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Application of DNA mini-barcoding reveals illegal trade in endangered shark products in southern Africa

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In recent decades, a combination of increasing demand and economic globalisation has created a global market for elasmobranch products, especially the highly prized shark fins for Asian markets. Morphological species identification, as well as traditional cytochrome *c* oxidase subunit I (COI) barcoding of shark fins and other products, become challenging when in a processed state (such as dried or bleached shark fins). Here a mini-barcoding multiplex assay was applied to determine the species of origin in case studies from southern Africa involving confiscated shark fins in different states of processing. This highlights that the illegal shark fin trade in southern Africa to a large extent comprises threatened species. Matching of sequences of the confiscated fins against public databases revealed several threatened species, including the CITES-listed species *Carcharodon carcharias, Carcharhinus longimanus*, *Isurus oxyrinchus*, *Rhynchobatus djiddensis* and *Sphyrna lewini*. The findings highlight the need for improved trade monitoring, such as to eliminate illegal trade in shark fins, which can in part be achieved through more widespread genetic sampling of internationally traded products. However, a major limitation to DNA barcoding in general lies in the lack of curated voucher specimens available on public databases. To facilitate the application of molecular methods in a more comprehensive evaluation of elasmobranch trade regionally, a concerted effort to create reliable curated sequence data is recommended.

Keywords: *Carcharhinus*, case studies, COI gene, elasmobranchs, multiplex assay, *Rhynchobatus djiddensis*, shark fin trade, wildlife trade monitoring

Introduction

Over the past few decades there has been overexploitation of sharks on a global scale, primarily to supply international markets with products such as meat, skin, fins, cartilage, liver and teeth (Clarke et al. 2006; Lack and Sant 2009; Dulvy et al. 2014). One of the most prominent of these markets is the shark fin trade whereby the fins of sharks and shark-like rays (such as wedgefishes and guitarfishes) are used for shark fin soup. This dish is a delicacy in some Asian countries and particularly in Hong Kong, which is considered a major fin trade hub (Fields et al. 2018; Cardeñosa et al. 2020). Worldwide, the main species targeted for the shark fin industry include blue shark *Prionace glauca*, shortfin mako shark *Isurus oxyrinchus*, silky shark *Carcharhinus falciformis*, dusky shark *C. obscurus*, sandbar shark *C. plumbeus*, tiger shark *Galeocerdo cuvier*, bull shark *C. leucas*, scalloped, smooth and great hammerhead sharks *Sphyrna lewini*, *S. zygaena* and *S. mokarran*, common, bigeye and pelagic thresher sharks *Alopias vulpinus*, *A. superciliosus* and *A. pelagicus*, oceanic whitetip shark *C. longimanus*, and more recently also shark-like rays of the families Rhinidae (wedgefishes) and Rhinobatidae (guitarfishes) (Amaral et al. 2017; Fields et al. 2018). These species are targeted directly or caught as incidental bycatch (Worm et al. 2013; Oliver et al. 2015) and used to supply a market that is largely unmonitored and unregulated. Therefore, more than half of the chondrichthyans that enter the fin trade are under threat (Dulvy et al. 2014).

Sharks and other chondrichthyans are vulnerable to overexploitation owing to their *K*-selected life-history characteristics, such as slow growth, late attainment of sexual maturity, low fecundity and long gestation periods (Dulvy et al. 2014; Hutchinson et al. 2015). Consequently, there is evidence of widespread shark and ray population declines (Davidson et al. 2016), and as of 2021, at least

32% of all shark and ray species globally are listed as threatened with high, very high or extremely high extinction risk (Vulnerable, Endangered or Critically Endangered, respectively) (Dulvy et al. 2021), according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2021). Even though a recent survey showed that at least 9% of the current global catch of sharks is biologically sustainable (Simpfendorfer and Dulvy 2017), mounting evidence suggests that apex shark populations are more vulnerable to exploitation than previously thought and ongoing declines are of major concern (Roff et al. 2018; MacNeil et al. 2020). The monitoring and sustainable use of sharks is especially important as they are among the most evolutionarily distinct fish lineages and play important structural and functional roles as apex predators or mesopredators, thus helping to maintain stable and functional marine ecosystems (Stevens et al. 2000; Heithaus et al. 2012).

For many commercially important shark species, catches are unregulated and seldom recorded to species level, preventing the development of effective shark management strategies (Barker and Schluessel 2005). Further lack of species-specific data (e.g. catch rate, annual landings and bycatch/discard level) stems from misidentified species or elasmobranchs that have been discarded at sea, and because fisheries report only retained (landed) catches (Lack and Sant 2009; FAO 2014). For multi-species fisheries, species identification during port inspections is highly challenging if using traditional morphological or taxonomic tools, as carcasses are usually processed at sea, where key distinguishing morphological features such as heads and fins of specimens are often removed (Abercrombie et al. 2005; Mendonça et al. 2010; Gulak et al. 2017). Additionally, morphological features are frequently similar between species—such as for carcharhinids like the common blacktip *C. limbatus* and the Australian blacktip *C. tilstoni* (Tillett et al. 2012)—making discriminant species identification difficult. In the case of morphologically similar species, catch data are often aggregated for several species, thus making catch and landings data of low resolution (Dulvy et al. 2000; Barausse et al. 2014; Williams 2017). Consequently, aggregated data may conceal trends within individual species, with the decrease of one species being compensated for by increases in others (Dulvy et al. 2000). Additionally, data from scientific surveys may also be confounded by misidentification where species lack an unambiguous phenotype-based identification method (Marino et al. 2017).

Molecular-based methods have regularly been used over the last decade as alternatives to morphological identification (Amaral et al. 2017). These molecular techniques include DNA barcoding and sequence-based identification methods (Ward et al. 2005; Blanco et al. 2008) as well as polymerase chain reaction (PCR) multiplex methods (Farrell et al. 2009; Mendonça et al. 2010). DNA barcoding entails using universal primers targeting a short, standardised gene region (~650 bp for animal species) of the mitochondrial gene encoding cytochrome *c* oxidase subunit I (COI) (Hebert et al. 2003). Specifically, for elasmobranchs, the use of the COI gene region has proven to be successful for identifying a broad range of species (Ward et al. 2008; Bineesh et al. 2017). Importantly, this method has also been effective in revealing the mislabelling of shark products, as well as identifying threatened species in the shark fin trade and trade of other shark products (Liu et al. 2013; Moore et al. 2014; Cardeñosa et al. 2017; Steinke et al. 2017; Hobbs et al. 2019).

Shark fins in the trade can, however, be found in numerous stages of processing, some of which can reduce the efficacy of the standard COI barcoding approach. Wet fins are those that have been removed from a recently harvested shark (not dried or processed further) and still contain skin (Abercrombie et al. 2018). Most fins entering the international trade are dried but unprocessed and are rigid, still containing both skin and cartilage. Both wet and dried, unprocessed fins generally contain genomic DNA of sufficient quality that can be amplified using PCR (Abercrombie et al. 2018). However, fins can also be processed, dried and chemically treated to remove the skin, and these processed fins are typically a yellow or golden colour. Processed fins often contain degraded genomic DNA, meaning that the DNA has broken down into very small DNA fragments, often incompatible with the use of standard genetic identification techniques that require non-degraded DNA (Abercrombie et al. 2018). To overcome this problem, a DNA mini-barcode assay was developed by Cardeñosa et al. (2017), whereby shorter COI gene fragments are amplified simultaneously in a single multiplex-PCR and one to two downstream DNA sequencing reactions, to achieve the genetic identification of species when dealing with processed shark fins. This method has been successfully applied in several cases, thereby leading to successful species identification despite the shorter information content of the generated sequences (Hellberg et al. 2019; Cardeñosa et al. 2020).

In South African fisheries, the misidentification of shark species in fisheries operations is a major concern (da Silva et al. 2015). The five commercially valuable inshore species that are commonly targeted in South Africa include the common smoothhound *Mustelus mustelus*, whitespotted smoothhound *M. palumbes*, tope shark *Galeorhinus galeus*, copper shark *C. brachyurus* and dusky shark *C. obscurus* (da Silva and Bürgener 2007; da Silva et al. 2015, 2018). When shark carcasses arrive at processing facilities, the fins are removed, after which the sharks are filleted and skinned. Most of the meat of processed demersal sharks is exported to Australia, primarily for the fish and chips trade, while fins are dried and exported to Hong Kong, particularly in the case of species with more-valuable fins (da Silva and Bürgener 2007). Under the Marine Living Resources Act (MLRA, Act No. 18 of 1998: RSA 1998), shark finning (the process of removing the fins and then discarding the carcass) is prohibited in South Africa. However, fins detached from carcasses of sharks that are caught in international waters may be landed in South Africa.

In Mozambique, shark fins have been exported for at least two decades, through several companies licenced to export them (Pierce et al. 2008). However, in legal instruments introduced recently in Mozambique—such as the biodiversity law (no. 5/2017, de 11 de Maio), the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) regulation (Decreto 34/2016, de 25 de Agosto)

and the marine fishing regulations (Decreto 89/2020, de 8 de Outubro)—greater attention has been given to CITES-listed species, which has led to increased and improved inspection of products destined for export. Commonly targeted and commercially valuable species include species of the hammerhead shark genus *Sphyrna*, the carcharhinid species *C. brevipinna* (spinner shark), *C. limbatus*, *C. plumbeus*, *C. leucas* and *C. albimarginatus* (silvertip shark), and the rhinid species whitespotted wedgefish *Rhynchobatus djiddensis*. Fins are immediately removed from the sharks when they are caught, after which they are dried and exported to other southern African countries and to Asian countries (Masquine and Pires 2018).

Considering the heavy exploitation of sharks in southern Africa and that shark fins are often in various states of processing, the aim of this research was to apply a mini-barcoding multiplex assay for the first time in southern African case studies involving confiscated fins of commercially exploited elasmobranch species. More specifically, we attempted to identify the species of origin of partially to heavily processed shark fins confiscated in different locations in the region. Ultimately, this allows for the detection of potential illicit trade in threatened species and those under the regulation of international conventions (e.g. CITES), as well as contributing to the knowledge of internationally traded species.

Materials and methods

Southern African case studies involving confiscated material

Case study 1 — The first case study involved 109 pieces of shark fins confiscated by the Mozambique Customs Authority in Maputo, Mozambique, on 12 December 2018 and 11 January 2019, and believed to originate from two different locations along the Mozambican coast, hereinafter referred to as Location A and Location B. The National Institute of Fishery Research (Instituto Nacional de Investigação Pesqueira, IIP), Mozambique, requested DNA analysis of the shark fin samples to confirm species identification. These samples comprised fin pieces that were cut into irregular shapes and were of different colours and forms (Figure 1). The samples were extremely desiccated and had apparently been treated with chemicals, which were visible upon inspection. DNA was successfully extracted from a total of 89 samples for further analysis: 43 samples from Location A, and 46 samples from Location B.

Case study 2 — Approximately 25 juvenile specimens were confiscated from an illegal fishing vessel, by the former South African Department of Agriculture, Forestry and Fisheries, during port inspections at the Cape Town Harbour, South Africa. The exact capture locations of these sharks are unknown, and the samples were morphologically identified as *M. mustelus*.

Case study 3 — Shark fins were confiscated at OR Tambo International Airport (Johannesburg, South Africa), and were believed to be in transit from outside of South Africa to Hong Kong. They were declared as *P. glauca* fins but were later suspected to be grey reef shark *C. amblyrhynchos* as well as hammerhead shark species (*Sphyrna* spp.), based on morphological identification. The former South African Department of Environmental Affairs requested DNA analysis of the shark fin samples to determine the species of origin. A subset of 10 fins was analysed.

Laboratory work and species identification

All shark fins received in each case study were hydrated in a saline solution (2% NaCl), after which fin-clip samples were taken and stored in 99% ethanol. To avoid sampling from the same specimen, and where applicable, samples of different colours, forms, shapes and processing stages were selected. Otherwise, sampling was done from each individual fin. Genomic DNA was extracted from fin-clip samples stored in 99% ethanol using an adjusted cetyltrimethylammonium bromide (CTAB) DNA extraction protocol (Sambrook and Russell 2001). DNA quantity (ng μl^{-1}) and quality (absorbance ratio: 260/280 and 260/230) was determined using a NanoDrop spectrophotometer and concentrations were adjusted accordingly to 50 ng μl^{-1}.

The mini-barcoding multiplex assay of Cardeñosa et al. (2017) makes use of five primers, which include one M13 tagged universal forward COI primer (VF2_tl), two M13 tagged universal reverse COI primers (FishR1_tl and FishR2_tl) and two internal mini-barcode primers (Shark150R and Shark474F) (Table 1). This multiplex PCR leads to the amplification of three mitochondrial COI gene fragments, with expected gene fragment sizes of ~150 bp (referred to as the Shark150 amplicon), ~200 bp (referred to as the Shark474 amplicon) and in some instances ~650 bp (referred to as the Full COI amplicon). PCR was carried out in a SimpliAmp™ Thermal Cycler in a 15-µl reaction volume that included 50 ng of template DNA, 1 x PCR buffer, 200 µM of each dNTP, varying concentrations of each primer (Table 1), 2 mM of $MgCl_2$ and 0.625 U of GoTaq® DNA polymerase (Promega). The multiplex PCR was amplified using the following cycling conditions: (i) one

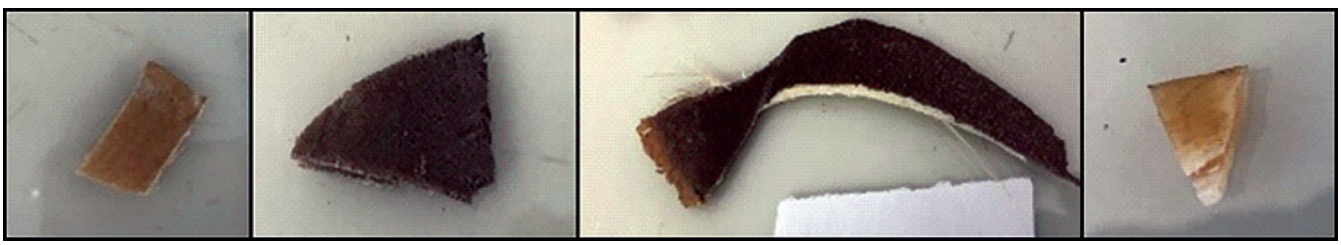

Figure 1: Shark fin samples of different shapes, sizes and forms confiscated in Maputo, Mozambique, and thought to originate from two separate locations (Locations A and B) on the Mozambique coast

Table 1: Five mitochondrial COI primer names, sequences and volumes (initial concentration = 10 µM) used in the mini-barcoding multiplex PCR of 15 µl (adapted from Cardeñosa et al. [2017]), amplifying three COI gene regions (150 bp, 200 bp, and 650 bp)

Primer name	Primer sequence (5´–3´)	Reference	Volume (µl)
VF2_tl	TGTAAAACGACGGCCAGTCAACCAACCACAAAGACATTGGCAC	Ward et al. (2005)	0.9000 [0.6 µM]
FishR1_tl	CAGGAAACAGCTATGACACTTCAGGGTGACCGAAGAATCAGAA	Ward et al. (2005)	0.4500 [0.3 µM]
FishR2_tl	CAGGAAACAGCTATGACACCTCAGGGTGTCCGAARAAYCARAA	Ward et al. (2005)	0.4500 [0.3 µM]
Shark150R	AAGATTACAAAAGCGTGGGC	Fields et al. (2015)	0.2250 [0.15 µM]
Shark474F	CHATTTCCCAATATCAAACACC	Cardeñosa et al. (2017)	0.1125 [0.075 µM]

cycle of initial denaturation at 95 °C for 2 min; (ii) 35 cycles of denaturation at 94 °C for 1 min, annealing at 54 °C for 1 min, elongation at 72 °C for 1 min; and (iii) a final elongation of one cycle at 72 °C for 10 min.

The PCR amplicons were visualised on a 3% (w/v) agarose electrophoresis gel for confirmation of successful amplification of the three amplicons (Shark150, Shark474, and Full COI). For standard Sanger sequencing chemistry (BigDye® Terminator 3.1 Cycle Sequencing Kit, Life Technologies, South Africa), the M13F primer (5'-TGTAAAACGACGGCCAGT-3') was used when the Shark150 amplicon was present, the M13R primer (5'-CAGGAAACAGCTATGAC-3') for the Shark474 amplicon, and both the M13F and M13R primers were used when the full COI amplicon was present. Capillary electrophoresis was performed at the DNA sequencing unit of Stellenbosch University, the Central Analytical Facility. Sequences were manually checked, edited, and trimmed in MEGA7 (Kumar et al. 2016). Species identification was determined by comparing sequences to the National Center for Biotechnology Information (NCBI) GenBank database using the basic local alignment search tool (BLAST), and using the Megablast algorithm for highly similar sequences (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Additionally, sequences were matched against species-level barcode records deposited in the Barcode of Life Data System (BOLD, https://www.boldsystems.org/index.php). A minimum 98% match is considered as reliable species-level identification (Barbuto et al. 2010); therefore, accurate species identification was based on 98–100% sequence similarity.

Finally, the success of the mini-barcoding approach was compared with the standard DNA barcoding method through testing nine samples randomly selected from the case studies. These samples were additionally amplified for the full standard COI barcoding gene region (655 bp) using universal primers FishF1 (5'TCAACCAACCACAAA GACATTGGCAC3') and FishR1 (5'TAGACTTCTGGGTG GCCAAAGAATCA3') and the recommended PCR protocol outlined in Ward et al. (2005). Amplification success was then compared through agarose gel electrophoresis.

Results

In the first case study of shark fins confiscated by the Mozambique Customs Authority in Maputo, Mozambique, all 89 samples tested amplified for either the 150-bp or the 200-bp COI gene region (the majority for the 150-bp region). The fact that the 655-bp fragment was not amplified could imply that all the genomic DNA obtained from these processed fins was degraded. Based on sequences from the 150-bp and 200-bp COI gene regions, 65 samples were unambiguously identified to species level and consisted of 13 different elasmobranch species (Figure 2), with all these samples showing a species match of >98%. The remaining 24 samples could not be identified to species level; however, the genus *Carcharhinus* was confirmed for all 24 samples. The IUCN Red List status of the identified species include the following categories: Critically Endangered (*R. djiddensis*, *Carcharhinus longimanus* and *S. lewini*), Endangered (*C. amblyrhynchos* and *I. oxyrinchus*), Vulnerable (*Hemipristis elongata*, *Carcharodon carcharias*, *Carcharhinus albimarginatus*, *C. amboinensis*, *C. leucas* and *C. brachyurus*) and Near Threatened (*P. glauca* and *G. cuvier*) (IUCN 2021). Five species were identified in multiple samples, namely *S. lewini*, *I. oxyrinchus*, *C. longimanus*, *G. cuvier* and *R. djiddensis*, which could be an indication for the targeting of species containing fins with a higher market value.

Application of the mini-barcoding assay to the second case study demonstrated that all samples amplified for the 150-bp and the 200-bp fragment, and one sample for the 650-bp fragment. After comparing specimen sequences to reference sequences on the BOLD and NCBI GenBank databases, it was concluded that, for the 200-bp sequences, species-level identification could not be made but confirmed them to be from the genus *Mustelus*. Top hits consisted of *M. manazo*, *M. asterias* and *M. palumbes*; however, *M. manazo* and *M. asterias* do not occur in South African waters so it is more likely that the specimens are whitespotted smoothhound *M. palumbes*. This indicates that the 200-bp COI fragment alone is not sufficient to identify *Mustelus* species to species level. Therefore, in cases involving closely related species such as within the genus *Mustelus*, sequence data from both the 150-bp fragment and the 200-bp fragment should be generated to potentially provide species-level identification.

In the third case study, which involved confiscated shark fins at OR Tambo International Airport, all samples amplified successfully for the 150-bp gene fragment, eight samples for the 200-bp, and two also for the 650-bp fragment. A total of six shark species were identified from the 10 fins sampled: *C. plumbeus*, *C. leucas*, graceful shark *C. amblyrhynchoides*, *C. limbatus*, *C. brevipinna* and pigeye shark *C. amboinensis* (Table 2). All samples showed >98% similarity to the respective reference sequences and were therefore considered reliable for species identification (Barbuto et al. 2010). The six species identified are all relatively large pelagic shark species, all belonging to the genus *Carcharhinus*. Based on the IUCN Red List, these species represent Endangered and Vulnerable categories (IUCN 2021). Three of these shark species, namely

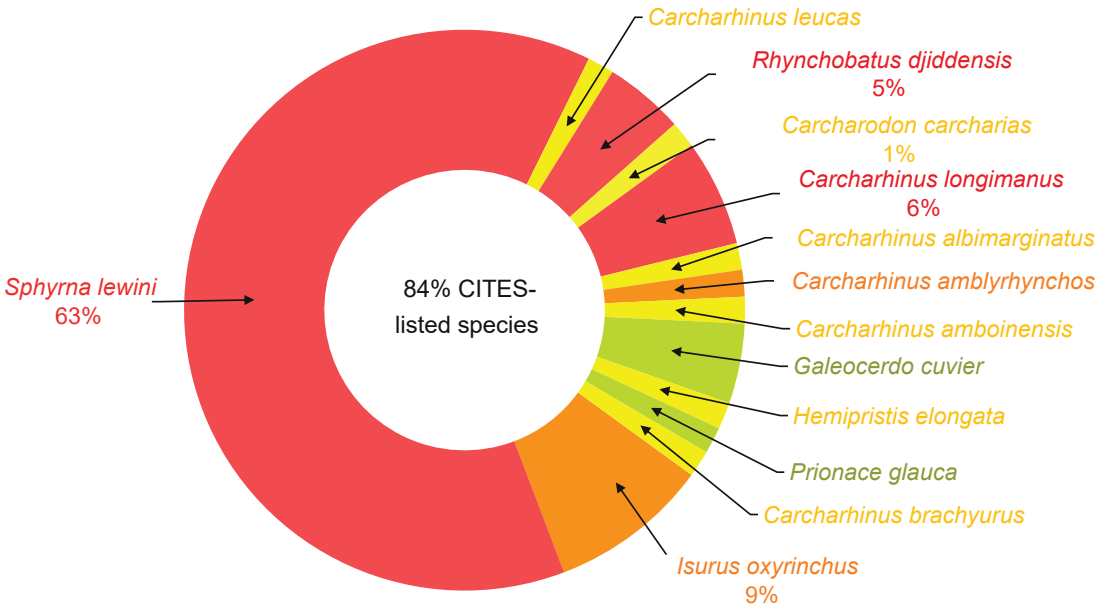

Figure 2: The 13 elasmobranch species identified from the shark fin samples confiscated in the Mozambique case study. Percentages of the five CITES-listed species are indicated, totalling 84% of the illegal catch. green = Near Threatened; yellow = Vulnerable; orange = Endangered; red = Critically Endangered

Table 2: Shark fin samples confiscated at OR Tambo International Airport, South Africa; species-level identification was performed using the mini-barcoding multiplex assay. The Barcode of Life Data System (BOLD) identification number and match percentage identity (%), and the IUCN Red List status are indicated (Endangered – very high risk of extinction in the wild; Vulnerable – high risk of extinction in the wild)

No. of samples	Most similar species	BOLD ID no. (%)	IUCN Red List status
1	*Carcharhinus plumbeus* (sandbar shark)	BOLD:AAA4896 (100)	Endangered
1	*Carcharhinus brevipinna* (spinner shark)	BOLD:AAA3388 (99.26)	Vulnerable
3	*Carcharhinus leucas* (bull shark)	BOLD:AAA6060 (100)	Vulnerable
2	*Carcharhinus amblyrhynchoides* (graceful shark)	BOLD:AAA5251 (100)	Vulnerable
2	*Carcharhinus limbatus* (blacktip shark)	BOLD:AAA5251 (100)	Vulnerable
1	*Carcharhinus amboinensis* (pigeye/Java shark)	BOLD:ACF2385 (100)	Vulnerable

C. leucas, *C. limbatus* and *C. amblyrhynchoides*, were represented more than once.

Of the nine fin-clip samples from the case studies that were tested using traditional COI barcoding amplification (FishF1 and FishR1 primers), only two amplified successfully for the full 655-bp region. However, using the multiplex assay, all nine samples amplified successfully for both the 150-bp and the 200-bp fragment, as well as two samples for the 650-bp fragment. These results confirm the limitations of using only the traditional COI barcoding primers when samples are processed, as was the case in the current study.

Discussion

Overall, the application of the mini-barcoding assay in case studies involving confiscated shark fin samples demonstrates that several CITES-listed and threatened elasmobranch species are traded through southern Africa. The multiplex assay was characterised by a high identification success rate compared with the traditional COI barcoding method for the processed (dried or chemically treated) samples tested here. Although there were some difficulties with species-level identification, this was not totally unexpected as the mini-barcoding assay was specifically designed for CITES-listed species and was previously found not to be successful for all *Carcharhinus* species (Cardeñosa et al. 2017).

Case study 1

At the time of the confiscations in Mozambique (Locations A and B), approximately 40% of the samples tested were from CITES-listed species; however, based on updated and current (2021) CITES listings, over 80% of the samples tested represent species listed on CITES Appendix II, which are thereby subject to trade regulation, including

Carcharodon carcharias, *Carcharhinus longimanus*, *I. oxyrinchus*, *R. djiddensis* and *S. lewini* (CITES 2021). Hammerhead sharks (*Sphyrna* spp.) are among the top sources of shark fins as they have the finest quality fin needles (ceratotrichia) for consumption and have a high commercial value in the Asian shark fin trade (Abercrombie et al. 2005). *Sphyrna lewini* is experiencing severe population declines throughout its distribution (Ferretti et al. 2008; Gallagher et al. 2014). In South Africa, a decline of 64% was observed for *S. lewini* populations over a 25-year period (1978–2003), with estimates based on catches in the bather protection nets along the coastline of KwaZulu-Natal Province (Dudley and Simpfendorfer 2006). The species was recently re-assessed as Critically Endangered (Rigby et al. 2019) on the IUCN Red List. Of greatest concern for *S. lewini*, in the context of this study, is its considerable contribution (46%) to the 89 sequenced fins that were confiscated in case study 1, indicative of the intense fishing pressure on this species.

In addition to its CITES listing that requires strict trade control, *C. longimanus* is required to be prohibited from capture in all fisheries within party states by virtue of its listing on Appendix I of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) (CMS 2020) and also is prohibited from capture in tuna and tuna-like fisheries in the Indian Ocean, through a retention ban defined under Resolution 13/06 of the Indian Ocean Tuna Commission (IOTC 2013). Mozambique is a party state with respect to both the CMS and IOTC and therefore the commercial exploitation and trade of this species in Mozambican waters contravenes the regulations of numerous multilateral environmental agreements.

Isurus oxyrinchus was identified as constituting the second-largest portion of the samples in case study 1. This is concerning for an Endangered species, as a recent study showed fishing mortality rates were well above those previously reported for the species in the western North Atlantic Ocean (Byrne et al. 2017). According to Fields et al. (2018), 2.77% of samples from the main fin markets in Hong Kong (i.e. Sheung Wan and Sai Ying Pun) consisted of *I. oxyrinchus*. This species was recently listed in CITES Appendix II (CITES 2019).

Also noteworthy is that three of the samples confiscated in Mozambique were identified as *R. djiddensis*. This species belongs to the batoid family Rhinidae (wedgefishes), which are large benthopelagic shark-like rays (Giles et al. 2016). *Rhynchobatus djiddensis* is exploited by fisheries that are driven by the high value of their fins in international trade, and declines have been noted throughout their range (Moore 2017; Jabado 2018). A recent trend shows that the fins of wedgefishes are becoming more common in the shark fin trade (Fields et al. 2018). Declines of *R. djiddensis* have been observed in South Africa (Daly et al. 2021) and in Mozambique, where this species was previously reported to be abundant (Pierce et al. 2008; Hopkins 2011). In South Africa, *R. djiddensis* was caught as bycatch by demersal prawn trawlers operating on the Thukela Bank (located off central KwaZulu-Natal), until the fishery closed in 2002 (Jordaan et al. 2021). Most specimens caught were alive and were released, although subsequent survival is not known (Fennessy 1994). In Mozambique, *R. djiddensis* is caught as a target and bycatch species in the artisanal and small-scale commercial fisheries operating in Inhambane and Sofala provinces (Pierce et al. 2008) and has become one of the most-exported species according to fin inspection reports from the fishery sector (INIP 2020). Heavy exploitation of wedgefishes also used to occur in Tanzania by means of bottom-set gillnets, prawn trawlers and possibly also spearfishing (Barnett 1997); however, their numbers are declining and it is now considered by some to be rare (Schaeffer 2004). Additionally, wedgefishes are targeted by foreign vessels off eastern Africa (offshore of Mozambique, Tanzania and Madagascar) (Kyne et al. 2020). Thus, for *R. djiddensis* the threat to the population seems not to be within South Africa, where this species is protected, but rather in neighbouring countries where the species is under severe threat of exploitation (Kyne et al. 2020; Daly et al. 2021). Recently, species in the family Rhinidae have shown severe population declines globally, resulting in 9 of the 10 species (90%) being assessed as Critically Endangered on the IUCN Red List (Kyne et al. 2020), including *R. djiddensis* (Kyne et al. 2019). All 10 rhinid species were also recently included in CITES Appendix II (CITES 2019).

The remaining 24 samples from case study 1 that could not be identified to species level were all identified to genus level (*Carcharhinus* spp.). The genomic DNA obtained from these samples was degraded because the samples were dried and apparently treated with chemicals.

In terms of the different locations, for Location A there was a greater diversity of species, with 10 different elasmobranch species identified. Three of these were represented more than once, namely *S. lewini*, *R. djiddensis* (both Critically Endangered) and *G. cuvier* (Near Threatened), while 23 samples were identified as belonging to the genus *Carcharhinus*. While incidental bycatch cannot be excluded, the findings are more likely due to the targeting of larger shark species and particularly those known to have higher-value fins. For Location B, four species were identified, *S. lewini*, *C. longimanus* (Critically Endangered), *I. oxyrinchus* (Endangered) and *P. glauca* (Near Threatened), the first three of which are CITES-listed. Both *S. lewini* and *I. oxyrinchus* are common in trade because of their high fin value (Abercrombie et al. 2005; Fields et al. 2018). Overall, the findings of this case study indicate the continuous exploitation of elasmobranch species listed by CITES or regarded as threatened by the IUCN (i.e. Critically Endangered, Endangered and Vulnerable), as well as (and possibly specifically for) the trade in their fins. Additionally, the fact that most of these fin samples were disguised into smaller pieces suggests that deliberate attempts were made to prevent identification of the species, highlighting the importance of molecular species identification—in addition to visual identification—for improved law enforcement with regard to the illicit shark fin trade.

Case study 2

Shark fins confiscated from Cape Town Harbour were morphologically identified as *M. mustelus*; however, based on COI sequencing (200-bp fragment), they were most

likely *M. palumbes*. This conclusion was drawn since the other *Mustelus* species with high sequence similarity do not occur in South Africa. For future case studies involving closely related species such as *Mustelus* spp., additional COI or other gene-region sequences should therefore be included if possible. The results highlight the problem of morphological misidentification, which in this case could be attributed to the fact that the samples were from juvenile specimens. Some identification features are not yet developed or visible in juveniles, making morphological identification more difficult and less accurate. For instance, spot patterns in *M. mustelus* can range from the absence of markings to the presence of large black spots, with the spots increasing in number with age (da Silva et al. 2018). *Mustelus palumbes*, by contrast, is covered with numerous small white spots (Compagno 1984; Farrell et al. 2009; da Silva et al. 2018). *Mustelus palumbes* is currently classified as Least Concern on the IUCN Red List and is endemic to southern Africa (Namibia, South Africa and Mozambique: Pollom et al. 2020). *Mustelus mustelus* and *M. palumbes* are both common species caught in the suite of commercial fisheries targeting inshore species in South African waters, including the demersal shark longline fishery, the commercial linefishery and the inshore trawl fishery (DAFF 2012). However, since the two species occur at different depths, the overall majority of aggregated *Mustelus* reported in the inshore trawl fishery is likely to be *M. mustelus.* In addition, a recent stock assessment for *M. mustelus* showed that they were not currently overexploited but that the stock is fished at unsustainable levels (da Silva et al. 2019).

Case study 3

Shark fins confiscated from OR Tambo International Airport were all identified to species level using the mini-barcoding approach (Table 2). Samples were assigned to six species in the genus *Carcharhinus* but none of them matched the original morphological identification of either *C. amblyrhynchos* or *Sphyrna* spp. In a recent study conducted in 2014–2015, *C. leucas*, *C. limbatus* and *C. brevipinna* were three of eight species that each comprised more than 1% of the fin trimmings from an assessment of a retail market (Sheung Wan and Sai Ying Pun fin market) in Hong Kong (Fields et al. 2018). In the same study, *C. amblyrhynchoides*, *C. amboinensis* and *C. plumbeus* are also mentioned as being sought after, specifically for the shark fin trade. A few *C. amblyrhynchoides* samples (0.13%) were identified from the 2014–2015 trimmings, while 54 samples of *C. amboinensis* (1.13%) were identified (Fields et al. 2018). This is concerning as *C. amboinensis* seems to be highly structured genetically, making coastal populations even more vulnerable to localised overexploitation (Chapman et al. 2015). Previously, *C. plumbeus* was commonly found in the Hong Kong shark fin auction trade, making up 2–3% of the fins auctioned (Clarke et al. 2006). However, in the recent study by Fields et al. (2018), *C. plumbeus* was rarely encountered, with only 11 samples (0.23%) identified from the trimmings collected during 2014–2015. Fisheries located on the coast of Western Australia and on the Atlantic coast of the United States were supplying large amounts of *C. plumbeus* from 1999–2001 (McAuley and Rowland 2012). Subsequently, significant population declines of this species led to large reductions in catch limits (McAuley and Rowland 2012). Thus, the current study further confirms that the above-mentioned species are of some importance for the shark fin trade and market in Hong Kong. These results also highlight that those policies aimed at mitigating the vulnerability to extinction of certain shark species need to be comprehensive and coordinated at the global level.

Conclusions

The above case studies involving confiscated shark fins demonstrate that the mini-barcoding multiplex assay can elucidate species-level identification for many threatened southern African shark and ray species, although for closely related species (such as *Mustelus* spp. and some *Carcharhinus* spp.) it is not always successful in identification to species level, and hence alternate COI or other gene fragments should also be analysed.

One important limitation is the lack of voucher information for many species, not just for the study region, but also globally. Studies have previously reported on the prevalence of misidentifications in databases such as NCBI and BOLD, which severely hampers accurate species identification in different taxa (Meiklejohn et al. 2019; Wannell et al. 2020). In elasmobranchs, levels of species misidentification based on morphology are high owing to the occurrence of cryptic species and the overlap of morphological traits between species. Additionally, taxonomic revisions commonly render sequence database depositions outdated and therefore require ongoing curation (Wannell et al. 2020). Complete curated data sources are undoubtedly the most important aspect for correct species identification of confiscated material, irrespective of the barcoding methodology used and state of processing (Fernandes et al. 2020). To facilitate the use of this barcoding assay in support of law enforcement, greater effort should be directed to the collection and curation of voucher DNA barcode sequences.

Although this study may not be representative of all elasmobranch species being traded through southern Africa, it confirms that several threatened species are targeted and exploited. Of great concern is the large percentage of confiscated shark fins from CITES-listed and threatened species (*S. lewini*, *I. oxyrinchus*, *C. longimanus* and *R. djiddensis*), including for illicit trade. Based on one of the case studies, South Africa possibly acts as an intermediate transportation zone (for example, between other western Indian Ocean countries and Hong Kong, in this case) for the export of shark fins. This highlights the importance of monitoring and enforcement of existing regulations and coordination among countries, which could to a certain extent be achieved through improved implementation and stricter enforcement of CITES trade controls.

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