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International fisheries threaten globally endangered sharks in the Eastern Tropical Pacific Ocean: the case of the Fu Yuan Yu Leng 999 reefer vessel seized within the Galápagos Marine Reserve

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Shark fishing, driven by the fin trade, is the primary cause of global shark population declines. Here, we present a case study that exemplifies how industrial fisheries are likely depleting shark populations in the Eastern Tropical Pacific Ocean. In August 2017, the vessel Fu Yuan Yu Leng 999, of Chinese flag, was detained while crossing through the Galápagos Marine Reserve without authorization. This vessel contained 7639 sharks, representing one of the largest seizures recorded to date. Based on a sample of 929 individuals (12%), we found 12 shark species: 9 considered as Vulnerable or higher risk by the IUCN and 8 listed in CITES. Four species showed a higher proportion of immature than mature individuals, whereas size-distribution hints that at least some of the fishing ships associated with the operation may have been using purse-seine gear fishing equipment, which, for some species, goes against international conventions. Our data expose the magnitude of the threat that fishing industries and illegal trade represent to sharks in the Eastern Tropical Pacific Ocean.

Amid the current biodiversity crisis, an era of unprecedented species extinction¹, our ability to document species loss and ecosystem collapse in marine environments has lagged behind compared with terrestrial ecosystems². This situation is particularly worrisome in the case of sharks, a group with a high proportion of top predators central to marine food web dynamics³. Some sharks have a high market value and hence are targeted by fisheries for their fins and other products⁴. Given the economic incentives for exploitation and the difficulties involved in controlling this trade, shark fishing has caused substantial population declines⁵. Consequently, at least 74 species of sharks (16% of shark diversity) are threatened worldwide⁶.

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Figure 1. Sample of shark carcasses seized in vessel Fu Yuan Yu Leng 999. A, inside one of the vessel freezers. B, unborn scalloped hammerhead sharks; C, whale shark. We assembled this figure using Adobe Creative Suite (<https://www.adobe.com>).

In response to global threats, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has identified the international shark fin trade as the primary driver of population declines, protecting 46 shark species under this convention. Further, 26 shark species are listed in Annex 1 of the Memorandum of Understanding on the Conservation of Migratory Sharks (www.cms.int/sharks/en/legalinstrument/sharks-mou), the first global instrument for the conservation of migratory species of elasmobranchs. Thus, management to prevent population collapses of some of the most heavily traded and vulnerable shark species has become a global priority (CITES, <https://www.citessharks.org>). Moreover, sharks benefit from marine protected areas that preserve habitats and populations⁷, and export biomass to non-protected areas, sustaining the yield of nearby fisheries^{8,9}.

Unfortunately, fisheries management regulations and benefits derived from marine protected areas become ineffective when sharks move into international waters¹⁰ or are undermined when international or local fleets fish protected species within countries' exclusive economic zones (EEZs)^{11,12}. Here, we present a case study from the Eastern Tropical Pacific Ocean as an example of how the operation of international fleets may hamper national and international efforts to preserve shark populations worldwide.

Our case is staged in the Galápagos Islands, an archipelago world-renowned for its iconic species and marine environments. Established in 1959, the Galápagos National Park (GNP) expanded to the Galápagos Marine

Family/species	Common name	Spanish name	Present in GMR	Total	Frequency	Conservation status IUCN	CITES
Family Alopidae							
<i>Alopias pelagicus</i>	Pelagic thresher	Tiburón rabón bueno	Yes	122	13.1%	Endangered	Appendix II
<i>Alopias superciliosus</i>	Bigeye thresher	Tiburón rabón amargo/ Tiburón zorro ojón	Yes	54	5.8%	Vulnerable	Appendix II
Family Charcharhinidae							
<i>Carcharhinus amblyrhynchus</i>	Grey reef shark	Tiburón gris de arrecife	Yes	2	0.2%	Endangered	No data
<i>Carcharhinus falciformis</i>	Silky shark	Tiburón mico/sedoso	Yes	257	27.7%	Vulnerable	Appendix II
<i>Carcharhinus longimanus</i>	Oceanic whitetip shark	Tiburón aletón/ puntas blancas oceánico	Yes	188	20.2%	Critically endangered	Appendix II
<i>Galeocerdo cuvier</i>	Tiger shark	Tiburón tigre	Yes	2	0.2%	Near threatened	No data
<i>Prionace glauca</i>	Blue shark	Tiburón azul o Aguado	Yes	109	11.7%	Near threatened	No data
Family Lamnidae							
<i>Isurus oxyrinchus</i>	Shortfin mako	Tiburón tinto	Yes	4	0.4%	Endangered	Appendix II
Family Rhincodontidae							
<i>Rhincodon typus</i>	Whale shark	Tiburón Ballena	Yes	1	0.1	Endangered	Appendix II
Family Sphyrnidae							
<i>Sphyrna lewini</i>	Scalloped hammerhead	Cachuda roja	Yes	122	13.1%	Critically endangered	Appendix II
<i>Sphyrna zygaena</i>	Smooth hammerhead	Cachuda blanca	Yes	67	7.2%	Vulnerable	Appendix II
Family Triakidae							
<i>Mustelus mustelus</i>	Common smooth-hound	Tollo	No	1	0.1%	Vulnerable	No data
				929	100%		

Table 1. Conservation status of species of sharks from vessel Fu Yuan Yu Leng 999 intercepted within the limits of the Galápagos Marine Reserve. Data from www.iucn.org and www.cites.org, updated to December 2020. All species except *Mustelus mustelus* have been reported for the Galápagos Marine Reserve (GMR) (Supplementary Information Table S1).

Reserve in 1998¹³, a protected area of about 133,000 km². This reserve has afforded over 20 years of protection for endemic and native marine species and holds at least 36 species of sharks (Supplementary Information Table S1).

On August 13th, 2017, an alert was issued to the Navy of Ecuador from the Monitoring Center of the GNP Directorate regarding a sizeable vessel crossing the Galápagos Marine Reserve. The reefer vessel Fu Yuan Yu Leng 999, of Chinese flag, was detained 12 miles north of Punta Pitt, on San Cristóbal Island. The vessel was escorted to Puerto Baquerizo Moreno, the Galápagos Islands' political and judicial capital, where an inquiry and subsequent trial began.

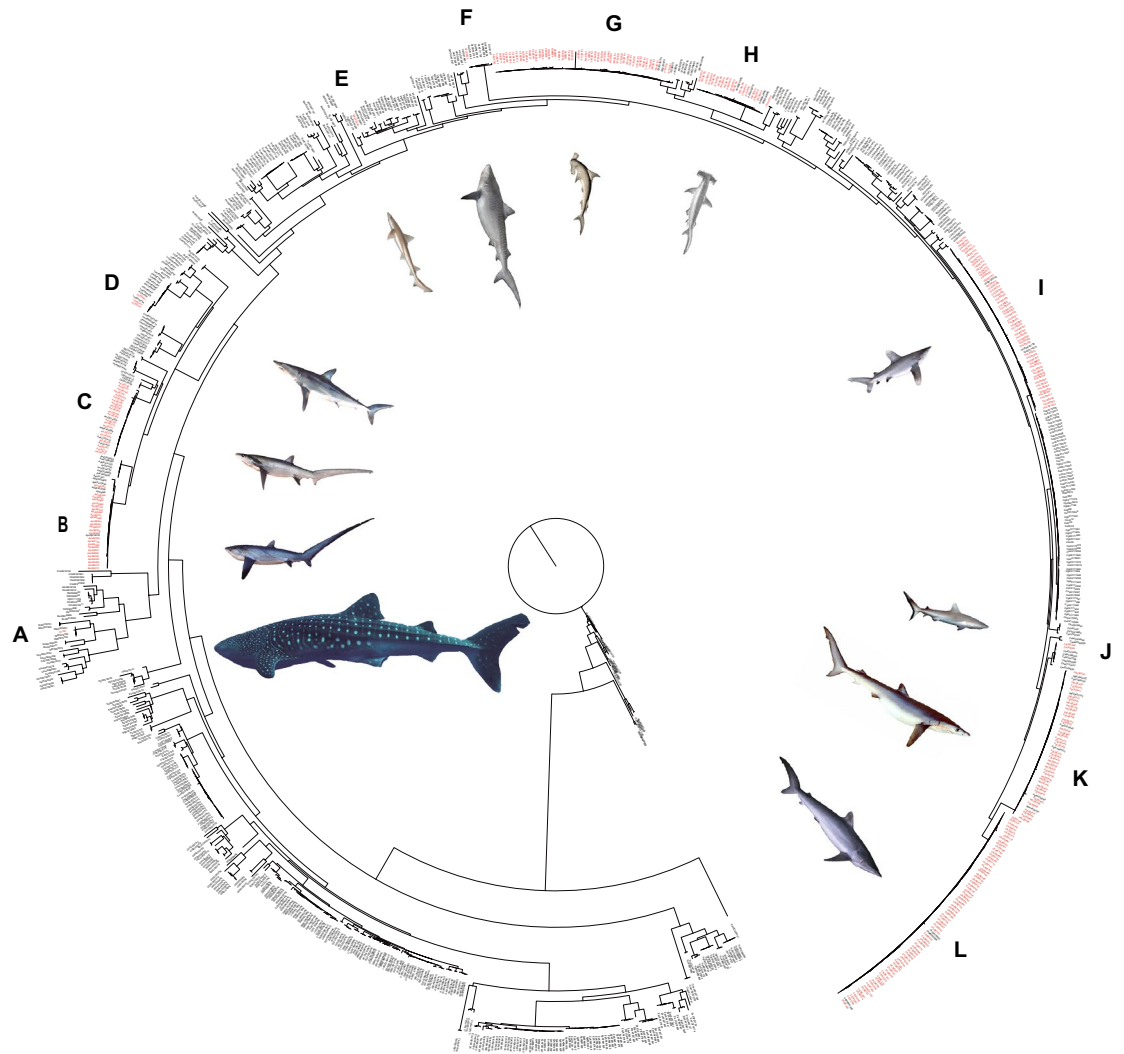
Here, we combined morphological identification with molecular barcoding to assess the identity of 12% of the carcasses contained in the vessel Fu Yuan Yu Leng 999 and estimated the size distribution of sharks targeted. We argue that the high shark biomass and the high proportion of endangered species transported by the reefer vessel, as well as the recent operation of international fleets around the Ecuadorian Exclusive Economic Zones, reveal a pattern of sustained exploitation of sharks in this region and, more generally, the Eastern Tropical Pacific Ocean. We discuss our results in terms of their implications for the impact of international fishing fleets on the conservation of shark species.

Results

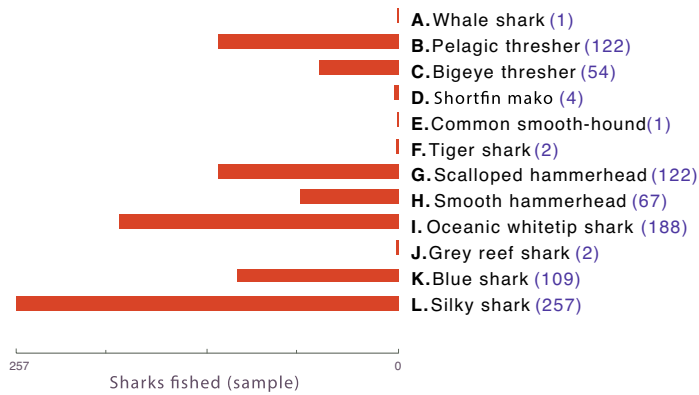
The vessel Fu Yuan Yu Leng 999 was carrying 572 tons of fish. The ship contained six freezer holds, and only one and ~ 1/3 were full. The cargo included 7639 sharks (7207 juveniles or adults, 432 unborn; see examples in Fig. 1A,B), 2114 bony fish, and 537 bags of shark fins. Out of the 7639 sharks found, 929 juveniles or adults (12% of the cargo) were morphologically identified and molecularly barcoded (GenBank accession numbers listed in Supplementary Data S1). This sample consisted of 12 species of sharks (Table 1), including a single specimen of the whale shark, *Rhincodon typus* (Fig. 1C).

Shark identification and geographic affinities. Out of 929 samples analyzed, 800 (86%) matched the morphological and molecular identifications (Supplementary Information Table S2). An overview of the phylogenetic tree is shown in Fig. 2. The complete maximum likelihood tree, with species names and bootstrap supports is available in the Supplementary Information Figure S1, where all samples were located in the same clade as samples of the species assigned by BLAST (bootstrap support $\geq 70\%$).

We could not determine the geographic affinities between our samples and those retrieved from GenBank because of the limited number of sequences per species from few geographic locations on this database. Also, at least 20% of GenBank sequences were not associated with specific localities and the overall level of individual variation in ND2 was low (see tree in Supplementary Information Figure S1). Still, the 929 sequences generated during this study, 86% of which are backed up by morphological diagnosis, will expand the availability of comparative shark data on GenBank, enhancing species identifications in future studies.



Sharks in the Fu Yuan Yu Leng 999
Species followed by number of individuals in the sample



◀ **Figure 2.** Phylogenetic tree obtained from 929 samples from 12 species of sharks found in vessel Fu Yuan Yu Leng 999, comparative sequences from GenBank (1275 individuals from 229 shark species distributed in the Pacific Ocean), and 9 Galapagos sharks from the Galápagos Islands. The figure also shows the number of identified carcasses per species found in the vessel (a total of 929 individuals); note that these numbers represent only a fraction of the 7639 sharks (7207 juveniles or adults, 432 unborn) found in the Fu Yuan Yu Leng 999. Photo credits: A, Whale shark (*Rhincodon typus*), Alex Hearn; B, Pelagic thresher (*Alopias pelagicus*), licenced by CSIRO; C, Bigeye thresher (*Alopias superciliosus*), licenced by CSIRO; D, Shortfin mako (*Isurus oxyrinchus*), licenced by CSIRO; E, Common smooth-hound (*Mustelus mustelus*), Henri Gervais (1877); F, Tiger shark (*Galeocerdo cuvier*), licenced by CSIRO; G, Scalloped hammerhead (*Sphyrna lewini*), Henri Gervais (1877); H, Smooth hammerhead (*Sphyrna zygaena*), Francys Day (1878); I, Oceanic whitetip shark (*Carcharhinus longimanus*), licenced by CSIRO; J, Grey reef shark (*Carcharhinus amblyrhynchos*), ReefLifeApps.com, licensed by Creative Commons Attribution-Share Alike 3.0; K, Blue shark (*Prionace glauca*), licenced by CSIRO; L, Silky shark (*Carcharhinus falciformis*), CSIRO. We assembled this figure using FigTree 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>) and Adobe Creative Suite (<https://www.adobe.com>).

Conservation status of seized sharks. From the 12 species of sharks found in the vessel Fu Yuan Yu Leng 999, 11 are found within the Galápagos Marine Reserve, 9 are listed as Vulnerable or higher risk by the IUCN (<https://www.iucnredlist.org>), and 8 are listed as CITES species (Appendix II; <http://checklist.cites.org>) (Table 1). The species most represented in the cargo were silky shark (Vulnerable; 28%), oceanic whitetip shark (Critically Endangered; 20%), scalloped hammerhead (*Sphyrna lewini*; Critically Endangered; 13%), pelagic thresher (Endangered; 13%), and blue shark (Near Threatened; 12%).

Size and estimation of size of sexual maturity. We obtained pre-caudal length measurements for 745 individuals of 11 species (Supplementary Data S2). Both sexually mature and immature individuals were present for all species except for tiger shark, grey reef shark *Carcharhinus amblyrhynchos*, and common smooth-hound (Table 2). Out of the seven species that had sufficient sampling, four—pelagic thresher, silky shark, oceanic whitetip shark, and blue shark—showed a higher proportion of immature than mature individuals. For oceanic whitetip shark (Critically Endangered), nearly all individuals were immature (96%; 157 out of 164), whereas for silky shark (Vulnerable), immature individuals comprised 86% of the sample (195 out of 228). Size structure for silky and oceanic whitetip sharks is presented in Fig. 3.

The legal case against vessel Fu Yuan Yu Leng 999. The provincial court of Galápagos, on San Cristobal Island, ruled in favor of the Galápagos National Park Directorate, imposing legal sanctions on the Fu Yuan Yu Leng 999 vessels' owner and crew. The process' legal base rested on the Ecuadorian law prohibiting the unauthorized possession and transport of protected species and on trespassing into the Galápagos Marine Reserve without authorization¹⁴. The final indictment resulted in the incarceration for 1–3 years of 20 crew members, confiscation of the vessel, and a fine of US\$ 6.1 million for damages inflicted to protected species¹⁵.

Discussion

The case of vessel Fu Yuan Yu Leng 999 represents the largest reported shark seizure in Ecuadorian waters to date. It reveals an unprecedented magnitude of targeted shark fisheries and highlights the vulnerability of crew members employed by international fishing fleets. Although based on a single case, the fisheries catch reported here exemplifies ongoing industrial operations that are likely depleting shark populations in the region on a vast scale. This situation might have profound implications for the management and conservation of shark populations in the Eastern Tropical Pacific.

There is no certainty about the origin of sharks found in the vessel Fu Yuan Yu Leng 999. However, machine-learning analysis of the data from the Automatic Identification System (AIS) of the vessel detected an anomaly in its trajectory 2735 km northwest of the Galápagos Marine Reserve¹⁶ (Fig. 4). Estimated locations of vessel rendezvous coincide with the movements of four Chinese flagged tuna long-liners, suggesting that the Fu Yuan Yu Leng 999 loaded cargo in the area without authorization, making the operation illegal¹⁷. These inferences are in line with the statements of crew members during legal procedures. Also, it is possible that some of the long-liners trespassed other countries' economic exclusive zones (EEZ) or received catch from coastal fishing ships. Our finding of two grey reef sharks, a non-pelagic species found in the western Pacific and the Central Pacific Islands¹⁸, supports this scenario. These detection anomalies highlight the importance of satellite technologies, such as AIS and vessel monitoring systems (VMS), in inferring true vessel trajectories, enforcing approved routes, and diminishing the probability of vessels trespassing into EEZs and marine protected areas¹⁹.

Whether the Fu Yuan Yu Leng 999 vessel would engage in potentially illegal operations around the Galápagos EEZ, remains unclear. Still, in its empty freezer holdings, the vessel had a gross capacity for at least 4.5 times the number of sharks found in this study (more than 30,000 additional individuals), which may have been received by the vessel along its south-bound trajectory if not been seized.

The number of individuals analyzed in this study constitutes a representative sample of the Fu Yuan Yu Leng 999 vessel's total cargo, which was highly biased towards sharks. The most common species found in the sample, the silky shark (28%), has been reported as the second most abundant species in the Hong Kong and Guangzhou markets in China, the largest shark fin retail centers in the world²⁰. Even more worrisome is the situation of the oceanic whitetip shark (20% of the sample), which is Critically Endangered. In 2011, in response to concerns about declining trends in catches of oceanic whitetip sharks, a ban by the Inter-American Tropical Tuna Commission (IATTC) was placed on the retention, transshipping, landing, storing, or selling of this species (Resolution

Species	Common name	Proportion of immatures	# Sexually immature (SI)	Size range SI (cm)	# Sexually mature (SM)	Size range SM (cm)	Length used	Size of sexual maturity*
<i>Alopias pelagicus</i>	Pelagic thresher	55%	52	63.0–137.8	42	139.0–174.0	PCL	138 cm ⁵¹
<i>Alopias superciliosus</i>	Bigeye thresher	48%	21	160.2–249.5	23	254.4–302.3	TL	253 cm ⁵²
<i>Carcharhinus amblyrhynchos</i>	Grey reef shark	–	0	NA	2	132.9–143.6	TL	116.7 ⁵³
<i>Carcharhinus falciformis</i>	Silky shark	86%	195	37.0–133.0	33	136.0–195.0	PCL	135–140 cm ³⁸
<i>Carcharhinus longimanus</i>	Oceanic whitetip shark	96%	157	76.7–169.9	7	189.1–257.6	TL	172 cm ³⁹
<i>Galeocerdo cuvier</i>	Tiger shark	–	2	145.1–212.3	0	NA	TL	276 cm ⁵⁴
<i>Prionace glauca</i>	Blue shark	86%	58	96.8–180.8	9	182.1–199.2	TL	182 cm ⁵⁵
<i>Isurus oxyrinchus</i>	Shortfin mako	–	2	120.4–171.2	1	203.4	TL	180 cm ⁵⁶
<i>Sphyrna lewini</i>	Scalloped hammerhead	27%	25	117.0–162.0	69	163.3–295.3	TL	162–181.2 cm ⁵⁷
<i>Sphyrna zygaena</i>	Smooth hammerhead	7%	3	118.4–172.8	43	179.7–289.9	TL	178.1 ⁵⁸
<i>Mustelus mustelus</i>	Common smoothhound	–	0	NA	1	161.9	TL	88 cm ⁵⁹
Total			515		230			

Table 2. Proportion of sexually mature individuals inferred from pre-caudal length. References are for studies reporting size for sexual maturity for males. *PCL* precaudal length, *TL* total length.

C-11-10²¹). Thus, our finding of 188 oceanic whitetip sharks implies that the Fu Yuan Yu Leng 999 crew was violating the ban of the IATTC, of which China is a signatory.

Another common species in the sample, the blue shark (12%), has been reported as the most abundant species in Asian markets²⁰. This species is not yet been listed by CITES because of its Near Threatened status (i.e., close to qualify for a threatened category in the near future; <https://www.iucnredlist.org/>). However, regionally, the blue shark represents the most common shark species landed in Peru²², and has been reported as by-catch in fisheries from Ecuador²³ and Chile²⁴. Other endangered shark species, such as hammerheads (collectively 20% of the sample), are highly vulnerable to non-target fisheries in the Eastern Pacific Ocean^{23, 25, 26}.

Additional threads may derive from the high proportion of immature individuals for some species in the sample. A comparison of fork length distribution of the seized silky and oceanic whitetip sharks (Fig. 3) with size-structured catch data from industrial fleets in the region²⁷, suggests that these species may have been caught using purse-seine gear. Consistent with these data, the semi-industrial longline fleet from mainland Ecuador caught mostly adults of silky shark and only a small proportion of oceanic whitetip shark in 2008–2012^{23, 28}. Samples of both species of hammerhead shark in the vessel were comprised mostly of adults, which is also consistent with the use of purse-seine gear²⁹. In 2016, the IATTC placed a precautionary ban for 2017–2019 on retention, transshipment, landing, or storing of silky sharks caught by purse seines in the convention area (Resolution C-16-06³⁰). Thus, our data, which suggest fishing a high proportion of silky sharks with purse seines, points to yet another violation of the IATTC by the Fu Yuan Yu Leng 999 crew. These data exemplify how the operation of international fishing fleets may be hampering the efforts of other IATTC members to protect shark species.

In recent years, international fleets comprising hundreds of vessels have been reported repeatedly near the Ecuadorian EEZs (Galápagos and Continental EEZs). In July 2017 and August 2017 (a few days before the seizure of vessel Fu Yuan Yu Leng 999), international fleets of ~300 ships (mostly Chinese flagged) were detected in the international waters bordering the Galápagos' EEZ³¹ and a similar event happened in March 2019³². More recently, on 16 July 2020, a fleet of 260 ships (mostly Chinese flagged) was reported along the southern border of Galápagos' EEZ³³. By 6 August 2020, the fleet had grown to 340 ships³⁴, and at least 6 were transmitting false coordinates that located them within New Zealand's waters³⁵.

These events suggest that the presence of international fishing fleets around the Ecuadorian EEZs may be systematic. Given the highly mobile nature of the targeted species identified here, international fleets are likely catching sharks that are demographically linked to populations protected under national legislation, undermining the efforts Ecuador has adopted for the conservation of sharks. Current proposals to enhance the protection of migratory marine life in the region include expanding Ecuador's EEZ along the Carnegie and Cocos ridges (Supplementary Information Figure S2). However, the seasonal return of large industrial fleets to the exact borders of the Ecuadorian EEZs implies that the resources within these zones are of particular interest.

The high seas in the Eastern Tropical Pacific, including those surrounding the Galápagos EEZ, harbor marine resources (in this case, sharks), which are targeted by international fishing fleets, with limited governance from Regional Fisheries Management Organizations (RFMOs). A better understanding of the demographic and genetic connectivity of targeted shark populations across jurisdictional boundaries is urgently needed to inform management and improve the conservation of the biological marine resources of the Eastern Tropical Pacific both within EEZs and in Areas Beyond National Jurisdiction (ABNJs).

Here, we provide the largest data set on shark species caught in the region and contribute to a growing data base of genetic information needed to assess the identity of fished sharks in the future. Improved governance of

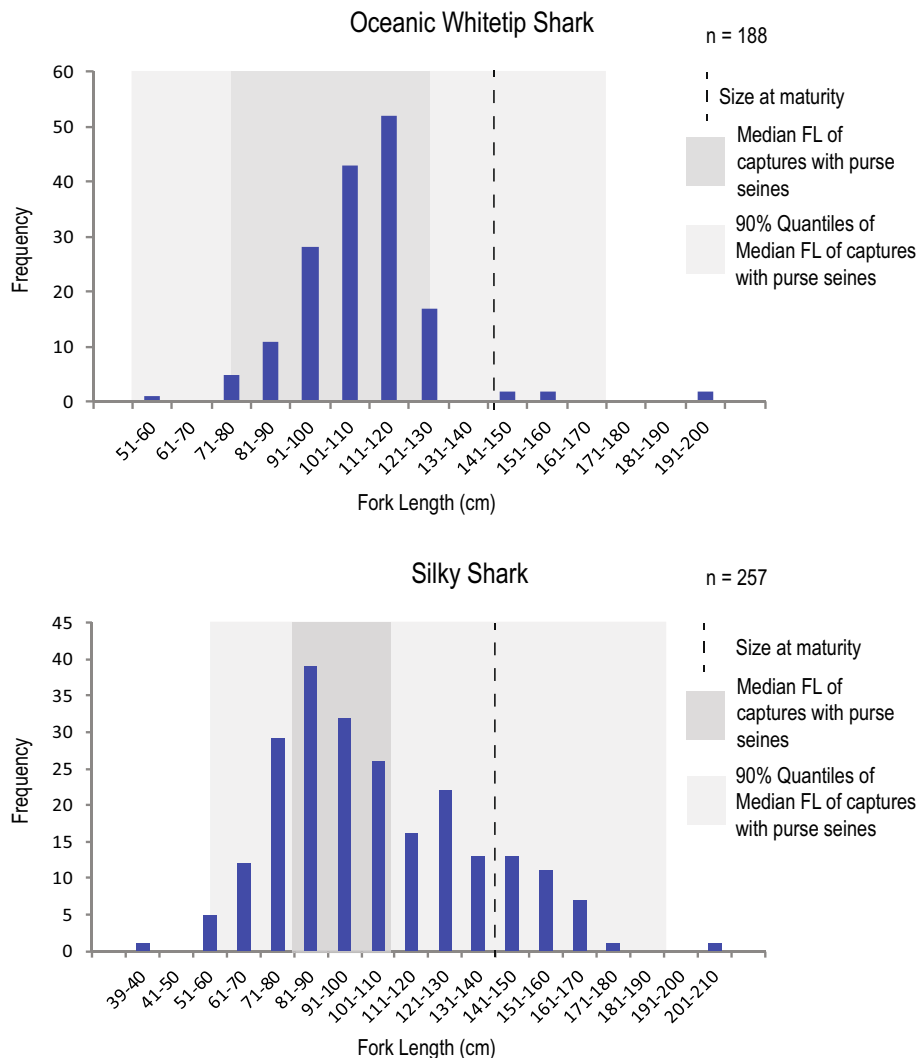


Figure 3. Size structure for oceanic whitetip and silky sharks seized in vessel Fu Yuan Yu Leng 999 (based on 188 and 257 individuals, respectively). Size to maturity for oceanic whitetip was based on Joung et al.³⁹, by transforming Total Length to Fork Length⁴⁹. Median Fork Length of captures with purse seines and 90% quantiles were approximated from Clarke et al.²⁷ Figure S3. we created this figure using Microsoft Excel Spreadsheet (<https://www.microsoft.com/en-ww/microsoft-365/excel>) and Adobe Creative Suite (<https://www.adobe.com>).

fisheries in ABNJs and their compliance with international treaties, will be paramount to preserve biological and economical marine resources of developing countries in the Eastern Tropical Pacific and tropical seas in general.

Methods

Sampling, morphological identification, and size of sexual maturity. Sampling was conducted onboard vessel Fu Yuan Yu Leng 999 in September and October 2017, in a collaborative effort between the National Army of Ecuador, the GNP Directorate, and the Galapagos Science Center (GSC) of Universidad San Francisco de Quito and the University of North Carolina at Chapel Hill (research permits PC-38-16 and PC-24-17). The procedure was performed under the time and logistic constraints imposed by the seizure's legal process, the low temperatures of the vessel holds, and the identifying and measuring of frozen samples—with limited personnel and the vessel in motion—while destruction/disposal of the cargo was taking place.

We tried to take a representative sample of all species present in the vessel, choosing a random sample of individuals within each species. Morphological identification was based on expert's knowledge and specialized literature^{18,28}. Tissue samples and pre-caudal body length were taken for as many individuals as possible. The total vessel cargo was weighed to the nearest 0.1 kg before disposal. The size of sexual maturity was inferred from the literature to estimate the ratio of immature-to-mature individuals in our sample. For pelagic thresher (*Alopias pelagicus*) and silky shark (*Carcharhinus falciformis*), size of sexual maturity was inferred from pre-caudal length. For other species, we used conversion factors to calculate total length from pre-caudal length, as

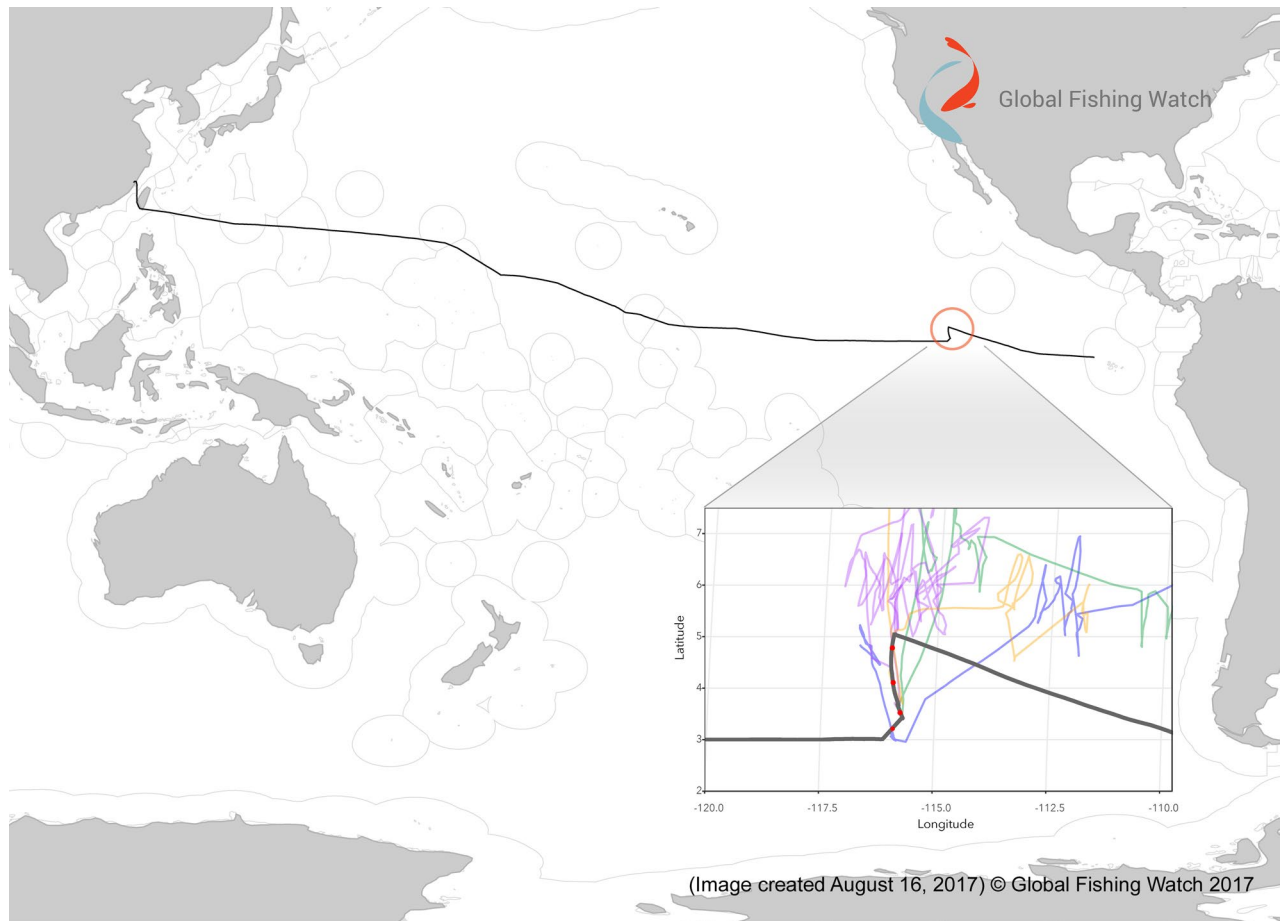


Figure 4. Trajectory of vessel Fu Yuan Yu Leng 999, including AIS-detected anomaly. The vessel departed from Fuzhou on the Chinese coast⁵⁰ and was detained at Punta Pitt, San Cristobal Island, within the Galápagos Marine Reserve. Figure from Cutlip¹⁷, its use authorized by Global Fishing Watch.

follows: for shortfin mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*), and smooth hammerhead (*Sphyrna zygaena*) we followed Mas et al.³⁶; for oceanic whitetip (*Carcharhinus longimanus*) D'Alberty et al.³⁷; for bigeye thresher (*Alopias superciliosus*), grey reef shark (*Carcharhinus amblyrhynchos*), tiger shark (*Galeocerdo cuvier*), and smooth-hound (*Mustelus mustelus*), FishBase (<https://www.fishbase.de>). For scalloped hammerhead (*Sphyrna lewini*), we used the conversion factor for smooth hammerhead³⁶. Since we lacked sex ID for all individuals, we defined minimum size at maturity using estimates for males only (which tend to be smaller than females). When a range was provided, we used the minimum size.

To compare the size structure of silky and oceanic whitetip sharks found in the vessel with that of sharks fished with long-lines and purse-seines²⁷, we converted pre-caudal length to fork length using Oshitani et al.³⁸ and Joung et al.³⁹ conversion factors, respectively.

Molecular identification. We sequenced the mitochondrial gene Nicotinamide Adenine Dehydrogenase subunit 2 (ND2), a barcode gene for sharks⁴⁰ (permits MAE-DNB-CM-2016-0041 and MAE-DNB-2018-0759-O). We conducted genomic DNA extractions on samples of subcutaneous muscle tissue (2 × 2 mm). Extraction followed a guanidine thiocyanate protein precipitation plus isopropanol DNA precipitation protocol⁴¹. Quality and concentration of genomic DNA were measured with a NanoDrop ND-1000 spectrophotometer v3.0.1 (NanoDrop, ThermoFisher Scientific) or an Epoch Microplate Spectrophotometer (BioTek).

The ND2 gen was amplified by PCR in 25 µl reactions comprised of 0.25 µl Paltinum Taq DNA Polymerase, Master Mix (Invitrogen), 2.50 µl 10X PCR Buffer, 1.5 mM of MgCl₂, 0.50 µl of 10 µM of each dNTP, 0.5 µl of each primer (10 µM), and different amounts of ultrapure water with 1 µl of template DNA (adjusted to 100 ng/mL of DNA). Thermocycling conditions included an initial denaturation at 94 °C/3 min; 35 cycles of denaturation at 93 °C/ 30 s, annealing at 58 °C/1 min, and extension at 72 °C/1 min; and a final extension at 72 °C/10 min. The resulting amplicons were visualized via electrophoresis in a 2% agarose gel (UltraPure Agarose). Excess nucleotides and dNTPs were removed from PCR products using ExoSAP-IT PCR Product Cleanup Reagent (Applied Biosystems). Purified amplicons were sequenced with big-dye chemistry and PCR primers, using capillary electrophoresis in an ABI3730xl sequencer. Inspection of chromatograms, contig assembly of forward and reverse sequences, and final sequence checking and edition were performed in Geneious 11.1.5 (Biomatters Ltd.⁴²).

To evaluate the similarity between sequences from the vessel's samples and those on GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>), we used BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>). To place the sample sequences in a phylogenetic framework, we consulted the Chondrichthyes Tree of Life (<https://sharkrays.org>) to assemble a list including all shark species from the Pacific Ocean, and downloaded the sequences for these species from Genbank. Locality information for sequences of the species present in the vessel was gathered, when possible, in an attempt to relate the seized samples to general geographic regions in the Pacific Ocean. Additionally, we sequenced samples from nine individuals of the Galapagos shark, *Carcharhinus galapagensis*, obtained from the Galápagos Marine Reserve (GNPD permit 065-2013).

Sequences of samples from vessel Fu Yuan Yu Leng 999, the Pacific Ocean (gathered from GenBank), and Galapagos shark were aligned using MAFFT 7⁴³. All sequences were inspected, translated into amino acids (to look for potential stop-codons), and trimmed to the size of the ND2 mitochondrial gen using Mesquite 3.6⁴⁴. To reduce the size of our matrix and facilitate phylogenetic analyses, we eliminated duplicates (identical sequences) in all datasets separately, using sRNAtoolbox⁴⁵. Then, we compiled the unique sequences from each dataset and re-aligned them in MAFFT 7.

We used IQ-TREE⁴⁶, as implemented in the IQ-TREE web server⁴⁷ (<http://iqtree.cibiv.univie.ac.at/>) to infer the best-fit model of nucleotide substitution, estimate the maximum likelihood tree, and assess nodal support. The best-model fit was estimated using ModelFinder⁴⁸ in "Auto" function and "FreeRate heterogeneity"; the best-fit model (GTR + F + R7) was chosen using the Bayesian information criterion. Nodal support was obtained using 1000 ultrafast bootstrap replicates, 1000 maximum iterations, and minimum correlation coefficient of 0.99. As outgroup, we used the rabbit fish, *Chimaera monstrosa* (GenBank accession number JQ518716).

Data availability

All the DNA sequences generated during this study are available on GenBank (Supplementary Data S1). All morphological data used is available from the Supplementary Information Data S1.

Received: 19 March 2021; Accepted: 30 June 2021

Published online: 22 July 2021

References

- Ceballos, G., Ehrlich, P. R. & Dirzo, R. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U. S. A.* **114**, E6089–E6096 (2017).
- Briggs, J. C. Marine extinctions and conservation. *Mar. Biol.* **158**, 485–488 (2011).
- Heupel, M. R., Knip, D. M., Simpfendorfer, C. A. & Dulvy, N. K. Sizing up the ecological role of sharks as predators. *Mar. Ecol. Prog. Ser.* **495**, 291–298 (2014).
- TRAFFIC East Asia. *Shark product trade in Hong Kong and mainland China and implementation of the CITES shark listings*. TRAFFIC East Asia (2004).
- Pacoureau, N. *et al.* Half a century of global decline in oceanic sharks and rays. *Nature* **589**, 567–571 (2021).
- Dulvy, N. K. *et al.* Extinction risk and conservation of the world's sharks and rays. *Elife* **3**, 1–34 (2014).
- Dwyer, R. G. *et al.* Individual and population benefits of marine reserves for reef sharks. *Curr. Biol.* **30**, 480–489.e5 (2020).
- Kerwath, S. E., Winker, H., Götz, A. & Attwood, C. G. Marine protected area improves yield without disadvantaging fishers. *Nat. Commun.* **4**, 1–6 (2013).
- Cabral, R. B. *et al.* A global network of marine protected areas for food. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 28134–28139 (2020).
- Camhi, M. D., Fordham, S. V. & Fowler, S. L. Domestic and International Management for Pelagic Sharks. in *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (eds. M. D. Camhi, E. K. Pikitch & E. A. Babcock) 418–444 (Blackwell, 2009). <https://doi.org/10.1002/9781444302516.ch34>.
- Schiller, L., Alava, J. J., Grove, J., Reck, G. & Pauly, D. The demise of Darwin's fishes: evidence of fishing down and illegal shark finning in the Galápagos Islands. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **25**, 431–446 (2015).
- Feitosa, L. M. *et al.* DNA-based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot. *Sci. Rep.* **8**, 1–11 (2018).
- Reck, G. Development of the Galápagos Marine Reserve. in *The Galapagos Marine Reserve. Social and Ecological Interactions in the Galapagos Islands* (ed. Denkinger, J. V. L.) 139–158 (Springer, 2014).
- PNG (Parque Nacional Galápagos). *Barco chino deberá pagar 6 millones por daño ambiental dispone Sala de lo Penal*. <https://www.galapagos.gob.ec/barco-chino-debera-pagar-6-millones-por-dano-ambiental-dispone-sala-de-lo-penal/> (2017).
- Fiscalía General del Estado Ecuatoriano. Boletín de Prensa FGE N. 096-DC-2019: Corte Nacional aceptó recurso de casación por delito contra la flora y fauna silvestres en Galápagos. <https://www.fiscalia.gob.ec/corte-nacional-acepto-recurso-de-casacion-por-delito-contra-la-flora-y-fauna-silvestres-en-galapagos/> (2019).
- D'Afflisio, E., Braca, P., Millefiori, L. M. & Willett, P. Maritime Anomaly Detection Based on Mean-Reverting Stochastic Processes Applied to a Real-World Scenario. in *2018 21st International Conference on Information Fusion, FUSION 2018* 1171–1177 (Institute of Electrical and Electronics Engineers Inc., 2018). <https://doi.org/10.23919/ICIF.2018.8455854>.
- Culip, K. Our Data Suggests Transshipment Involved in Refrigerated Cargo Vessel Just Sentenced to \$5.9 Million and Jail Time for Carrying Illegal Sharks. <https://globalfishingwatch.org/impacts/policy-compliance/transshipment-involved-in-reefer-sentenced-for-carrying-illegal-sharks/> (2017).
- Compagno, L., Dando, M. & Fowler, S. *Sharks of the World* (Princeton University Press, 2005).
- Bradley, D. *et al.* Leveraging satellite technology to create true shark sanctuaries. *Conserv. Lett.* **12**, 1–8 (2019).
- Cardenosa, D. *et al.* Species composition of the largest shark fin retail-market in mainland China. *Sci. Rep.* **10**, 1–10 (2020).
- IATTC. *Resolution C-11-10. Resolution on the conservation of oceanic whitetip sharks caught in association with fisheries in the Antigua convention area.* (IATCC, 2011).
- Gonzalez-Pestana, A., Kouri J., C. & Velez-Zuazo, X. Shark fisheries in the Southeast Pacific: A 61-year analysis from Peru. *F1000Research* **3**, 164 (2014).
- Martínez-Ortiz, J., Aires-Da-silva, A. M., Lennert-Cody, C. E. & Maunder, M. N. The Ecuadorian artisanal fishery for large pelagics: Species composition and spatio-temporal dynamics. *PLoS ONE* **10**, 1–29 (2015).
- Bustamante, C. & Bennett, M. B. Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean. *Fish. Res.* **143**, 174–183 (2013).
- Hinton, M. G. *et al.* Stock Status Indicators for Fisheries of the Eastern Pacific Ocean. INTER-AMERICAN TROPICAL TUNA COMMISSION, 19, 142–182 (2011).

26. Duffy, L. M., Lennert-Cody, C. E., Olson, R. J., Minto-Vera, C. V. & Griffiths, S. P. Assessing vulnerability of bycatch species in the tuna purse-seine fisheries of the eastern Pacific Ocean. *Fish. Res.* **219**, 105316 (2019).
27. Clarke, S. C., Harley, S. J., Hoyle, S. D. & Rice, J. S. Population trends in Pacific Oceanic sharks and the utility of regulations on shark finning. *Conserv. Biol.* **27**, 197–209 (2013).
28. Martínez Ortiz, J. *et al.* Abundancia estacional de Tiburones desembarcados en Manta-Ecuador. EPESPO-PMRC, 9–27 (2007).
29. Román-Verdesoto, M. Updated summary regarding hammerhead sharks caught in the tuna fisheries in the Eastern Pacific Ocean 6th Meeting of the Scientific Advisory Committee IATTC. (2015).
30. IATTC. *Resolution C-16-06: Conservation Measures for Shark Species, with Special Emphasis on the Silky Shark (Carcharhinus falciformis), for the years 2017, 2018, and 2019.* (IATTC, 2016).
31. Alava, J. J. Massive Chinese Fleet Jeopardizes Threatened Shark Species around the Galápagos Marine Reserve and Waters off Ecuador. *Int. J. Fish. Sci. Res.* **1**, 8–10 (2017).
32. El Universo. Se detectan tres flotas pesqueras chinas cerca de Galápagos. <https://www.eluniverso.com/Noticias/2019/03/21/Nota/7244318/Se-Detectan-Tres-Flotas-Pesqueras-Chinas-Cerca-Galapagos> (2019).
33. El Universo. Armada del Ecuador detecta flota pesquera con 260 barcos en las cercanías de Galápagos. <https://www.eluniverso.com/noticias/2020/07/16/nota/7908768/armada-ecuador-detecta-flota-pesquera-260-barcos-cercanias>. (2020).
34. El Universo. Varios barcos chinos, que integran la flota extranjera que pesca cerca de Ecuador, estarían emitiendo 'falsas coordenadas'; aparecen en Nueva Zelanda. https://www.eluniverso.com/noticias/2020/08/06/nota/7932429/flota-china-pesquera-galapagos-ecuador-nueva-zelanda-ecuador#cxrecs_s. (2020)
35. Stuff. Chinese vessels off Galapagos 'cloaking' in New Zealand. <https://www.stuff.co.nz/environment/122339295/chinese-vesse-ls-off-galapagos-cloaking-in-new-zealand>. (2020).
36. Mas, F., Forselledo, R. & Domingo, A. Length-length relationships for six pelagic shark species. *Collect. Vol. Sci. Pap. ICCAT* **70**, 2441–2450 (2014).
37. D'Alberto, B. M. *et al.* Age, growth and maturity of oceanic whitetip shark (*Carcharhinus longimanus*) from Papua New Guinea. *Mar. Freshw. Res.* **68**, 1118–1129 (2017).
38. Oshitani, S., Nakano, H. & Tanaka, S. Age and growth of the silky shark *Carcharhinus falciformis* from the Pacific Ocean. *Fish. Sci.* **69**, 456–464 (2003).
39. Joung, S. J., Chen, N. F., Hsu, H. H. & Liu, K. M. Estimates of life history parameters of the oceanic whitetip shark, *Carcharhinus longimanus*, in the Western North Pacific Ocean. *Mar. Biol. Res.* **12**, 758–768 (2016).
40. Naylor, G. J. P. *et al.* A DNA sequencebased approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. *Bull. Am. Museum Nat. Hist.* **21**, 1–262 (2012).
41. Peñafiel, N., Flores, D. M., Rivero De Aguilar, J., Guayasamin, J. M. & Bonaccorso, E. A cost-effective protocol for total DNA isolation from animal tissue. *Neotrop. Biodivers.* **5**, 69–74 (2019).
42. Kearse, M. *et al.* Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**, 1647–1649 (2012).
43. Katoh, K., Rozewicki, J. & Yamada, K. D. MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. *Brief. Bioinform.* **20**, 1160–1166 (2018).
44. Maddison, W. P. & Maddison, D. R. Mesquite: A modular system for evolutionary Mesquite installation for evolutionary analysis. (2003).
45. Aparicio-Puerta, E. *et al.* SRNAbench and sRNAtoolbox 2019: intuitive fast small RNA profiling and differential expression. *Nucleic Acids Res.* **47**, W530–W535 (2019).
46. Nguyen, L. T., Schmidt, H. A., Von Haeseler, A. & Minh, B. Q. IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* **32**, 268–274 (2015).
47. Trifinopoulos, J., Nguyen, L. T., von Haeseler, A. & Minh, B. Q. W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Res.* **44**, W232–W235 (2016).
48. Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., Von Haeseler, A. & Jermini, L. S. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nat. Methods* **14**, 587–589 (2017).
49. Seki, T., Taniuchi, T., Nakano, H. & Shimizu, M. Age, growth and reproduction of the oceanic Whitetip shark from the Pacific Ocean. *Fish. Sci.* **64**, 14–20 (1998).
50. Bergman, B. Reefer Fined \$5.9 Million for Endangered Catch in Galapagos Recently Rendezvoused with Chinese Longliners. <https://skytruth.org/2017/08/galapagos-reefer-fined-5-9-million/> (2017).
51. Romero-Caicedo, A. F., Galván-Magaña, F. & Martínez-Ortiz, J. Reproduction of the pelagic thresher shark *Alopias pelagicus* in the equatorial Pacific. *J. Mar. Biol. Assoc. U. K.* **94**, 1501–1507 (2014).
52. Chen, C., Liu, K. & Chang, Y. Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839) (Chondrichthyes: Alopiidae), in the northwestern Pacific. *Ichthyol. Res.* **44**, 227–236 (1997).
53. Bradley, D. *et al.* Growth and life history variability of the grey reef shark (*Carcharhinus amblyrhynchos*) across its range. *PLoS ONE* **12**, 1–20 (2017).
54. Holmes, B. J. *et al.* Age and growth of the tiger shark *Galeocerdo cuvier* off the east coast of Australia. *J. Fish Biol.* **87**, 422–448 (2015).
55. Nakano, H. Stevens, J. The biology and ecology of the blue shark, *Prionace glauca*. in *Sharks of the open ocean: Biology, fisheries and conservation (Vol. 1)* (ed. Camhi, Merry D. Pikitch, E. K. Babcock, E. A.) 140–151 (Blackwell Scientific Publications, 2008).
56. Gubanov, Y. E. The reproduction of some species of pelagic sharks from the equatorial zone of the Indian Ocean. *J. Ichthyol.* **18**, 781–792 (1978).
57. Fahmi & Sumadhiharga, K. Size, sex and length at maturity of four common sharks caught from Western Indonesia. *Mar. Res. Indones.* **32**, 7–19 (2007).
58. Nava, P. N. & Márquez-Farías, J. F. Talla de madurez del tiburón martillo, *Sphyrna zygaena*, capturado en el Golfo de California. *Hidrobiologica* **24**, 129–135 (2014).
59. Saïdi, B., Bradaï, M. N. & Bouaïn, A. Reproductive biology of the smooth-hound shark *Mustelus mustelus* (L.) in the Gulf of Gabès (south-central Mediterranean Sea). *J. Fish Biol.* **72**, 1343–1354 (2008).

Acknowledgements

We are grateful to the national army of Ecuador, Fuerzas Armadas Nacionales, and especially Comander Dario Ortega (Zona Naval de San Cristóbal, Galápagos), for their support during the vessel seizure. To the Galápagos National Park Directorate for its institutional support and to its staff—Galo Quezada, Daniel Lara-Solis, Jorge Carrión, Gabriel Vásquez, and Maryuri Yépez—Galápagos National Park rangers, and Ingrid Jaramillo for their assistance during sampling. Special thanks to our volunteers Diego Iglesias, Jacob Salinas, Jens Mayorga, Alice Skehel, Jaime Grijalva, and Jason Castañeda, who assisted during sample collection under such hard conditions. Gabriela Gavilanes and Nathalia Valencia assisted during sequencing procedures. Finally, we want to thank GSC staff—Carlos Mena, Stephen Walsh, Philip Page, Sofia Tacle, Sylvia Sotamba, Cristina Vintimilla, and Soledad Sarzosa—for their continuous support. This study was funded by The National Geographic Society (Grant Award

NGS-421C-18), Universidad San Francisco de Quito (HUBI 10140), and a generous donation from Michael Smith towards shark conservation in the Galápagos (USFQ, HUBI 12204).

Author contributions

E.B.: Study concept and design of molecular component; acquisition of funding; final data analyses; drafting of the manuscript. N.O.-G.: acquisition and preliminary analyses of data; partial drafting of the manuscript. D.A.P.: comparative data compilation; morphological data analysis; provision of Galápagos shark samples; critical revision of the manuscript. A.H.: comparative data compilation; partial drafting of the manuscript; critical revision of the manuscript. D.P.-R.: acquisition of research permits; sampling logistics; critical revision of the manuscript. S.C.: morphological identification; photography; critical revision of the manuscript. J.P.M.-P.: sample collection and sampling logistics; review of the manuscript. E.E.: sample collection and sampling logistics. J. S.: sample collection and taking of morphological measurements; L.D.M.-R.: sample collection and taking of morphological measurements. A.V.: sample collection and taking of morphological measurements. J.A.C.: acquisition of funding; critical revision of the manuscript. M.L.T.: laboratory support; critical revision of the manuscript. W.B.: logistic and institutional support; critical revision of the manuscript. D. R.: logistic and institutional support. M.H.: morphological identification; partial drafting of the manuscript; critical revision of the manuscript. J.M.G.: Study concept and design of molecular component; sampling logistics; acquisition of funding; critical review of the manuscript.

Competing interests

Sebastián Cruz (SC) declares competing interest given its involvement as subject expert hired during the legal inspection of vessel Fu Yuan Yu Leng 999 for the morphological identification of shark species.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-021-94126-3>.

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