

Population genetics reveals global and regional history of the apex predator *Galeocerdo cuvier* (carcharhiniformes) with comments on mitigating shark attacks in north-eastern Brazil

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Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 306290/2015-4; Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco, Grant/Award Number: APQ1203-2.02/10

Abstract

The knowledge of the population structure of a given species is of great importance for its conservation and for the management of its fishing exploitation, especially for sharks. The tiger shark (*Galeocerdo cuvier* Péron&Lesueur, 1822) is an apex predator species that is currently listed as “Near Threatened” on the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species. In this study, the tiger shark's genetic structure in the Metropolitan Region of Recife (MRR) and oceanic archipelago of Fernando de Noronha (FN) was investigated based on one mitochondrial and two nuclear DNA markers. In addition, sequenced data from other geographic sites were added into the mitochondrial analysis. The data showed moderate-to-high genetic diversity, and it is consistent with good resilience of *G. cuvier* in ecological terms. The structuring tests reinforced a global distinction of the species in two lineages, one being from the Indo-Pacific and the other from the North Atlantic. Also, this analysis showed the close relationship between tiger sharks from Indo-Pacific and South-eastern coast of Brazil. The Bayesian and AMOVA tests indicated that tiger sharks from FN and MRR are genetically similar, forming a cohesive population. These analyses support live specimen translocations from beaches (where the attacks occur) to distant marine areas given we detected a historical cohesive population occurring between those beaches from MRR and FN Islands where the sharks migrate. This research is the first that has validated individual translocations as a green strategy in South-western Atlantic.

KEYWORDS

Galeocerdo cuvier genetics, global and regional connectivity, population structure, shark attacks

1 | INTRODUCTION

The understanding of the population genetic structure of the species is of great importance because it reveals information about the geographic limits of populations by analysing the gene flow between locations. This approach can be also used as possible drivers for their conservation (Castro et al., 2007; Reiss et al., 2009;

Dudgeon et al., 2012; Bellafronte et al., 2013; Chapman et al., 2015; Quintanilla et al. 2015; Sigsgaard et al., 2016; Domingues et al. 2018a; Flanagan et al., 2018; Carmo et al., 2019), given the possibility of identification of evolutionary and management units (Domingues et al., 2019; Dudgeon et al., 2012; Giles et al., 2016; King et al., 2015; Larson et al., 2015; Laurrabaquio-A et al., 2019). Studies on the levels of genetic variation of species also allow

estimating effective population size and can help to enlighten questions about species vulnerability, especially for exploited marine species and sharks, as fishing and environmental changes can cause a decline in populations and the reduction in the genetic variability (Garcia et al., 2008; Allendorff et al. 2014; Rosa et al., 2014; Rosa et al., 2017; Pinsky & Palumbi, 2014; Ferrette et al., 2015).

Knowledge on genetic structure is also greatly relevant for the conservation of sharks, given that evolutionary lineages can be masked by conserved external morphologies (Gaither et al., 2016), and also due to the fact that several species across the world show signs of stock depletion (Baum et al., 2003; Burgess et al. 2005; Myers et al., 2007; Dulvy et al., 2008; Davidson et al., 2016; Roff et al., 2018). As such, population genetics have been studied for several species helping to identify cryptic species, endogamy, low genetic diversity, fitness reduction and endangered populations, and being of great use in species management and conservational plans (Amos & Balmford, 2001; Domingues et al., 2019; Dudgeon et al., 2012; Frankham et al., 2008; Giles et al., 2016; Karl et al., 2011, 2012; Larson et al., 2015).

Population genetics have been studied for sharks, such as black-tip sharks (*Carcharhinus limbatus* Müller & Henle, 1839) (Keeney & Heist, 2006), blue sharks (*Prionace glauca* Linnaeus, 1758) (Veríssimo et al., 2017), whale sharks (*Rhincodon typus* Smith, 1828) (Castro et al., 2007; Sigsgaard et al., 2016), great white sharks (*Carcharodon carcharias* Linnaeus, 1758) (Blower et al., 2012; Gubili et al., 2010, 2015) and tiger sharks (*Galeocerdo cuvier* Péron & Lesueur, 1822) (Carmo et al., 2019; Pirog et al., 2019), the target species of this paper.

Genetic data for *G. cuvier* from different parts of the world have revealed a better condition of the species in adaptive terms, considering the values of genetic diversity observed in mitochondrial and nuclear regions (Bernard et al., 2016; Carmo et al., 2019). Recently, this species has presented moderate genetic diversity estimates and strong genetic structuring from samples from the Atlantic and the Pacific (Carmo et al., 2019; Pirog et al., 2019). The Archipelago of Fernando de Noronha (FN) has also been suggested as a refuge zone for the conservation of the species, considering the high degree of genetic diversity in this area (Carmo et al., 2019). Despite this information very little is known about the history of possible connections between the Archipelago and coastal regions from North-eastern Brazil. Possibly the tiger sharks involved in the systemic contacts of them with humans in the metropolitan region of Recife (MRR—State of Pernambuco) can compose a single historical population with those from Archipelago of Fernando de Noronha, favouring the management of animals to other sites as recommended in the literature (Clua et al., 2020). Importantly, FN and MRR are components of two different eco-regions, which mean different seascapes hosting different ecological/geological profiles. However, there are no evidences on the genetic structure of this possible population along those zones.

In Brazil, interactions between sharks and humans are ancient. Zooarcheological studies have shown that pre-Columbian people

already exploited these animals for fishing using an active search strategy (Fossile et al., 2020; Gilson & Lessa, 2019). The contacts of humans and sharks are increasing worldwide since 1960s (Midway et al., 2019), and in Brazil (MRR), this is not different as in other parts of the world (Meyer et al. 2018). In the North-eastern Brazil, the management of the contacts/attacks has been difficult and controversial. The Shark Monitoring Program of Recife (SMPR) uses as mitigation methods the translocation of individuals from hazardous areas to more distant areas (offshore) that was responsible for diminish the shark attack rate in the region (Hazin & Afonso, 2014). The monitoring of some translocated individuals via telemetry from the beaches of the city of Recife to coastal zones further away has revealed the movement of the species northwards (Hazin et al., 2013). One of the emerging questions about this mitigation strategy for attacks in the region is whether this strategy favours the introduction of a non-historical genetic composition in the region given the species' northward movement pattern. These effects would make this strategy less viable, once it would not favour the species but simply it would minimize the contact of sharks with humans. In order to test whether the SMPR strategy might affect the historical movement pattern, we accessed mitochondrial and nuclear genetic data to test for the occurrence or absence of a historically connected population in the area between beaches from Recife and areas in the northern tropical Atlantic (Fernando de Noronha Islands). The results of this study might validate whether the translocations comprehend a suitable strategy for the mitigation of shark attacks in terms of the maintenance of the historical connectivity between regions. Furthermore, due to the aspects of the conservation status of *G. cuvier*, from the evolutionary potential point of view (genetic variation) of the species, and the literature-based data sets available on the species worldwide, this study aimed to (a) test for the level of general genetic variation of the species as an indication of its vulnerability; (b) test for the Archipelago of Fernando de Noronha as a refuge zone of genetic variation, through nuclear diversity and (c) test the global connectivity of the species by adding new genetic data.

2 | MATERIALS AND METHODS

A total of seventy-six tiger shark specimens were sampled in two coastal areas of North-eastern Brazil: 43 specimens from the metropolitan region of the city of Recife (MRR) and the other 33 were from an insular environment of the Archipelago of Fernando de Noronha (FN; Figure 1). All sampling animals from MRR followed procedures approved by the Committee on Ethics for the Use of Animals of the Universidade Federal Rural de Pernambuco (permit #23082.025519/2014) and did not involve anaesthesia, euthanasia or any kind of animal sacrifice. Fieldwork permit was issued by the Instituto Chico Mendes para a Conservação da Biodiversidade (permit #43305-6). In Fernando de Noronha Islands, the sampling was conducted in accordance with Brazilian regulations for wildlife research and it was approved by the Instituto Chico Mendes

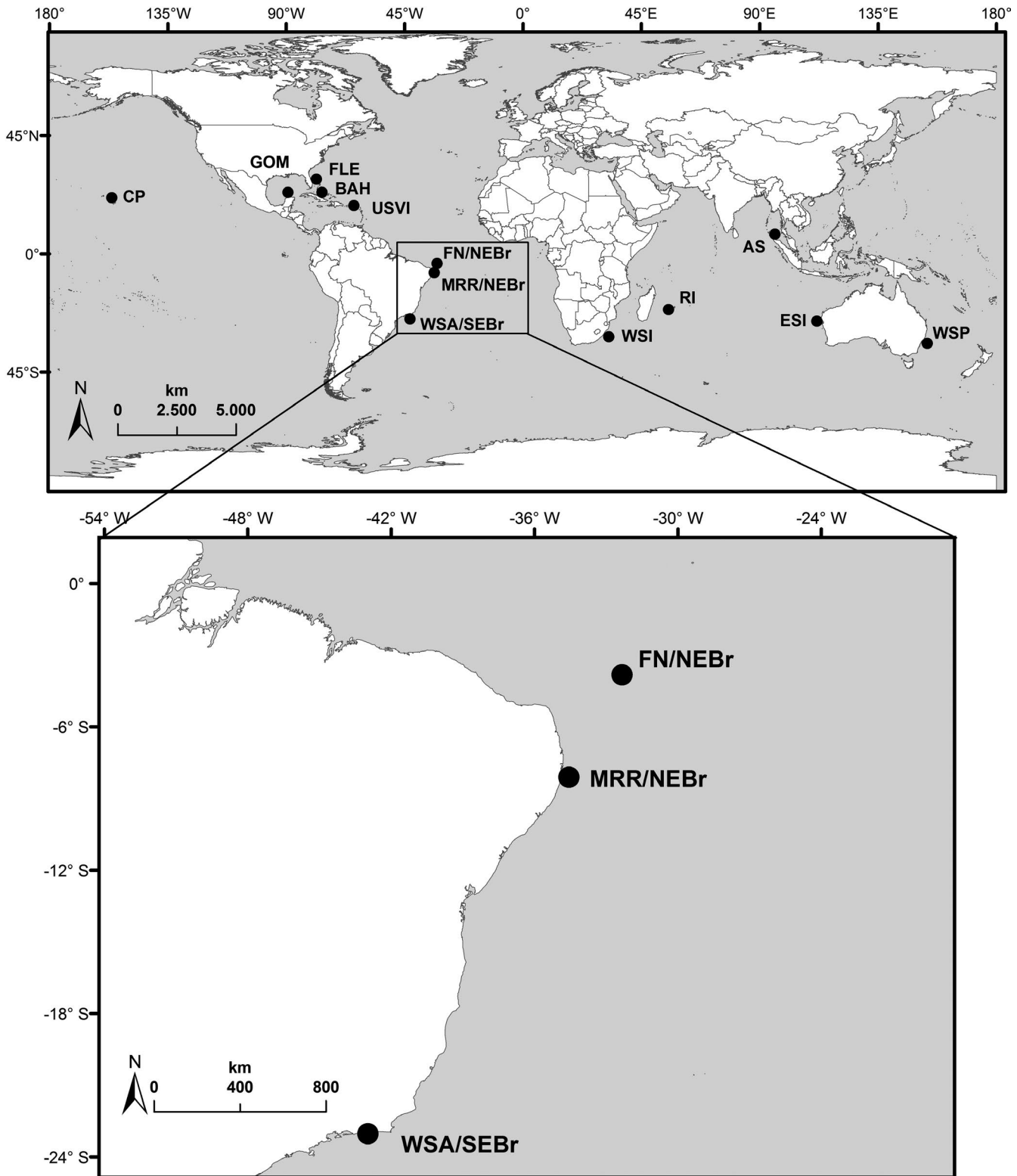


FIGURE 1 Localities of study samples. Study areas; Fernando de Noronha, Brazil (FN/NEBr), Metropolitan Region of Recife, Brazil (MRR/NEBr). Pirog et al., 2015; Réunion Islands (RI). Bernard et al., 2016; Southern Brazil (WSA/SEBr), East Coast of Florida (FLE), Central Pacific Ocean (CP), Gulf of Mexico (GOM), Bahamas (BAH), American Virgin Islands (USVI), South-West India (WSI), Andaman Sea (AS), East Indian Ocean (ESI), West South Pacific (WSP)

de Conservação da Biodiversidade of the Brazilian Ministry of the Environment (permit #15083-8). Tiger shark capture and handling was approved and carried out in full compliance with the

recommendations of the Regiment of the Commission of Ethics on the Usage of Animals from the Universidade Federal Rural de Pernambuco (permit #23082.009679/2009).

Tissue samples were preserved in 96% ethanol at -20°C . The total DNA was extracted using the *DNeasy Blood & Tissue* (QIAGEN®) extraction kit, following the dealer instructions.

The molecular procedures were concentrated on the amplification, via PCR, of three genetic regions: the control region of mtDNA (CR), the intron 6 of the nuclear lactate dehydrogenase gene subunit A (LDHA) and an internal transcribed spacer 2 (ITS-2).

The PCRs were performed using the primers ElasmCR15642F (5-TTGGCTCCCAAAGCCAARATTCTG-3) and ElasmCR16638R (5-CCCTCGTTTTWGGGG-3) for the Control Region (CR), ElasmLDHAF1 (5-GCTTATGARGTGATWAAACTGAA-3), ElasmLDHA6F2 (5-GGGWTGTCTGTGGCAGACCTCGC-3) and ElasmLDHAR1 (5-GAARACCTCRTTYTYWATRCCATA-3) for the LDHA (Stoner et al., 2003) and the universal primers Fish5.8SF (5-TTA GCGGTGGATCACTCGGCTCGT-3) and Fish28SR (5-CCTCCGCTTAGTAATATGCTTAAATTCAGC-3) for the ITS-2 (Pank et al., 2001). The PCR solution contained a final volume of $25\mu\text{L}$ and consisted of $12.5\mu\text{L}$ of 2X taq Master Mix (Vivantis®—0.05U/ulTaq polymerase 2X ViBuffer A), 15–20mM of each primer, 0.25U of Taq Polymerase (Invitrogen), 0.5mM of MgCl_2 , 70–150mg of genomic DNA and enough ultrapure water to complete $25\mu\text{L}$. The PCRs were performed in the *Applied Biosystems*® 2,720 (Life Technologies) thermocycler, following the cycling conditions suggested by Stoner et al. (2003) and Pinhal et al. (2012).

All the PCR products were enzymatically purified using ExoSap-IT® (Affymetrix), following the fabrication instructions. The sequences were obtained from the ABI 3,500—*Applied Biosystems* sequencer, using the *Big Dye™ Terminator v 3.1* (*Applied Biosystems*) kit.

The sequences obtained were aligned using the Clustal W programme (Thompson et al., 1994), implemented on BioEdit (Hall, 1999), visually edited, and the gaps were treated as missing data. The CR data were incremented with the addition of 28 more tiger shark sequences from various areas, made available by Pirog et al. (2015), Bernard et al. (2016) and Carmo et al. (2019). These data were discriminated here using the following abbreviations: South-eastern Brazil (SEBr), North Atlantic (AtINo) and Indo-Pacific (IndPac).

The genetic diversity data, such as the number of haplotypes, number of polymorphic sites, haplotypic and nucleotide diversities, were calculated using DnaSP v5 (Librado & Rozas, 2009; Rozas & Rozas, 1999). To test the hypotheses of the neutrality of genetic variation, tests on the distribution of segregated sites (Tajima's D, Tajima, 1989 and R^2 ; Ramos-Onsins & Rozas, 2002), haplotype distribution (Fu's F_S , Fu, 1997) and the different of pairwise sequences (Raggedness—Rg, Harpendings, 1994 and sum of squared deviations—SSD) were performed, with significance based on 1,000 permutations using the DnaSP v5 (Librado & Rozas, 2009) and Arlequin (Excoffier & Lischer, 2010). The significance index (p) used was 5%.

The relationship among the CR haplotypes and the variants from nuclear regions (LDHA and ITS-2) was evaluated using the software PopArt 1.7 (Leigh, 2016). The evolutionary models that best explained the variance of the sites of all three data sets were collected

using Modeltest 2.1.7 (Felsenstein, 2005; Posada 2008; Darrriba 2012) using Akaike's information criteria (AIC) (Akaike, 1979, 1983; Wagenmakers & Farrell, 2004).

The demographic history of the species was examined using DnaSP for each of the three data sets, for the construction of histograms of different pairwise nucleotides (mismatch distributions). The changes in *G. cuvier*'s demographic history over time were estimated, using the CR data, by Bayesian skyline plot (BSP) on BEAST 1.8 (Drummond et al., 2012) and Tracer 1.5 (Rambaut et al. 2014) in 10–40 million generations of MCMC. For this analysis, an average mutational rate 0.55% per million years was used in the CR data set. This was calculated using the average mutational rates reported for other sharks species: 0.43% for *Carcharhinus limbatus* (Keeney & Heist, 2006), 0.67% for *Negaprion brevirostris* (Schultz et al., 2008) and 0.54% for *Ginglymostoma cirratum* (Karl et al., 2012).

The phylogenetic analysis was obtained using Bayesian inference (BI) utilizing the BEAUti and BEAST 1.8. software (Drummond et al. 2012), in 10 million generations of Markov chains (MCMC). The analysis used *Cetorhinus maximus* (KF597303, NC023266) as the outgroup, and the majority consensus topology was obtained using a burn-in period of 10% of the MCMC generations.

The analysis of molecular variance (AMOVA) was performed in order to test for the genetic structure (Excoffier et al., 1992) computing the conventional statistics of θ (theta), the haplotype frequency data, with 1,000 permutations, using the Arlequin software. This method was applied in order to calculate the general (Φ_{ST}) and pairwise (F_{ST}) fixation indexes. The values were computed in two rounds: using the three data sets to compare MRR and FN and CR data to compare North-eastern (Pernambuco) and South-eastern Brazil, following Bernard et al. (2016). Through this last approach, we classified four groups: North-eastern Brazil (NEBr), South-eastern Brazil (SEBr), North Atlantic (AtINo) and Indo-Pacific (IndPac).

The population structure of *G. cuvier*, in regional and global terms, was further evaluated through the Bayesian designation analysis using the BAPS v3.1 software (Bayesian analyses of population structure—Corander et al., 2003; Corander and Martinen 2006). The number of populations (k) was estimated in 10 replicas with a maximum k value of 10. Furthermore, the population structure was also evaluated using another Bayesian designation, with the inclusion of geographic information, using the Geneland package (Guillot et al., 2005a, b). This analysis, in regional terms (comparing MRR and FN), was carried out using two data sets; CR + ITS-2 and CR + LDHA. The comparison between the genetic variation observed in North-eastern Brazil (Pernambuco) and in South-eastern Brazil (São Paulo), as well as the global analysis, was performed using only one set of CR data.

3 | RESULTS

The analysis of 88 CR sequences (28 MRR samples, 32 FN samples and 28 sequences from the data bank) produced an alignment of 672pb. A total of 20 polymorphic sites characterizing 28 haplotypes

were found. The average values of haplotype (Hd) and nucleotide (π) diversity were 0.897 and 0.005, respectively (Table 1). For the regional analysis (MRR-FN), four haplotypes were shared between these areas, as well as with other regions (Figure 2). For the global analysis, of the 28 haplotypes found for the CR data, 18 were exclusive (6 IndPac, 11 SEBr and 1 AtINO) and 10 were shared between all areas (Figure 2). The Bayesian inference (IB) topology of the CR data showed the presence of two clades (Figure 4). These two clades included lineages with relatively different distributions. One of the clades comprised all the exclusive genetic variants of the Indo-Pacific, the largest part of the genetic variation observed for South-eastern Brazil (SEBr), the smallest part of the genetic variation of North-eastern Brazil (NEBr) and a very small part of the North Atlantic (AtINO) variation. The other clade comprised the smallest part of the genetic variation observed in South-eastern Brazil (SEBr) and the major part of the genetic variation observed in

North-eastern Brazil (NEBr) and North Atlantic (AtINO). The dating analysis pointed out to the origin of those clades between 0.05 Mya and 2.2 Mya (mean = 380Kya).

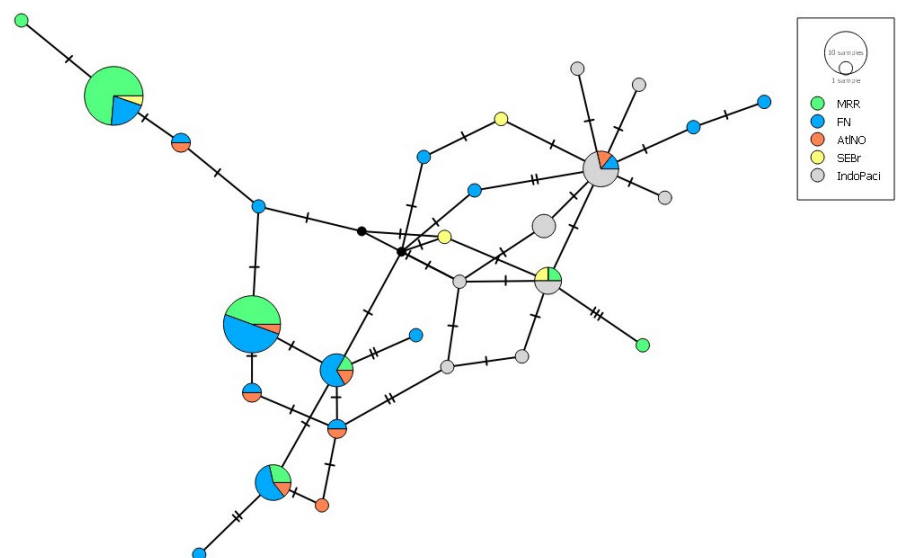
For the nuclear analyses, the sequences of the intron LDHA (15 samples of MRR, 5 samples of FN) produced an alignment of 206pb, whereas the paired ITS-2 sequences (25 samples of MRR, 23 samples of FN) generated a final alignment of 352pb. A total of 18 polymorphic sites were found in the intron LDHA and 10 polymorphic sites in the ITS-2, totalling 11 and 10 haplotypes, respectively. The genetic diversity data were Hd = 0.805 and π = 0.018 for the intron LDHA and Hd = 0.198 and π = 0.00178 for the ITS-2 (Table 1).

The allele network of the intron LDHA (Figure 3a) presented nine exclusive alleles and only two shared alleles between MRR and FN, whereas the allele network of ITS-2 (Figure 3b) was organized by a central shared allele with 89.6% frequency, as well as the nine exclusive alleles.

TABLE 1 Synthesis of genetic diversity informations and of the neutrality tests obtained with CR data, LDHA intron (Ld), ITS-2. In the table, the total number of specimens sampled (n), number of haplotypes (h), haplotype diversity (Hd), nucleotide diversity (π), Tajima's D test of neutrality (D), Fu's FS (FS), R_2 - sum of squared deviations (SSD) and Raggedness (Rg) (* $p < 5\%$; ** $p < 2\%$)

| | CR | | | | Ld | | | ITS | | |
|-------|---------|--------|-------|-------|---------|--------|--------|---------|-------|--------|
| | General | FN | MRR | NEBr | General | FN | MRR | General | FN | MRR |
| N | 88 | 32 | 28 | 60 | 20 | 5 | 15 | 48 | 23 | 25 |
| h | 28 | 15 | 7 | 18 | 11 | 3 | 10 | 10 | 7 | 4 |
| Hd | 0.897 | 0.89 | 0.715 | 0.822 | 0.805 | 0.7 | 0.857 | 0.198 | 0.283 | 0.118 |
| π | 0.005 | 0.005 | 0.004 | 0.005 | 0.018 | 0.0098 | 0.021 | 0.0017 | 0.003 | 0.0005 |
| D | -0.32 | -0.59 | -0.34 | -0.64 | -1.23 | 0.27 | -0.87 | -2.1** | -1.8* | 1.764 |
| FS | -14* | -6.14* | -0.17 | 6.17* | -2.17 | -0.58 | -3.77* | -2.45 | -1.89 | 3.01* |
| Rg | 0.015 | 0.01 | 0.19 | 0.033 | 0.058 | 0.07 | 0.046 | 0.49 | 0.33 | 0.65 |
| SSD | 0.0045 | 0.0028 | 0.068 | 0.093 | 0.148 | 0.0148 | 0.015 | 0.003 | 0.001 | 0.005 |
| R_2 | 0.085 | 0.098 | 0.115 | 0.083 | 0.115 | 0.25 | 0.131 | 0.023 | 0.04 | 0.07 |

FIGURE 2 Haplotype network based on CR data. The vertical lines over the connections among the haplotypes show the quantity of mutational steps. The diameter of each circle represents haplotype frequency. The black dots indicate lost or not sampled haplotypes. For acronyms, please consult Figure 1



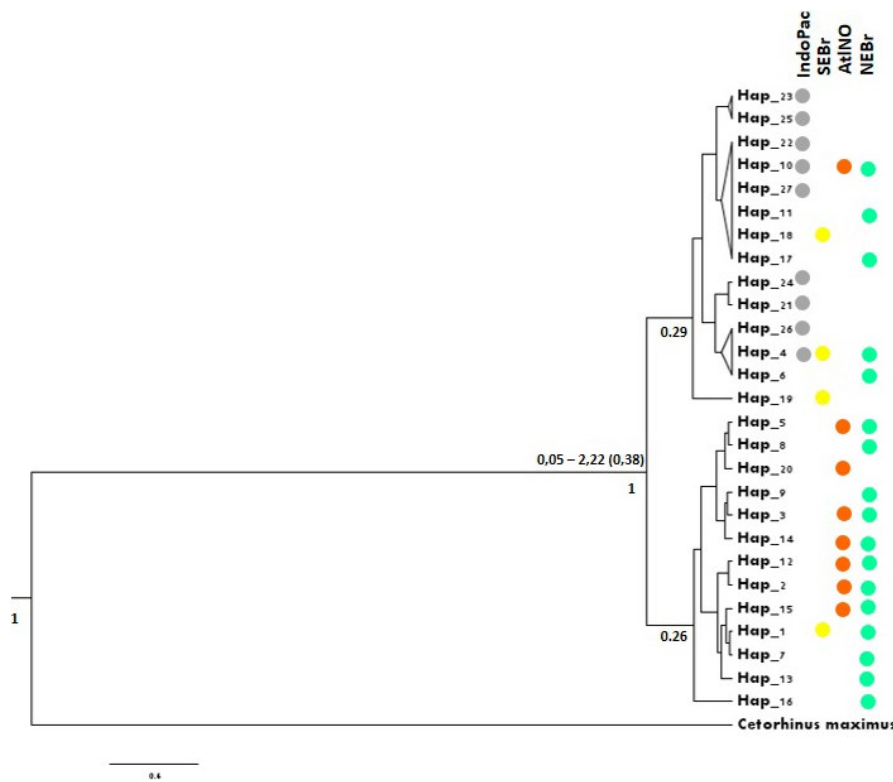


FIGURE 4 Bayesian topology of the control region data evidencing the two lineages. The values above the nodes represent the time intervals obtained [minimum - maximum values and (average)]. The values below the branches show the posterior probabilities

3.1 | Population structure and demographic history

The AMOVA with the CR data revealed for the regional comparison between MRR and FN, a general $\Phi_{ST} = 0.066$ ($p > .05$). The comparison between the observed genetic variation in North-eastern and South-eastern Brazil resulted in a $\Phi_{ST} = 0.035$ ($p > .05$). In the pairwise comparisons, a significant F_{ST} estimation of 0.144 between the Indo-Pacific and North-eastern Brazil ($p < .05$) (Table 2). In addition, it was observed the $\Phi_{ST} = 0.146$ ($p < .01$) between the clades recovered by the Bayesian inference with the CR data (Figure 4).

The analysis of the Bayesian structure (BAPS) revealed, for the regional data, a similar genetic profile among specimens from MRR and FN for all the markers (CR, ITS-2 and LDHA; Figure 5). The regional comparison between the genetic variation in North-eastern (NEBr = MRR+FN) and South-eastern Brazil (SEBr) showed a modified genetic profile (Figure 5a). The global CR data analysis demonstrated a value of $k = 3$ (Figure 5a) and a clear distinction in the genetic profile between the Indo-Pacific population and the other studied areas. Furthermore, it was observed distinct genetic profiles between the *G. cuvier* populations from North Atlantic (AtINO) and South-eastern Brazil (SEBr). But among the Atlantic populations relatively similar genetic repertoires were observed (Figure 5a).

The Bayesian analysis of the Geneland (Figure 6) showed the existence of a single ($k = 1$) *G. cuvier* population in Pernambuco (MRR + FN; Figure 6a) and the occurrence of two populations ($k = 2$) in NEBr and SEBr (Figure 6b). The global analysis (Figure 6c) showed the existence of two populations ($k = 2$), which comprised the genetic variation of the Indo-Pacific in relation to the rest of the study areas.

The mismatch distribution analyses (Figure 7) showed bimodal or multimodal pairwise differences in the majority of the graphs (Figure 7b-g). The results obtained with the ITS-2 data presented a unimodal distribution (Figure 7h-j). The statistical deviations for non-neutral variation obtained through Tajima's D and Fu's FS neutrality tests presented in general negative values. The Raggedness (Rg) and SSD values were in general low and non-significant. The R_2 tests (Ramos-Onsis and Rozas, 2002) presented also low values. All the values obtained for each of the markers are summarized in Table 1.

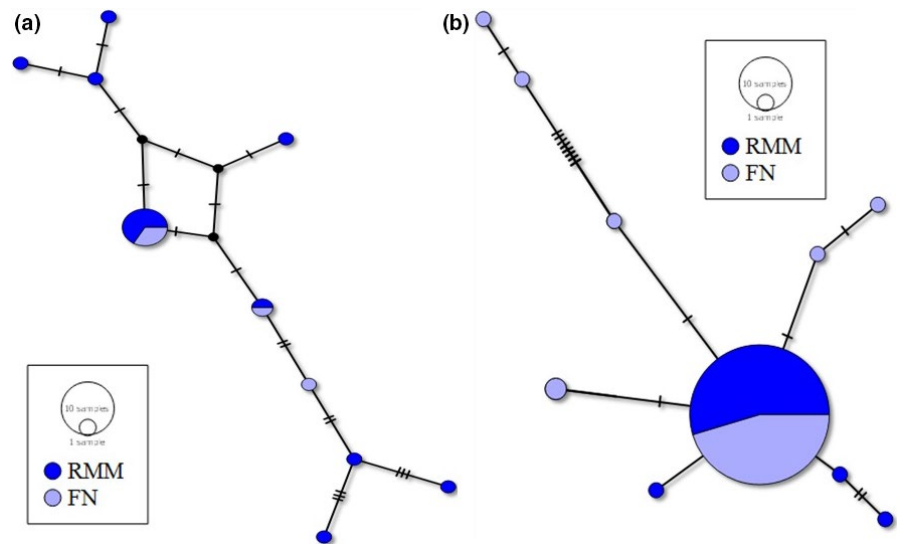
The analysis of deviations in the effective population size, performed using the Bayesian Skyline Plot (Figure 8), demonstrated evidence of population fluctuations over time, both regionally (NEBr, FN) and globally (Figure 8).

4 | DISCUSSION

4.1 | Genetic diversity, demographic history and conservation status

According to the IUCN data, *G. cuvier* is considered as "Near threatened" (Simpfendorfer, 2009). The data obtained from the CR and LDHA showed moderate-to-high diversity values. Pelagic sharks tended to present in CR similar diversity values, as seen in *Prionace glauca* (Veríssimo et al., 2017), *Carcharhinus falciformes* (Domingues et al., 2018) and *Sphyrna lewini* (Quintanilla et al. 2015). This comparison suggests that *G. cuvier* present similar values to other species. Among studied sites, the Archipelago of Fernando de Noronha (FN)

FIGURE 3 Haplotype network based on nuclear data:(a) lactate dehydrogenase intron A and (b) ITS-2



showed the highest diversity values, for both CR and intron LDHA, suggesting that the FN population contributed significantly to the magnitude of tiger shark genetic variation in the region, reinforcing the importance of the region for conservation (Carmo et al., 2019). The data from ITS-2 reinforced this hypothesis given the high allele diversity observed even being a more conserved genomic region. This information allows for the suggestion that the extent of genetic variation observed in this study is consistent with the conservation status of the species.

The demographic history of species is one of the most important pieces of evidence for their conservation, as historic oscillations of effective population sizes (N_e) outline the trajectory of persistence or cessation of species over time (Frankham et al., 2008). In the regional approach [FN, MRR and NEBr (MRR + FN)], the neutrality tests (Fu's F_S , R_2 , SSD and R_g) suggested a demographic pattern possibly different from stability, suggesting a slight expansion of the population based on the inspected loci. This is further reinforced by the analysis of temporal effective population size oscillations (Bayesian Skyline Plotting—BSP) and the haplotype and nuclear networks. The BSP graphs indicated gradual events of increasing effective population size in NEBr, starting at approximately 1,000 years ago (1kya). In

FN, a subtle expansion was observed around 2000 years ago (2kya), and globally, an abrupt phenomenon beginning at also around 1kya was observed. In general, these evidences suggest that *G. cuvier* has been experiencing population expansion. These increases in N_e observed in this study are not easily detected, since they are recent according to our dating parameters (Holocene). However, the use of the more variable mitochondrial marker (control region—CR) was fundamental in the observation of these signs of population expansion and reinforces which has been observed in the literature (Hewitt et al. 2004; Domingues et al. 2018; Carmo et al., 2019), even with different data sets, as were analysed in this study. The observed pattern of haplotype and allele networks reinforces this hypothesis that both networks demonstrated low variation at high frequencies and high variation at low frequencies, typical of a history of population expansion, which has been observed for other species of sharks (Domingues et al. 2018; Ramirez-Amaro et al. 2018; Kuguru et al., 2019).

Global warming has been greatly studied in recent years, and the implications that this could have exercise influence on many taxa have been greatly discussed, including changes in distribution, abundance and density of species, as well as the phenotypic and physiological

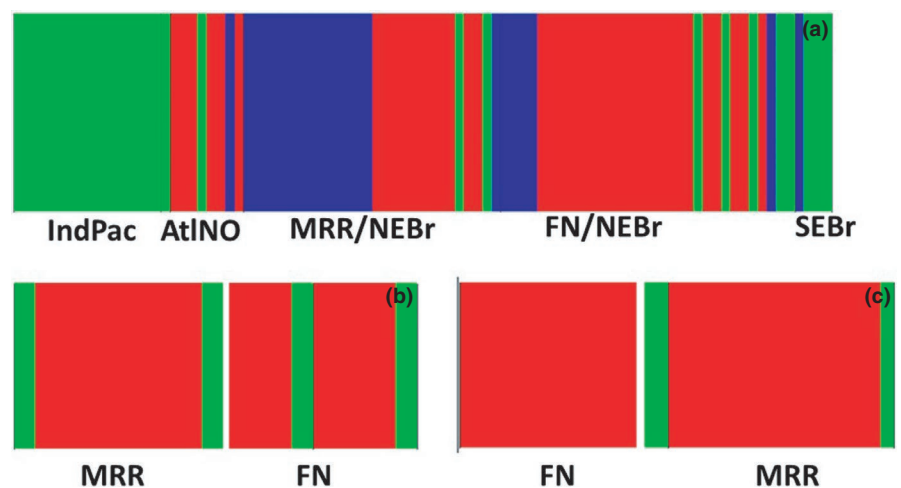


FIGURE 5 BAPS (Bayesian Analyses of Population Structure): (a) CR, (b) LDHA and (c) ITS-2. For acronyms, please consult Figure 1

changes in organisms (Hughes, 2000; Walther et al., 2002; Hughes et al., 2003; Root et al., 2003; Thomas et al., 2004; Parmesan, 2006; Mawdsley et al., 2009; Poloczanska et al., 2013; Alcarez-Romero et al. 2018; Watson et al., 2018). Global temperature increasing events are indicated during the Holocene (11,300 years until present) in tropical zones (Marcott et al., 2013), and their effects can cause significantly important oscillations in the demography and in the population genetics of many species including tiger sharks as observed herein. These signs of N_e oscillations over time have been demonstrated at several different species (Torres & Ribeiro, 2009; Von der Heyden et al., 2011; der Heyden et al., 2013; Teske et al., 2013; Lima et al., 2016; Baggio et al., 2017; Machado et al., 2017). Despite the occasional capability on reaching temperatures below 15°C, tiger sharks seem to prefer warmer waters. Specimens from Hawaiian Archipelago were monitored and in around 75% of the observations occurred above 22°C (Meyer et al. 2018). Thus, the biological and ecological features of the tiger sharks such as wide distribution, high longevity, high fecundity rate, generalist predator (Randall 1992;

Lowe et al. 1996; Simpfendorfer, 1992; Shibuya et al. 2005; Pickard et al. 2016) and great movement (mainly horizontal and occasional vertical) (Afonso et al., 2017; Afonso & Hazin, 2015; Hammerschlag et al., 2012; Hazin et al., 2013; Holmes et al., 2014; Lea et al., 2015; Vaudo et al., 2014; Meyer et al. 2018), compared to others sharks (Compagno 1984; Randall 1992; Whitney et al. 2000), help the species possibly and occasionally overcome unfavourable conditions.

4.2 | Connectivity: global and regional as a validation for translocations as a green strategy

Significant structuring was detected in tiger shark when global comparisons were made in relation to Atlantic and Pacific provinces, according to the fixation index of genetic variation (Φ_{ST}). Importantly, the inclusion of a significant amount ($n = 43$) of new data from coastal North-eastern Brazil might have favoured this evidence. Naylor et al. (2012) proposed the existence of two

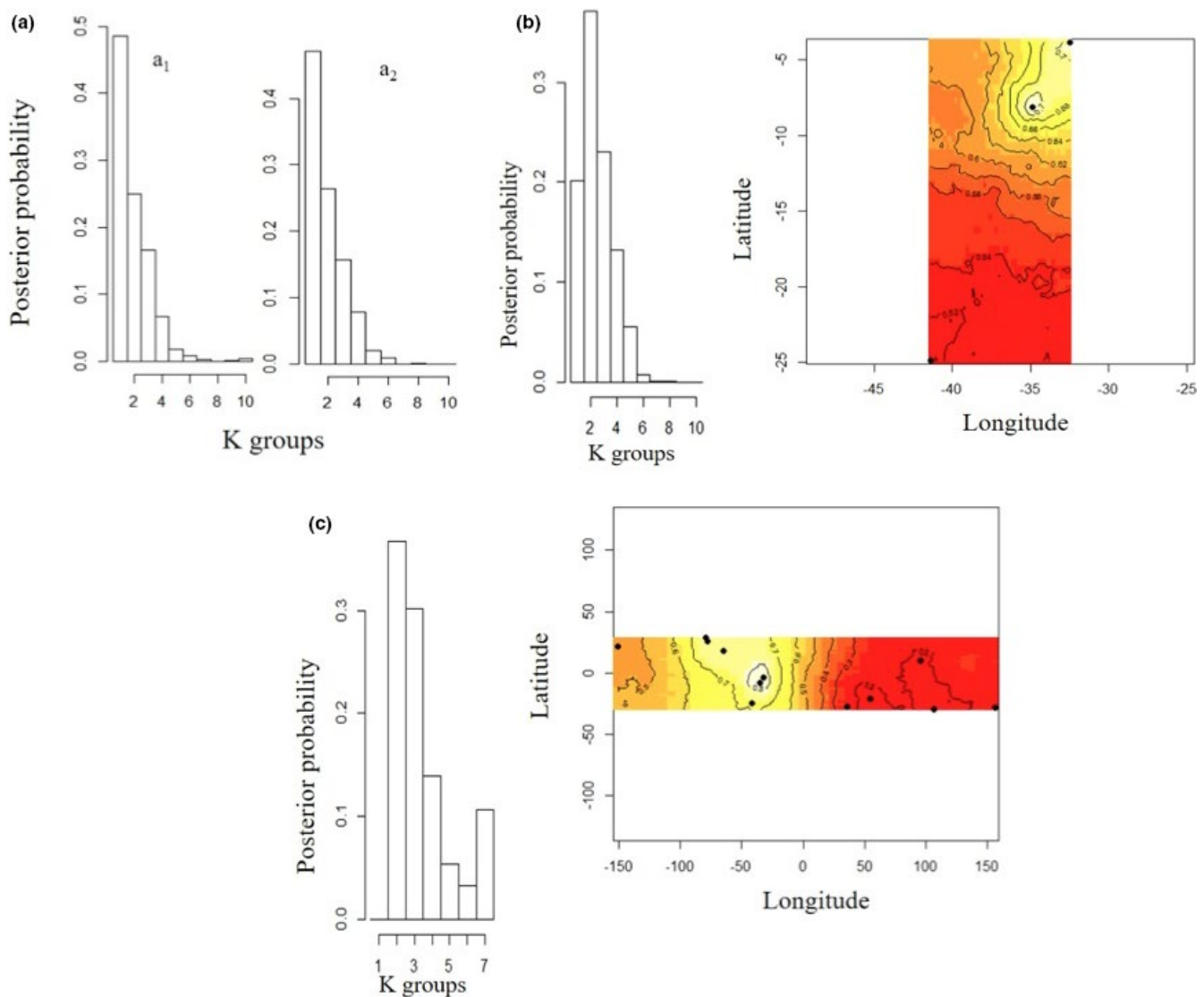


FIGURE 6 Geneland results: (a_1) CR + LDHA and (a_2) CR + ITS-2 for the MRRxFN; CR: (b) NE x SE and (c) global data

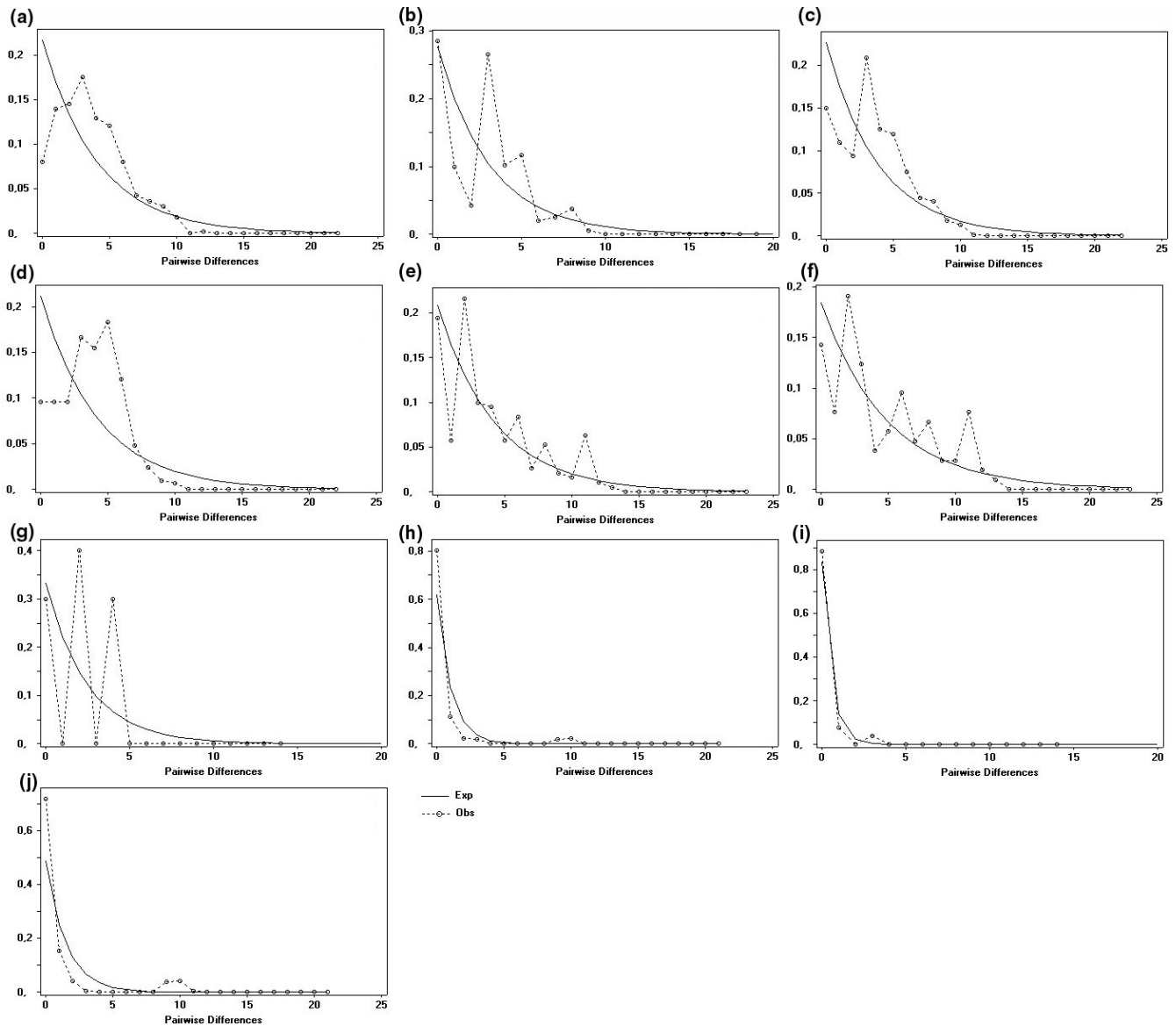


FIGURE 7 Mismatch distribution results: (a)FN, (b)MRR, (c)FN + MRR and (d) (CR data);(e)FN + MRR, (f)MRR, and (g)FN(Lactate dehydrogenase intron A data); (h)FN + MRR, (i)MRR, (j) FN (ITS-2 data)

allopatric species occurring in the regions. However, molecular data rejected this hypothesis and suggested the existence of two populations recently separated (<1 million years ago), sharing haplotypes with the Brazilian population (Bernard et al., 2016; Carmo et al., 2019; Holmes et al., 2017). The genetic-evolutionary division between the Pacific and Atlantic basins has been reported for other animals (Craig et al., 2016; Ceballos et al., 2016), including sharks (Quattro et al., 2006; Duncan et al. 2006; Castro et al., 2007; Dudgeon et al., 2012; Gubili et al., 2010; Sigsgaard et al., 2016). The Φ_{ST} and the calibrated Bayesian topology obtained here are consistent with previous molecular studies pointing to the existence of differences between the Indo-Pacific and Atlantic regions. Also, the Bayesian topology obtained in this study using the CR data recovered the time of differentiation, reinforcing the Isthmus of Panama as a consistent oceanographic barrier. The mismatch data obtained also supported the coexistence of

different lineages found for the species, indicating a possible secondary contact between populations. Secondary contact has been recently demonstrated for marine species in the tropical Atlantic (Jacobina et al., 2020). Such contact between these tiger shark lineages may have been gradually facilitated by a steady increase in sea level over the past millennia, as has been previously mentioned above for the whole community of marine species.

Geneland reinforced $K = 2$ populations found by Bernard et al. (2016) and Holmes et al. (2017). The Bayesian topology obtained supported this result and also demonstrated the Pacific West samples as a third population, given the observed posterior probability to $K = 3$. The Bayesian topology, the haplotype networks and the BAPS analysis recovered the three genetic lineages ($K = 3$) for *G. cuvier*. These data indicate the isolation of IndPac specimens but with a closer similarity to the SEBr region. This relationship implies large connectivity between the areas and also reinforces the ability

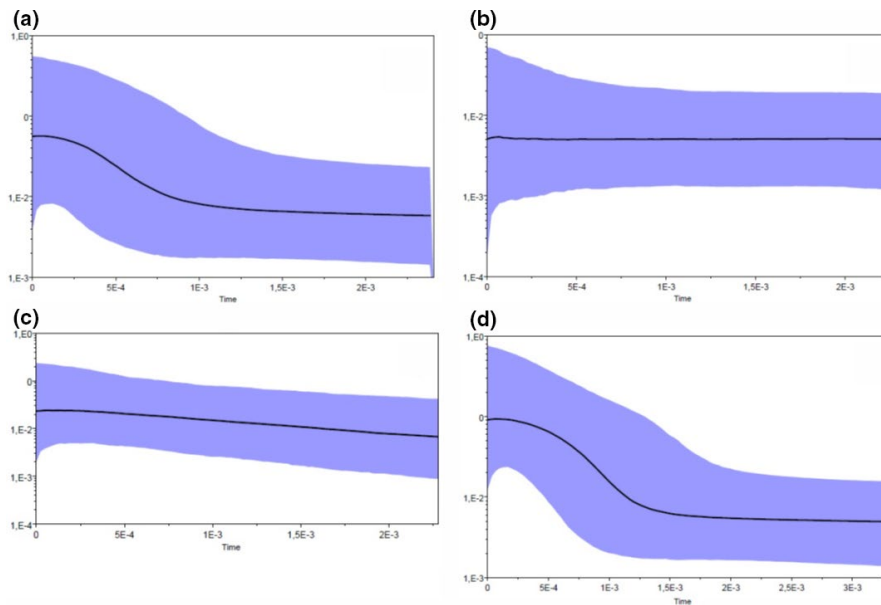


FIGURE 8 BSP results (Bayesian Skyline Plots) with CR data (mutation rate of 0.55% of divergence between lineages per million years): (a)MRR + FN, (b) MRR, (c) FN and (d) global. The logarithmic “y” axis represents the population size in function of the effective population size (Ne) and the “x” axis divergence time (Myr)

TABLE 2 Pairwise AMOVA (F_{ST}) against the CR data for *Galeocerdo cuvier*. NEBr = North-eastern Brazil; SEBr = South-eastern Brazil; AtINO = North Atlantic; IndPac = Indo-Pacific (** $p < 1\%$; ns = non-significant).

| | NEBr | SEBr | AtINO | IndPac |
|--------|---------------------|---------------------|---------------------|--------|
| NEBr | - | | | |
| SEBr | 0.035 ^{ns} | - | | |
| AtINO | 0.036 ^{ns} | 0 | - | |
| IndPac | 0.144** | 0.041 ^{ns} | 0.024 ^{ns} | - |

of horizontal movement by *G. cuvier*, even throughout the South Atlantic, which houses dispersion barriers for many fish such as the warm Benguela current (Floeter et al., 2008; Joyeux et al., 2001; Rocha, 2003). This hypothesis is further supported by the results of the pairwise fixation index (F_{ST}) obtained in this study that revealed the absence of statistically significant evolutionary and genetic differences between the genetic variation of the IndPac and the SEBr and the latter with NEBr, suggesting the South-eastern region of Brazil as a route of communication between the Indo-Pacific basin with equatorial zones of the South Atlantic.

This study also and importantly revealed the population genetic homogeneity of *G. cuvier* in Pernambuco. The parameters of the population genetics, such as fixation indices Φ_{ST} , the relationship between the observed genetic variants (haplotype/allele networks) and the Bayesian population structure tests (BAPS and Geneland), revealed that the specimens from FN and those from MRR are genetically very similar, based on all three analysed loci (mitochondrial and nuclear). The cohesion found herein between MRR and FN suggests high gene flow between these areas, which supports the existence of a single panmictic population in the region. This pattern is quite different to the previous hypothesis, suggesting the occurrence of a barrier between the coast of North-eastern Brazil and FN islands, and the lack of specimens sampled in the coast of North-eastern Brazil

explains that observed original pattern (Carmo et al., 2019). Thus, the tiger's shark high mobility (capacity of travel for long distances), by the movement of the species northwards (Hazin et al., 2013) and by the South Equatorial Under Current (SEUC) which favours a route in the direction of FN (Peterson & Stramma, 1991), possibly due to the preference of these animals to warmer temperature as already shown in Heithaus (2001) Holmes et al. (2014) Wirsing et al. (2006) and Meyer et al. (2018) was attested by the high gene flow between the areas observed herein. Importantly and in general, water temperature has been considered as a driver to some biological features in fishes as fecundity (Chen et al. 2020). Specifically, the temperature has been closely associated with movements in several aquatic species (Andrzejczak et al., 2019; Kiyofuji et al., 2019; Staveley et al., 2019), including sharks (Lee et al., 2019; Verissimo et al., 2017;). Therefore, the combination of this species' behavioural attributes, with the dynamic of currents and with the genetic data observed here, suggests high gene flow between FN and MRR, supporting the existence of a single cohesive and panmictic population in the region.

Another interesting approach to regional connectivity is the comparison between the observed genetic variation in Pernambuco (MRR + FN) and in South-eastern Brazil (Bernard et al., 2016). The CR data obtained here allow for such a comparison, in which the Bayesian Analysis of Population Structure (BAPS) and Geneland pointed to the division of the genetic variation of this species between areas, suggesting two distinct genetic profiles ($k = 2$). Despite the fixation index (Φ_{ST}) suggested the absence of structuring between the regions, both BAPS and Geneland can detect subtle structurings (Corander et al. 2008; Guillot et al. 2011; Cheng et al., 2013; Bourgeois et al. 2017). Thereby, such evidences suggest a subtle division in the genetic variation between Pernambuco (MRR + FN) and South-eastern Brazil. This hypothesis reinforced partially the original idea of a barrier occurring between FN Islands and South-eastern Brazil (Carmo et al., 2019). On the other hand, the results obtained

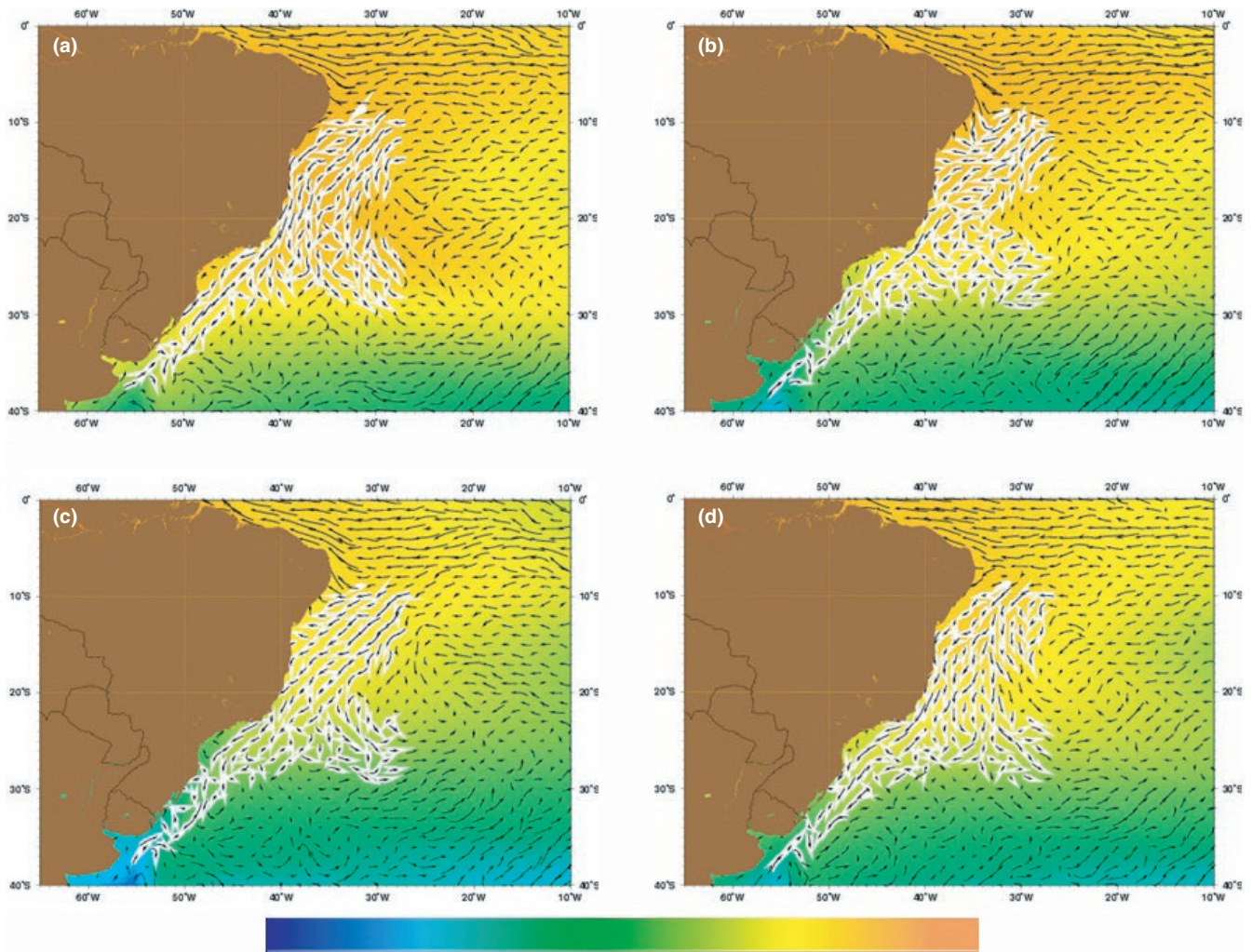


FIGURE 9 Pattern of the annual positioning of the Brazil Current (BC; in white) and of the South Equatorial Current axis (SEC) off the coast of Brazil. The arrows indicate the flow of currents: BD in a southward direction and SEC in a northward direction from the latitude 12°S. In (a), (b), (c) and (d), January, February and March; April, May and June, July August and September; and October, November and December, respectively. The gradient bar below indicates colder temperatures (blue) and hotter temperatures (orange). Taken from Bischof et al. (2004) (<http://oceancurrents.rsmas.miami.edu/atlantic/brazil.html>.)

here also modified the map of the distribution of genetic variation of tiger sharks along the South-western Atlantic by suggesting a probable population division between North-eastern and South-eastern coasts of Brazil.

In conclusion, using the overall set of findings and hypotheses found in this study it is possible to reinforce that *Galeocerdo cuvier* is regionally and globally resilient based on the moderate to eventually high levels of genetic diversity. This fits well with IUCN status of this species. The regional connectivity patterns suggest a lack of structuring between MRR and FN using the multiloci approach, which sustains a single cohesive population between the areas. Furthermore, it is possible to apply this information to the increment of mitigation for attacks on humans in the MRR. The strategy used by the State Committee of the Monitoring of Incidents with Sharks (CEMIT) in the state of Pernambuco to mitigate the attacks has been the translocation of live individuals of *G. cuvier* from beach regions (MRR; risk area) to those located further

from the coast (Hazin & Affonso 2014). The monitoring of *G. cuvier* in the region has suggested a movement route of the species in a south–north direction (Hazin et al., 2013). The issue with this method was due to the lack of scientific validation of this strategy, as this could favour contact between historically disjunct populations. The mixing of evolutionary isolated populations is considered to be one of the worst methods in preserving biological diversity (Candall et al. 2000; Moritz, 2002). However, the evolutionary and genetic findings obtained herein indicate that the translocation strategy does not cause anthropogenic changes, as it favours the maintenance of a historically consolidated population. Therefore, the present genetic analyses validated the translocation of individuals as a green strategy to minimize contacts among sharks and humans in recreation areas. Finally, the data presented here suggest that similar procedures could be adopted in another areas worldwide where interactions among sharks and humans are very common.

ACKNOWLEDGEMENTS

The study was funded by INCT—Ciências do Mar em Ambientes Marinhos Tropicais—CNPq/Fapesb (2014/17) and the Government Scholarship (2014–2016) for master's degree provided by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), the Ministry of Education. This study was also funded by Projeto CAPES CIMAR II and Protuba-Governo do Estado de Pernambuco, Brazil. RAT is grateful for the research fellowship provided by CNPq (grant no. 306290/2015-4).

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REFERENCES

- Afonso, A. S., Garla, R., & Hazin, F. H. V. (2017). Tiger sharks can connect equatorial habitats and fisheries across the Atlantic Ocean basin. *PLoS One*, 12, e0184763. <https://doi.org/10.1371/journal.pone.0184763>
- Afonso, A. S., & Hazin, F. H. V. (2015). Vertical movement patterns and ontogenetic niche expansion in the tiger shark, *Galeocerdo cuvier*. *PLoS ONE*, 10, e0116720. <https://doi.org/10.1371/journal.pone.0116720>
- Akaike, H. (1979). A Bayesian extension of the minimum AIC procedure of autoregressive model fitting. *Biometrika*, 66, 237–242. <https://doi.org/10.1093/biomet/66.2.237>
- Akaike, H. (1983). Information measures and model selection. *Proceedings of the 44th Session of the International Statistical Institute*, 1, 277–291.
- Allendorf, F. W., Berry, O., & Ryman, N. (2014). So long to genetic diversity, and thanks for all the fish. *Molecular Ecology*, 23, 23–25. <https://doi.org/10.1111/mec.12574>
- Álvarez-Romero, J. G., Munguía-Vega, A., Beger, M., Mar Mancha-Cisneros, M., Suárez-Castillo, A. N., Gurney, G. G., ... Torre, J. (2018). Designing connected marine reserves in the face of global warming. *Global Change Biology*, 24, e671–e691. <https://doi.org/10.1111/gcb.13989>
- Amos, W., & Balmford, A. (2001). When does conservation genetics matter? *Heredity*, 87, 257–265. <https://doi.org/10.1046/j.1365-2540.2001.00940.x>
- Andrzejczek, S., Gleiss, A. C., Pattiaratchi, C. B., & Meekan, M. G. (2019). Patterns and drivers of vertical movements of the large fishes of the epipelagic. *Reviews in Fish Biology and Fisheries*, 29, 335–354. <https://doi.org/10.1007/s11160-019-09555-1>
- Baggio, R. A., Stoiev, S. B., Spach, H. L., & Boeger, W. A. (2017). Opportunity and taxon pulse: The central influence of coastal geomorphology on genetic diversification and endemism of strict estuarine species. *Journal of Biogeography*, 44, 1626–1639. <https://doi.org/10.1111/jbi.12934>
- Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., & Doherty, P. A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science*, 299, 389–392. <https://doi.org/10.1126/science.1079777>
- Bellafronte, E., Mariguela, T. C., Pereira, L. H., Oliveira, C., & Moreira-Filho, O. (2013). DNA barcode of Parodontidae species from the La Plata river basin - applying new data to clarify taxonomic problems. *Neotropical Ichthyology*, 11, 497–506. <https://doi.org/10.1590/S1679-62252013000300003>
- Bernard, A. M., Feldheim, K. A., Heithaus, M. R., Wintner, S. P., Wetherbee, B. M., & Shivji, M. S. (2016). Global population genetic dynamics of a highly migratory, apex predator Shark. *Molecular Ecology*, 25, 5312–5329. <https://doi.org/10.1111/mec.13845>
- Bischof, B., Rowe, E., Mariano, A. J., & Ryan, E. H. (2004). *The Brazil current*. Ocean Surface. Currents., (access in april 24th 2020) <https://oceancurrents.rsmas.miami.edu/atlantic/brazil.html>
- Blower, D. C., Pandolfi, J. M., Bruce, B. D., Gomez-Cabrera, M. C., & Ovenden, J. R. (2012). Population genetics of Australian white sharks reveals fine-scale spatial structure, transoceanic dispersal events and low effective population sizes. *Marine Ecology Progress Series*, 455, 229–244. <https://doi.org/10.3354/meps09659>
- Bourgeois, Y. X. C., Hazzouri, K. M., & Warren, B. H. (2017). Going down the rabbit hole: A review on methods characterizing selection and demography in natural populations. *bioRxiv*, 052761. <https://doi.org/10.1101/052761>
- Burgess, G. L., Beerkircher, L. R., Gregor, M., Cailliet, G. M., Carlson, J. K., Cortés, E., ... Simpfendorfer, C. A. (2005). Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? *Fisheries*, 30, 19–26. [https://doi.org/10.1577/1548-8446\(2005\)30](https://doi.org/10.1577/1548-8446(2005)30)
- Carmo, C. B., Ferrette, B. L. S., Camargo, S. M., Roxo, F. F., Coelho, R., Garla, R. C., ... Mendonça, F. F. (2019). A new map of the tiger shark (*Galeocerdocuvier*) genetic population structure in the western Atlantic Ocean: Hypothesis of an equatorial convergence centre. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 1–13.
- Castro, A. L., Stewart, S., Wilson, G., Hueter, R. E., Meekan, M. G., Motta, P. J., ... Karl, S. (2007). Population genetic structure of Earth's largest fish, the whale shark (*Rhincodon typus*). *Molecular Ecology*, 16, 5183–5192.
- Ceballos, S. G., Lessa, E. P., Licandeo, R., & Fernández, D. A. (2016). Genetic relationships between Atlantic and Pacific populations of the notothenioid fish *Eleginops maclovinus*: The footprints of Quaternary glaciations in Patagonia. *Heredity*, 116, 372–377. <https://doi.org/10.1038/hdy.2015.106>
- Chapman, D. D., Feldheim, K. A., Papastamatiou, Y. A., & Hueter, R. E. (2015). There and back again: A review of residency and return migrations in Sharks, with implications for population structure and management. *The Annual Review of Marine Science*, 7, 547–570. <https://doi.org/10.1146/annurev-marine-010814-015730>
- Chen, Y.-S., Jeng, Z.-Y., & Wang, H.-Y. (2020). Changes in reproduction for subtropical cutlassfish *Trichiurus japonicus* reflect variation in temperature and population demography. *Marine Ecology*, 41, e12578.
- Cheng, L., Connor, T. R., Sirén, J., Aanensen, D. M., & Corander, J. (2013). Hierarchical and spatially explicit clustering of DNA sequences with BAPS software. *Molecular Biology and Evolution*, 30, 1224–1228. <https://doi.org/10.1093/molbev/mst028>
- Clua, E. E. G., Linnell, J. D. C., Planes, S., & Meyer, C. G. (2020). Selective removal of problem individuals as an environmentally responsible approach for managing shark bites on humans. *Ocean and Coastal Management*, 194, 105266. <https://doi.org/10.1016/j.ocecoaman.2020.105266>
- Compagno, L. J. V. (1984). *FAO Species Catalogue, Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1 – Hexanchiformes to Lamniformes*. FAO Fisheries. Synopsis, 125, 4/1, 1–249.
- Corander, J. & Marttinen, P. (2006). Bayesian identification of admixture events using multilocus molecular markers. *Molecular Ecology*, 15, 2833–2843. <https://doi.org/10.1111/j.1365-294X.2006.02994.x>
- Corander, J., Marttinen, P., Sirén, J., & Tang, J. (2008). Enhanced Bayesian modelling in BAPS software for learning genetic structures of populations. *BMC Bioinformatics*, 9, 539.
- Corander, J., Waldmann, P., & Sillanpää, M. J. (2003). Bayesian analysis of genetic differentiation between populations. *Genetics*, 163, 367–374.
- Craig, M. T., Graham, R. T., Torres, R. A., Hyde, J. R., Freitas, M. O., Ferreira, B. P., Hostim-Silva, M., Gerhardinger, L. C., Bertoncini, A. A., & Robertson, D. R. (2009). How many species of goliath grouper are there? Cryptic genetic divergence in a threatened marine fish and the resurrection of a geopolitical species. *Endangered Species Research*, 7, 167–174.

- Crandall, K. A., Bininda-Emonds, O. R. P., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary processes in conservation biology. *Trends in Ecology and Evolution*, *15*(7), 290–295.
- Darriba, D., Taboada, G. L., Doallo, R., & Pousada, D. (2012). jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods*, *9*, 772. <https://doi.org/10.1038/nmeth.2109>
- Davidson, L. N. K., Krawchuk, M. A., & Dulvy, N. K. (2016). Why have global shark and ray landings declined: Improved management or overfishing? *Fish and Fisheries*, *17*, 438–458. <https://doi.org/10.1111/faf.12119>
- Domingues, R. R., Bruels, C. C., Gadig, O. B. F., Chapman, D. D., Hilsdorf, A. W. S., & Shivji, M. S. (2019). Genetic connectivity and phylogeography of the night shark (*Carcharhinus signatus*) in the western Atlantic Ocean: Implications for conservation management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*, 102–114.
- Domingues, R. R., Hilsdorf, A. W. S., & Gadig, O. B. F. (2018). The importance of considering genetic diversity in shark and ray conservation policies. *Conservation Genetics*, *19*, 501–525. <https://doi.org/10.1007/s10592-017-1038-3>
- Domingues, R. R., Hilsdorf, A. W. S., Shivji, M. M., Hazin, F. V. H., & Gadig, O. B. F. (2018). Effects of the Pleistocene on the mitochondrial population genetic structure and demographic history of the silky shark (*Carcharhinus falciformis*) in the western Atlantic Ocean. *Reviews Fish Biology Fisheries*, *28*, 213–227. <https://doi.org/10.1007/s11160-017-9504-z>
- Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. <https://doi.org/10.1093/molbev/mss075>
- Dudgeon, C. L., Blower, D. C., Broderick, D., Giles, J. L., Holmes, B. J., Kashiwagi, T., ... Ovenden, J. R. (2012). A review of the application of molecular genetics for fisheries management and conservation of sharks and rays. *Journal of Fish Biology*, *80*, 1789–1843. <https://doi.org/10.1111/j.1095-8649.2012.03265.x>
- Duncan, K. M., Martin, A. P., Bowen, B. W., & DeCouet, H. G. (2006). Global phylogeography of the scalloped hammerhead shark (*Sphyrna lewini*). *Molecular Ecology*, *15*, 2239–2251.
- Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortés, E., Domingo, A., ... Valenti, S. (2008). You can swim but you can't hide: The global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *18*, 459–482. <https://doi.org/10.1002/aqc.975>
- Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, *10*, 564–567. <https://doi.org/10.1111/j.1755-0998.2010.02847.x>
- Excoffier, L., Smouse, P. E., & Quattro, J. M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes application to human mitochondrial-DNA restriction data. *Genetics*, *131*, 479–491.
- Felsenstein, J. (2005). PHYLIP. (Phylogeny Inference Package) version 3.6. Distributed by the author. : Department of Genome Sciences, University of Washington.
- Ferrette, B. L. S., Mendonça, F. F., Coelho, R., Oliveira, P. G. V., Hazin, F. H. V., Romanov, E. V., ... Foresti, F. (2015). High connectivity of the Crocodile Shark between the Atlantic and Southwest Indian oceans: Highlights for conservation. *PLoS One*, *10*, e0117549.
- Flanagan, S. P., Forester, B. R., Latch, E. K., Aitken, S. N., & Hoban, S. (2018). Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. *Evolutionary Applications*, *11*, 1035–1052. <https://doi.org/10.1111/eva.12569>
- Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., ... Bernardi, G. (2008). Atlantic reef fish biogeography and Evolution. *Journal of Biogeography*, *35*, 22–47.
- Fossile, T., Ferreira, J., Bandeira, D. R., Dias-da-Silva, S., & Colonese, A. C. (2020). Integrating zooarchaeology in the conservation of coastal-marine ecosystems in Brazil. *Quaternary International*, *545*, 38–44. <https://doi.org/10.1016/j.quaint.2019.04.022>
- Frankham, R., Ballou, J. D., & Briscoe, D. A. (2008). Fundamentos da Genética da Conservação. Sociedade Brasileira De Genética, p. 280.
- Fu, Y.-X. (1997). Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, *147*, 915–925.
- Gaither, M. R., Bowen, B. W., Rocha, L. A., & Briggs, J. C. (2016). Fishes that rule the world: Circumtropical distributions revisited. *Fish and Fisheries*, *17*, 664–679. <https://doi.org/10.1111/faf.12136>
- Garcia, V. B., Lucifora, L. O., & Myers, R. A. (2008). The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 83–89. <https://doi.org/10.1098/rspb.2007.1295>
- Giles, J. L., Riginos, C., Naylor, G. J., Dharmadi, & Ovenden, J. R. (2016). Genetic and phenotypic diversity in the wedgetfish *Rhynchobatus australiae*, a threatened ray of high value in the shark fin trade. *Marine Ecology Progress Series*, *548*, 165–180. <https://doi.org/10.3354/meps11617>
- Gilson, S.-P., & Lessa, A. (2019). Human-Sharks interaction in chroniclers' accounts from the XVIth and XVIIIth centuries: A rich source of information for Brazilian zooarchaeological studies. *Archaeofauna*, *28*, 157–167.
- Gubili, C., Bilgin, R., Kalkan, E., Karhan, S. U., Jones, C. S., Sims, D. W., ... Noble, L. R. (2010). Antipodean white sharks on a Mediterranean walkabout? Historical dispersal leads to genetic discontinuity and an endangered anomalous population. *Proceedings of the Royal Society B*, *278*, 1679–1686. <https://doi.org/10.1098/rspb.2010.1856>
- Gubili, C., Robinson, C. E. C., Cliff, G., Wintner, S. P., De Sabata, E., De Innocentiis, S., ... Jones, C. S. (2015). DNA from historical and trophic samples provides insights into white shark population origins and genetic diversity. *Endangered Species Research*, *27*, 233–241. <https://doi.org/10.3354/esr00665>
- Guillot, G., Estoup, A., Mortier, F., & Cosson, J. F. (2005b). A spatial statistical model for landscape genetics. *Genetics*, *170*, 1261–1280. <https://doi.org/10.1534/genetics.104.033803>
- Guillot, G., Mortier, F., & Estoup, A. (2005a). Geneland: A computer package for landscape genetics. *Molecular Ecology Notes*, *5*, 712–715. <https://doi.org/10.1111/j.1471-8286.2005.01031.x>
- Hall, T. (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, *41*, 95–98.
- Hammerschlag, N., Gallagher, A. J., Wester, J., Luo, J., & Ault, J. S. (2012). Don't bite the hand that feeds: Behavioral impacts of provisioning ecotourism on an apex marine predator. *Functional Ecology*, *26*, 567–576.
- Harpending, H. C. (1994). Signature of ancient population growth in a low resolution mitochondrial DNA mismatch distribution. *Human Biology*, *66*, 591–600.
- Hazin, F. H. V., & Afonso, A. S. (2014). A green strategy for shark attack mitigation off Recife, Brazil. *Animal Conservation*, *17*, 287–296.
- Hazin, F. H. V., Afonso, A. S., Castilho, P. C., Ferreira, L. C., & Rocha, B. C. L. (2013). Regional movements of the tiger shark, *Galeocerdo cuvier*, off northeastern Brazil: Inferences regarding shark attack hazard. *Anais Da Academia Brasileira De Ciências*, *85*, 1053–1062. <https://doi.org/10.1590/S0001-37652013005000055>
- Heithaus, M. R. (2001). The biology of tiger sharks, *Galeocerdo cuvier*, in Shark Bay, Western Australia: Sex ratio, size distribution, diet, and seasonal changes in catch rates. *Environmental Biology of Fishes*, *61*(1), 25–36.
- Heithaus, M. R., Hamilton, I. M., Wirsing, A. J., & Dill, L. M. (2006). Validation of a randomization procedure to assess animal habitat preferences: Microhabitat use of tiger sharks in a seagrass

- ecosystem. *Journal of Animal Ecology*, 75, 666–676. <https://doi.org/10.1111/j.1365-2656.2006.01087.x>
- Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society B*, 359, 183–195. <https://doi.org/10.1098/rstb.2003.1388>
- Holmes, B. J., Pepperell, J. G., Griffiths, S. P., Jaine, F. R. A., Tibbetts, I. R., & Bennett, M. B. (2014). Tiger shark (*Galeocerdocuvier*) movement patterns and habitat use determined by satellite tagging in eastern Australian waters. *Marine Biology*, 16, 2645–2658. <https://doi.org/10.1007/s00227-014-2536-1>
- Holmes, B. J., Williams, S. M., Otway, N. M., Nielsen, E. E., Maher, S. L., Bennett, M. B., & Ovenden, J. R. (2017). Population structure and connectivity of tiger sharks (*Galeocerdocuvier*) across the Indo-Pacific Ocean basin. *Royal Society Open Science*, 4, 170309.
- Hughes, L. (2000). Biological consequences of global warming: Is the signal already. *Trends in Ecology & Evolution*, 15, 56–61.
- Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., ... Hoegh-Guldberg, O. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929–933. <https://doi.org/10.1126/science.1085046>
- Jacobina, U. P., Torres, R. A., Afonso, P. R. A. M., Santos, E. V., Calado, L. L., & Bitencourt, J. A. (2020). DNA barcoding reveals cryptic diversity and peculiar phylogeographic patterns in mojarras (Perciformes: Gerreidae) from the Caribbean and Southwestern Atlantic. *Journal of the Marine Biological Association of the United Kingdom*, 100, 277–283.
- Joyeux, J. C., Floeter, S. R., Ferreira, C. E. L., & Gasparini, J. L. (2001). Biogeography of tropical reef fishes: The South Atlantic puzzle. *Journal of Biogeography*, 28, 831–841. <https://doi.org/10.1046/j.1365-2699.2001.00602.x>
- Karl, S. A., Castro, A. L. F., & Garla, R. C. (2012). Population genetics of the nurse shark (*Ginglymostoma cirratum*) in the western Atlantic. *Marine Biology*, 159, 489–498. <https://doi.org/10.1007/s00227-011-1828-y>
- Karl, S. A., Castro, A. L. F., Lopez, J. A., Charvet, P., & Burgess, G. H. (2011). Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred from mitochondrial and microsatellite DNA. *Conservation Genetics*, 12, 371. <https://doi.org/10.1007/s10592-010-0145-1>
- 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. *Molecular Ecology*, 15, 3669–3679. <https://doi.org/10.1111/j.1365-294X.2006.03036.x>
- King, J. R., Wetklo, M., Supernault, J., Taguchi, M., Yokawa, K., Sosa-Nishizaki, O., & Withler, R. E. (2015). Genetic analysis of stock structure of blue shark (*Prionace glauca*) in the north Pacific ocean. *Fisheries Research*, 172, 181–189. <https://doi.org/10.1016/j.fishres.2015.06.029>
- Kiyofuji, H., Aoki, Y., Kinoshita, J., Okamoto, S., Masujima, M., Matsumoto, T., ... Kitagawa, T. (2019). Northward migration dynamics of skipjack tuna (*Katsuwonus pelamis*) associated with the lower thermal limit in the western Pacific Ocean. *Progress in Oceanography*, 175, 55–67. <https://doi.org/10.1016/j.pocean.2019.03.006>
- Kuguru, G., Gennari, E., Wintner, S., Dicken, M. L., Klein, J. D., Rhode, C., & der Merwe, A. E. B.-v. (2019). Spatio-temporal genetic variation of juvenile smooth hammerhead sharks in South Africa. *Marine Biology Research*, 15(10), 568–579. <https://doi.org/10.1080/17451000.2019.1695058>
- Larson, S., Farrer, D., Lowry, D., & Ebert, D. A. (2015). Preliminary observations of population genetics and relatedness of the broadnose sevengill Shark, *Notorynchus cepedianus*, in two Northeast Pacific Estuaries. *PLoS One*, 10, e0129278. <https://doi.org/10.1371/journal.pone.0129278>
- Laurraquiuo-A, N. S., Islas-Villanueva, V., Adams, D., Uribe-Alcocer, M., Alvarado-Bremer, J. R., & Díaz-Jaimés, P. (2019). Genetic evidence for regional philopatry of the Bull Shark (*Carcharhinus leucas*), to nursery areas in estuaries of the Gulf of Mexico and western North Atlantic ocean. *Fisheries Research*, 209, 67–74. <https://doi.org/10.1016/j.fishres.2018.09.013>
- Lea, J. S., Wetherbee, B. M., Queiroz, N., Burnie, N., Aming, C., Sousa, L. L., ... Shivji, M. S. (2015). Repeated, long-distance migrations by a philopatric predator targeting highly contrasting ecosystems. *Scientific Reports*, 5, 11202. <https://doi.org/10.1038/srep11202>
- Lee, K. A., Smoothy, A. F., Harcourt, R. G., Roughan, M., Butcher, P. A., & Peddemors, V. M. (2019). Environmental drivers of abundance and residency of a large migratory shark, *Carcharhinus leucas*, inshore of a dynamic western boundary current. *Marine Ecology Progress Series*, 622, 121–137. <https://doi.org/10.3354/meps13052>
- Leigh, J. W. (2016). PopART – Population Analysis with Reticulate Trees. <http://popart.otago.ac.nz>. Accessed 15 August 2016.
- Librado, P., & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25, 1451–1452. <https://doi.org/10.1093/bioinformatics/btp187>
- Lima, S. M. Q., Vasconcellos, A. V., Berbel-Filho, W. M., Lazoski, C., Russo, C. A. M., Sazima, I., & Solé-cava, A. M. (2016). Effects of Pleistocene climatic and geomorphological changes on the population structure of the restricted-range catfish *Trichogenes longipinnis* (Siluriformes: Trichomycteridae). *Systematics and Biodiversity*, 1, 1–16.
- Lowe, C. G., Wetherbee, B. M., Crow, G. L., & Tester, A. L. (1996). Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian Waters. *Environmental Biology of Fishes*, 47, 203–211.
- Machado, K. F., Damasceno, J. S., Bertoncini, A. A., Tosta, V. C., Farro, A. P. C., Hostim-Silva, M., & Oliveira, C. (2017). Population genetic structure and demographic history of the spadefish, *Chaetodipterus faber* (Ephippidae) from Southwestern Atlantic. *Journal of Experimental Marine Biology and Ecology*, 487, 45–52. <https://doi.org/10.1016/j.jembe.2016.11.005>
- Marcott, S. A., Shakun, J. D., Clark, P. U., & Mix, A. C. (2013). A reconstruction of regional and global temperature for the past 11,300 years. *Science*, 339, 1198–1201. <https://doi.org/10.1126/science.1228026>
- Mawdsley, J. R., Malley, R., & Ojima, D. S. (2009). A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. *Conservation Biology*, 23, 1080–1089. <https://doi.org/10.1111/j.1523-1739.2009.01264.x>
- Meyer, C. G., Anderson, J. M., Coffey, D. M., Hutchinson, M. R., Royer, M. A., & Holland, K. N. (2018). Habitat Geography around Hawaii's Oceanic Islands Influences Tiger Shark (*Galeocerdo cuvier*) Spatial Behavior and Shark Bite Risk at Ocean Recreation sites. *Scientific Reports*, 8, 4945.
- Midway, S. R., Wagner, T., & Burguess, G. H. (2019). Trends in global shark attacks. *PLoS One*, 14(2), e0211049. <https://doi.org/10.1371/journal.pone.0211049>
- Moritz, C. (2002). Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, 51(2), 238–254.
- Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, 315, 1846–1850. <https://doi.org/10.1126/science.1138657>
- Naylor, G. J. P., Caira, J. N., Jensen, K., Rosana, K. A. M., White, W. T., & Last, P. R. (2012). A DNA sequence-based approach to the identification of Shark and ray species and its implications for global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History*, 367, 1–262. <https://doi.org/10.1206/754.1>
- Pank, M., Stanhope, M., Natanson, L., Kohler, N., & Shivji, M. (2001). Rapid and simultaneous identification of body parts from the morphologically similar sharks *Carcharhinus obscurus* and *Carcharhinus plumbeus* (Carcharhinidae) using multiplex PCR. *Marine Biotechnology*, 3, 231–240. <https://doi.org/10.1007/s101260000071>

- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Peterson, R. G., & Stramma, L. (1991). Upper-level circulation in the South Atlantic Ocean. *Progress in Oceanography*, 26, 1–73. [https://doi.org/10.1016/0079-6611\(91\)90006-8](https://doi.org/10.1016/0079-6611(91)90006-8)
- Pickard, A. E., Vaudo, J. J., Wetherbee, B. M., Nemeth, R. S., Blondeau, J. B., Kadison, E. A., & Shivji, M. S. (2016). Comparative use of a Caribbean mesophotic coral ecosystem and association with fish spawning aggregations by three species of shark. *PLoS One*, 11, e0151221.
- Pinhal, D., Shivji, M. S., Nachtigall, P. G., Chapman, D. D., & Martins, C. (2012). A streamlined DNA tool for global identification of heavily exploited coastal shark species (Genus *Rhizoprionodon*). *PLoS One*, 7, e34797. <https://doi.org/10.1371/journal.pone.0034797>
- Pinsky, M. L., & Palumbi, S. R. (2014). Meta-analysis reveals lower genetic diversity in overfished populations. *Molecular Ecology*, 23, 29–39. <https://doi.org/10.1111/mec.12509>
- Pirog, A., Blaison, A., Jaquemet, S., Soria, M., & Magalon, H. (2015). Isolation and characterization of 20 microsatellite markers from *Carcharhinus leucas* (bull shark) and cross-amplification in *Galeocerdo cuvier* (tiger shark), *Carcharhinus obscurus* (dusky shark) and *Carcharhinus plumbeus* (sandbar shark). *Conservation Genetics Resources*, 7, 121–124. <https://doi.org/10.1007/s12686-014-0308-3>
- Pirog, A., Jaquemet, S., Ravigné, V., Cliff, G., Clua, E., Holmes, B. J., ... Magalon, H. (2019). Genetic population structure and demography of an apex predator, the tiger shark *Galeocerdo cuvier*. *Ecology and Evolution*, 9, 5551–5571.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., ... Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, 3, 919–925. <https://doi.org/10.1038/nclimate1958>
- Posada, D. (2008). jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, 25(7), 1253–1256. <https://doi.org/10.1093/molbev/msn083>
- Quattro, J. M., Stoner, D. S., Driggers, W. B., Anderson, C. A., Priede, K. A., Hoppmann, E. C., Campbell, N. H., Duncan, K. M., & Grady, J. M. (2006). Genetic evidence of cryptic speciation within hammerhead sharks (Genus *Sphyrna*). *Marine Biology*, 148, 1143–1155.
- Quintanilla, S., Gómez, A., Mariño-Ramírez, C., Sorzano, C., Bessudo, S., Soler, G., Bernal, J. E., & Caballero, S. (2015). Conservation genetics of the scalloped hammerhead shark in the Pacific Coast of Colombia. *Journal of Heredity*, 106, 448–458. Symposium Article, Special Issue.
- Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2014). Tracer v1.6. <http://beast.bio.ed.ac.uk/Tracer>. Accessed 20 July 2016.
- Ramírez-Amaro, S., Picornell, A., Arenas, M., Castro, J. A., Massutí, E., Ramon, M. M., & Terrasa, B. (2018). Contrasting evolutionary patterns in populations of demersal sharks throughout the western Mediterranean. *Marine Biology*, 165, 3.
- Ramos-Onsins, S. E. & Rozas, J. (2002). Statistical properties of new neutrality tests against population growth. *Molecular Biology and Evolution*, 19, 2092–2100. <https://doi.org/10.1093/oxfordjournals.molbev.a004034>
- Randall, J. E. (1992). Review of the biology of the tiger shark (*Galeocerdo cuvier*). *Australian Journal of Marine and Freshwater Research*, 43, 21–31.
- Reiss, H., Hoarau, G., Dickey-Collas, M., & Wolff, W. J. (2009). Genetic population structure of marine fish: Mismatch between biological and fisheries management units. *Fish and Fisheries*, 10, 361–395.
- Rocha, L. A. (2003). Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography*, 30, 1161–1171. <https://doi.org/10.1046/j.1365-2699.2003.00900.x>
- Roff, G. A., Brown, C. J., Priest, M. A., & Mumby, P. J. (2018). Decline of coastal apex shark populations over the past half century. *Communications Biology*, 1, 223. <https://doi.org/10.1038/s42003-018-0233-1>
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57–60. <https://doi.org/10.1038/nature01333>
- Rosa, R., Baptista, M., Lopes, V. M., Pegado, M. R., Ricardo Paula, J., Trubenbach, K., ... Repolho, T. (2014). Early-life exposure to climate change impairs tropical shark survival. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141738.
- Rosa, R., Rummer, J. L., & Munday, P. L. (2017). Biological responses of sharks to ocean acidification. *Biology Letters*, 13, 20160796. <https://doi.org/10.1098/rsbl.2016.0796>
- Rozas, J., & Rozas, R. (1999). DnaSP version 4.0: An integrated program for molecular population genetics and molecular evolution analysis. *Bioinformatics*, 15, 174–175.
- Simpfendorfer, C. A., Goodreid, A. B., & McAuley, R. B. (2001). Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from western Australian waters. *Environmental Biology of Fishes*, 61, 37–46.
- Schultz, J. K., Feldheim, K. A., Gruber, S. H., Ashley, M. V., McGovern, T. M., & Bowen, B. W. (2008). Global phylogeography and seascape genetics of the lemon shark (genus *Negaprion*). *Molecular Ecology*, 17, 5336–5348.
- Shibuya, A., Rosa, R. S., & Gadig, O. B. F. (2005). Stomach contents of *Galeocerdo cuvier* and *Carcharhinus plumbeus* (Elasmobranchii: Carcharhinidae) caught off Paraíba State, Brazil. *Arquivos de Ciências do Mar*, 38, 105–107.
- Sigsgaard, E. E., Nielsen, I. B., Bach, S. S., Lorenzen, E. D., Robinson, D. P., Knudsen, S. W., ... Thomsen, P. F. (2016). Population characteristics of a large whale shark aggregation inferred from seawater environmental DNA. *Nature Ecology & Evolution*, 1, 0004.
- Simpfendorfer, C. (1992). Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. *Australian Journal of Marine and Freshwater Research*, 43, 33–43. <https://doi.org/10.1071/MF9920033>
- Simpfendorfer, C. (2009). *Galeocerdo cuvier*. The IUCN Red List of Threatened Species 2009, eT39378A10220026. <http://dx.doi.org/10.2305/IUCN.UK.2009.RLTS.T39378A10220026.en>. Accessed 04 April 2016.
- Staveley, T. A. B., Jacoby, D. M. P., Perry, D., van der Meijs, F., Lagenfelt, I., Cremlé, M., & Gullström, M. (2019). Sea surface temperature dictates movement and habitat connectivity of Atlantic cod in a coastal fjord system. *Ecology and Evolution*, 9(16), 9076–9086. <https://doi.org/10.1002/ece3.5453>
- Stoner, D. S., Grady, J. M., Priedel, K. A., & Quattro, J. M. (2003). Amplification primers for the mitochondrial control region and sixth intron of the nuclear-encoded lactate dehydrogenase: A gene in elasmobranch fishes. *Conservation Genetics*, 4, 805–808. <https://doi.org/10.1023/B:COGE.0000006122.47004.c2>
- Tajima, F. (1989). Statistical methods for testing the neutral mutation hypothesis for DNA polymorphism. *Genetics*, 123, 585–595.
- Teske, P. R., Zardi, G. I., McQuaid, C. D., & Nicastro, K. (2013). Two sides of the same coin: Extinctions and originations across the Atlantic/Indian Ocean boundary as a consequence of the same climate oscillation. *Frontiers in Biogeography*, 5, 48–59.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature02121>
- Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680. <https://doi.org/10.1093/nar/22.22.4673>

- Torres, R. A., & Ribeiro, J. (2009). The remarkable species complex *Mimagoniates microlepis* (Characiformes: Glandulocaudinae) from the Southern Atlantic Rain forest (Brazil) as revealed by molecular systematic and population genetic analyses. *Hydrobiologia*, 617, 157–170. <https://doi.org/10.1007/s10750-008-9543-5>
- Vaudo, J. J., Wetherbee, B. M., Harvey, G., Nemeth, R. S., Aming, C., Burnie, N., Howey-Jordan, L. A., & Shivji, M. S. (2014). Intraspecific variation in vertical habitat use by tiger sharks (*Galeocerdo cuvier*) in the western North Atlantic. *Ecology and Evolution*, 4, 1768–1786.
- Veríssimo, A., Sampaio, Í., McDowell, J. R., Alexandrino, P., Mucientes, G., Queiroz, N., ... Noble, L. R. (2017). World without borders—genetic population structure of a highly migratory marine predator, the blue shark (*Prionace glauca*). *Ecology and Evolution*, 7, 4768–4781.
- Von der Heyden, S., Bowie, R. C. K., Prochazka, K., Bloomer, P., Crane, N. L., & Bernardi, G. (2011). Phylogeographic patterns and cryptic speciation across oceanographic barriers in South African intertidal fishes. *Journal of Evolutionary Biology*, 24, 2505–2519. <https://doi.org/10.1111/j.1420-9101.2011.02382.x>
- Von der Heyden, S., Gildenhuis, E., Bernardi, G., & Bowie, R. C. K. (2013). Fine-scale biogeography: Tidal elevation strongly affects population genetic structure and demographic history in intertidal fishes. *Frontiers of Biogeography*, 5, 29–38.
- Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin & Review*, 11, 192–196. <https://doi.org/10.3758/BF03206482>
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., ... Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. <https://doi.org/10.1038/416389a>
- Watson, S.-A., Allan, B. J. M., McQueen, D. E., Nicol, S., Parsons, D. M., Pether, S. M. J., ... Munday, P. L. (2018). Ocean warming has a greater effect than acidification on the early life history development and swimming performance of a large circumglobal pelagic fish. *Global Change Biology*, 24, 4368–4385. <https://doi.org/10.1111/gcb.14290>
- Whitney, N. M., Pyle, R. L., Holland, K. N., & Barcz, J. T. (2012). Movements, reproductive seasonality, and fisheries interactions in the whitetip reef shark (*Triaenodon obesus*) from community-contributed photographs. *Environmental Biology of Fishes*, 93, 121–136.
- Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2006). Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: Evidence from 7 years of standardized fishing effort. *Marine Biology*, 149(4), 961–968. <https://doi.org/10.1007/s00227-006-0278-4>

How to cite this article: Andrade FRS, Afonso AS, Hazin FHV, Mendonça FF, Torres RA. Population genetics reveals global and regional history of the apex predator *Galeocerdo cuvier* (carcharhiniformes) with comments on mitigating shark attacks in north-eastern Brazil. *Mar Ecol*. 2021;42:e12640. <https://doi.org/10.1111/maec.12640>