

Marine Record

Cite this article: O'Connell CP, Prasetyo AP, Stewart M, Fahmi (2024). From where I belong: using mitochondrial DNA analysis to investigate the origin of a white shark (*Carcharodon carcharias*) captured in Indonesian waters. *Journal of the Marine Biological Association of the United Kingdom* **104**, e75, 1–6. <https://doi.org/10.1017/S0025315424000778>

Received: 6 January 2024

Revised: 11 June 2024

Accepted: 8 July 2024

Keywords:

Carcharodon carcharias; D-loop sequences; Indonesia; mtDNA; white shark

Corresponding author:

C. P. O'Connell;

Email: oseasfdn@gmail.com

From where I belong: using mitochondrial DNA analysis to investigate the origin of a white shark (*Carcharodon carcharias*) captured in Indonesian waters

C. P. O'Connell^{1,2} , A. P. Prasetyo³, M. Stewart⁴ and Fahmi⁵

¹O'Seas Conservation Foundation, Inc., Yonkers, NY, 10701, USA; ²School for Marine Science and Technology, University of Massachusetts Dartmouth, New Bedford, MA 02740, USA; ³Research Center for Conservation of Marine and Inland Water Resources, National Research and Innovation Agency, Cibinong 16911, Bogor, Indonesia; ⁴Project Hiu, Brisbane, QLD 4001, Australia and ⁵Research Center for Oceanography, National Research and Innovation Agency, Pademangan 14430, Jakarta, Indonesia

Abstract

In 2013 and 2019, two separate encounters with a white shark (*Carcharodon carcharias*) were documented within Indonesian waters. Of particular importance was *ca.* 6.0 m male *C. carcharias* that was captured in Lombok, Indonesia in 2013, where an upper lateral tooth was retained. Using the D-loop sequences of the mitochondrial DNA (mtDNA) associated with this captured white shark, the mtDNA was compared to the available mtDNA sequences in GenBank[®] associated with the Northwest Pacific and Australian (i.e. Southern-Western and Eastern) *C. carcharias* subpopulations to determine its point of origin. Results from the mtDNA analyses suggest that the point of origin for this captured *C. carcharias* is from one of the Australian subpopulations. When compared to primary literature, this migration presents a northerly range extension for this species; however, since it is unclear what Australian subpopulation this shark was from it is uncertain what subpopulation this range extension applies to. Although *C. carcharias* presence within Indonesian waters is likely a rare occurrence, being that Indonesia represents the largest shark fin exporter in the world, the utilization of these waters and potential unsustainable exploitation poses a definitive threat to this highly migratory top predator. Therefore, further research investigating the purpose and site fidelity of *C. carcharias* within these waters is critical to future multijurisdictional protection of this top predator.

Introduction

Top predators, such as some shark species, play a critical role and have been demonstrated to help maintain the balance within their respective food webs (Burkholder *et al.*, 2013; Hussey *et al.*, 2015). In some locations or even on a global scale, the retention of certain shark species is prohibited (e.g. Convention on International Trade in Endangered Species of Wild Fauna and Flora; Tolotti *et al.*, 2015); however, in other locations, the increased demand and exploitation rates, both legal and illegal, raise concern about the health of certain shark populations (Shivji *et al.*, 2005). Understanding the population structure, range, and abundance of a particular shark population can provide fisheries managers with essential information regarding the sustainable or unsustainable exploitation of that particular population (e.g. Chapman *et al.*, 2015; Pérez-Jiménez and Mendez-Loeza, 2015) and consequently can provide regulations to help restore the population to pre-existing levels (Hoffmann *et al.*, 2010).

In the instance of white sharks (*Carcharodon carcharias*), there are nine known *C. carcharias* subpopulations: Southern-Western Australia (Bruce, 2016; McAuley *et al.*, 2017), Western North Atlantic (WNA, Skomal *et al.*, 2017), Northeastern Pacific (NEP, Domeier and Nasby-Lucas, 2013), Eastern Australian and New Zealand (Bruce *et al.*, 2019), Mediterranean (Leone *et al.*, 2020), South African (Kock *et al.*, 2013), Northwest Pacific (Tanaka *et al.*, 2011), South American Atlantic (Cione and Barla, 2008), and South American Pacific (Bustamante *et al.*, 2014; Figure 1). Due to its low rebound potential and current estimated population status, *C. carcharias* is listed as vulnerable on a global scale (Rigby *et al.*, 2019) according to the International Union for the Conservation of Nature Red List. The white shark is particularly vulnerable to exploitation since this species is characterized by having low fecundity, producing an average of 2–14 pups per litter (Francis, 1996; Uchida *et al.*, 1996), slow growth (Wintner and Cliff, 1999; Natanson and Skomal, 2015), and late sexual maturity (Natanson and Skomal, 2015), which is estimated to be >3.80 m total length (TL) for males and >4.50 m TL for females (Francis, 1996; Pratt, 1996; Wintner and Cliff, 1999). However, despite international protection of *C. carcharias*, this species exhibits transoceanic movements, making it susceptible to a variety of anthropogenic sources of mortality (e.g. Bonfil *et al.*, 2005). While extensive tagging efforts have provided a baseline understanding of the movements of most *C. carcharias* populations (e.g. Skomal *et al.*, 2017; Bruce *et al.*, 2019), there remains uncertainty as to the structure, size, and range of



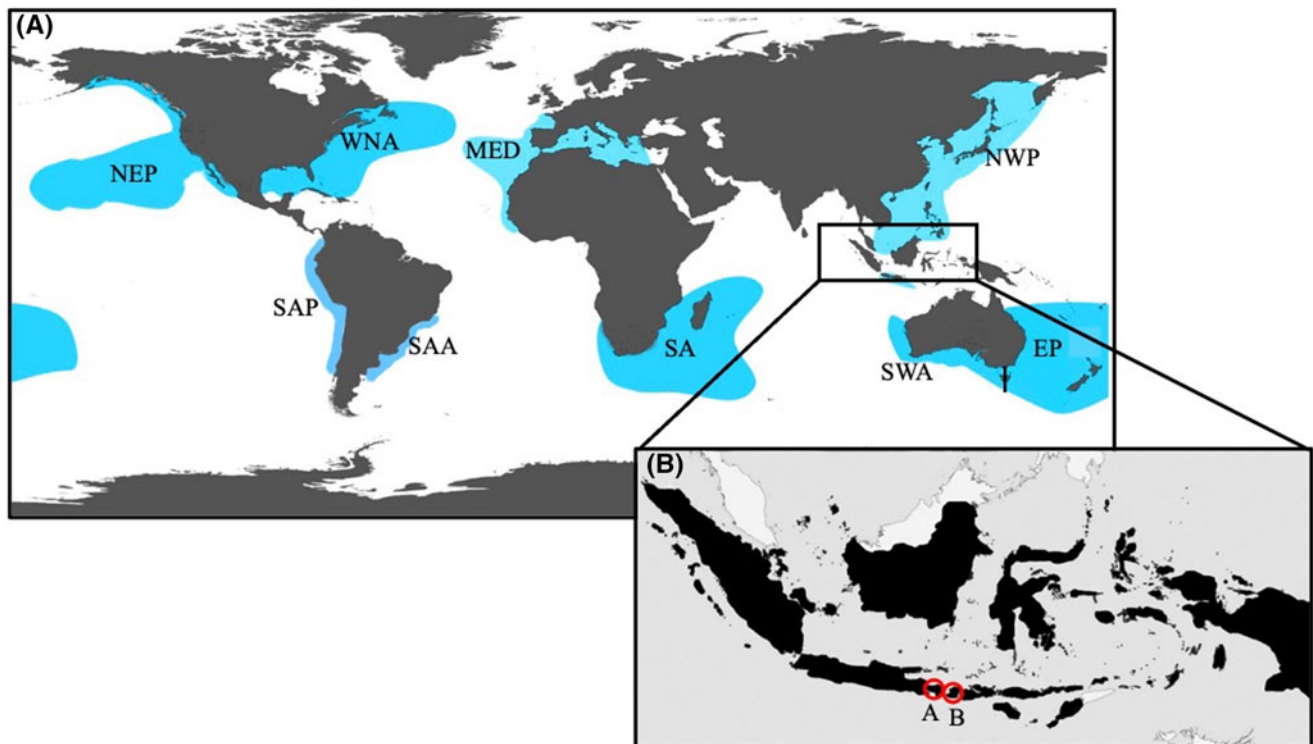


Figure 1. (A) Map illustrating the relative locations of white shark (*C. carcharias*) populations (modified from Huvneers *et al.*, 2018). The populations are: Northeastern Pacific (NEP), Western North Atlantic (WNA), Mediterranean (MED), South African (SA), Northwest Pacific (NWP), Southern-Western Australian (SWA), Eastern Australian and New Zealand (EA), South American Pacific (SAP), and South American Atlantic (SAA). The rectangular region highlights the location of Indonesia. (B) Map representing Indonesia (area in black), as well as the white shark (*C. carcharias*) sightings within the region: (A) Nusa Penida in Bali, Indonesia ($8^{\circ}44'S$; $115^{\circ}32'E$; 5.0 m female) and (B) Lombok, Indonesia ($08^{\circ}51'S$; $118^{\circ}18'E$; 6.0 m male).

most subpopulations, particularly in the Northwest Pacific population (Christiansen *et al.*, 2014).

In recent years, sparse sightings of *C. carcharias* have occurred within Indonesian waters (Fahmi and Dharmadi, 2014; Coleman,

personal communication, 2019). More specifically, in 2019 within Nusa Penida in Bali, Indonesia ($8^{\circ}44'S$; $115^{\circ}32'E$; Figure 1A), scuba divers encountered an approximately 5.0 m TL female *C. carcharias* (Figure 2A). In 2013, a *ca.* 6.0 m TL male

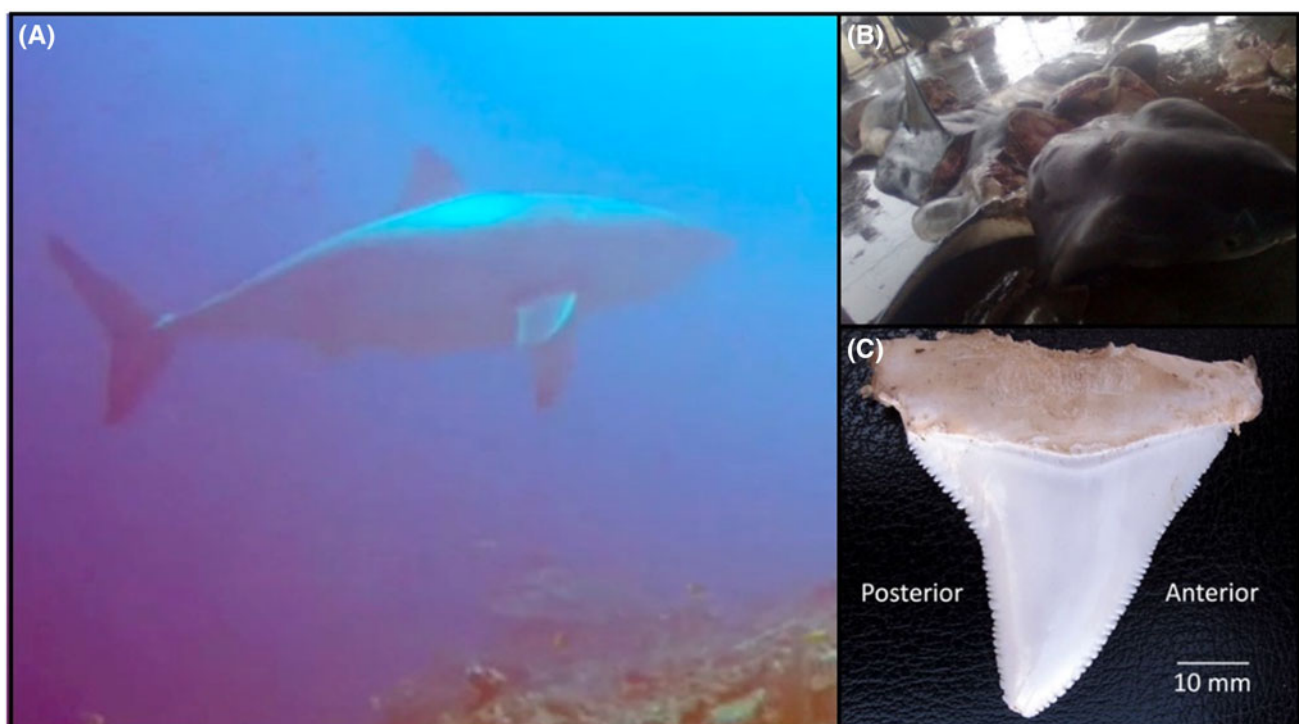


Figure 2. Recent and documented white shark (*C. carcharias*) sightings within Indonesian waters. (A) An estimated 5.0 m TL female *C. carcharias* sighted by divers at Nusa Penida in Bali, Indonesia in 2019 © Two Fish Divers. (B) A 6.0 m TL male *C. carcharias* captured by fishermen in eastern Lombok, Indonesia in 2013 © Fahmi and Dharmadi (2014). (C) Upper lateral tooth collected from the white shark *C. carcharias* landed in eastern Lombok, Indonesia in 2013. © Fahmi and Dharmadi (2014).

C. carcharias (Figure 2B) was captured by demersal longline fishermen off Dompu in West Nusa Tenggara, Indonesia (08°51'S; 118°18'E; Figure 1B). Although multiple *C. carcharias* subpopulations have been identified in the waters surrounding Indonesia, including the Northwest Pacific, the Southern-Western Australian, and Eastern Australian and New Zealand, there exists no record of any tagged sharks associated with these stocks travelling into these tropical waters. Therefore, using a sample collected from the upper lateral tooth of the *C. carcharias* captured in the Lesser Sunda region and comparing it to the publicly available mitochondrial DNA (mtDNA) database (GenBank®; Bethesda, MD, USA), the present study aimed to determine which subpopulation this *C. carcharias* may be most closely related to, thus suggesting site of origin.

Methods

In 2013, a *C. carcharias* was captured by demersal longline fishermen and brought to a fishing market where scientists were able to collect both photographic evidence and one upper lateral tooth (Fahmi and Dharmadi, 2014; Figure 2C). At the Centre Laboratory of Sequencing, National Research and Innovation Agency in West Java, Indonesia from February to April 2023, DNA was extracted from the 10-year-old upper lateral tooth using a DNeasy Tissue Kit (Qiagen™) and the addition of ethylenediaminetetraacetic acid to the incubation stage (modified from Swig and Collier, 2021). A polymerase chain reaction (PCR) was used to amplify about 500 bp of the mtDNA D-loop region. The two primers for the D-loop region were: GWDL-L (TTG ACG CGA TCA AGG ACG AA) and GWDL-H (CAA ACA TCC ATT TGG CCT TC) (Pardini *et al.*, 2000). A total volume of 24 µl included 12.5 µl MyTaq™ HS Red Mix PCR kit, 1 µl of the 5 µM pre-mixed forward and reverse primers (IDT™), 3 µl of a standardized amount (10–15 ng µl⁻¹) of DNA, and 7.5 µl of sterile water. The PCR profile included a 1 min initial denaturing step at 95°C, 40 cycles at 95°C for 15 s, 55°C for 30 s, 72°C for 1 min, and a 5 min final extension step at 72°C (Tanaka *et al.*, 2011). The negative control (Borneo river shark [*Glyphis fowlerae*]) was used to validate the GWS primer. To confirm species, two additional primers were run (i.e. Elas02; Taberlet *et al.*, 2012 and Leray-XT; Wangensteen *et al.*, 2018) by following the PCR mix and PCR profile (Prasetyo *et al.*, 2023). After PCR, each replicate was visually examined on a 1.2% agarose gel and stained with GelRed® Nucleic Acid Gel Stain. Each well received 2 µl of the sample and a 100 bp ladder from Invitrogen™ was included in the gel for reference.

PCR products are then purified using a QIAquick PCR Purification Kit (Qiagen). The purification products were then Sanger sequenced using the Genetic Analyzer 3500 (ABI™) at the Sequencing Centre, Genomic Laboratory, National Research and Innovation Agency, Bogor, Indonesia. All positions containing gaps and missing data were eliminated from the dataset ('Complete deletion' option). After trimming and quality control have been conducted, the sequences (GenBank accession no. PP078820) were then aligned using software UGENE (Okonechnikov *et al.*, 2012) and compared with the National Center for Biotechnology Information (NCBI) sequences for the Japanese (GenBank accession nos. AB598394–AB598397) (Tanaka *et al.*, 2011) and Australian–New Zealand (GenBank accession nos. KY067571–KY067590) subpopulations. To further examine the phylogenetic tree, maximum-likelihood was constructed using the neighbour-joining method with the Kimura-2 model for 1000 bootstrap replications in MEGA-X with default parameters. To improve the clarity of the phylogenetic tree, FigTree v1.4.4 and Inkscape were used.

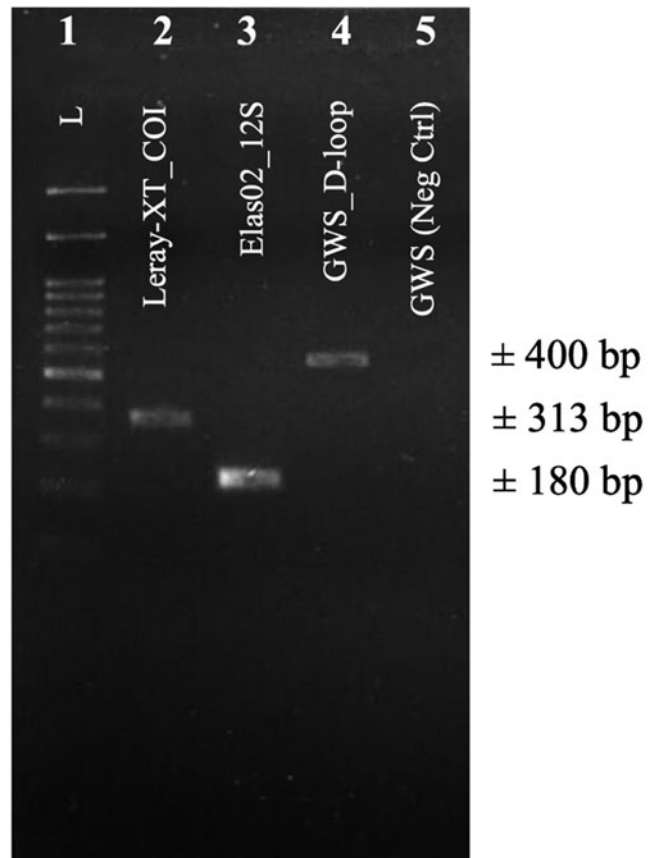


Figure 3. Gel electrophoresis image of the amplified sequence associated with the 6.0 m TL white shark (*C. carcharias*) captured in 2013 by demersal longline fishermen off of eastern Lombok, Indonesia. The 100 bp DNA Ladder by Geneaid™ was used (lane 1). Experiments were conducted using three distinct primer sets: Leray-XT (Wangensteen *et al.*, 2018), Elas02 (Taberlet *et al.*, 2012), and GWS (Pardini *et al.*, 2000). Each primer set was designed to target specific regions, namely cytochrome c oxidase I region (COI; lane 2), 12S ribosomal RNA region (12S; lane 3), and D-loop region (D-loop; lane 4), respectively. The Leray-XT and 12S primers amplified sequences were used to confirm the identification of species, whereas the GWS primer sequences were utilized for further investigation. The negative control (Borneo river shark [*G. fowlerae*]) was used to validate GWS primer (lane 5).

Results

The modified DNA extraction protocol successfully resulted in the DNA extraction from the 10-year-old upper lateral tooth. However, the DNA concentration was very low by 7.75 ng µl⁻¹. Despite the low DNA concentration, the three primer sets successfully amplified the targeted sequence. A short-targeted sequence was chosen to anticipate fragmented DNA extracted from the tooth (GenBank accession no. PP078820; Figure 3).

Sanger sequencing confirmed that the tooth was from a *C. carcharias* based on three different primers (Table 1). Moreover, the neighbour-joining tree associated with the mtDNA in the D-loop region (about 400–500 bp) revealed that the shark has a

Table 1. BLAST result using the NCBI for the 6.0 m TL male white shark (*C. carcharias*) captured in eastern Lombok, Indonesia

Number	Code	Identification source	Similarity (%)
1	GWS_01 D-Loop	<i>C. carcharias</i> (GenBank: KY067577.1)	100
2	GWS_01 Elas02	<i>C. carcharias</i> (KY067590.1)	99.54
3	GWS_01 Leray-XT	<i>C. carcharias</i> (GenBank: KY922993.1)	92.02

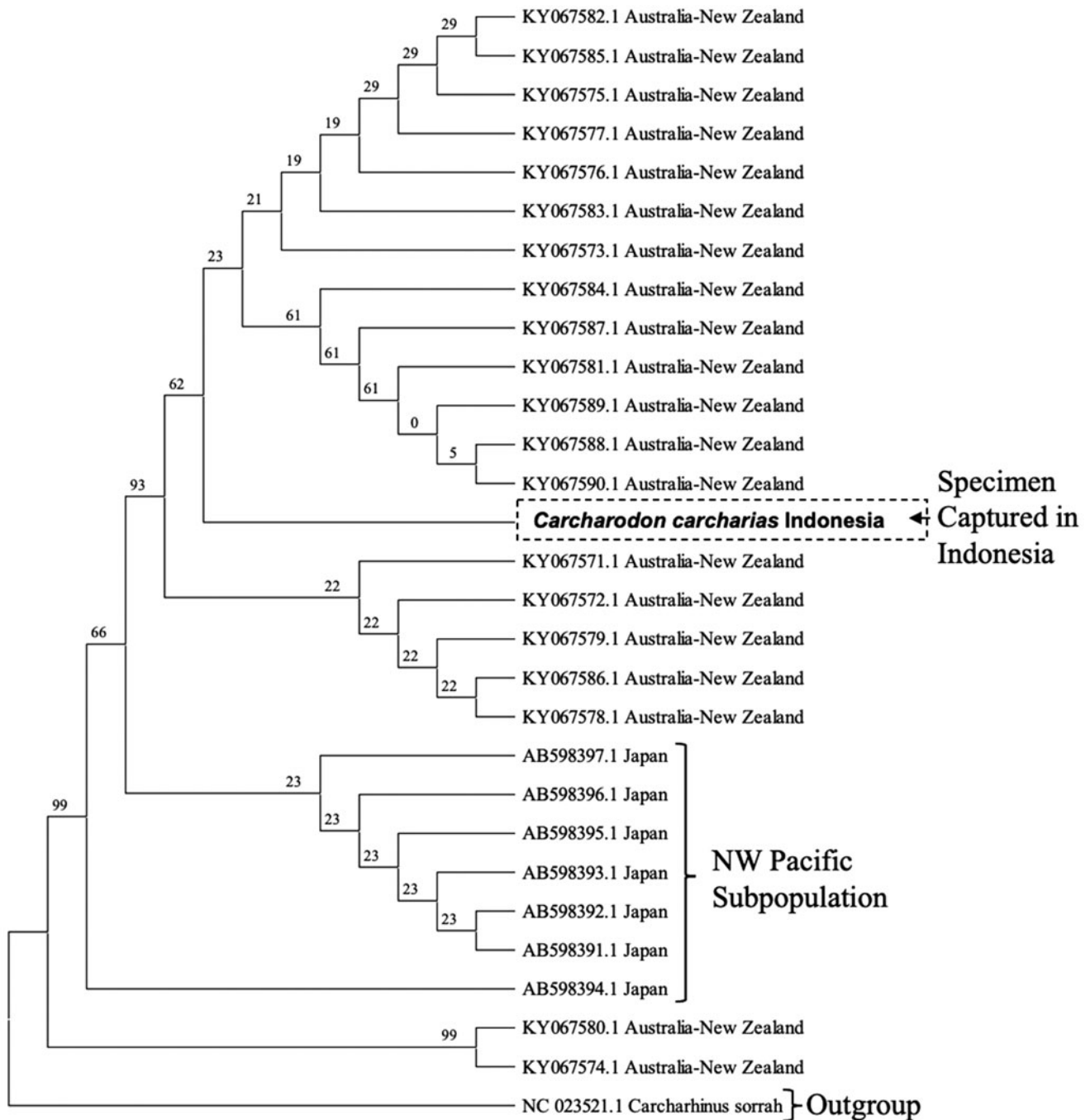


Figure 4. Genetic relationship of 29 white sharks (*C. carcharias*) from the Northwest Pacific (Japan) and Australia-New Zealand subpopulations in comparison to the Indonesian specimen using the D-loop region inferred using the neighbour-joining method with the Kimura-2 model for 1000 bootstrap replications. There was a total of 412 positions in the final dataset. Bootstrap support values are shown near internal nodes.

closer or nested clade with the Australian subpopulations rather than the Japanese subpopulation (Figure 4) with a bootstrap value at 93%. Although these results suggest the site of origin for this individual *C. carcharias* is from the Australian subpopulations, the available GenBank database does not differentiate between the two subpopulations (i.e. Southern-Western and Eastern Australian and New Zealand). Therefore, determining the specific Australian subpopulation that this *C. carcharias* was most closely associated with was not possible.

Discussion

Understanding the migratory habits of marine top predators is important as it provides critical information about stock structure

and potential threats that may negatively impact population health and abundance. Using the present mtDNA analysis of the D-loop region, this study is the first to demonstrate at least one site of origin (e.g. from Australia) for *C. carcharias* that enter Indonesian waters. While it is currently uncertain as to whether this shark came from the Southern-Western Australian (e.g. Bradford *et al.*, 2020) or Eastern Australian and New Zealand (e.g. Spaet *et al.*, 2022) *C. carcharias* subpopulation, this study provides an initial step to further understanding the true range of this highly migratory top predator. Presently the range associated with both Australian subpopulations has not been demonstrated to extend into Indonesian waters (e.g. Spaet *et al.*, 2020); however, the Eastern Australian and New Zealand subpopulation has been documented as far north as Papua New

Guinea (PNG; Spaet *et al.*, 2020). Therefore, the present study suggests a range extension for Australia-associated *C. carcharias*. Although it is likely that the documented *C. carcharias* encounters from the present study are associated with the Eastern Australian and New Zealand subpopulation due to the proximity of Indonesia to PNG, due to the lack of tangible satellite telemetry or genetic data it is uncertain which subpopulation this range extension pertains to.

Furthermore, while little is known about the migratory patterns of the Northwest Pacific *C. carcharias* stock (Christiansen *et al.*, 2014), DNA analyses suggest that this is a reproductively isolated stock (Tanaka *et al.*, 2011). More specifically, Tanaka *et al.* (2011) demonstrated through the use of mtDNA analyses that the Northwest Pacific *C. carcharias* form a monophyletic clade and exhibit unique life-history characteristics in comparison to other *C. carcharias* stocks. Therefore, although likely a rare occurrence, *C. carcharias* that utilize Indonesian waters are likely only from one or both of the Australia-associated stock (i.e. Southern-Western Australian and Eastern Australian and New Zealand) or if they are from the Northwest Pacific, they are not utilizing this region for mating purposes as this would be evidenced through previous DNA analyses (e.g. Tanaka *et al.*, 2011).

Although it is uncertain if all *C. carcharias* that utilize Indonesian waters are from the Australian subpopulations (e.g. Southern-Western Australian and Eastern Australian and New Zealand) or from the Northwest Pacific subpopulation, it is further uncertain as to why, how frequently, and for what duration they are utilizing these tropical waters. It is not uncommon for *C. carcharias* to utilize tropical waters as they have a global distribution in temperate, subtropical, and tropical seas (Bonfil *et al.*, 2005, 2010; Duffy *et al.*, 2012; Skomal *et al.*, 2017). However, research illustrates that *C. carcharias* movement patterns have been suggested to be correlated with a variety of both biotic and abiotic variables, including reproductive behaviour (e.g. mating or parturition; Domeier, 2012), water temperature (e.g. Skubel *et al.*, 2018), and prey (Nasby-Lucas *et al.*, 2009). While all three are plausible explanations for their presence within Indonesian waters, insufficient data make it difficult to make any sound conclusions.

Indonesia is considered one of the world's largest shark fin exporters in the world (Okes and Sant, 2019; FAO, 2022) with serious challenges on managing fisheries and its trade (Prasetyo *et al.*, 2021). While *C. carcharias* may not be commonly utilizing these waters, the potential anthropogenic threats are a cause for concern. Therefore, future research should aim at distinguishing what subpopulation(s) these Indonesian *C. carcharias* originated from, with a focus on satellite tagging efforts that may shed light on the potential ecological importance of Indonesia's waters to this top predator.

Acknowledgements. We acknowledge the facilities, scientific, and technical support from the Sequencing Centre, Genomic Laboratory at the National Research and Innovation Agency (BRIN).

Author contributions. C. P. O., A. P. P., M. S., and Fahmi all formulated the research question and assisted with writing the manuscript. Fahmi provided the white shark sample. C. P. O., A. P. P., and Fahmi helped design the study, whereas A. P. P. carried out the study, analysed the data, and interpreted the findings.

Financial support. This work was partially supported by O'Seas Conservation Foundation, Inc.; Discovery Channel, Inc. and Talesmith TV; and Mrs. Uli Pandjaitan.

Competing interests. None.

Data availability. The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

References

- Bonfil R, Francis MP, Duffy C, Manning MJ and O'Brien S (2010) Large-scale tropical movements and diving behavior of white sharks *Carcharodon carcharias* tagged off New Zealand. *Aquatic Biology* **8**, 115–123.
- Bonfil R, Mejer M, Scholl MC, Johnson R, O'Brien S, Oosthuizen H, Swanson S, Kotze D and Paterson M (2005) Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science (New York, N.Y.)* **310**, 100–103.
- Bradford R, Patterson TA, Rogers PJ, McAuley R, Mountford S, Huveneers C, Robbins R, Fox A and Bruce BD (2020) Evidence of diverse movement strategies and habitat use by white sharks, *Carcharodon carcharias*, off southern Australia. *Marine Biology* **167**, 1–12.
- Bruce BD (2016) *Determining the size and trend of the West Coast white shark population*. Marine Biodiversity Hub, National Environmental Science Program report. Hobart: CSIRO. <https://www.nespmarine.edu.au/document/determining-size-and-trend-west-coast-white-shark-population>
- Bruce BD, Harasti D, Lee K, Gallen C and Bradford R (2019) Broad-scale movements of juvenile white sharks *Carcharodon carcharias* in eastern Australia from acoustic and satellite telemetry. *Marine Ecology Progress Series* **619**, 1–15.
- Burkholder DA, Heithaus MR, Fourqurean JW, Wirsing A and Dill LM (2013) Patterns of top-down control in a seagrass ecosystem: could a roving apex predator induce a behaviour-mediated trophic cascade? *Journal of Animal Ecology* **82**, 1192–1202.
- Bustamante C, Vargas-Caro C and Bennett MB (2014) Not all fish are equal: functional biodiversity of cartilaginous fishes (Elasmobranchii and Holocephali) in Chile. *Journal of Fish Biology* **85**, 1617–1633.
- Chapman DD, Feldheim KA, Papastamatiou YP and Hueter RE (2015) There and back again: a review of residency and return migrations in sharks, with implications for population structure and management. *Annual Review of Marine Science* **7**, 547–570.
- Christiansen HM, Lin V, Tanaka S, Velikanov A, Mollet HF, Wintner SP, Fordham SV, Fisk AT and Hussey NE (2014) The last frontier: catch records of white sharks (*Carcharodon carcharias*) in the Northwest Pacific Ocean. *PLoS ONE* **9**, e94407.
- Cione AL and Barla MJ (2008) Causes and contrasts in current and past distribution of the white shark (Lamniformes: *Carcharodon carcharias*) off southeastern South America. *Revista del Museo Argentino de Ciencias Naturales* **10**, 175–184.
- Domeier ML (2012) A new life-history hypothesis for white sharks, *Carcharodon carcharias*, in the Northeastern Pacific. In Domeier ML (ed.), *Global Perspectives on the Biology and Life History of the White Shark*. Boca Raton, FL: CRC Press, pp. 199–224.
- Domeier ML and Nasby-Lucas N (2013) Two-year migration of adult female white sharks (*Carcharodon carcharias*) reveals widely separated nursery areas and conservation concerns. *Animal Biotelemetry* **1**, 1–9. <https://doi.org/10.1186/2050-3385-1-2>
- Duffy CAJ, Francis MP, Manning MJ and Bonfil R (2012) Regional population connectivity, oceanic habitat, and return migration revealed by satellite tagging of white sharks, *Carcharodon carcharias*, at New Zealand aggregation sites. In Domeier ML (ed.), *Global Perspectives on the Biology and Life History of the White Shark*. Boca Raton: CRC Press, pp. 301–318.
- Fahmi and Dharmadi (2014) First confirmed record of the white shark *Carcharodon carcharias* (Lamniformes: Lamnidae) from Indonesia. *Marine Biodiversity Records* **7**, e53.
- FAO (2022) Fishery and aquaculture statistics. Global capture production 1950–2020 (FishStatJ). In *FAO Fisheries and Aquaculture Division [online]*. Updated 2022. Rome, Italy: FAO UN. www.fao.org/fishery/statistics/software/fishstatj/en.
- Francis MP (1996) Observations on a pregnant white shark with a review in reproduction biology. In Klimley AP, Ainley DG (ed.), *Great White Sharks: The Biology of *Carcharodon carcharias**. San Diego, CA: Academic Press, pp. 157–172.
- Hoffmann M, Hilton-Taylor C, Angulo A, Böhm M, Brooks TM, Butchart SHM, Carpenter KE, Chanson J, Collen B, Cox NA, Darwall WRT, Dulvy NK, Harrison LR, Katariya V, Pollock CM, Quader S, Richman NI, Rodrigues ASL, Tognelli MF, Vié J-C, Aguiar JM, Allen DJ, Allen GR, Amori G, Ananjeva NB, Andreone F, Andrew P, Ortiz ALA, Baillie JEM, Baldi R, Bell BD, Biju SD, Bird JP, Black-Decima P, Blanc JJ, Bolaños F, Bolivar-G W, Burfield IJ, Burton JA, Capper DR, Castro F, Catullo G, Cavanagh RD, Channing A, Chao NL, Chenery AM, Chiozza F, Clausnitzer V, Collar NJ, Collett LC, Collette BB,

- Fernandez CFC, Craig MT, Crosby MJ, Cumberlidge N, Cuttelod A, Derocher AE, Diesmos AC, Donaldson JS, Duckworth JW, Dutton G, Dutta SK, Emslie RH, Farjon A, Fowler S, Freyhof J, Garshelis DL, Gerlach J, Gower DJ, Grant TD, Hammerson GA, Harris RB, Heaney LR, Hedges SB, Hero J-M, Hughes B, Hussain SA, Icochea M J, Inger RF, Ishii N, Iskandar DT, Jenkins RKB, Kaneko Y, Kottelat M, Kovacs KM, Kuzmin SL, La Marca E, Lamoreux JF, Lau MWN, Lavilla EO, Leus K, Lewison RL, Lichtenstein G, Livingstone SR, Lukoschek V, Mallon DP, McGowan PJK, McIvor A, Moehlman PD, Molur S, Alonso AM, Musick JA, Nowell K, Nussbaum RA, Olech W, Orlov NL, Papenfuss TJ, Parra-Olea G, Perrin WF, Polidoro BA, Pourkazemi M, Racey PA, Ragle JS, Ram M, Rathbun G, Reynolds RP, Rhodin AGJ, Richards SJ, Rodríguez LO, Ron SR, Rondinini C, Rylands AB, Sadovy de Mitcheson Y, Sanciangco JC, Sanders KL, Santos-Barrera G, Schipper J, Self-Sullivan C, Shi Y, Shoemaker A, Short FT, Sillero-Zubiri C, Silvano DL, Smith KG, Smith AT, Snoeks J, Stattersfield AJ, Symes AJ, Taber AB, Talukdar BK, Temple HJ, Timmins R, Tobias JA, Tsytsulina K, Tweddle D, Ubeda C, Valenti SV, Paul van Dijk P, Veiga LM, Veloso A, Wege DC, Wilkinson M, Williamson EA, Xie F, Young BE, Akçakaya HR, Bennun L, Blackburn TM, Boitani L, Dublin HT, da Fonseca GAB, Gascon C, Lacher TE, Mace GM, Mainka SA, McNeely JA, Mittermeier RA, Reid GM, Rodríguez JP, Rosenberg AA, Samways MJ, Smart J, Stein BA and Stuart SN (2010) The impact of conservation on the status of the world's vertebrates. *Science* **330**, 1503–1509.
- Hussey NE, MacNeil MA, Siple MC, Popp BN, Dudley SF and Fisk AT (2015) Expanded trophic complexity among large sharks. *Food Webs* **4**, 1–7.
- Huveneers C, Apps K, Becerril-García EE, Bruce B, Butcher PA, Carlisle AB, Chapple TK, Christiansen M, Cliff G, Curtis TH and Daly-Engel TS (2018) Future research directions on the “elusive” white shark. *Frontiers in Marine Science* **17**, 455.
- Kock A, O’Riain MJ, Mauff K, Mejer M, Kotze D and Griffiths C (2013) Residency, habitat use and sexual segregation of white sharks, *Carcharodon carcharias* in False Bay, South Africa. *PLoS ONE* **8**, 55048.
- Leone A, Puncher GN, Ferretti F, Sperone E, Tripepi S, Micarelli P and Tinti F (2020) Pliocene colonization of the Mediterranean by great white shark inferred from fossil records, historical jaws, phylogeographic and divergence time analyses. *Journal of Biogeography* **47**, 1119–1129.
- McAuley RB, Bruce BD, Keay IS, Mountford S, Pinnell T and Whoriskey FG (2017) Broad-scale coastal movements of white sharks off Western Australia described by passive acoustic telemetry data. *Marine and Freshwater Research* **68**, 1518–1531.
- Nasby-Lucas N, Dewar H, Lam CH, Goldman KJ and Domeier ML (2009) White shark offshore habitat: a behavioral and environmental characterization of the Eastern Pacific shared offshore foraging area. *PLoS ONE* **4**, e8163.
- Natanson LJ and Skomal GB (2015) Age and growth of the white shark, *Carcharodon carcharias*, in the Western North Atlantic Ocean. *Marine and Freshwater Research* **66**, 387–398.
- Okes N and Sant G (2019) *An Overview of Major Shark and Ray Catchers, Traders, and Species*. Cambridge, UK: TRAFFIC.
- Okonechnikov K, Golosova O, Fursov M and Team TU (2012) Unipro UGENE: a unified bioinformatics toolkit. *Bioinformatics (Oxford, England)* **28**, 1166–1167.
- Pardini AT, Jones CS, Scholl MC and Noble LR (2000) Isolation and characterization of dinucleotide microsatellite loci in the great white shark, *Carcharodon carcharias*. *Molecular Ecology* **9**, 1176–1178.
- Pérez-Jiménez JC and Mendez-Loeza I (2015) The small-scale shark fisheries in the southern Gulf of Mexico: understanding their heterogeneity to improve their management. *Fisheries Research* **172**, 96–104.
- Prasetyo AP, McDevitt AD, Murray JM, Barry J, Agung F, Muttaqin E and Mariani S (2021) Shark and ray trade in and out of Indonesia: addressing knowledge gaps on the path to sustainability. *Marine Policy* **133**, 104714.
- Prasetyo AP, Murray J, Agung F, Sales N, McDevitt A and Mariani S (2023) Shark-dust: application of high-throughput DNA sequencing of processing residues for trade monitoring of threatened sharks and rays. *Conservation Letters* **16**, e12971. <https://doi.org/10.1111/conl.12971>
- Pratt HL (1996) Reproduction in the male white shark. In Klimley AP and Ainley DG (eds), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego, CA: Academic Press, pp. 131–138.
- Rigby CL, Barreto R, Carlson J, Fernando D, Fordham S, Francis MP, Jabado RW, Liu KM, Marshall A, Pacoureaux N, Romanov E, Sherley RB and Winker H (2019) White shark (*Carcharodon carcharias*). IUCN Red List of Threatened Species.
- Shivji MS, Chapman DD, Pikitch EK and Raymond PW (2005) Genetic profiling reveals illegal international trade in fins of the great white shark, *Carcharodon carcharias*. *Conservation Genetics* **6**, 1035–1039.
- Skomal GB, Braun CD, Chisholm JH and Thorrold SR (2017) Movements of the white shark *Carcharodon carcharias* in the North Atlantic Ocean. *Marine Ecology Progress Series* **580**, 1–16.
- Skubel RA, Kirtman BP, Fallows C and Hammerschlag N (2018) Patterns of long-term climate variability and predation rates by a marine apex predator, the white shark *Carcharodon carcharias*. *Marine Ecology Progress Series* **587**, 129–139.
- Spaet JL, Butcher PA, Manica A and Lam CH (2022) Spatial dynamics and fine-scale vertical behaviour of immature eastern Australasian white sharks (*Carcharodon carcharias*). *Biology* **11**, 1689.
- Spaet JL, Patterson TA, Bradford RW and Butcher PA (2020) Spatiotemporal distribution patterns of immature Australasian white sharks (*Carcharodon carcharias*). *Scientific Reports* **10**, 10169.
- Swig B and Collier RS (2021) Novel method for the extraction of DNA from Lamniformes tooth and denticle enamel suitable for PCR. *Dental Research and Oral Health* **6**, 25–27. 2021.01.18.427093.
- Taberlet P, Coissac E, Hajibabaei M and Rieseberg LH (2012) Environmental DNA. *Molecular Ecology* **21**, 1789–1793.
- Tanaka S, Kitamura T, Mochizuki T and Kofuji K (2011) Age, growth and genetic status of the white shark (*Carcharodon carcharias*) from Kashima-nada, Japan. *Marine and Freshwater Research* **62**, 548–556.
- Tolotti MT, Filmlalter JD, Bach P, Travassos P, Seret B and Dagorn L (2015) Banning is not enough: the complexities of oceanic shark management by tuna regional fisheries management organizations. *Global Ecology and Conservation* **4**, 1–7.
- Uchida S, Toda M, Teshima K and Yano K (1996) Pregnant white sharks and full-term embryos from Japan. In Klimley AP, Ainley DG (eds), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego, CA: Academic Press, pp. 139–155.
- Wangenstein OS, Palacín C, Guardiola M and Turon X (2018) DNA metabarcoding of littoral hard-bottom communities: high diversity and database gaps revealed by two molecular markers. *PeerJ* **6**, e4705.
- Wintner SP and Cliff G (1999) Age and growth determination of the white shark, *Carcharodon carcharias*, from the east coast of South Africa. *Fisheries Bulletin* **97**, 153–169.