenecks and the slow rate of molecular evolution, regardless of whether the cause is historical or cotemporary, the current levels of genetic diversity should be taken into account for conservation policies (Martin et al. 1992; Hoelzel et al. 2006; O'Brien et al. 2013; Allendorf et al. 2013).

Traditional management plans seek to increase the number of individuals in different populations (Hauser and Carvalho 2008). However, even large populations (census

population size— $N_c$ ) may face a substantial loss of genetic variation because the  $N_e$ , which determines the strength of genetic drift in a population, is often much smaller than  $N_c$  in overexploited marine fish species (Ryman et al. 1995; Allendorf et al. 2008; Hare et al. 2011). For example, millions of individuals may be equivalent to a  $N_e$  of only hundreds or thousands (Ryman et al. 1995; Hauser et al. 2002). Therefore, as  $N_e$  decreases, genetic drift erodes genetic variation, increasing the probability of fixation of deleterious alleles and reducing the resilience of overfished species (Hare et al. 2011). Although  $N_e$  is one of the most important genetic parameters of wildlife populations, estimations of contemporary  $N_e$  are highly limited for shark and ray species (Table 2). Several studies have shown  $N_e$  values lower than 500 for some shark and ray species, such as the zebra shark (*Stegostoma fasciatum*, Stegostomidae) (Dudgeon and Ovenden 2015) and the smalltooth sawfish (Chapman et al. 2011) (Table 2). Recent studies suggest that at a minimum, an  $N_e$  of  $\geq 100$  individuals is suggested to prevent short-term genetic erosion and a 10% loss of fitness over five generations, whereas the minimal threshold to retain long-term evolutionary potential is at least 1000 individuals (Frankham 2014). The  $N_e$  values estimated for elasmobranch populations suggest the need for long-term monitoring and can be informative for management decisions. Therefore, we believe that  $N_e$  is an important genetic parameter to be applied to future fisheries management plans because of its importance in assessing the level of genetic diversity (Willoughby et al. 2015) and because of its role as a proxy of abundance [(IUCN Red List criterion C) (Ovenden et al. 2016)], as determined by previous studies (e.g., Dudgeon et al. 2012; Frankham 2014; Ovenden et al. 2016).

## Conservation policies have overlooked and neglected shark and ray genetic diversity

Many shark and ray species are highly migratory and overexploited; therefore, they may require international management efforts such as bilateral and multilateral fisheries management agreements (Musick et al. 2000; Herndon et al. 2010). The conservation status and management measures for many shark and ray species have been evaluated by international conservation organizations, and the policies for conservation are mainly based on retention bans, finning bans and trading bans intended to promote the recovery of shark populations (Tolotti et al. 2015). Like many other international policies these organizations do not have any initiatives that deal specifically with genetic diversity.

Recently, a consortium representing various organizations of experts, The Global Sharks and Rays Initiative

**Table 1** Genetic diversity metrics for shark and ray species

Species*	Regions**	Molecular markers***	He	Ho	Ra	<i>h</i>	$\pi$	References	IUCN
<b>Sharks</b>									
<i>Squatina argentina</i> (Squatiniidae)	Brazil	A	–	0.2860 (4)	–	–	–	Solé-Cava et al. (1983)	EN
<i>Squatina argentina</i> (Squatiniidae)	Brazil	A	–	0.3670 (4)	–	–	–	Solé-Cava et al. (1983)	EN
<i>Mustelus antarcticus</i> (Triakidae)	Australia	A	–	0.0057 (32)	–	–	–	MacDonald (1988)	LC
<i>Carcharhinus tilstoni</i> (Carcharhinidae)	Australia	A	–	0.0370 (13)	–	–	–	Lavery and Shackle (1989)	LC
<i>Carcharhinus sorrah</i>	Australia	A	–	0.0350 (13)	–	–	–	Lavery and Shackle (1989)	NT
<i>Carcharhinus plumbeus</i>	NAO, GM	A/RFLP	–	0.0050 (27)	–	–	0.0004	Heist et al. (1995)	VU
<i>Isurus oxyrinchus</i>	Global	RFLP	–	–	–	0.75	0.0035	Heist et al. (1996a)	VU
<i>Rhizoprionodon terraenovae</i> (Carcharhinidae)	NAO, GM	RFLP	–	–	–	0.71	0.0013	Heist et al. (1996b)	LC
<i>Squatina californica</i> (Squatiniidae)	California	A/RFLP	–	0.0056 (7)	–	–	–	Gaida (1997)	NT
<i>Mustelus antarcticus</i>	Australia	A/RFLP	–	0.0990 (28)	–	0.53	0.0016	Gardner and Ward (1998)	LC
<i>Carcharodon carcharias</i>	SA, Australia, NZ	CR mtDNA/MS	–	0.68 (5)	–	–	0.0203	Pardini et al. (2001)	VU
<i>Negaprion brevirostris</i> (Carcharhinidae)	WAO	MS	0.79	0.77 (15)	–	–	–	Feldheim et al. (2001)	NT
<i>Carcharhinus limbatus</i> (Carcharhinidae)	NAO, GM	CR mtDNA	–	–	–	0.71	0.0011	Keeney et al. (2003)	NT
<i>Isurus oxyrinchus</i>	Global	MS	0.87	0.85 (4)	–	–	–	Schrey and Heist (2003)	VU
<i>Carcharhinus limbatus</i>	NAO, GM, CS	CR mtDNA/MS	0.5	0.50 (8)	–	0.81	0.0021	Keeney et al. (2005)	NT
<i>Carcharhinus limbatus</i>	Global	CR mtDNA	–	–	–	0.84	0.0041	Keeney and Heist (2006)	NT
<i>Carcharias taurus</i>	SA, Australia	CR mtDNA/AFLP	–	–	–	0.39	0.0025	Stow et al. (2006)	VU
<i>Sphyrna lewini</i>	Global	CR mtDNA	–	–	–	0.80	0.0013	Duncan et al. (2006)	EN
<i>Cetorhinus maximus</i> (Cetorhinidae)	Global	CR mtDNA	–	–	–	0.72	0.0013	Hoelzel et al. (2006)	VU
<i>Rhincodon typus</i>	Global	CR mtDNA	–	–	–	0.97	0.0110	Castro et al. (2007)	VU
<i>Triakis semifasciata</i> (Triakidae)	California	CR mtDNA/ISSR	–	–	–	–	0.0067	Lewallen et al. (2007)	LC
<i>Somniosus microcephalus</i> (Somniosidae)	NPO, SO, NA	CytB mtDNA	–	–	–	0.78	0.0022	Murray et al. (2008)	NT

**Table 1** (continued)

Species*	Regions**	Molecular markers***	He	Ho	Ra	<i>h</i>	$\pi$	References	IUCN
<i>Somniosus pacificus</i> (Somniosidae)	NPO, SO, NA	CytB mtDNA	–	–	–	0.82	0.0037	Murray et al. (2008)	DD
<i>Somniosus antarcticus</i> (Somniosidae)	NPO, SO, NA	CytB mtDNA	–	–	–	0.67	0.0023	Murray et al. (2008)	DD
<i>Negaprion brevirostris</i>	PAO	CR mtDNA/MS	0.81	0.73 (9)	8.5	0.78	0.0059	Schultz et al. (2008)	NT
<i>Negaprion acutidens</i> (Carcharhinidae)	IPO	CR mtDNA/MS	0.67	0.58 (9)	2.6	0.28	0.0006	Schultz et al. (2008)	VU
<i>Carcharias taurus</i>	Global	CR mtDNA/MS	0.74	0.65 (6)	3.3	0.73	0.00003	Ahonen et al. (2009)	VU
<i>Galeorhinus galeus</i> (Triakidae)	Global	CR mtDNA	–	–	–	0.92	0.0071	Chabot and Allen (2009)	VU
<i>Stegostoma fasciatum</i>	IWPO	ND4 mtDNA/MS	0.73	–	–	0.75	0.0014	Dudgeon et al. (2009)	VU
<i>Carcharodon carcharias</i>	PO	CR mtDNA	–	–	–	0.79	0.0034	Jorgensen et al. (2009)	VU
<i>Prionace glauca</i>	IAA	CR mtDNA	–	–	–	0.92	0.0080	Ovenden et al. (2009)	NT
<i>Carcharhinus sorrah</i>	IAA	CR mtDNA	–	–	–	0.60	0.0030	Ovenden et al. (2009)	NT
<i>Carcharhinus obscurus</i>	IAA	CR mtDNA	–	–	–	0.60	0.0050	Ovenden et al. (2009)	VU
<i>Sphyrna lewini</i>	IAA	CR mtDNA	–	–	–	0.61	0.0098	Ovenden et al. (2009)	EN
<i>Sphyrna lewini</i>	WAO	CR mtDNA	–	–	–	0.38	0.0013	Chapman et al. (2009)	EN
<i>Rhincodon typus</i>	Global	MS	0.68	0.66 (8)	9	–	–	Schmidt et al. (2009)	VU
<i>Carcharhinus plumbeus</i>	Global	CR mtDNA/MS	0.81	0.81 (8)	11.1	0.96	0.0048	Portnoy et al. (2010)	VU
<i>Mustelus schmitti</i>	SAO	CytB mtDNA	–	–	–	0.23	0.0015	Pereyra et al. (2010)	EN
<i>Chiloscyllium plagiosum</i> (Hemiscylliidae)	Japan	CytB mtDNA	–	–	–	0.72	0.0025	Fu et al. (2010)	NT
<i>Carcharhinus leucas</i> (Carcharhinidae)	WAO	CR mtDNA/MS	0.84	0.83 (5)	–	0.51	0.0012	Karl et al. (2011)	NT
<i>Squalus acanthias</i> (Squalidae)	Global	ND2 mtDNA/MS	0.60	0.61 (8)	5.6	0.84	0.0086	Veríssimo et al. (2010)	VU
<i>Squalus mitsukurii</i> (Squalidae)	HA	CR mtDNA/MS	0.56	0.57 (8)	8.4	0.54	0.0010	Daly-Engel et al. (2010)	DD
<i>Rhizoprionodon porosus</i> (Carcharhinidae)	WAO	CR mtDNA	–	–	–	0.88	0.0028	Mendonça et al. (2011)	LC
<i>Sphyrna lewini</i>	EPO	CR mtDNA/MS	0.79	0.77 (15)	–	0.53	0.0011	Nance et al. (2011)	EN
<i>Rhizoprionodon acutus</i> (Carcharhinidae)	EA, Indonesian	ND4 mtDNA/MS	0.63	0.48 (6)	–	0.82	0.0034	Ovenden et al. (2011)	LC

**Table 1** (continued)

Species*	Regions**	Molecular markers***	He	Ho	Ra	<i>h</i>	$\pi$	References	IUCN
<i>Sphyrna lewini</i>	EA, Indonesian	ND4 mtDNA/MS	0.75	0.69 (8)	–	0.34	0.0018	Ovenden et al. (2011)	EN
<i>Carcharhinus brachyurus</i>	Global	CR mtDNA	–	–	–	0.76	0.0160	Benavides et al. (2011a)	NT
<i>Carcharhinus obscurus</i>	Global	CR mtDNA	–	–	–	0.83	0.0050	Benavides et al. (2011b)	VU
<i>Centroscymnus coelolepis</i> (Somniosidae)	EA	CR mtDNA/MS	0.77	0.77 (8)	8.1	0.65	0.0018	Veríssimo et al. (2011)	NT
<i>Carcharhinus leucas</i>	Australia	ND4 mtDNA/MS	0.77	0.77 (3)	–	0.48	0.0791	Tillet et al. (2012b)	NT
<i>Carcharhinus limbatus</i>	Brazil	CR mtDNA	–	–	–	0.80	0.0021	Sodré et al. (2012)	NT
<i>Ginglymostoma cirratum</i>	WAO	CR mtDNA/MS	0.58	0.58 (8)	–	0.48	0.0008	Karl et al. (2012)	DD
<i>Carcharodon carcharias</i>	Australia	CR mtDNA/MS	0.68	0.68 (6)	–	0.88	0.0086	Blower et al. (2012)	VU
<i>Sphyrna lewini</i>	MP, GM	CR mtDNA/MS	0.53	0.62 (5)	4.0	0.49	0.0110	Castillo-Olguín et al. (2012)	EN
<i>Carcharhinus amboinensis</i> (Carcharhinidae)	Northern Australia	ND/CR mtDNA	–	–	–	0.78	0.0065	Tillet et al. (2012a)	DD
<i>Centrophorus squamosus</i> (Centrophoridae)	Entire distribution range	ND2 mtDNA/MS	–	0.74 (6)	12.4	0.57	0.0018	Veríssimo et al. (2012)	VU
<i>Triaenodon obesus</i> (Carcharhinidae)	IPO	CR mtDNA	–	–	–	0.55	0.0021	Whitney et al. (2012)	NT
<i>Sphyrna lewini</i>	Global	MS	0.77	0.71 (13)	7.6	–	–	Daly-Engel et al. (2012)	EN
<i>Mustelus antarcticus</i>	IPO, Australasia	ND2/ND4/CR mtDNA	–	–	–	0.46	0.0008	Boomer et al. (2012)****	LC
<i>Mustelus lenticalatus</i> (Triakidae)	IPO, Australasia	ND2/ND4/CR mtDNA	–	–	–	0.53	0.0009	Boomer et al. (2012)****	LC
<i>Rhizoprionodon terraenovae</i>	GM	AFLP	0.32	–	–	–	–	Suarez-Moo et al. (2013)	LC
<i>Carcharhinus brevipinna</i> (Carcharhinidae)	Southern IPO	ND4 mtDNA	–	–	–	0.68	0.0013	Geraghty et al. (2013)	NT
<i>Rhizoprionodon lalandii</i> (Carcharhinidae)	WAO	CR mtDNA	–	–	–	0.88	0.0028	Mendonça et al. (2013)	DD
<i>Rhizoprionodon porosus</i>	–	CR mtDNA	–	–	–	0.88	0.0041	Tavares et al. (2013)	LC
<i>Carcharhinus porosus</i> (Carcharhinidae)	–	CR mtDNA	–	–	–	0.88	0.0044	Tavares et al. (2013)	DD
<i>Carcharhinus limbatus</i>	–	CR mtDNA	–	–	–	0.54	0.0022	Tavares et al. (2013)	NT
<i>Sphyrna tudes</i> (Sphyrnidae)	–	CR mtDNA	–	–	–	0.20	0.0005	Tavares et al. (2013)	VU



**Table 1** (continued)

Species*	Regions**	Molecular markers***	He	Ho	Ra	<i>h</i>	$\pi$	References	IUCN
<i>Carcharhinus falciformis</i>	IPO	CR mtDNA	–	–	–	0.48	0.0009	Galván-Tirado et al. (2013)	NT
<i>Carcharhinus melanopterus</i> (Carcharhinidae)	FP	MS	0.58	0.57 (17)	–	–	–	Mourier and Planes (2013)	NT
<i>Negaprion acutidens</i>	FP	MS	0.63	0.62 (16)	–	–	–	Mourier et al. (2013)	VU
<i>Carcharhinus melanopterus</i>	FP	MS	–	0.49 (11)	–	–	–	Vignaud et al. (2013)	NT
<i>Carcharhinus acronotus</i> (Carcharhinidae)	US Atlantic, GM	CR mtDNA/MS	0.66	(23)	9.7	0.85	0.0006	Portnoy et al. (2014b)	NT
<i>Carcharhinus melanopterus</i>	FP	CR mtDNA/MS	0.55	0.54 (14)	5.2	0.46	0.0011	Vignaud et al. (2014b)	NT
<i>Alopias pelagicus</i> (Alopiidae)	PO	COI mtDNA/MS	0.64	0.59 (7)	–	0.57	0.0031	Cardeñosa et al. (2014)	VU
<i>Rhincodon typus</i>	IPO	CytB CR mtDNA/MS	0.63	0.62 (14)	4.5	0.92	0.0120	Vignaud et al. (2014a)	VU
<i>Carcharhinus sorrah</i>	IPO	CR mtDNA	–	–	–	–	0.0025	Giles et al. (2014)	NT
<i>Carcharhinus plumbeus</i>	Australia	ND4 mtDNA	–	–	–	0.28	0.0009	Geraghty et al. (2014)	VU
<i>Carcharhinus obscurus</i>	Australia	ND4 mtDNA	–	–	–	0.52	0.0012	Geraghty et al. (2014)	VU
<i>Pseudocarcharias kamoharai</i> (Pseudocarchariidae)	AO, SIO	CR mtDNA	–	–	–	0.63	0.0017	Ferretti et al. (2015)	NT
<i>Carcharhinus falciformis</i>	Global	CR mtDNA	–	–	–	0.93	0.0032	Clarke et al. (2015)	NT
<i>Mustelus henlei</i> (Triakidae)	Northeastern PO	CR mtDNA/MS	0.56	0.45 (6)	4.1	0.77	0.0040	Chabot et al. (2015)	LC
<i>Sphyrna tiburo</i>	NAO	CR mtDNA	–	–	–	0.93	0.0032	Escatel-Luna et al. (2015)	LC
<i>Prionace glauca</i>	North PO	MS	0.61	0.60 (14)	6.7	–	–	King et al. (2015)	NT
<i>Sphyrna lewini</i>	Colombia	CR mtDNA/MS	0.64	0.56 (15)	–	0.58	0.0012	Quintanilha et al. (2015)	EN
<i>Mustelus henlei</i>	GC	CR mtDNA/MS	0.68	0.71 (12)	–	0.84	0.0033	Sandoval-Castillo and Beheregaray (2015)	LC
<i>Prionace glauca</i>	IPO	CytB mtDNA	–	–	–	0.80	0.0021	Taguchi et al. (2015)	NT
<i>Notorynchus cepedianus</i> (Hexanchidae)	California	MS	0.53	0.41 (7)	–	–	–	Larson et al. (2015)	DD
<i>Carcharodon carcharias</i>	Northeastern PO	CR mtDNA	–	–	–	0.77	0.0018	Oñate-González et al. (2015)	VU
<i>Triakis semifasciata</i>	California, BJ	CR mtDNA/MS	0.80	0.81 (15)	4.9	–	–	Barker et al. (2015)	LC
<i>Galeorhinus galeus</i>	SA	MS	0.63	0.65 (12)	–	–	–	Bitalo et al. (2015)	VU
<i>Mustelus mustelus</i> (Triakidae)	SA	MS	0.53	0.68 (12)	–	–	–	Bitalo et al. (2015)	VU

**Table 1** (continued)

Species*	Regions**	Molecular markers***	He	Ho	Ra	<i>h</i>	$\pi$	References	IUCN
<i>Carcharodon carcharias</i>	SA	CR mtDNA/MS	0.63	0.67 (14)	–	0.21	0.0027	Andreotti et al. (2015)	VU
<i>Carcharhinus amblyrhynchos</i> (Carcharhinidae)	Australia	MS	0.78	0.79 (15)	6.6	–	–	Momigliano et al. (2015)	NT
<i>Carcharhinus limbatus</i>	AP	CR mtDNA/MS	0.75	0.61 (20)	–	0.33	0.0007	Spaet et al. (2015)	NT
<i>Sphyrna lewini</i>	AP	CR mtDNA/MS	0.76	0.72 (20)	–	0.48	0.0001	Spaet et al. (2015)	EN
<i>Carcharhinus sorrah</i>	AP	CR mtDNA/MS	0.65	0.62 (20)	–	0.39	0.0012	Spaet et al. (2015)	NT
<i>Rhizoprionodon acutus</i>	AP	CR mtDNA/MS	0.56	0.53 (20)	–	0.70	0.0013	Spaet et al. (2015)	LC
<i>Galeorhinus galeus</i>	Global	MS	0.43	0.40 (11)	3.9	–	–	Chabot (2015)	VU
<i>Galeorhinus galeus</i>	SPO	CR mtDNA/MS	0.61	0.55 (8)	4.8	0.75	0.0010	Hernandez et al. (2015)	VU
<i>Carcharodon carcharias</i>	Northwest AO, SA	CR mtDNA/MS	0.67	0.56 (14)	8.5	0.74	0.0045	O’Leary et al. (2015)	VU
<i>Scyliorhinus canicula</i> (Scyliorhinidae)	MS	COI mtDNA/MS	0.59	0.57 (12)	5.3	0.81	0.0032	Kousteni et al. (2015)	LC
<i>Negaprion brevirostris</i>	WAO	CR mtDNA/MS	0.79	0.78 (9)	–	0.83	0.0020	Ashe et al. (2015)	NT
<i>Squatina guggenheim</i> (Squatinae)	SAO	CytB/ITS2 mtDNA	–	–	–	0.38/0.26	0.0110/0.0070	Garcia et al. (2015)	EN
<i>Centroscymnus coelolepis</i>	Australia, SA, European	CR mtDNA/MS	0.81	(11)	8.3	0.65	0.0018	Catarino et al. (2015)	NT
<i>Sphyrna tiburo</i>	Florida, GM	CR mtDNA/SNPs	–	–	–	0.88	0.0020/0.3129	Portnoy et al. (2015)	VU
<i>Galeocerdo cuvier</i> (Carcharhinidae)	Global	CR mtDNA/MS	0.65	0.64 (10)	8.2	0.82	0.0027	Bernard et al. (2016)	NT
<i>Carcharhinus isodon</i> (Carcharhinidae)	US waters WAO	CR mtDNA/MS	0.67	(16)	9.0	0.16	0.0002	Portnoy et al. (2016)	LC
<i>Mustelus mustelus</i>	South IO, AO	ND4 mtDNA/MS	0.50	0.50 (8)	2.1	0.47	0.0010	Maduna et al. (2016)	VU
<i>Carcharhinus longimanus</i>	IO, AO	CR mtDNA	–	–	–	0.60	0.0013	Camargo et al. (2016)	VU
<b>Rays</b>									
<i>Pseudobatos productus</i> (Rhinobatidae)	GC	CR mtDNA	–	–	–	0.77	0.0119	Sandoval-Castillo et al. (2004)	NT
<i>Raja clavata</i> (Rajidae)	NA, MS	CytB mtDNA/MS	0.67	0.65 (5)	–	0.50	0.0060	Chevolot et al. (2006)	NT
<i>Amblyraja radiata</i> (Rajidae)	NAO	CytB mtDNA	–	–	–	0.80	0.0090	Chevolot et al. (2007)	VU
<i>Aetobatus narinari</i> (Aetobatidae)	IPO	CytB/CR mtDNA	–	–	–	0.80/0.81	0.0126/0.0085	Schluessel et al. (2010)	NT
<i>Urobatis halleri</i> (Urotrygonidae)	SC, GC	MS	0.24	(7)	–	–	–	Plank et al. (2010)	LC

**Table 1** (continued)

Species*	Regions**	Molecular markers***	He	Ho	Ra	<i>h</i>	$\pi$	References	IUCN
<i>Pristis pectinata</i>	NAO	MS	0.82	0.84 (8)	–	–	–	Chapman et al. (2011)	CR
<i>Pristis zijsron</i> (Pristidae)	Australia	CR mtDNA	–	–	–	0.56	0.0036	Phillips et al. (2011)	CR
<i>Pristis clavata</i> (Pristidae)	Australia	CR mtDNA	–	–	–	0.49	0.0040	Phillips et al. (2011)	EN
<i>Pristis pristis</i> (Pristidae)	Australia	CR mtDNA	–	–	–	0.65	0.0044	Phillips et al. (2011)	CR
<i>Raja straeleni</i> (Rajidae)	Eastern AO, MS, WIO	CR mtDNA	–	–	–	0.67	0.0025	Parsolini et al. (2011)	DD
<i>Rhinoptera steindachneri</i> (Rhinopteridae)	BC	ND2 mtDNA	–	–	–	0.08	0.0026	Sandoval-Castillo and Rocha-Olivares (2011)	NT
<i>Raja clavata</i>	Eastern AO, MS, WIO	CR mtDNA	–	–	–	0.55	0.0023	Parsolini et al. (2011)	NT
<i>Bathytoshia brevicaudata</i> (Dasyatidae)	IPO	CR mtDNA	–	–	–	0.78	0.0009	Le Port and Lavery (2012)	LC
<i>Paratrygon aier-eba</i> (Potamotrygonidae)	Amazon	ATPase 6	–	–	–	0.99	0.0349	Frederico et al. (2012)	DD
<i>Neotrygon kuhlii</i> (Dasyatidae)	CTR	COI mtDNA	–	–	–	0.76	0.0060	Arlyza et al. (2013)	DD
<i>Hemitrygon akajei</i> (Dasyatidae)	PO	AFLP	0.23	–	–	–	–	Li et al. (2013)****	NT
<i>Zapteryx exasperata</i> (Trygonorrhinidae)	NMP	ND2 CR mtDNA	–	–	–	0.76/0.39	0.0013/0.0007	Castillo-Páez et al. (2014)	DD
<i>Aetobatus narinari</i>	GM, CS	CytB mtDNA/MS	0.74	0.73 (10)	9.6	0.60	0.0023	Sellas et al. (2015)	NT
<i>Aetobatus narinari</i>	Florida, GM	MS	0.70	0.66 (8)	–	–	–	Newby et al. (2014)	NT
<i>Hemitrygon akajei</i>	PO	CR mtDNA	–	–	–	0.94	0.0069	Li et al. (2015)	NT
<i>Pristis pristis</i>	Australia	Mitogenome	–	–	–	0.92	0.0011	Feutry et al. (2015)	CR
<i>Rhynchobatus australiae</i> (Rhino-nidae)	IPO	CR mtDNA	–	–	–	0.85	0.0061	Giles et al. (2016)****	LC
<i>Raja polystigma</i> (Rajidae)	MS	CR COI 16S mtDNA/MS	0.55	0.51 (7)	2.8	0.94	0.0032	Frodella et al. (2016)****	LC
<i>Raja montagui</i> (Rajidae)	MS	CR COI 16S mtDNA/MS	0.65	0.55 (7)	3.3	0.25	0.0002	Frodella et al. (2016)	LC

*He* expected heterozygosity, *Ho* observed heterozygosity (with number of alleles in parentheses), *Ra* allelic richness, *h* haplotype diversity,  $\pi$  nucleotide diversity

\*The systematics and nomenclatural arrangement follows a major recent revision summarized in Last et al. (2016)

\*\*Geographical regions SA South African, NZ New Zealand, WAO Western Atlantic Ocean, NAO Northwest Atlantic Ocean, GM Gulf of Mexico, CS Caribbean Sea, NPO North Pacific Ocean, SO Southern Ocean, NA North Atlantic Ocean, PAO Pacific and Atlantic Oceans, IPO Indo-Pacific Ocean, IWPO Indo-West Pacific Ocean, PO Pacific Ocean, IAA Indo-Australian Archipelago, SAO Southwest Atlantic Ocean, HA Hawaiian Archipelago, EPO Eastern Pacific Ocean, EA Eastern Australian, MP Mexican Pacific, SIO Southwest Indian Ocean, GC Gulf of Mexico, AP Arabian Peninsula, SPO South Pacific Ocean, MS Mediterranean Sea, IO Indian Ocean, BJ Baja California, WIO Western Indian Ocean, SC Southern California, CTR Coral Triangle Region, NMP Northern Mexican Pacific, FP French Polynesia

\*\*\*Molecular Markers A allozymes, RFLP restriction fragment length polymorphism, AFLP amplified fragment length polymorphism, SNP single-nucleotide polymorphism, MS microsatellites, CR mtDNA control region mitochondrial DNA, CytB mtDNA cytochrome b mitochondrial DNA, ND4 mtDNA NADH dehydrogenase subunit 4 mitochondrial DNA, ND2 mtDNA NADH dehydrogenase subunit 2 mitochondrial DNA, COI mtDNA Cytochrome oxidase subunit 1 mitochondrial DNA, 16S mtDNA 16S RNA ribosomal mitochondrial DNA, MS Microsatellites, ITS2 internal transcribed spacer 2 nuclear DNA

**Table 1** (continued)

\*\*\*Concatenated data

**Table 2** Contemporary effective population size ( $N_e$ ) parameters for shark and ray species

Species	Regions*	Sample size	Loci	$N_e$ (CI 95%)	$N_e/N_c$	Method**	References
<b>Sharks</b>							
<i>Carcharhinus plumbeus</i>	DEL/ES	481/506	8	4890/2709	0.5 (DEL)	LD	Portnoy et al. (2009)
<i>Pristis pectinata</i>	SWFL	137	8	230–250 (142–955)	NA	M-ratio	Chapman et al. (2011)
<i>Carcharodon carcharias</i>	Australia	97	6	1512 (122–∞)	NA	LD	Blower et al. (2012)
<i>Carcharodon carcharias</i>	NWA/SA	35/131	14	32.2 (25.2–42.6)/346.6 (220.2–728.1)	NA	LD	O’Leary et al. (2014)
<i>Stegostoma fasciatum</i>	Australia	105	14	377 (274–584)	0.82	LD	Dudgeon and Ovenden (2015)
<i>Prionace glauca</i>	NPO	844	14	5468 (2802–52,352)	$2 \times 10^{-3}$ – $10^{-4}$	LD	King et al. (2015)
<i>Carcharodon carcharias</i>	SA	302	14	333 (247–487)	0.76	LD	Andreotti et al. (2016)
<i>Carcharhinus isodon</i>	US WAO	345	16	12 798	NA	LD	Portnoy et al. (2016)
<b>Rays</b>							
<i>Raja clavata</i>	IS	363	5	283 (45–857)	$9 \times 10^{-5}$ – $6 \times 10^{-4}$	PL	Chevolot et al. (2008)
<i>Aetobatus narinari</i>	Florida	143	8	2265.7 (243.3–∞)	NA	LD	Newby et al. (2014)

\*Geographical regions DEL Delaware Bay, ES Eastern shore of Virginia, SWFL Southwest Florida, NWA Northwest Atlantic Ocean, SA South Africa, NPO North Pacific Ocean, US WAO United States Western Atlantic Ocean, IS Irish Sea

\*\*Methods LD Linkage disequilibrium, M-ratio (Garza and Williamson 2001), PL Pseudo-maximum likelihood

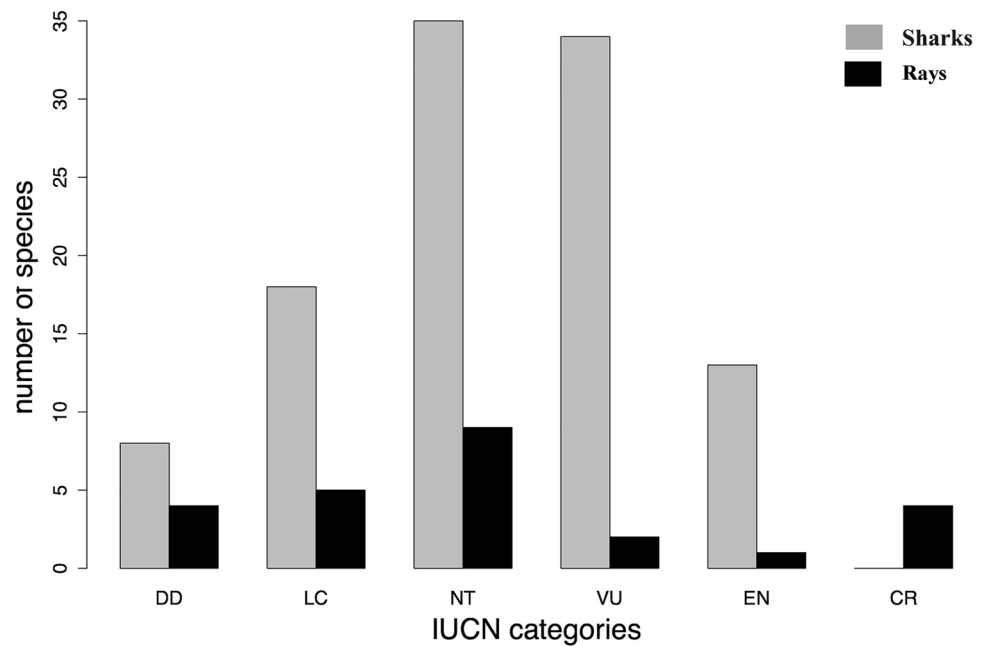
(GSRI), launched the Global Strategy for the Conservation of Sharks and Rays (2015–2025). This document summarizes the global priorities for shark and ray conservation (Bräutigam et al. 2015) and highlights the urgent need to prevent the extinction of imperiled coastal sharks and rays in many diverse and endangered hotspots, including the coastal waters near Argentina, Australia, Brazil, Colombia, Indonesia, Japan, Madagascar, Mozambique, South African and Uruguay (Lucifora et al. 2011; Bräutigam et al. 2015). Similarly to the other conservation initiatives for shark and ray species, the GSRI does not recognize the importance of genetic diversity as a criterion for its management plan. Population genetics metrics, including genetic diversity levels, population structure and demographic history, could help the GSRI assess the genetic health of populations and determine priority areas for conservation. This approach could provide an excellent match between the use of common genetics tools in management and their relevant applications in the policy arena (Hoban et al. 2013a, b).

The same problem extends to the one of the most influential conservation organizations in the world, the International Union for Conservation of Nature (IUCN). Currently, the framework developed by the IUCN for assessing extinction risk of species is the most widely used even though the IUCN Red List does not hold any legal weight (Fung and Waples 2017). Although the IUCN considers genetic diversity as one of the three levels of biodiversity that must be conserved (McNelly et al. 1990), there are no specific

genetic criteria listed that would categorize sharks and rays or other species as being under any level of threat (Laikre 2010; Rivers et al. 2014). Although the IUCN Red Lists take into account a range of quantitative species-specific criteria, such as distribution, number of individuals and declines in abundance, other than for rare exceptions, the categorization of a given species into Red List categories (IUCN 2001) largely ignores genetic diversity in its evaluation criteria. This shortcoming suggests that any shark and ray species listed under an IUCN Red List category could be overlooked in long-term management plans (Laikre et al. 2008; Willoughby et al. 2015).

According to Dulvy et al. (2014), 1041 shark and ray species are currently listed under the IUCN Red List threat categories. Of these, 181 shark and ray species fall into categories that represent varying degrees of threat (Dulvy et al. 2014). A Web of Science® search that we conducted, selecting data up to August, 2016, indicated that the number of shark and ray species for which genetic information is available has increased over the last 20 years, though these studies have mainly focused on sharks rather than rays (Fig. 1). However, some genetic data (genetic diversity metrics and population genetic structures) exist for only 10% of the 1041 shark and ray species currently listed by the IUCN, and approximately 25% of the species fall into some threat category (Fig. 2). Even with nearly half of all shark species listed by the IUCN as ‘Data Deficient’ (DD) due to incomplete data in terms of life history and population

**Fig. 2** Numbers of articles published that describe the genetic diversity of shark and ray species for each IUCN category. *DD* data deficient, *LC* least concern, *NT* near threatened, *VU* vulnerable, *EN* endangered, *CR* critically endangered



abundance dynamics (Hoffman et al. 2010), for some species in this category, there are genetic data that could be used for assessment when combined with other information. Moreover, the lowest values of observed heterozygosity are for species listed as DD and Least Concern (LC), whereas the lowest nucleotide diversity values are for species listed as LC (Fig. 3). This pattern is similar to those found by Willoughby et al. (2015) for bony fish, birds, mammals, and reptiles. For example, artisanal fisheries represent a main threat to nurse sharks (*Ginglymostoma cirratum*, Ginglymostomatidae), which inhabit coastal waters and are found throughout the Atlantic Ocean (Ebert et al. 2013). Although the IUCN lists nurse sharks as DD globally (Rosa et al. 2006), this species has been genetically analyzed, and these data could be used to help assess their populations. The nurse shark population in the western Atlantic Ocean shows low genetic diversity in the control region of the mtDNA (CR mtDNA) ( $h = 48 \pm 5\%$ ;  $\pi = 0.08 \pm 0.06\%$ ) and microsatellites ( $H_o = 0.58$ ). Furthermore, nurse shark populations show significant and distinct genetic differences between offshore islands and the mainland in the western Atlantic Ocean, and there is a high degree of genetic variability (78.2%) within populations (Karl et al. 2012). These genetic isolation patterns and genetic diversity parameters are comparable to those of other shark species categorized by the IUCN as threatened, including the sand tiger shark and the bonnethead shark (*Mussetelus schmitti*, Triakidae) (Table 1). Although genetically depauperate shark populations result mainly from historical fluctuations in population size (O'Brien et al. 2013), these examples clearly highlight the usefulness of genetic diversity metrics, including haplotype and nucleotide diversity and heterozygosity, at least as indicators of the health of

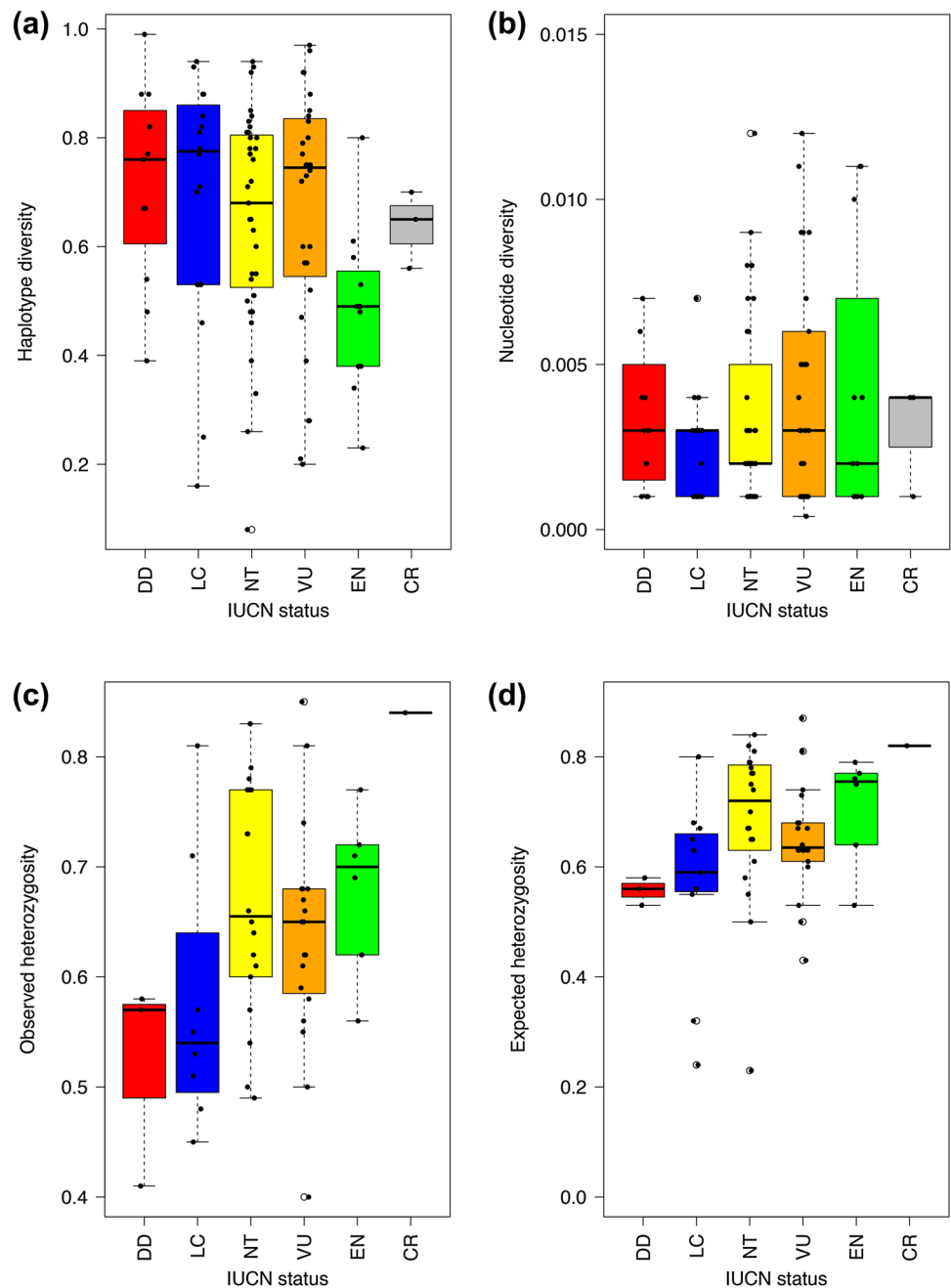
the population and the conservation status of a particular shark species. Specifically, high levels of genetic diversity can increase individual fitness and population resilience, and there is currently no framework for the direct use of genetic diversity metrics in management plans.

As advised in previous studies (Frankham 2010, 2014; Laikre 2010; Rivers et al. 2014; Willoughby et al. 2015), genetic diversity metrics imply that the IUCN should include genetic diversity as another criterion for categorizing threatened species. This could be completed using a novel approach for identifying vertebrate species with conservation needs based on the number of generations ( $t$ ) until, using  $N_e$  as an index, the species loses significant genetic diversity (Willoughby et al. 2015). Obviously, we recognize that estimating  $N_e$  for shark and ray species can be difficult, mainly because these species tend to have overlapping generations; thus, estimated  $N_e$  must not be used as an autonomous criterion. However, this parameter is very informative in regard to the conservation and management of wildlife populations because it provides information regarding how quickly genetic diversity may be lost (Leberg 2005; Dudgeon and Ovenden 2015). From this prediction, it is possible to direct conservation efforts to mitigate this loss (Uzans et al. 2015). Therefore, given the potential association between  $N_e$  and the probability of extinction, estimates of  $N_e$  may be useful as an additional criterion in the assessment of species vulnerability (Leberg 2005; Willoughby et al. 2015).

Although the use of genetic parameters is largely overlooked and neglected in fisheries management plans and, consequently, in conservation policies for shark and ray species, there are a few good examples of their use. One such example is the Red List assessment of *Stegostoma fasciatum*



**Fig. 3** Boxplot of genetic diversity metrics of shark and ray species pooled for each IUCN category. **a** Haplotype diversity, **b** Nucleotide diversity, **c** Observed heterozygosity and **d** Expected heterozygosity. *DD* data deficient, *LC* least concern, *NT* near threatened, *VU* vulnerable, *EN* endangered, *CR* critically endangered



(Stegostomatidae). In this case, the population genetic structure was used to analyze the two main populations, the Indian Ocean-Southeast Asian and Eastern Indonesian-Oceania populations, which were then assessed independently. Furthermore,  $N_e$  was used to estimate the approximate census size of the Eastern Indonesian-Oceania population. In another case, genetic data were used for stock delineation in the assessment of scalloped hammerhead populations (Miller et al. 2013), thus helping this shark species become the first shark species to be protected by the U.S. Endangered Species Act (Federal Register 80 FR 71774). For the scalloped hammerhead, stock delineation is important not only

for increasing its population size but also for safeguarding its evolutionary dynamics. These examples clearly demonstrate the many advantages of adding genetic information to species assessments and management plans.

## Limitations

Although the number of studies of shark and ray species has increased over recent decades, several significant limitations remain and can be highlighted, such as sampling protocols

and population coverage, methodological issues, and appropriate use of molecular markers.

### Sampling and geographical coverage

Similar to other marine apex predators and highly mobile species, there are many challenges to properly investigating the population structure and genetic diversity of sharks and rays. In general, sampling schemes are not always adequate in terms of sample size, geographical coverage, and collection method (Hindrikson et al. 2017; Letessier et al. 2017). A good strategy for solving this problem is the use of simple simulation software (e.g., POWSIM or SPOTG) that estimates statistical power (i.e., the probability of rejecting the null hypothesis when it is false) to simulate optimal combinations of sample size, number of loci, and allele frequency for any hypothetical degree of true differentiation (Ryman and Palm 2006; Hoban et al. 2013b). Additionally, recently, an initiative has been adopted to overcome these problems. Shark Share Global (SSG) (<https://www.sharkshareglobal.org>) provides an online database to which researchers can submit tissue samples, search, and request them from colleagues around the world. This allows researchers to obtain robust collections of tissues samples from various locations throughout the range of a species, enabling a better understanding of the population genetic structure and genetic diversity of the species studied. Despite aid from SSG to increase the sample size and geographical coverage, obtaining systematic and planned (as opposed to opportunistic) sampling for one specific location, sex, age, and time remains a challenge. Consequently, few studies based on such planned sampling have been performed to date (e.g., Chevlot et al. 2008; Verissimo et al. 2017).

### Methodological issues

While fin clipping has been the most commonly used method for collecting genetic data from sharks and rays, this method has some drawbacks, such as stress, injury, and even death after release (Wasko et al. 2003). In the past decade, a variety of less invasive techniques, including noninvasive genetic sampling, have been developed especially for internationally protected shark and ray species, in order to minimize such drawbacks (Larson et al. 2017). For example, Lieber et al. (2013) tested the potential of mucus swabs from a vulnerable species, the basking shark (*Cetorhinus maximus*, Cetorhinidae), at three molecular markers (cytochrome oxidase I (COI), CR mtDNA, and ITS2). Similarly, Kashiwagi et al. (2015) evaluated the PCR success of mtDNA ND5 and nuclear DNA RAG1 for manta rays, as well as microsatellite loci from manta ray mucus collected underwater using toothbrushes. Such collection methods combined with new DNA technology, which require less representative

sampling, show promise as a solution for more sustainable and less invasive genetics studies.

### Molecular markers

Another way to increase the geographical coverage and understanding of the population genetic structure and genetic diversity of sharks and rays is the use of common methods and sets of genetic markers, which could be universally comparable between studies. To date, several methods and molecular markers have been used for shark and ray genetic studies (Table 1). However, CR mtDNA is the most commonly used, either in part (e.g., Duncan et al. 2006; Frodella et al. 2016; Domingues et al. 2017) or in whole (e.g., Clarke et al. 2015; Bernard et al. 2016, 2017). Similarly, a set of highly polymorphic microsatellite loci, such as those used by Daly-Engel et al. (2012), could be standardized and used for multiple shark and ray species. However, the rapidly developing field of genomics holds great promise developing other DNA markers (SNPs) for shark and ray population analysis.

### Future challenges

Recently, many authors have claimed that the use of genetic diversity as should be at the forefront of conservation policy and management and not used only as supporting information (Laikre 2010; Hoban et al. 2013a, b). However, we note that making genetic diversity data more promptly useful to policymakers requires overcoming some challenges in either scientific or policy arenas, as described below:

- Prioritize shark and ray species that have narrow geographic distributions and are currently overexploited
- Conduct genetic monitoring by sampling in temporal series to assess genetic variations over time
- Apply genomics to shark and ray genetic research
- Include more conservation geneticists in developing conservation policies
- Improve communication between scientists and policymakers

### Prioritize shark and ray species that have narrow geographic distributions and are currently overexploited

From a conservation genetics perspective, the worst situation is the representation of an endangered species as a single population (Frankham et al. 2002). Frequently, small populations are most likely to be affected by the loss of genetic diversity due to overfishing, which affects their

evolutionary potential and results in an elevated risk of extinction (Frankham et al. 2002; Allendorf et al. 2008). Therefore, obtaining information at the level of genetic diversity for a species either with a narrow geographic distribution or within an isolated population is important for indicate the population fragility of that species. For example, the narrownose shark is a species endemic to the Southwest Atlantic Ocean with a narrow geographic distribution, which extends from Rio de Janeiro, Brazil, to Patagonia, Argentina. This shark species has experienced intense overfishing along its entire geographic range, including its nursery grounds (Massa et al. 2006). Moreover, the genetic diversity of the narrownose shark is among the lowest among all sharks (Table 2), making this species highly susceptible to overfishing in the short term and to low genetic diversity in the long term. This situation could affect other elasmobranch species that have narrow geographic distributions and are currently overfished, including critically endangered elasmobranchs such as the daggernose shark (Lessa et al. 2016), the Brazilian guitarfish (*Pseudobatos horkelii*, Rhinobatidae) (Vooren et al. 2005, as *Rhinobatos horkelii*) and the common angel shark (*Squatina squatina*, Squatinidae) (Ferretti et al. 2015). On the other hand, widely distributed shark and ray species are rarely panmictic from one end of their distribution area to the other, and instead, they show partitioning genetics (Castro et al. 2007; Ahonen et al. 2009; Clarke et al. 2015). However, low population genetic differentiation may not be informative on the appropriate spatial scale for management decisions. For example, Schmidt et al. (2009) found only low levels of genetic differentiation between geographically distinct whale shark populations, suggesting that conservation efforts must target international protection for this species. Furthermore, the asymmetric dispersal (females non-roving and males roving), consistent with male-mediated gene flow, that is common in many shark and ray species (e.g., Feldheim et al. 2014; Sellas et al. 2015) is another factor that must be considered in management decisions. Therefore, obtaining information regarding the extent of gene flow among populations is important for determining whether a species requires the maintenance of genetic diversity through migration (Frankham et al. 2002; Allendorf et al. 2013).

### Genetic monitoring by sampling in temporal series to assess genetic variations over time

Genetic monitoring, as defined by Schwartz et al. (2007), is the quantification of temporal changes in population genetic parameters or other population data generated using molecular markers. This technique can be performed using ancient DNA (aDNA) from the dried jaws and vertebrae of sharks and rays archived in museums and private collections and even kept as exotic souvenirs (Nielsen et al. 2016). These data allow for retrospective monitoring to assess historical

conditions, such as the temporal stability of the population structure, the loss of genetic diversity, and changes in the  $N_e$ , which are difficult to determine using traditional methods (Schwartz et al. 2007; Nielsen and Hansen 2008). Good examples of the use of this approach are mainly demonstrated in bony fish (e.g., Hauser et al. 2002; Nielsen and Hansen 2008; Bonamoni et al. 2016). However, there are currently a few examples of the use of aDNA for shark species. Gubili et al. (2015) sequenced a small fragment (135–228 bp) of mtDNA (D-loop) from 34- to 129-year-old dried cartilage and skin samples from six *Carcharodon carcharias* individuals and found greater genetic diversity (number of haplotypes and nucleotide and haplotype diversity) in the historical samples than in contemporary samples found in the Mediterranean Sea. Moreover, Li et al. (2015) used the complete mitochondrial genome of aDNA to infer the phylogeny and gene flow of endangered river sharks (*Glyphis* spp., Carcharhinidae). Therefore, the management of genetically depauperate populations must embrace the identification of source founders from genetically diverse populations (Allendorf et al. 2013) and genetic monitoring through sampling in temporal series to assess genetic variation over time (Allendorf et al. 2008; Laikre et al. 2008).

### Applications of genomics in elasmobranch genetic research

DNA sequences, especially the control regions of mitochondrial DNA and microsatellites, are the markers most widely used in elasmobranchs to date (Table 1). However, the availability of new high-resolution molecular markers such as single-nucleotide polymorphisms (SNPs), promises a marked advance in genetic studies in the future. Currently, with the advances in next-generation sequencing (NGS), there are many methods to uncover and genotype thousands of SNPs that cover the entire genome in a single step at minimal cost, thus making NGS feasible for most labs (Stapley et al. 2010). We will not attempt to describe NGS, its methods, or associated analyses in detail, as these have been covered in other reviews (e.g., Rocha et al. 2013; Goodwin et al. 2016). Instead, we intend to highlight the need for using NGS approaches to better answer questions pertaining to shark and ray population genetics in the near future.

Even though 10–20 microsatellites are estimated to be equivalent to 100 SNPs, with the recent development of new methods such as the use of restriction-site-associated DNA tags (RAD-tags), tens of thousands of SNPs can be recovered from multiple individuals at the same time, thereby increasing the statistical power of fine-scale detection in discrete populations (Nielsen et al. 2009; Davey and Blaxter 2011; Rocha et al. 2013). Consequently, SNP analysis requires relatively small numbers of samples from a given location, which in turn is an advantage due to the numbers of

shark and ray species that are currently threatened. Another advantage of using SNPs is that this approach aids in determining which parts of the genome are responsible for local adaptation even in cases of high gene flow, thereby enabling the identification of priority areas to be conserved (Nielsen et al. 2009). However, future studies using approaches based on genomic population outliers must be conducted carefully because these approaches still pose several challenges, including genotyping errors, the underlying population structure and false positives, variation in the mutation rate and limited sensitivity (false negatives) (Narun and Hess 2011; Tiffin and Ross-Ibarra 2014; Hoban et al. 2016; Flanagan et al. 2017). In fact, NGS technologies are having substantial effects on many areas of biology, including the analysis of genetic diversity in populations, and they promise an abrupt advance in genetic studies in the coming years (review in Nielsen et al. 2009). However, the use of NGS technologies in developing countries may still be cost-prohibitive, due to limited funding for basic research and because they require sophisticated bioinformatics systems, fast data processing and large data storage capabilities (Willette et al. 2014; Puckett 2017). Furthermore, although the pitfalls of mtDNA and microsatellite studies are fairly well known and can usually be recognized and tested, the drawbacks of NGS approaches are still being identified (Bowen et al. 2014).

To date, only one study has used neutral and outlier SNPs to infer the local adaptation of sharks. Using neutral SNPs (648,035 SNPs), Portnoy et al. (2015) found differences in the population structure of the bonnethead shark between the North Atlantic (North Carolina) and the Gulf of Mexico (Florida Bay, Tampa Bay and Panama City), whereas the use of 30 outlier SNPs showed fine-scale differences in population structures among all locations except for Tampa Bay and Florida Bay, where the population structures were homogenous. The authors attributed this local adaptation to north–south (latitudinal) clinal patterns in allele frequencies. More recently, Pazmiño et al. (2017) conducted a genome-wide analysis using 8103 neutral SNPs to investigate the population structure of the Galapagos shark (*Carcharhinus galapagensis*) over a small geographic range (Galapagos Marine Reserve). Those authors found two differentiated populations and a low estimated  $N_e$  of 200, suggesting that these populations are susceptible to extinction and are of concern for long-term conservation. In another recent paper, Corrigan et al. (2017) performed a genome-wide analysis using 2152 SNPs to examine the patterns of genetic admixture between the Galapagos shark and the dusky shark (*Carcharhinus obscurus*), two closely related sharks. However, even with genomic data providing novel insights, its use in the analysis of shark and ray species remains limited (e.g., Feutry et al. 2015; Portnoy et al. 2015; Delsler et al. 2016; Pazmiño et al. 2017; Corrigan et al. 2017).

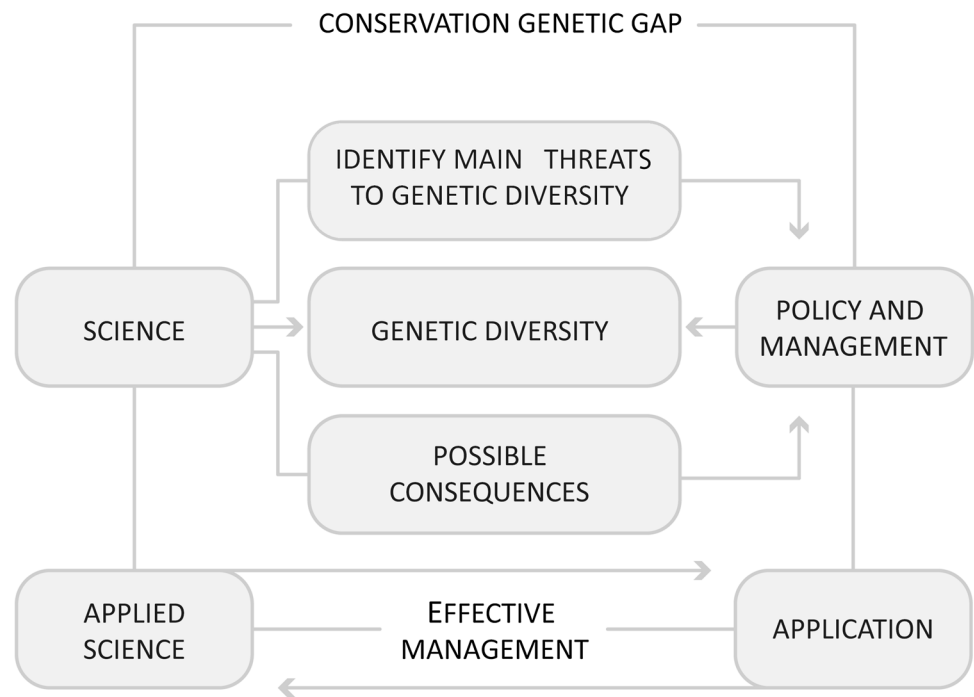
## Including more conservation geneticists in international developing conservation policy making

The importance of genetic criteria to guarantee long-term population viability and conservation is well known in academia. However, outside academia, genetics is still largely overlooked and neglected in practical management and in national and international policies, though there are some exceptions (Laikre 2010). The main agencies interested in the conservation of shark and ray species do not have many conservation genetics specialists integrated into their teams. Members of these organizations are mainly fisheries scientists interested in assessing stock abundance, which demonstrates the lack of concern for genetics in assessing species (Laikre 2010). Therefore, we recommend the inclusion of more conservation geneticists in conservation organizations. This inclusion would facilitate the addition of genetic criteria to assessments and future management plans for shark and ray species.

## Bridging the gap between genetic science and shark and ray conservation policies

Currently, there remains a gap between the genetics research that generates knowledge about genetic data (e.g., genetic diversity, population genetic structure and demographic history) and conservation organizations that use these data to establish protection measures that aim to allow populations to recover (Laikre 2010; Hoban et al. 2013a, b; Haig et al. 2016). Typically, policymakers and managers are not geneticists, and they have difficulty interpreting genetic data correctly; consequently, these data are often used incorrectly in the creation of management plans (Hoban et al. 2013a, b; Haig et al. 2016). This issue could be resolved, for example, by providing training to national and international conservation organizations. Workshops, courses and lectures for non-genetics researchers, conservation practitioners and decision-makers interested in sharks and rays could be organized to show how genetic diversity can be effectively used in management plans. This approach would provide an excellent opportunity to show that genetic diversity data could reveal a wide variety of information for conservation policies. Furthermore, the inclusion of genetics experts among national and international policymakers could be a good start for incorporating genetic information into conservation policy (Fig. 4). For example, the IUCN Conservation Genetics Specialist Group (CGSG) (<http://www.cgsg.uni-freiburg.de>), whose mission is to promote the use of genetics in conservation management and decision-making, was recently created. However, the inclusion of geneticists among policymakers requires improvement in the

**Fig. 4** The link between scientific knowledge and conservation policies aimed at preserving the genetic diversity of shark and ray species. Scientists must generate knowledge that identifies the main threats to genetic diversity and their deleterious effects on shark and ray populations, whereas policymakers must consider the information provided by scientists and apply this information to their conservation policies in order to effectively manage species populations



communication between scientists and policymakers. To bridge the divide between conservation genetics research and practice, Conservation Genetic Resources for Effective Species Survival (ConGRESS), a freely available online resource (<http://congressgenetics.eu>) that increases access to current knowledge, facilitates implementation of studies and interpretation of available data, and fosters collaboration between researchers and practitioners, was recently launched (Hoban et al. 2013c). Thus, geneticists' research could help with elaborating on and revising regional and global reports on sharks and rays and proposals that incorporate genetic data for the management and research of these species.

## Conclusions

In light of the above considerations, we can assume that the increasing overexploitation of shark populations, mainly by fisheries, will have a long-term impact on the genetic variability of these populations and thus will reduce their fitness and responsiveness to environmental changes. Therefore, future assessments of shark and ray populations by conservation organizations should definitely include genetic parameters. Furthermore, as an important outcome of this synthesis, we highlighted the limitations and future challenges to overcoming the gap in current knowledge through genetic studies of sharks and rays. Finally, we argue that geneticists can inform

policymakers when and where genetic diversity will be important for shark and ray conservation.

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