COI-Barcoding evidences mislabelling and the use of endangered species in German shark products

Kilian Niedermeier, Matthias Affenzeller, Andreas Tribsch

Recent estimations categorize about 37 % of all cartilaginous fish species (sharks, rays and chimaeras) as endangered. Especially sharks show severe population declines and many species are protected by CITES and other international conventions. Shark meat and other body parts are sold as various products internationally, often via complex trade routes. As most shark products (like cartilage pills, liver oil or smoked meat) are heavily processed, correct species identification can only be achieved via DNA based methods. It has been shown that a large proportion of shark products ends up mislabelled at the consumer in Europe. Moreover, fraudulent and economically motivated substitution with cheaper meat is a strong driver for illegal and non-transparent shark trade. Interestingly, the German market is one of the most significant key drivers of the legal trade with Squalus acanthias, the spiny dogfish, which is appreciated in gastronomy as 'Schillerlocken' although the species is listed as vulnerable by the IUCN. Additionally, cartilage pills are a popular 'health' product in 'alternative medicine'. We wanted to find out whether mislabelled and substituted shark products exist in the German market. Hence seven 'Schillerlocken' and 17 products of 'shark cartilage pills' were analyzed by DNA-Barcoding. We used various primer cocktails to amplify and sequence between 127 bp ('minibarcodes') and 650 bp of the mitochondrial Cytochrome C Oxidase subunit I. We identified 45.8 % Squalus acanthias (including all 'Schillerlocken') and 8.3% critically endangered shark species (Galeorhinus galeus), as well as 4.2 % Prionace glauca. In addition, we report 70.6 % of the cartilage pills as mislabelled or substituted. The analysis revealed the use of an undeclared teleost species (Merluccius merluccius, European hake), as well as Gallus gallus (chicken) and Solanum sp. (potato). Our results support earlier demands for better transparency and stronger regulation of the shark product market and hold implications for conservation as well as for consumer's health.

Niedermeier K, Affenzeller M, Tribsch A (2023) COI-Barcoding belegt Fehlkennzeichnung und Verarbeitung gefährdeter Arten in deutschen Haiprodukten. Jüngsten Schätzungen zufolge gelten etwa 37 % aller Knorpelfische als gefährdet. Besonders Haie weisen starke Populationsabfälle auf und einige Arten werden bereits von CITES oder anderen internationalen Konventionen geschützt. Haifleisch und andere Körperteile werden global als unterschiedliche Produkte gehandelt, oftmals über komplexe Handelsnetze. Da ein Großteil aller Haiprodukte (wie Knorpelpillen, Leberöl oder Räucherfisch) stark verarbeitet ist, kann eine korrekte Artbestimmung meist nur mittels DNA basierten Methoden erzielt werden. Nachweislich landet ein großer Anteil von Haiprodukten fehlgekennzeichnet beim Konsumenten in Europa. Zusätzlich ist die betrügerisch und ökonomisch motivierte Substitution mit billigerem Fleisch ein starker Treiber für den illegalen und intransparenten Haihandel. Interessanterweise stellt der deutsche Markt einen der stärksten Treiber des Handels mit Squalus acanthias, dem Gemeinen Dornhai, dar, weil dieser in der Gastronomie als "Schillerlocken" wertgeschätzt wird, obwohl die Art von der IUCN als gefährdet gelistet wird. Außerdem sind Haiknorpelpillen ein beliebtes Gesundheitsprodukt und Nahrungsergänzungsmittel in der "alternativen Medizin". Wir wollten herausfinden, ob fehlgekennzeichnete und substituierte Haiprodukte im deutschen Markt existieren. Daher wurden 7 "Schillerlocken" und 17 "Ĥaiknorpelpillen" mittels DNA-Barcoding untersucht. Wir verwendeten verschiedene Primer-Cocktails, um 127 bp ("Mini-Barcodes") und 650 bp der mitochondrialen Cytochrom C Oxidase Untereinheit I zu amplifizieren und zu sequenzieren. Aus der Stichprobe konnten 45,8 % Squalus acanthias (einschließlich aller "Schillerlocken") und 8,3 % einer vom Aussterben bedrohten Haiart (Galeorhinus $\it galeus)$ sowie 4,2 % $\it Prionace$ $\it glauca$ identifiziert werden. Außerdem melden wir 70,6 % der Knorpelprodukte als fehlgekennzeichnet oder substituiert, da in der Analyse Treffer mit einem undeklarierten Teleosten (Merluccius merluccius, dem Europäischen Seehecht), wie auch mit *Gallus gallus* (Huhn) und *Solanum* sp. (Kartoffel) erzielt wurden. Unsere Ergebnisse unterstützen frühere Forderungen nach besserer Transparenz und stärkerer Regulierung im Handel mit Haiprodukten und könnten Auswirkungen auf Naturschutz und Verbrauchergesundheit beinhalten.

Keywords: species identification, seafood mislabelling, shark trade, DNA-barcoding, food fraud.

Introduction

While sharks have already been a culinary part of various cultures for hundreds if not thousands of years (Charpentier et al. 2020), mass trade of shark products only started in the previous century. Though the shark trade is only a minor business in the global seafood industry, landings as well as demand increased exponentially. Since many shark species show a generally high sensitivity to overfishing and exploitation given their low fecundity, slow generation rates and late maturation, all over the world populations have started declining (Barker & Schluessel 2005). Official catch statistics combined with estimations of unreported fisheries reckon that annually between 63 and 273 million sharks are being harvested (Worm et al. 2013). Assuming that data-deficient species are endangered in an equal proportion as assessed species, about 37 % of Chondrichthyes (sharks, rays and chimaeras) could be threatened with extinction by now (Dulvy et al. 2021).

Western societies mostly blame Asian markets for the exploitation of sharks. Yet, the trade with shark derived products is a global network consisting of complex phases of processing, importing and re-exporting, which often makes their routes hard to track (Dent & Clarke 2015). An additional factor, which complicates the tracing of catch rates and trade routes and therefore conservation and monitoring efforts, is the mislabelling and substitution of products with other, visually indistinguishable species. Reasons for this type of fraud in the seafood industry are mostly suggested as either economically motivated or to circumvent consumers apprehensions to buy threatened species. Previous studies have identified the practice of mislabelling in most big shark trading hubs and in application for a variety of different products (Bornatowski et al. 2013).

Within Europe shark-mislabelling largely appears in coastal states like e.g. Spain, Italy, Greece or the UK (Pardo & Jiménez 2020; Barbuto et al. 2010; Pazartzi et al. 2019; Hobbs et al. 2019). Even though mislabelling has been confirmed in the German seafood industry, as well as inadequate enforcement of CITES regulations in traded shark fins, the German market still lacks studies concerning themselves with mislabelling of shark products in particular (Pardo et al. 2018, Villate-Moreno et al. 2021). Furthermore, German consumers' demand has been reported to be one of the most significant drivers for the fisheries of the Spiny dogfish, *Squalus acanthias*, which is a vulnerable shark species. Its smoked belly flaps are mostly sold under the misleading umbrella term 'Schillerlocken' (Fordham 2006).

It can be hypothesized that mislabelling and substitution also exist in the German shark market. Using DNA-Barcoding, we analyzed the two most accessible shark products available: 1) the so-called 'Schillerlocken' as well as 2) 'Shark cartilage pills', which are used as food supplement or health product. Moreover, to obtain a clearer picture of the markets species composition we wanted to find out whether threatened shark species are available.

Materials and Methods

Sample collection

Samples were bought either from German or Austrian Fish Vendors and Pharmacies or ordered online from inside Germany or Austria. A total of 24 samples was collected, of which seven were 'Schillerlocken', 13 shark cartilage pills, one shark cartilage tablets, one shark cartilage globules and two were only labelled as 'cartilage pills'. All samples are listed in Table 1. While all cartilage products were stored at room temperature, meat was stored in a freezer at -20° C. Samples (gelatine capsules and frozen meat) were only opened for extraction. The meat was sampled from the 'Schillerlocken' using a scalpel, anatomical scissors and dissection needles. To maximize DNA yield as many different layers as possible were dissected out of the smoked meat filling the tip of a 1.5 mL Eppendorf' tube. Cartilage powder was retrieved by screwing open the respective gelatine capsules and again filling the tip of a 1.5 mL Eppendorf' tube with a spatula. Globules and tablets were inserted into 1.5 mL Eppendorf' tubes and ground up using a spatula.

DNA extraction

DNA extractions were executed for all sampled product categories by following the manufacturers' instructions of the QIAGEN DNeasy' Blood & Tissue Kit. Concentrations of the respective extracts were then measured with a NanoDrop' 2000c spectrophotometer and noted in [ng/ μ L], followed by a check of DNA quality and degradation with gel electrophoresis on 1% agarose gel (See Table 1). All gels were cast in 1% TAE and 3 or 5 μ L Midori Green stain. Gel electrophoresis ran in a PowerPacTM Basic Power Supply by BIO-RAD Laboratories at 100 V for 15 minutes and results were visualized with a BIO-RAD Laboratories Universal Hood II UV-Transilluminator and the analysis software Quantity One. To eliminate contamination as much as possible negative controls were included in every performed step and each sample was individually extracted, amplified and sequenced at least twice. Pipette tips were purchased from LabConsulting (Vienne, Austria) or VWR (Vienna, Austria).

Polymerase chain reactions (PCRs)

Every PCR was conducted with undiluted DNA extract, since in a test run no difference between diluted and undiluted extracts was observed. Primers were obtained from Eurofins Genomics Europe Shared Services GmbH and diluted to $10 \, \mu M$.

Polymerase chain reactions (PCRs) were carried out in 30 μ l containing 100-1000 ng of genomic DNA, 0.2 mM of each dNTP (Promega, Germany), 10 pmol of each primer, 1x Green GoTaqTM Reaction Buffer (Promega, Germany), and 1.5 units of GoTaqTM (Promega, Germany) DNA polymerases. All steps were executed on ice. PCRs were conducted in a GeneAmp' PCR-System 9700 Thermocycler.

Conditions for samples amplified using the primers 'FishF2' and 'FishR2' started with a denaturation at 95°C for 2 minutes, followed by 35 cycles of denaturation at 94°C for 30 seconds, annealing at 53°C for 30 seconds and elongation at 72°C for 1 minute, with an extension of 10 minutes at 72°C (Pazartzi et al. 2019).

For samples amplified with shark mini-barcodes 3 different protocols were used. The primer mix using 'VF2_t1 + FishF2_t1' and 'Shark COI-MINIR' initiated with 15 minutes at

Tab. 1: List of all samples analyzed in this study (N=24). The origin column indicates the locations of purchase with product types in brackets, as well as nations and results are included. – Tab. 1: Liste aller in dieser Studie analysierten Proben (N=24). In der Herkunftsspalte sind die Einkaufsorte mit den Produkttypen in Klammern angegeben. Ein Sternchen weist auf starke DNA-Degradation des Produkts nach der Extraktion hin. Außerdem sind die strong DNA degradation of the product after extraction if marked with an asterisk. Additionally, fishing zones, declared content, utilized primer combi-Fanggebiete, der ausgewiesene Inhalt, die verwendeten Primerkombinationen und die Ergebnisse angegeben.

Origin (Product type)	Fishing zone	Declared content	Primer combination	BLAST Result	Red list status	Mislabeled
Freilassing, D (Schillerlocken)	FAO 20 North- West Atlantic	Squalus acanthias	Α	S. acanthias (99.41 %)	VU	u
Ostfriesland, D (Schillerlocken)	FAO 27 North-East Atlantic	S. acanthias	Α	S. acanthias (99.56 %)	VU	u
Hamburg, D (Schillerlocken)	FAO 20 North- West Atlantic	S. acanthias	Α	S. acanthias (99.41 %)	VU	n
Wilhelmshaven, D (Schillerlocken)	FAO 21 North- West Atlantic	S. acanthias	Α	S. acanthias (99.41 %)	VU	u
Bremerhaven, D (Schillerlocken)	FAO 21 North- West Atlantic	S. acanthias	Α	S. acanthias (99.56 %)	VU	n
Osnabrück, D (Schillerlocken)	FAO 21 North- West Atlantic	S. acanthias	Α	S. acanthias (99.11 %)	VU	u
Vienna, AUT (Schillerlocken)	FAO 21 North- West Atlantic	S. acanthias	Α	S. acanthias (99.08 %)	VU	n
Eisenstadt, AUT (cartilage globules)	NA	shark cartilage	NA	NA	NA	У
Kusterdingen, D (cartilage capsules)*	NA	glucosamine, chondroitin sulfate, net- tle, turmeric, pepper, ginger	D, B	Gallus gallus (100 %), Solanum sp. (100 %)	TC	y
Ludwigshafen, D (capsules)*	NA	shark cartilage	C	S. acanthias (99.38 %)	VU	и
Ludwigshafen, D (capsules)*	NA	shark cartilage powder	D	Merluccius merluccius (99.53 %)	TC	y

Origin (Product type)	Fishing zone	Declared content	Primer combination	BLAST Result	Red list status	Mislabeled
Hagen, D (capsules)*	NA	shark cartilage powder	С	M. merluccius (99.06 %)	ГС	у
Ludwigshafen, D (capsules)*	NA	Shark cartilage extract	D	S. acanthias (85.5 %)	VU	u
Blankenburg, D (capsules)*	NA	Shark cartilage powder	D	G. gallus (100 %)	ГС	у
Blankenburg, D (capsules)*	NA	Shark cartilage extract	D	G. gallus (100 %)	ГС	у
Köln, D (capsules)*	NA	Shark cartilage	D	Galeorhinus galeus (99.27 %)	CR	u
Rheda-Wiedenbrück, D (capsules)*	NA	Shark	D	G. gallus (99.15 %)	ГС	у
Rheda-Wiedenbrück, D (capsules)*	NA	Shark	D	G. gallus (100 %)	ГС	у
Online (capsules)*	POR	Shark cartilage	D	G. galeus (100 %)	CR	n
Online (capsules)*	NA	Shark cartilage	D	Prionace glauca (99.07 %)	NT	n
Online (capsules)*	E	Shark cartilage	D	G. gallus (99.38 %)	TC	у
Online (capsules)*	E	Shark cartilage	D	G. gallus (99.19 %)	TC	у
Online (cartilage tabs)*	E	Chondroitin	D	S. acanthias (96.91 %)	VU	У
Online (capsules)*	NA	Carcharodon carcharias, Carcharhinus limbatus, Isurus oxyrinchus, P. glauca, Alopias sp.	D	S. acanthias (100 %)	VU	У

95°C, followed by 35 cycles of denaturation at 94°C for 1 minute, annealing at 52°C for 1 minute and elongation at 72°C for 2 minutes, with an extension of 5 minutes at 72°C (Hellberg et al. 2019). The identical protocol was used for mixtures containing 'VF2_t1 + FishF2_t1' along with 'Shark_Mini_V1_R' or 'Shark_Mini_V2_R', only changing the annealing temperatures to 46°C or 54°C respectively (Zahn et al. 2020).

As Hellberg et al. (2019) also discovered sequences of *Oryza rufipogon* (Wild rice) in their analysis, we additionally executed PCRs using the plant primers c and d targeting the *trn*L (UAA) intron after Taberlet et al. (2007). PCR success was confirmed on 2 % TAE cast with 5 μL Midori Green stain, running at 90 mV for 30 minutes.

Tab. 2: Utilized Primers and primer combinations used as capital letters [A-E]: FishF2 + FishR2 [A], trn L (UAA) intron c + trn L (UAA) intron d [B] or VF2_t1 + FishF2_t1 as forward primers mixed with either Shark COI-MINIR [C], Shark_mini_V1_R [D] or Shark_Mini_V2_R [E] as reverse primers. – Tab. 2: Verwendete Primer und Primer-Kombinationen in Großbuchstaben [A-E]: FishF2 + FishR2 [A], trn L (UAA) intron c + trn L (UAA) intron d [B] oder VF2_t1 + FishF2_t1 als Vorwärtsprimer gemischt mit entweder Shark COI-MINIR [C], Shark_mini_V1_R [D] oder Shark_Mini_V2_R [E] als Rückwärtsprimer.

Primer [combinations]	Direction	Primer sequence	Amplicon Length	Literature source
FishF2 [A]	forward	5´TCGACTAATCATAAAGA TATCGGCAC3´	670 bp	Pazartzi et al. 2019
FishR2 [A]	reverse	5´ACTTCAGGGTGACCGAAGAAT CAGAA3´	670 bp	Pazartzi et al. 2019
VF2_t1 [C, D, E]	forward	5 ['] TGTAAAACGACGGCCAGTCAAC CAACCACAAAGACATTGGCAC3 [']	127 bp	Hellberg et al. 2019
FishF2_t1 [C, D, E]	forward	5´TGTAAAACGACGGCCAGTCGAC TAATCATAAAGATATCGGCAC3´	127 bp	Hellberg et al. 2019
Shark COI-MINIR [C]	reverse	5´AAGATTACAAAAGCGTGGGC3´	127 bp	Hellberg et al. 2019
Shark_Mini_V1_R [D]	reverse	5´AAGATTATTACAAA AGCRTGRGC3´	127 bp	Zahn et al. 2020
Shark_Mini_V2_R [E]	reverse	5´AAGATTATTA- CRAADGCRTGRGC3´	127 bp	Zahn et al. 2020
trn L (UAA) intron c [B]	forward	5´CGAAATCGGTAGACGCTACG3´	456 bp	Taberlet et al. 2007
trn L (UAA) intron d [B]	reverse	5´GGGGATAGAGGGACTTGAAC3´	456 bp	Taberlet et al. 2007

Sequencing and Analysis

Successful PCR products were sent for Sanger-sequencing to Eurofins Genomics Europe Shared Services GmbH and resulting DNA sequences assembled and edited with the program Geneious version 8.1.9. (Biomatters Ltd.). All sequences were matched using the NCBI Nucleotide Basic Local Alignment Search Tool and identity hits of 98% or higher were taken into account as genus or species identifications. Assembled forward and reverse sequences were mapped to the highest matching reference sequence of the NCBI Genbank in order to compare the similarity and confirm the identity of each sequence obtained in our study.

Results

Extractions were successful for 23 samples (seven meat and 16 cartilage products). Only one product (the cartilage globules) failed to yield any DNA. Still, all extracted DNA was affected by DNA degradation. Samples from meat were moderately degraded while DNA obtained from cartilage pills showed highly degraded DNA (See Table 1). PCRs were successful with all 23 samples and at least one PCR product in the desired bp length (between 107 and 685 bp for both cartilage and meat) was generated with at least one primer set for all of these.

Meat was primarily successfully analyzed using the 'FishF2'/FishR2'. This particular primer mix, however, failed with cartilage products showing highly degraded DNA. Instead, the shark mini-barcodes were successfully applied for those. The 'Mini_V2' set did not work for any samples, while 'Shark COI-MINIR' was successful for most of the extracts. The 'Mini_V1' primer set, on the other hand, proved the most efficient primer mix to amplify cartilage products and supplied PCR products for all samples that otherwise posed challenges.

DNA sequences generated from meat DNA showed sequence lengths of around 685 bp with high HQ values and few ambiguities, which facilitated identification as all seven matched with only *Squalus acanthias* at an identity of at least 99% after BLAST search. These results corresponded with the shark species indicated on each of the Schillerlocken. Thus, every sampled shark meat fillet was correctly labelled and hence always compliant with EU legislation. Consequently, the mislabelling rate in the investigated 'Schillerlocken' was 0%.

Shark cartilage PCR products were sometimes of insufficient quality and ranged in length between 107 and 680 bp, as mini-barcodes target a shorter region in COI. Still, the com-

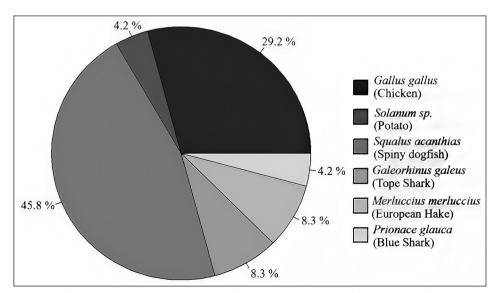


Fig. 1: All detected species present in the samples sequenced (N=23). – Abb. 1: Alle nachgewiesenen Arten in den sequenzierten Proben (N=23).

bination of different primer sets allowed for the identification of sequences from all examined cartilage samples, except the globules. Four cartilage products (three pills and the tabs) also contained *Squalus acanthias*. This resulted in an overall share of eleven samples containing *Squalus acanthias* in our study. Besides, the tope shark *Galeorhinus galeus* could be identified in two samples, as well as the blue shark *Prionace glauca* in one. For the remaining nine cartilage products no shark sequences were present. In seven of those *Gallus gallus* was proven, the marine teleost European hake (*Merluccius merluccius*) in two and *Solanum* sp. (presumably potato) in one. Fig. 1 illustrates all detected species of the present study in their individual proportion.

The cartilage sample in which *Prionace glauca* was discovered needed many trials until a proper sequence could be generated. It is possible that other species were mixed in this product, because the sequences obtained in some tries were often overlapping and indistinguishable.

Products in which shark sequences could be determined were not considered as mislabelled except for two cases. One of those clearly stated the presence of only five particular species, yet another was detected, while the other did not mention the presence of shark, but was only labelled as containing cartilage. Nevertheless, *Squalus acanthias* was proven to be in this product. The rest indicated the presence of either 'shark' or 'shark cartilage' on the labels, but without explicitly naming any shark species, but as shark DNA was proven those were not considered as mislabelled.

Overall, our study revealed a mislabelling proportion of 50%, and 70.6% in cartilage products alone. All products with *Merluccius merluccius* were categorized as mislabelled, as no teleost species was declared to be contained, as well as all products in which only signals of *Gallus gallus* were detected. The cartilage product in which sequences of *Solanum* sp. in addition to sequences of *Gallus gallus* were found, was classified as mislabelled even though it did not specifically claim to incorporate shark cartilage. There was, however, no mention of potato as an ingredient.

Discussion

Our study highlights that DNA barcoding proved to be an easy way to get an overview of potentially mislabelled or generally suspicious seafood products. An economically motivated substitution of shark cartilage with cheaper cartilage from species like *Merluccius merluccius* or *Gallus gallus* as well as with fillers like *Solanum* sp. seems a plausible explanation for their presence, given the fact that similar fraud has been proven to occur on a global scale. Since most other cartilage food supplements also use *Gallus gallus* it would be easy for manufacturers to sell one and the same product under differing labels.

There could still always be the risk of contamination somewhere along the laboratory process or even already while sampling, especially as a substitution of shark cartilage products with *Gallus gallus* has hitherto never been reported, at least to our knowledge. But none of the results changed after repeating extraction and PCR, except for an improvement on some sequences displaying higher sequence quality in the second run. This, in addition to the fact that all steps were executed as sterile as possible for our lab, is the reason we consider the risk of contamination as minimal.

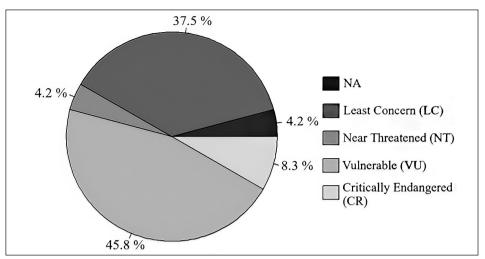


Fig. 2: Threat categories according to the IUCN red list of threatened species and their respective proportions for all species detected in the analyzed sample size (N=24). – Abb. 2: Gefährdungskategorien gemäß der IUCN Roten Liste und ihre jeweiligen Anteile für alle in der analysierten Stichprobe (N=24) nachgewiesenen Arten.

An explanation for the amplification of *Gallus gallus* sequences that were contained in the extract could be that low annealing temperatures may have caused the shark-primers to bind less specifically. That would also explain why the 'V1' primer set worked best. Even though the mini-barcodes deliver only short fragments as products, the possibility of an overlap in the concerning gene regions between the respective examined species is very slim since too many point mutations were detected in this region and the samples match at least 98 % to the references in the database.

Overall the total share of vulnerable species present in both product categories is 45.8%, all of those being *Squalus acanthias*. Concerning all examined meat, the respective fish vendors still do set a positive example to the global shark trade, as none were mislabelled. Besides, six of them were supposedly harvested from the FAO 21 fishing area in the northwestern Atlantic. This subpopulation is currently classified as not endangered, though it has fluctuated heavily in the previous decades. Only one vendor imported their meat from the FAO 27 area in the north-eastern Atlantic, where *Squalus acanthias* is at this time classified as critically endangered but was last assessed in 2006 (IUCN 2020). Still, shark meat mislabelling could be happening at a timescale unnoticed by our study, as the samples were taken at more or less the same time and are therefore just a momentary depiction of the market.

The critically endangered shark species *Galeorhinus galeus* was observed in two samples and was only present in shark cartilage pills. It was not traceable whether the processing of this shark had been monitored by officials or if it appears in an official trade statistic, as neither label nor shop mentioned a distinct species.

Most mislabelled cartilage samples were comprised of *Merluccius merluccius* or *Gallus gallus*, with one additionally indicating the supplementation with *Solanum* sp.. All three species are categorized as Least Concern, so the lack of threatened species can be reported in

37.5% of samples, additionally to the globules, where no DNA was found. Non-declaration of their presence is nonetheless food fraud (at a share of 70.6% in the analyzed cartilage products) and persons with allergies (for e.g. fish-protein) could hypothetically come to harm. This, however, likewise holds true for people consuming actual shark cartilage, because it has been shown to contain toxins (Mondo et al. 2014).

Even the low sample size of this study already revealed a large portion of mislabelling as well as threatened species in shark cartilage products, which indicates the need for an increased monitoring effort and for legal adaptations to enhance transparency. Future studies at a larger scale are needed to assess the true extent of mislabelling in the German shark market and how the German consumers affect the exploitation of threatened shark species.

Accessibility

Sequence data were deposited on DRYAD and can be accessed via https://doi.org/10.5061/dryad.ngf1vhhxw.

Acknowledgments

Our study was funded by the Project 'Aufbau von universitären DNA-Barcoding-Pipelines für ABOL - Austrian Barcoding of Life', a collaborative Infrastructure project financed by the Austrian Ministry of Science.

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Received: 2023 03 07

Addresses:

Kilian Niedermeier, E-Mail: kilian.niedermeier@stud.sbg.ac.at

Matthias Affenzeller, E-Mail: kilian.niedermeier@stud.sbg.ac.at

Andreas Tribsch, E-Mail: andreas.tribsch@plus.ac.at Department Environment and Biodiversity, University of Salzburg, Hellbrunner Straße 34, A-5020 Salzburg.

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<u>Frueher: Verh.des Zoologisch-Botanischen Vereins in Wien. seit 2014 "Acta ZooBot Austria"</u>

Jahr/Year: 2023

Band/Volume: 159

Autor(en)/Author(s): Niedermeier Kilian, Affenzeller Matthias, Tribsch Andreas

Artikel/Article: COI-Barcoding evidences mislabelling and the use of endangered

species in German shark products 275-285