Genome scans discriminate independent populations of the blue shark *Prionace glauca*

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Abstract

The blue shark *Prionace glauca* is a cosmopolitan species that inhabits all oceans worldwide except the poles. Several IUCN regional assessments have classified it as Near Threatened, mostly due to overfishing. Previous genetic studies that have used classical genetic markers failed to reject the hypothesis that the species is a single worldwide population (panmixia). As such, the blue shark was proposed to be an archetype of the 'grey zone of population differentiation', named to signify those cases common in the marine realm, where the split among population is too recent or too faint to be detected using classical genetic markers. Here, samples collected across the majority of the global range of blue shark were sequenced (using a specific genome scan method named DArTseq) and screened through genome scan using 37,655 single nucleotide polymorphisms. Significant differences distinguished locations from the northern (Mediterranean and North Atlantic) vs. southern (southeastern Atlantic, Indian Ocean and southwestern Pacific) oceanic regions. Furthermore, F_{ST}

values were significant, albeit low, between locations from distinct regions within the Atlantic Ocean (northern vs. northeastern vs. southeastern Atlantic). In addition, F_{ST} values were significant between these Atlantic locations and Mediterranean, Indian, and Pacific locations. These results illustrate the power of genome scans to delineate independent populations in marine species and to accurately identify distinct management units.

Keywords

Blue shark, population genetics, SNP, bycatch, pelagic, stock assessments

Introduction

The blue shark *Prionace glauca* is considered as the most abundant and widely distributed shark worldwide (Compagno 1984; Nakano and Seki 2003), occurring in all oceans except in polar seas (i.e., from 60°N to 50°S). The blue shark is the most frequently caught shark species in fisheries worldwide (Baum and Blanchard 2010; Campana et al. 2006). It is mostly a bycatch of tuna and swordfish longline fisheries (Carvalho et al. 2015; Coelho et al. 2018), although occasionally targeted for its meat (e.g., western coast of Baja California Sur (Galvan-Magana et al. 2019)) and by recreational fisheries (Campana et al. 2006; Mejuto and García-Cortés 2005). Post-release mortality is estimated to reach 35% (Campana et al. 2009). With an estimate of 20 million individuals caught annually, the blue shark is considered by the IUCN as a Near Threatened worldwide (Rigby et al. 2019) and Critically Endangered in the Mediterranean Sea (Sims et al. 2016).

The blue shark's nomadic pelagic behaviour and wide distribution (Stevens 1990) means stock assessments rely on the assumption of regional homogeneity of stocks in the Atlantic (North Atlantic and South Atlantic; ICCAT 2015) and Pacific basins (North Pacific and South Pacific; ISC 2018) and in the Indian Ocean (assumption of a single homogeneous entity; IOTC 2017). Among other unverified assumptions, the treatment of stock as a homogeneous entity may lead to erroneous results if the stock is comprised of more than one population with differing levels of productivity and/or connectivity. Electronic tags confirmed that blue shark have the capacity to swim very large distances, even inter-oceans (Maxwell et al. 2019; Vandeperre et al. 2014; Kohler et al. 2002; Queiroz et al. 2012; da Silva et al. 2010). However, trans-equatorial migration is suspected to be limited (Kohler and Turner 2008) and non-overlapping reproductive cycles have been reported for the northern and southern hemispheres (Nakano and Seki 2003; Nakano and Stevens 2008). Based on mitochondrial DNA or/and microsatellite markers, no consistent pattern of genetic differentiation has been detected even between northern and southern hemispheres (Bitencourt et al. 2019; King et al. 2015; Li et al. 2017;

Taguchi et al. 2015; Verissmo et al. 2017), except faint signs of differentiation of the Mediterranean sea (Bailleul et al. 2018; Leon et al. 2017), and off Western Australia; both are interpreted as possible distinction between stocks of the Indian and Pacific Oceans (Taguchi et al. 2015). Traditional genetic methods only detect extreme restriction to exchange (i.e. far below the threshold of demographic independence; Waples 1998; Waples and Gaggiotti 2006) and integrate migratory exchanges over a number of generations increasing with the effective population size at stake (Hedgecock, Barber, and Edmands 2007). Effective population sizes of marine species can be extremely large, a situation likely to apply to the blue shark, considering its known distribution range and observed relative density. In fact, the blue shark has been used as a case species to illustrate the concept of 'population grey zone' (Bailleul et al. 2018), the often inconclusive results obtained when applying population genetics to define management units in pelagic species. The 'population grey zone' effect describes the potentially very long time-lag (hundreds to thousands of generations) between the demographic split of a population into two independent entities and the ability to capture the signal of such spatial-temporal dynamics using a handful molecular markers (Bailleul et al. 2018).

A far denser array of markers can be characterized using high throughput sequencing, typically thousands of single nucleotide polymorphisms (SNPs) throughout the genome. This substantially increases the resolution of population structure analyses, allowing to the detection much lower levels of genetic differentiation. Here, we used Diversity Arrays Technology sequencing (DArTseq™; Georges et al. 2018) on a total sample of 376 blue sharks from the Atlantic, Pacific and Indian Oceans, as well as from the Western Mediterranean Sea, to test the hypothesis of large-scale panmixia reported in previous studies. Our aim is to take advantage of the power offered by genome scan analysis to provide a genetically-based delineation of management units for blue shark.

Material and Methods

Sampling

A total of 376 samples collected in the Mediterranean Sea, and the Atlantic (northern and southern hemispheres), Indian and Pacific Oceans were used in this study, of which only 364 samples passed the DArT library constructions' quality checks (Figure 1). All were caught by longline, except the samples from Indonesia (eastern Indian Ocean) which were obtained by purse seine. Phenotypic information such as length (cm) and sex, geographic locations (latitude and longitude), as well vessel information were usually recorded - except for 93 individuals missing length data and 149 individuals not sexed due to handling limitations during large catches. Individual measures reported as curved fork length,

precaudal length, and interdorsal space were converted to fork length (FL) based on the equations of Cramer, Bertolino, and Scott (1997). Small pieces of tissue (a superficial part of the fins or a muscle piece depending whether the individual was released after bycatch or not) were preserved in ethanol 96% for all sampling locations except Indonesia (tissue was silica dried) and La Réunion Island (tissues were kept in RNA later).

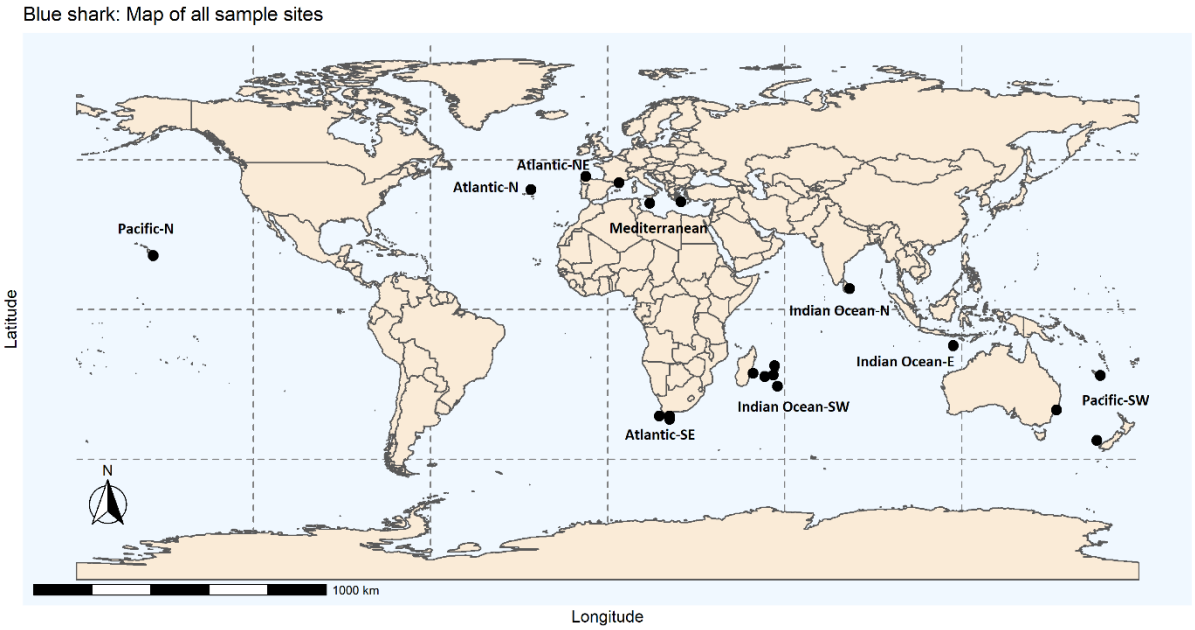

Figure 1. Sampling locations for blue shark with 49 individuals in the North Atlantic (Atlantic-N), 26 individuals in the Northeast Atlantic (Atlantic-NE), 110 individuals in the Southeast Atlantic (Atlantic-SE or South Africa), 54 individuals in Mediterranean sea (Mediterranean), 29 individuals in the Southwest Indian Ocean (Indian Ocean-SW), 27 individuals in the North Indian Ocean (Indian Ocean-N), 8 individuals in the East central Indian Ocean (Indian Ocean-EC), 4 individuals in the North Pacific (Pacific-N), and 57 individuals in the Southwest Pacific (Pacific-SW).

Molecular processing: DNA extraction, DarT libraries preparation and sequencing

Genomic DNA was extracted from 15 mg of tissue subsampled from 376 individual biopsies (mainly skin and muscle) on an Eppendorf EP motion 5057 liquid robotic handler using a modification of the QIAamp® 96 DNA QIAcube HT Kit (QIAGEN, Hilden, Germany). This extraction includes a lysis step in the presence of Proteinase K followed by bind-wash-elute QIAGEN technology. Low quality/degraded samples were extracted using the modified CTAB method following Grewe et al. (1993).

Genomic DNA was processed for the construction of a reduced representation library, sequenced, and genotyped by Diversity Arrays Technology (DarT Pty Ltd, Canberra) using the DArTseq™ technique. DNA sample libraries were created in digestion/ligation reactions using two methylation-sensitive restriction enzymes, *PstI* and *SphI*. The *PstI* site was compatible with a forward adapter that included

a flow cell (Illumina, San Diego) attachment sequence and a sequencing primer sequence incorporating a "staggered", varying length barcode region. *SphI*- generated a compatible overhang sequence that was ligated to a reverse adapter containing a flow cell attachment region and reverse priming sequence. Only "mixed fragments" (*PstI-SphI*) were effectively amplified by PCR. PCR conditions consisted of an initial denaturation at 94°C for 1 min followed by 30 cycles of 94°C for 20 sec, 58°C for 30 sec and 72°C for 45 sec, with a final extension step at 72°C for 7 min. After PCR, equimolar amounts of amplification products from each sample of the 96-well microtiter plate were bulked and applied to cBot (Illumina) bridge PCR, followed by sequencing on an Illumina Hiseq2000. The sequencing (single read) was run for 77 cycles. The fragments of DNA selected by this process are about 75 bp in length. More details on the method can be found in Sansaloni et al. (2011), Kilian et al. (2012), and Georges et al. (2018).

For initial assessment of read quality and sequence representation, raw reads were processed using Illumina CASAVA v.1.8.2 software. DNA genotype data was generated from sequencing runs completed at DArT using a proprietary DArTseq analytical pipeline (DArT-Soft14 version). The DArTtoolbox was then used to perform filtering and variant calling (e.g. filter away poor-quality sequences and applying more stringent selection criteria to the barcode region), and generate final genotypes (Kilian et al. 2012). More details in the sequences process to generate SNP genotyping can be found in Georges et al. (2018). A total of 172,384 SNPs from 364 samples were retained. Data from 364 samples contained 109 technical replicates (DNA library constructed and sequenced from original genomic DNA templates).

SNPs filtering

SNP data were filtered for reproducibility, monomorphic markers, minor allele count, departure from heterozygosity distribution, coverage, missingness, short-linkage disequilibrium and Hardy-Weinberg Equilibrium (see details in Supplementary material, S1) using radiator package v1.1.5 (Gosselin 2018; Gosselin et al. 2020) in R v3.5.3 (R Development Core Team 2018). Individuals were filtered based on missingness, heterozygosity (a soft threshold was set based on the mean heterozygosity of all populations combined and a more stringent threshold was chosen based on the mean heterozygosity of each sampling location) and duplicate individuals. Following this filtering, our dataset contained 45,810 SNPs for 312 individuals.

Sex-linked markers identification

The unfiltered data were tested for the presence of sex-linked markers using the *sexy_markers* function in the radiator package (Gosselin et al. 2020). To reduce false positive results, the raw data was filtered on individual missingness and heterozygosity, as well as monomorphic markers and short-distance linkage of SNP (i.e. multiple SNPs per locus). Next, we identified markers on Y or W chromosomes by looking if a marker was present in one sex, but absent in the other. Similarly, X- or Z-linked markers were found based on the heterozygosity and coverage patterns between sexes. Any sex-linked markers were removed from the data.

Potentials outliers

After discarding sex-linked markers, two algorithms were run to identify putative outliers: *PCAdapt* v4.1.0 (Luu, Bazin, and Blum 2017) and *OutFLANK* v0.2 (Whitlock, Lotterhos, and Editor: Judith 2015). We also ran *BayeScan* v2.1 (Foll and Gaggiotti 2008) to identify potential balancing or purifying selection (i.e. negative alpha). The last step of filtering consisted in removing loci with minor allele frequencies (MAF) lower than 0.01 using dartR v1.5.5 (Georges et al. 2018).

Population genetic analyses

Genetic polymorphism metrics including heterozygosity, Fis, and Hardy-Weinberg equilibrium (HWE) were estimated using the *diveRsity* package v1.9.90 (Keenan et al. 2013).

Pairwise F_{ST} and average pairwise differences were estimated using the *strataG* package v2.4.91 (Archer, Adams, and Schneiders 2017). Principal component analysis (PCA) on allelic frequencies (Jombart 2008; Jombart and Ahmed 2011) was run using *adegenet* v2.1.1 (Jombart and Ahmed 2011).

Hierarchical genetic clustering was performed using *ADMIXTURE* v1.3 (Alexander, Novembre, and Lange 2009) assuming two to six ancestral populations (K). The value of K with lowest associated error value was identified using ADMIXTURE's cross-validation procedure. Then, the R package *stockR* v1.0.73 (Foster 2020) was used with K values (designed in StockR to correspond to a number of differentiated groups, rather than a number of ancestral populations) from two to six and the approach outlined in Foster et al. (2018), designed to discriminate groups with no contemporary mixture based on probability for classification.

Results

Samples

The body length of individuals ranged from 74.5 cm FL to 330 cm FL with a mean of 140.4 cm FL; females exhibited lower mean size than males. The smallest individuals were sampled in the northeastern Atlantic and the largest in the Mediterranean Sea (Figure 2). However only 23 of the 54 individuals sampled from the Mediterranean were measured and so caution should be taken when interpreting this result, especially since Mediterranean blue sharks have been reported as having similar growth rates to those observed in the Atlantic and Pacific Oceans (Megalofonou, Damalas, and de Metrio 2009).

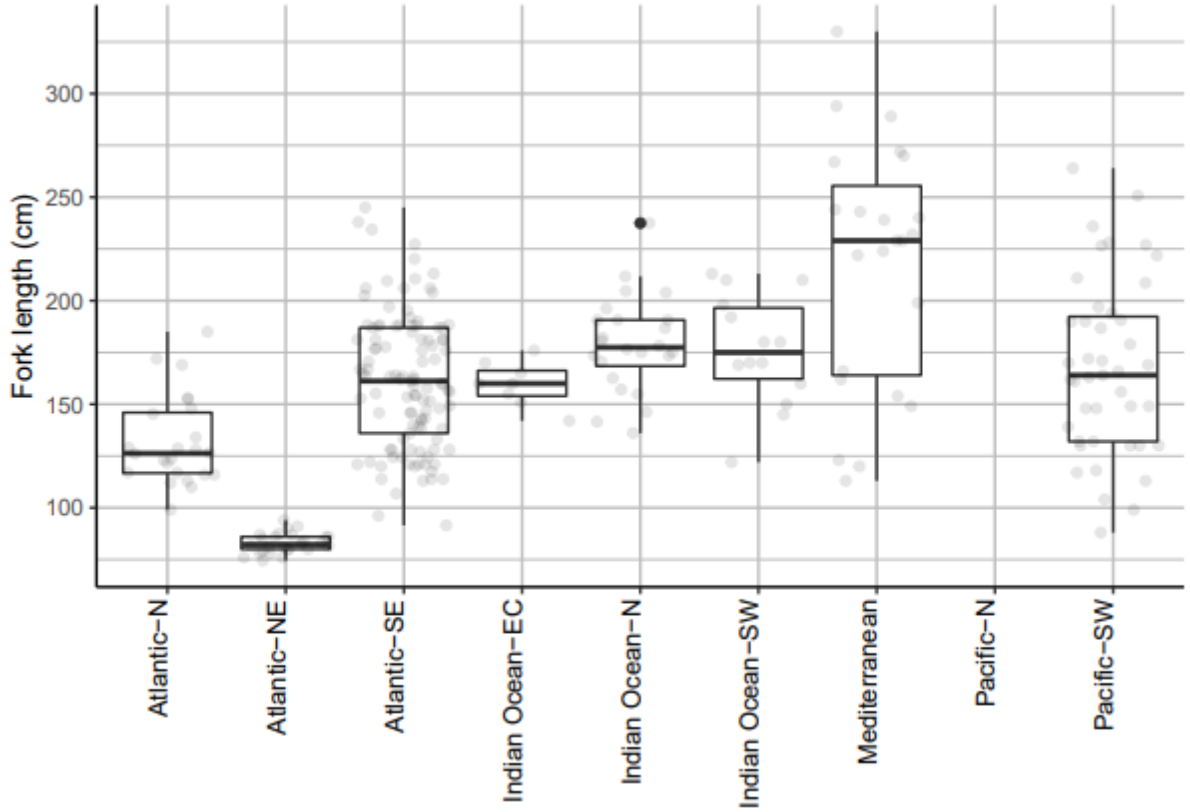

Figure 2. Fork length of blue shark per main area sampled.

Sequencing and quality control

Total genotypes count from the sequencer ranged from 545,764 to 2,702,952 reads per individual with an average of 1,805,674 counts.

After the first DArTseq™ bioinformatic processing (see material and method section), all analyses were performed under R 3.5.3. The different filtering steps using radiator (detailed S1) resulted in a dataset of 45,666SNPs (one SNP per *de novo* assembled fragment) from 312 individuals. The North Pacific area was removed during this process as it contained only eight individuals with high missingness (an indication of low-quality DNA). The last steps of filtering removed sex linked markers (112), outliers (9) detected with both *OutFLANK* (Whitlock, Lotterhos, and Editor: Judith 2015) and *PCAdapt* (Luu, Bazin, and Blum 2017), and SNPs with low MAF, yielding a final dataset of 35,755SNPs on a total of 312 samples. *BayeScan* did not identify any SNP under potential balancing or purifying selection.

Diversity

All locations exhibited low heterozygosity (observed around 14% and expected around 16-17%) on the final dataset of 35,755SNPs and 312 samples. Except for the East Indian Ocean (probably due to the low number of samples, 8 individuals), all FIS values were positive (0.031-0.115; confidence intervals not overlapping with 0). The global test on Hardy-Weinberg disequilibrium was not significant, except for Atlantic-SE (South Africa) and Southwest Pacific which still exhibited a significant heterozygote deficiency.

Genetic differentiation

The F_{ST} values were extremely low (in the of order of 10^{-3} to 10^{-4}), although significant between the three Atlantic locations. Significant F_{ST} values also characterized comparisons between locations inside and outside the Atlantic Ocean (Table 1).

PCA (Figure 3) and clustering with stockR (Figure 4) and Admixture (S2) revealed that each Ocean hosts a distinct genetic group, with the exception of the Indian and South-western Pacific Oceans between which no significant structure was detected. The southeastern Atlantic samples (comprised of individuals captured in South Africa) had an admixture profile. Although the F_{ST} presented differentiation, the results of PCA and ADMIXTURE revealed a mix on membership in South Africa while stockR assigned mainly to a single group (Indo-Pacific) because it does not assume admixture.

Table 1. Pairwise F_{ST} values and their level of significance after correction with q-value (* p<0.01, and **p<0.001). MED Mediterranean Sea; ATL Atlantic Ocean; IO Indian Ocean; PAC Pacific Ocean; IO-EC eastern-central Indian Ocean. Sample size in brackets

Location	MED (45)	ATL-N (42)	ATL-NE (21)	ATL-SE (105)	IO-EC (8)	IO-N (16)	IO-SW (22)	PAC-SW (53)
MED		0.0007**	0.0010**	0.0015**	0.0023*	0.0017**	0.0017**	0.0022**
ATL-N			0.0006*	0.0013**	0.0010*	0.0011**	0.0015**	0.0017**
ATL-NE				0.0018**	0.0015*	0.0015**	0.0015**	0.0020**
ATL-SE					0.0000	0.0000	0.0000	0.0000
IO-EC						0.0004	0.0000	0.0000
IO-N							0.0000	0.0000
IO-SW								0.0001
PAC-SW								

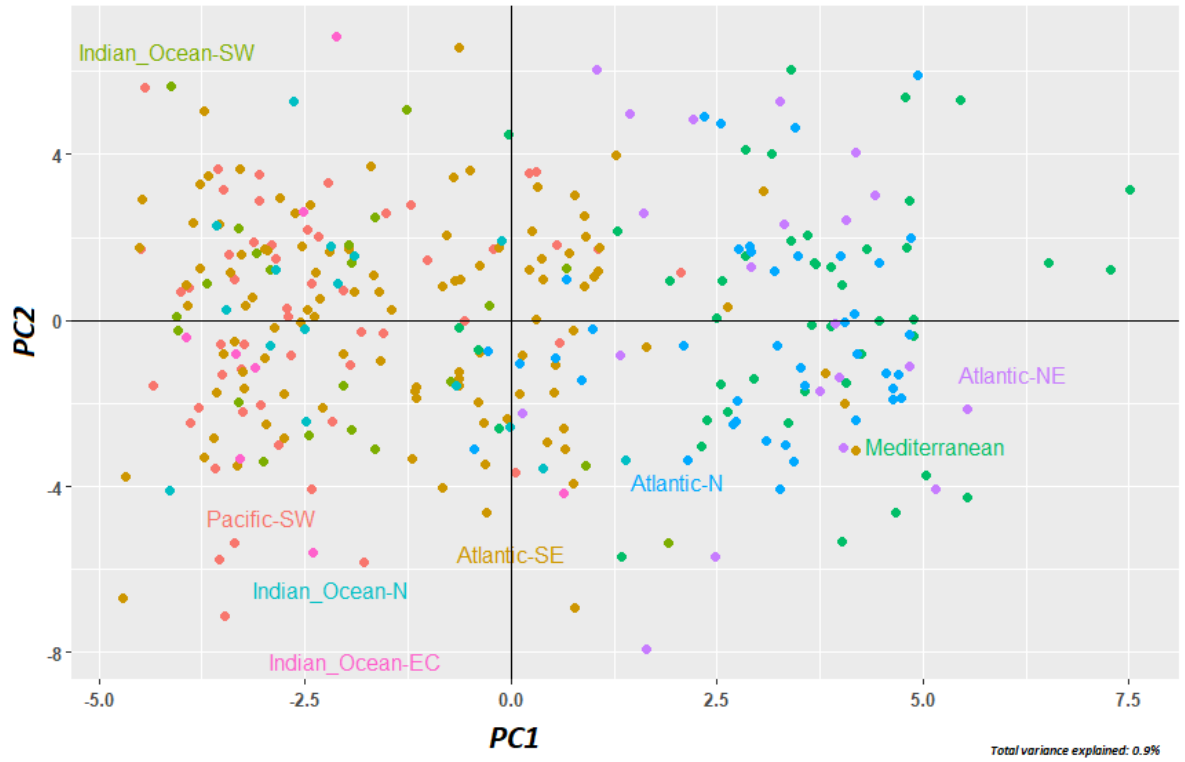

Figure 3. PCA results on 312 blue sharks characterized by 37,655 SNPs. Colors correspond to main area sampled.

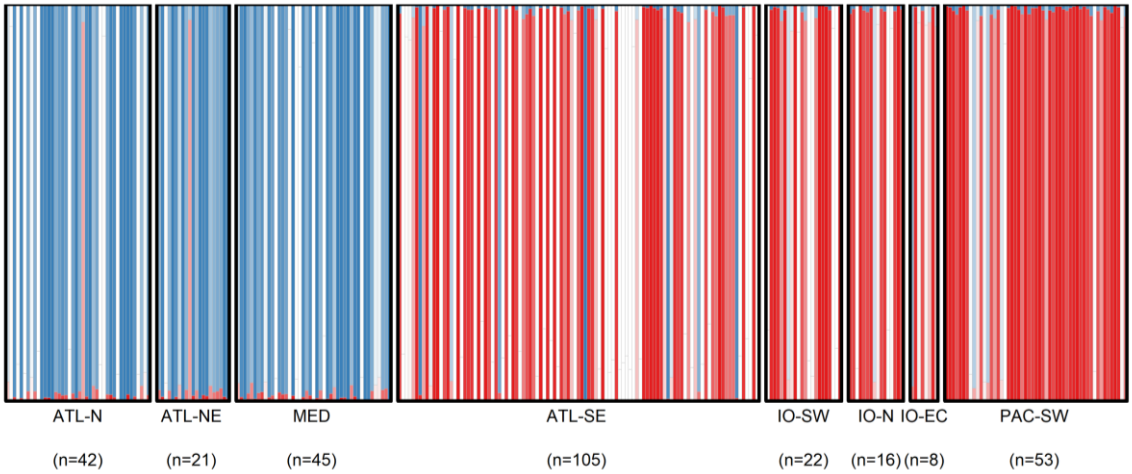

Figure 4. Genetic clustering from stockR with the final dataset (37,655 SNPs on 312 blue sharks). Individuals with admixed background were indicated in white, as stockR does not test admixture.

Discussion

For the first time, clear signatures of population genetic structure were detected in blue shark. This study supports the possible explanation of Bailleul et al. (2018) that a population differentiation is present in blue shark. This was called the 'grey zone' effect of population differentiation. Based on simulations, Bailleul et al. (2018) showed that the time-lag between a demographic event (e.g., a population split or a drastic reduction of population size) and its detectable imprint in the population genetic structure of a species could exceed several hundred or thousand years, and that this 'grey zone' of low detectability increases with effective population size and the number of exchange migrants. They also suggested that genome scans may have the necessary power to detect patterns of population structure difficult to detect with a limited set of microsatellites. Here we showed that working with higher numbers of loci allowed the detection of subtle genetic differences among blue shark populations. While this approach requires increased computation time and data handling, high throughput sequencing allowed us to distinguish blue shark populations between Ocean basins. This study revealed two main genetic clusters for blue shark: (1) the northern Atlantic Ocean region, including the Mediterranean Sea, and (2) the Indo-Pacific region. The southeastern Atlantic region might be an important area of admixture between these two regions. Further study of in southern Atlantic blue sharks, including larger sampling sizes and more locations, are needed to fully resolve the level of mixing in that region.

The levels of genetic diversity at the 37,655 SNP were low and very similar among all sample collections (heterozygosity observed around 14% and expected around 16% to 17%), which is consistent with previous studies on blue shark (Leone 2018) and others sharks of the *Carcharhinus* genus (Pazmiño et al. 2017; Momigliano et al. 2017; Green et al. 2019).

The results presented here have implications for Regional Fisheries Management Organizations (RFMOs) as they will inform the assumptions and model structure when assessing the stock, as well as provide a more accurate representation of the likely population structure to facilitate appropriate management interventions. Fisheries management requires the identification of demographically independent units (Carvalho and Hauser 1995; Waples, Punt, and Cope 2008). The current IOTC (Indian Ocean Tuna Commission) blue shark assessment assumes a single stock in the Indian Ocean. This study does not provide any evidence of genetic structure within the Indian Ocean. It is possible, however, that limited demographic connectivity exists between regions within the Indian Ocean that is not detected with the approach deployed here. At the western border of the IOTC convention area, genetic information indicates possible admixture with the Atlantic Ocean, although additional samples would be needed in the southwest Atlantic Ocean to confirm whether the South African region has a distinct blue shark population. The possibility of a parturition and nursery area off the Cape and the movement of sharks into both adjacent ocean basins have been noted in a previous study (da Silva et al. 2010). Based on observations and tag-recapture information, Da Silva et al. (2010) suggest that the South African blue sharks are part of a single stock that straddles the South Atlantic and the Indian Ocean, and possibly the entire Southern Hemisphere. Considering the spatial distribution of longline blue shark catches and the existence of a specific biogeochemical provinces along South Africa (EAFR; Longhurst, 1998), the western boundary of the Indian Ocean blue shark area could be set to 35°E (instead of 20°E as presently used). The genetic analyses also show a strong coherence between the Indian Ocean and the Southwest Pacific. Tagging results from Southwest Pacific individuals revealed long migration cross Indian Ocean until South Africa (West et al. 2004). Provided that our easternmost samples came from New Zealand, Southeast Australia, and New-Caledonia (Figure 1), the eastern boundary of the Indian Ocean blue shark stock could therefore be set at 170°E. An alternative and complementary assessment within these new boundaries (35°E to 170°E) would require a joint work between IOTC and WCPFC. In order to provide the necessary information to support this preliminary consideration, we encourage an additional genetic study with a focus on samples from the Southeast and North Pacific to refine the level of connectivity with the Indian Ocean.

Acknowledgements

We are grateful to skippers Morgan Le Guernic, Rudy Levian, Mathias Hoarau, Samuel Kazambo, Sébastien Laffont, Rudy Levian, Leopold Corbrejaud of the domestic longline fleet for their continued support of the "PSTBS" project. We also thank Reunimer and Enez, particularly Hubert Chenede and Frédéric Payet for facilitating access to work plans for sampling in good condition. We thank Estelle Crochelet and Loïc Le Foulgoc for their participation in the sampling. Many thanks to Denham Parker (DAFF) and Steward Norman (CapFish) for their huge help to collect samples in South Africa. We thank all the CSIRO team for their help on production of DArT genotype data and collection of samples in Pacific and eastern Indian Ocean. We also thank Thierry Gosselin for very interesting exchanges on genetic analysis and help on filter_rad. Finally, we thank Arthur Georges for his advice on dartR package and contributors to the dartR forum (https://groups.google.com/forum/#!topic/dartr/).

Funding

This work is part of the PSTBS project supported by funding from CSIRO Oceans and Atmosphere, AZTI Tecnalia, Institut de recherche pour le développement (IRD), and Research Institute for Tuna Fisheries (RITF) and financial assistance of the European Union (GCP/INT/233/EC – Population structure of IOTC species in the Indian Ocean), and POPSIZE project supported by FEAMP (2014-2020 UE N°508/2014).

Authorizations

Permit: 0001500212. This permit is issued under Biosecurity Act 2015 Section 179 (1).

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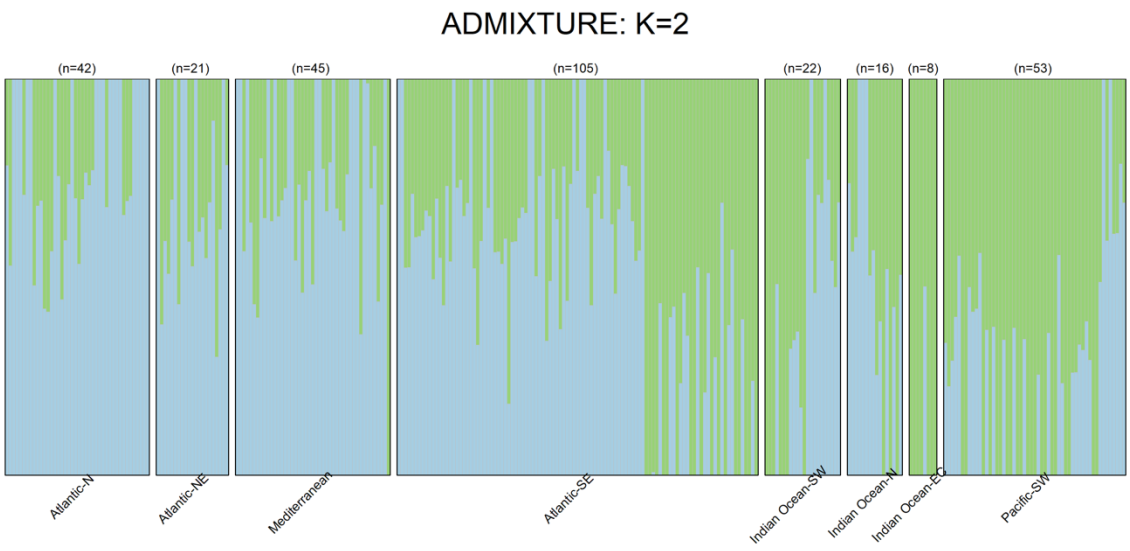
Supplementary material

S1. Radiator filtering steps for the blue shark Prionace glauca, including threshold values and the number of individuals, locus and markers after each step (the raw dataset consisted in 20,220 SNPs SNPs on 312 samples analysed). Last lines also detail the number of SNPs removed after radiator filters because detected as outliers by applying approach OutFLANK, and removed from the dataset before further analysis.

Filters	VALUES	Individuals / Locus / Markers
Filter DArT marker reproducibility	0.959(outliers)	364 / 95699 / 156195
Filter monomorphic markers		364 / 95699 / 156195
Filter markers in common		364 / 85836 / 142272
Filter individuals based on missingness	0.185(outliers)	332 / 85836 / 142272
Filter individuals based on heterozygosity	0.0601-0.0779 (outliers)	312 / 85836 / 142272
Filter monomorphic markers		312 / 84082 / 136648
Filter minor allele count	4	312 / 71622 / 110261
Filter marker coverage (min / max)	7/200	312 / 60859 / 95216
Filter marker missingness	0.1	312 / 46128 / 68083
Filter SNPs position on the read	8bp (outliers)	312 / 46128 / 68083
Filter number of SNPs per locus	4 (outliers)	312 / 45889 / 66837
Filter short linkage disequilibrium	MAC	312 / 45889 / 45889
Detect mixed genomes (ind. heterozygosity)	0.117-0.15	312 / 45889 / 45889
Detect duplicate genomes (duplicated individuals)	0.1	312 / 45889 / 45889
Filter Hardy-Weinberg Equilibrium	Min 3 pops; p<0.0001	312 / 45810 / 45810
Post radiator: remove sex-linked markers		312 / 45667/ 45667
Post radiator: filtering based on outlier detected using PCAdapt and OutFLANK		312 / 45658/ 45658
Post radiator: filtering monomorphic markers based on MAF with dartR	0.01	312 / 37655/ 37655



S2. Genetic clustering from ADMIXTURE of blue shark samples characterized with 37,655 SNPs on 312 blue sharks, with number of clusters (K) = 2.