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Confirmed record of the roughear scad *Decapterus tabl* in the Cabo Verde Archipelago based on morphological and genetic data

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RESUMO

A ocorrência de *Decapterus tabl* é confirmada pela primeira vez no arquipélago de Cabo Verde. vários espécimes capturados nos anos 2015 e 2020 demostraram serem muito diferentes de *Decapterus macarellus* e *Decapterus punctatus*, ambas as espécies já assinaladas para as águas de Cabo Verde, com base em dados morfométricos, merísticos e moleculares. Morfologicamente, esta cavala atinge maior tamanho do que as congéneres, possui barbatana caudal avermelhada, margem serrilhada na membrana do opérculo, 10 a 12 branquispinhas (primeiro arco branquial) na porção superior e 30 a 33 na inferior (incluindo rudimentares). O *barcoding* genético baseado no citocromo oxidase I mitocondrial corrobora os dados merísticos e morfométricos, validando a presença local da chamada "cavala americana" no arquipélago de Cabo Verde.

Palavras-chave: Atlântico Nordeste, Carangidae, *Decapterus* spp., mtDNA

ABSTRACT

The occurrence of *Decapterus tabl* is confirmed for the first time for the Cabo Verde Archipelago. Several specimens from fisheries catches in the years 2015 and 2020 proved to differ unambiguously from *Decapterus macarellus* and *Decapterus punctatus*, both species already reported from Cabo Verde waters, based on morphometric, meristic and molecular data. Morphologically, the roughear scad reaches larger sizes than its congeners, presents reddish caudal fin, serrated margin on the operculum membrane, 10 to 12 gill rakers in the upper limbs and 30 to 33 gill rakers in lower limbs (including rudiments). A genetic barcoding analysis based on mitochondrial cytochrome oxidase I corroborates the meristic and morphometric data, validating the presence of the locally called '*cavala americana*' in the Cabo Verde Archipelago.

Keywords: Carangidae, *Decapterus* spp., mtDNA, Northeastern Atlantic

INTRODUCTION

The carangid genus *Decapterus* Bleeker, 1851 is well represented in the pelagic zone of central Eastern Atlantic shelfs, with a northern distribution limit of some of the northern species around the Strait of Gibraltar and the southern species reaching South African coasts. Of the ten species listed in this genus, four occur along the West African coast: *Decapterus macarellus* (Cuvier, 1833), *Decapterus punctatus* (Cuvier, 1829), *Decapterus muroadsi* (Temminck & Schlegel, 1844), and *Decapterus tabl* Berry, 1968 (Smith-Vaniz 2016).

To date, only two species have been reported for the Cabo Verde Archipelago: the mackerel scad *D. macarellus* and the round scad *D. punctatus* (Reiner 2005, Wirtz *et. al.* 2013, Hanel & John 2015). In the southeastern Atlantic, the amberstripe scad *D. muroadsi* and the roughear scad *D. tabl* are known only from Saint Helena surroundings (Smith-Vaniz *et al*. 1990, Kimura *et al.* 2013, Smith-Vaniz, 2016, Wirtz *et al.* 2017). In the Northeastern Atlantic, Bañón *et al.* (2019) only recently reported *D. tabl* for Madeira.

Decapterus tabl is an epipelagic oceanic and coastal (reef-associated) circumtropical species (Berry & Smith-Vaniz 1978). On the global scale, the species has been reported for Bermuda and from North Carolina to Venezuela in the Western Atlantic Ocean, for the Indian Ocean, and the Indo-West Pacific eastwards to Hawaii (Berry 1968, Kim & Koh 1994, Kimura *et al.* 2013, Smith-Vaniz 2016). Adult specimens use the whole water column from near the surface and mid-water to near the bottom. The recorded maximum total length (TL) is 50 cm and maximum weight 560 g (Berry & Smith-Vaniz 1978, Smith-Vaniz 1986), while the most commonly observed size is around 25–35 cm TL (Cervigón *et al*. 1992, Smith-Vaniz 2016). It feeds on small planktonic invertebrates, primarily copepods (Cervigón *et al*. 1992, Smith-Vaniz 2016).

The present study aims at confirming the regular occurrence of *D. tabl* in Cabo Verde based on meristic counts and molecular markers. An unambiguous differentiation of the three distinct *Decapterus* species found in the archipelago will facilitate accurate landing data and, therefore, better knowledge on population dynamics and stock size, ultimately leading to better scientific advice for fisheries management.

MATERIAL AND METHODS

The first specimens of *D. tabl* used in this study were collected in 2015 near Flamengo Bay off São Vicente's southern coast, standing out due to their large size and reddish caudal fin. The vessel landed several tons of scad captured at 50 m deep. One specimen was brought to Instituto do Mar (IMAR), former Instituto Nacional de Desenvolvimento das Pescas at Mindelo, São Vicente, for photo recording. It was not possible to get biometric or molecular data for this specimen because it was lost. In addition, four *Decapterus* specimens (KV293a, KV294a, KV302a, KV303a), one with reddish caudal fin, were photographed and a muscle tissue sample collected at São Vicente's fish market on May 18, 2015 (Fig 1). Tissues were deposited in Thünen Institute, Germany, and used to extract DNA for molecular identification.

In February 2020, three additional specimens were collected at São Nicolau's fish market for morphometric characterization (Fig 1). Muscle tissue samples were deposited in the newly established biodiversity reference collection at the 'Universidade Técnica do Atlântico' at Mindelo, Cabo Verde (UCV00341–UCV00343).

Biometric measurements of these three specimens were performed with a calliper and a 50 cm length millimeter ruler. All specimens were sexed and photographed. Molecular identification of these specimens was not possible to be performed due to logistic constraints caused by the COVID-19 pandemics.

All photographs were deposited in MorphoBank (M740012–M740018; M740101 –M740102; username: P3974). The meristic characters and body proportions of the specimens were compared with the metrics data retrieved from Berry (1968), Kim & Koh (1994) and Kimura (2013). Counts and measurements generally followed Hubbs & Lagler (1958) except for body depth, which was measured from the origin of the first dorsal fin (D1) to the pelvic fin in sagittal plane (P2) and from the second dorsal fin (D2) to the first spine of the anal fin (A1). All data were compared primarily to the three Northeastern Atlantic species of *Decapterus*.

DNA extraction from samples KV293a, KV294a, KV302a and KV303a was conducted using Invisorb Spin Tissue Mini Kit (Stratec, Birkenfeld, Germany). Four fragments of approximately 650 base pairs (bp) of the cytochrome oxidase I (COI) gene were amplified using Ivanova *et al.* (2007) – Ward *et al.* (2005) cocktail primers, modified with M13 sequencing sites: VF2_t1_M13 (5′-TGT-AAA-ACG-ACG-GCC-AGT-CAA-CC A-CCA-CAA-AGA-CAT-TGG-CAC-3′), FishF2_t1_M13 (5′-TGT-AAA-ACG-ACG-GCC-AGT-CGA-CTA-ATC-ATA-AAG-AT A-TCG-GCA-C-3′), FishR2_t1_M13 (5′-CAG-GAA-ACA-GCT-ATG-ACA-CTT-CA G-GGT-GAC-CGA-AGA-ATC-AGA-A-3′), and FR1d_t1_M13 (5′-CAG-GAA-ACA-GCT-ATG-ACA-CCT-CAG-GGT-GTC-CG A-ARA-AYC-ARA-A-3′).

PCR reactions were performed using Phusion High-Fidelity PCR Master Mix with HF Buffer for KV293 & KV294 samples and Q5 High-Fidelity 2X Master Mix for KV302 & KV303. The reactions were performed in a thermocycler, in a total volume of 20 µL/reaction, including 3 µL of genomic DNA, 1X PCR Master Mix and 0.25 µM of each primer. The cycling conditions started with an initial denaturation of 98°C for 30 s, followed by 32 cycles of 98°C for 10 s, 53°C for 30 s, 72°C for 20 s and a final extension at 72°C for 8 min. For quality check, 5 µL of each PCR product were visualized in agarose gel 1% stained with SERVA DNA Stain Clear G and observed in a transilluminator under UV light.

Samples were sequenced at GATC Services Eurofins Genomics (Ebersberg, Germany) using primers designed by Messing (1983): M13F(-21) (5´-TGT-AAA-ACG-ACG-GCC-AGT-3´) and M13R(-27) (5´-CAG-GAA-ACA-GCT-ATG-AC-3´).

Fig. 1. The five specimens of the roughear scad *Decapterus tabl* collected in Cabo Verde. **A)** Specimen caught at Flamengo Bay, off the southern São Vicente coast (photo by A. Martins). **B**) Specimen photographed from São Vicente's fish market on May 18 2015 (KV302a; photo by R. Hanel). **C**) Specimens collected at São Nicolau's fish market (from top to bottom: UCV00341 to UCV00343; photo by E. Lopes).

Sequences were assembled with CodonCode Aligner version 9.0 (www.codoncode.com/aligner/index.htm) and compared with available sequences in GenBank to taxonomically identify the specimens. The translation of mitochondrial genes was deduced using the mtDNA genetic code of vertebrates in Unipro UGENE version 1.29 (Okonechnikov et al. 2012) allowing to inspect the existence of stop codons and the presence of pseudogenes. The global alignment was done using ClustcalW algorithm present in BioEdit v.7.0.5.3 (Hall 1999). A total of 36 COI sequences with 648 bp of nine *Decapterus* species deposited in GenBank were included in the phylogenetic analyses together with four new sequences and two outgroup sequences of *Selar crumenophthalmus* (Bloch, 1793) (Table 1).

Table 1. List of samples included in the genetic analyses. Their code and taxonomic identification are given, as well as their distribution range, climatic zone, location, and GenBank accession number.

Species	**Distribution**	**Climatic zone**	**Location**	**GenBank**
Decapterus sp. (KV303a)	–	–	São Vicente, Cabo Verde	MT435950
Decapterus sp. (KV293a)	–	–	São Vicente, Cabo Verde	MT435951
Decapterus sp. (KV294a)	–	–	São Vicente, Cabo Verde	MT435952
Decapterus sp. (KV302a)	–	–	São Vicente, Cabo Verde	MT435953
Decapterus akaadsi	Western Pacific	Subtropical	China Sea	EF607334
			China Sea	EF607333
			South Japan	JF952716
Decapterus kurroides	Indo-West Pacific	Deep-water	Indonesia	JN312966
			Indonesia	HQ564303
			Indonesia	HQ564304
Decapterus macarellus	All oceans	Subtropical	Malaysia	KY570732
			Malaysia	KY570733
			Madeira Islands	MH980014
			Indonesia	HQ564302
Decapterus macrosoma	Indo-Pacific and Southeast Atlantic	Tropical	Indonesia	HQ564442
			Indonesia	HQ564377
			Panama	MF956639
Decapterus maruadsi	Indo-Pacific and Southeast Atlantic	Tropical	Malaysia	KY570749
			Malaysia	KY570751
			California	HQ010055
Decapterus punctatus	Atlantic	Subtropical	Northwest Atlantic, USA	KT883653
			Guatemala	KR086824
			North Carolina, USA	MH378676
			México	GU224777
Decapterus russelli	Indo-West Pacific	Tropical	South Africa, KwaZulu	JF493352
			Malaysia, Kuala Kedah	KY570767
			Malaysia, Kuala Kedah	KY570768
Decapterus tabl	Pacific Ocean, Western and South Atlantic	Subtropical	Portugal, Madeira Islands	MH980015
			Portugal, Madeira Islands	MH980016
			Portugal, Madeira Islands	MH980017
			China, South China Sea	KY371432
			China, South China Sea	KY371433
			China, South China Sea	KY371434
Selar crumenophthalmus	Circumtropical	Subtropical	China Sea	MH638715
			China Sea	MH638727

PartitionFinder v2.1.1 (Lanfear *et al*. 2012) was used to determine the best-fit partitioning schemes and models of molecular evolution to each dataset, according to Akaike's Information Criterion (Akaike 1973). The following models of molecular evolution were applied to COI partitions: GTR+G (1st partition), GTR+I (2nd partition), F81+I (3rd partition). Maximum likelihood (ML) and Bayesian inference (BI) methods were used to reconstruct *Decapterus* phylogeny. For BI analyses, performed in MrBayes v3.2.6 (Ronquist *et al.* 2012), settings included five million generations, sampling every 1000 generations, and discarding the first 25% generations as burn-in. The convergence of parameter values was assessed using Tracer v1.7 (Rambaut *et al*. 2018), excluding an initial 10% for each run. All parameter estimates for each run showed ESS values >100. A final Bayesian majority-rule consensus tree was obtained for each data set. For ML RAxML v8.1.16 (Stamatakis 2006) with the rapid hill-climbing algorithm and

10,000 bootstrap pseudoreplicates was used. The consensus trees inferred for each method were improved using FigTree v1.4.3 (http://tree.bio.ed.ac.uk/software/fgtree/).

To identify the relationships among *D. tabl* specimens used in the present study, a non-rooted network of haplotypes based on the 95% parsimony method was built in TCS1.21 (Clement *et al*. 2000), with deletions treated as a fifth state. The final manipulation was performed in tcsBU (Santos *et al.* 2016).

RESULTS

The macroscopic analysis of the three scad specimens collected on São Nicolau and two specimens previously collected on São Vicente showed a very elongated, almost rounded body, metallic blue dorsally, silver and whitish ventrally (Fig. 1), and moderately large eye with well-developed adipose eyelid, completely covering the eyes (Fig. 2). Even though the roughear scad shares characters with the mackerel scad, some morphological features make a differentiation relatively simple, including the presence of reddish caudal fin, edges of dorsal, red anal and pectoral fins, white muscle tissue significantly darker and a little firmer, more rounded eyes, and overall lighter external colouration. Also, 30 gill rakers on the lower limb and serrated opercular margin pointed to the roughear scad *Decapterus tabl* (Fig. 2).

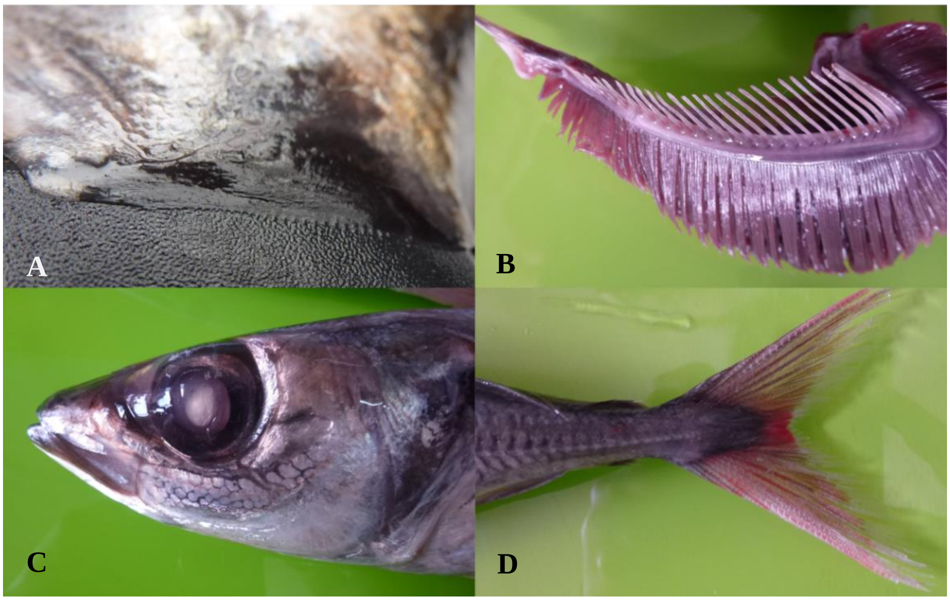

Fig. 2. Diagnostic characters of *D. tabl* from specimens acquired at the fish markets of São Nicolau, Cabo Verde (photos by E. Lopes; Morphobank M740012–M740018; M740101–M740102). **A)** Serrated margin of the opercular membrane, **B**) 30 lower gill rakers, **C**) posterior margin of the head straight, and **D**) reddish caudal fin.

In the comparison among the three species present in Cabo Verde, it was clear that the body proportions of the two females and one male *Decapterus* collected on São Nicolau, and the one collected on São Vicente, matched to *D. tabl* (Table 2). These data were in agreement with the size and weight ranges, body proportions, and gill rakers, second anal fin, lateral line scutes counts and colour reported for this species (Berry 1968, Berry & Smith-Vaniz 1978, Kimura *et al*. 2013, Wirtz *et al*. 2017).

Table 2. Number of specimens, measurements and counts of *Decapterus tabl* collected on São Nicolau (SN) and São Vicente (SV), Cabo Verde, compared with data from Kim & Koh (1994) for Korea, Kimura et al. (2013) for Caribean Sea (CS) and Berry (1968) for Western Atlantic (WA) and St. Helena (SH) and close-related species. Measurements are presented in percentage of standard length. D1 and D2 stand for first and second portion of dorsal fin, respectively, P2 for pelvic fin in sagittal plane, and A1 for first spine of anal fin. True spines were counted and are reported in uppercase Roman numerals and soft rays in Arabic numerals.

Variables	**Present study**		**Kim & Koh (1994)**	**Kimura (2013)**	**Berry (1968)**			
	D. tabl		*D. tabl*	*D. tabl*	*D. tabl*		*D. punctatus*	*D. macarellus*
	SN	SV	Korea	CS	WA	SH		
Number of specimens	3	1	1	8	50	2	–	–
Standard length (mm)	313–348	–	180	156–203	156–199	351–360	140–183	145–256
Total length	118–118	–	115	–	113–115	114	116–117	115
Fork length	106–108	–	106	–	104–106	106	106–108	106–107
Head length	29.0–30.3	–	27.6	27.4–30.5	27.5–29.0	28.8–30.0	25.5–27.5	25.2–26.8
Eye diameter	6.7–7.4	–	6.8	7.1	6.5–7.4	7.1–8.5	7.1–7.9	5.9–6.9
Snout length	10.1–10.6	–	10.0	9.8	8.3–10.4	9.4–10.7	7.3–9.1	8.3–9.4
Postorbital head length	14.7–14.7	–	16.7	12.4	11.8–13.0	11.4–11.9	10.2–12.3	10.5–11.4
Upper jaw length	9.4–9.9	–	9.2	9.6	9.2–9.9	10.0–10.3	8.3–8.6	7.8–8.5
Maxillary depth	2.7–3.3	–	3.1	–	2.8–3.4	3.1–3.2	2.9–3.2	2.7–3.1
Body depth D1–P2	18.5–18.7	–	9.2	–	17.0–20.2	20.1–20.2	18.8–22.0	17.4–19.2
Body depth D2–A1	19.4–20.7	–	24.1	–	16.5–20.0	19.8–20.0	19.5–23.1	17.3–18.9
Maximum body depth	19.8–21.8	–	22.8	16.6–23.0	16.7–19.8	19.5–19.7	18.8–23.0	16.1–18.9
Pectoral-fin length	20.1–21.0	–	24.3	17.8–21.5	16.4–18.1	18.8–19.4	18.2–23.5	15.3–17.5
Pelvic-fin length	11.0–11.8	–	13.0	10.8–13.0	10.5–12.1	11.4–12.9	11.0–13.0	9.9–12.1
Longest dorsal spine	11.6–15.1	–	14.9	10.7–15.0	12.4–13.9	13.2–13.8	12.4–15.6	10.3–13.6
Longest dorsal soft ray	9.4–12.2	–	10.4	–	10.2–11.2	10.9–11.4	11.5–12.4	8.9–9.5
Longest anal spine	2.4–2.7	–	1.3	2.0–3.9	2.9–3.7	2.9–2.9	4.2–4.6	3.2–3.8
Longest anal soft ray	9.0–10.5	–	–	–	8.8–9.5	9.5–9.9	10.1–11.3	7.5–8.7
Lateral-line ratio	0.7	–	–	–	0.6–0.9	0.7–0.8	0.9–1.2	0.8–1.0
Dorsal fin	VIII, I+33	–	VIII, I+32	–, 29–32	VIII, I–29–34	–	VIII, I+29–34	VIII, I+31–37
Anal fin	II+I+26	–	II+I+26	–, 23–26	II+I+24–27	–	II+I+26–30	II+I+27–31
Pectoral fin	21	–	21	–, 20–21	20–22	–	18–20	21–23
Pelvic fin	I+5	–	I+5	I+5	I+5	–	I+5	I+5
Upper gill rakers	10	–	11	9–10	10–12	–	11–13	9–13
Lower gill rakers	30	30	31	30–32	30–33	–	32–37	31–39
Branchiostegal rays	7	–	7	–	7	–	7	7
Lateral-line scutes	36–38	–	37	35–38	39	–	32–56	23–32

Bayesian and Maximum Likelihood analyses showed identical results, revealing well-supported clades for most of the species described for this genus. Three *Decapterus* individuals (KV293a, KV294a, KV303a) collected at São Vicente grouped within the clade of *D. macarellus*, and one (KV302a), morphologically distinct, grouped with *D. tabl* sequences (Fig. 3A). The haplotype network of *D. tabl* showed two distinct groups separated by several mutational steps: one belonging to the Pacific (China Sea) with two haplotypes, and another belonging to the Atlantic (Madeira and Cabo Verde Islands) with three haplotypes (Fig. 3B). The individuals from Cabo Verde shared the same haplotype with a sample from Madeira Island (Fig. 3B).

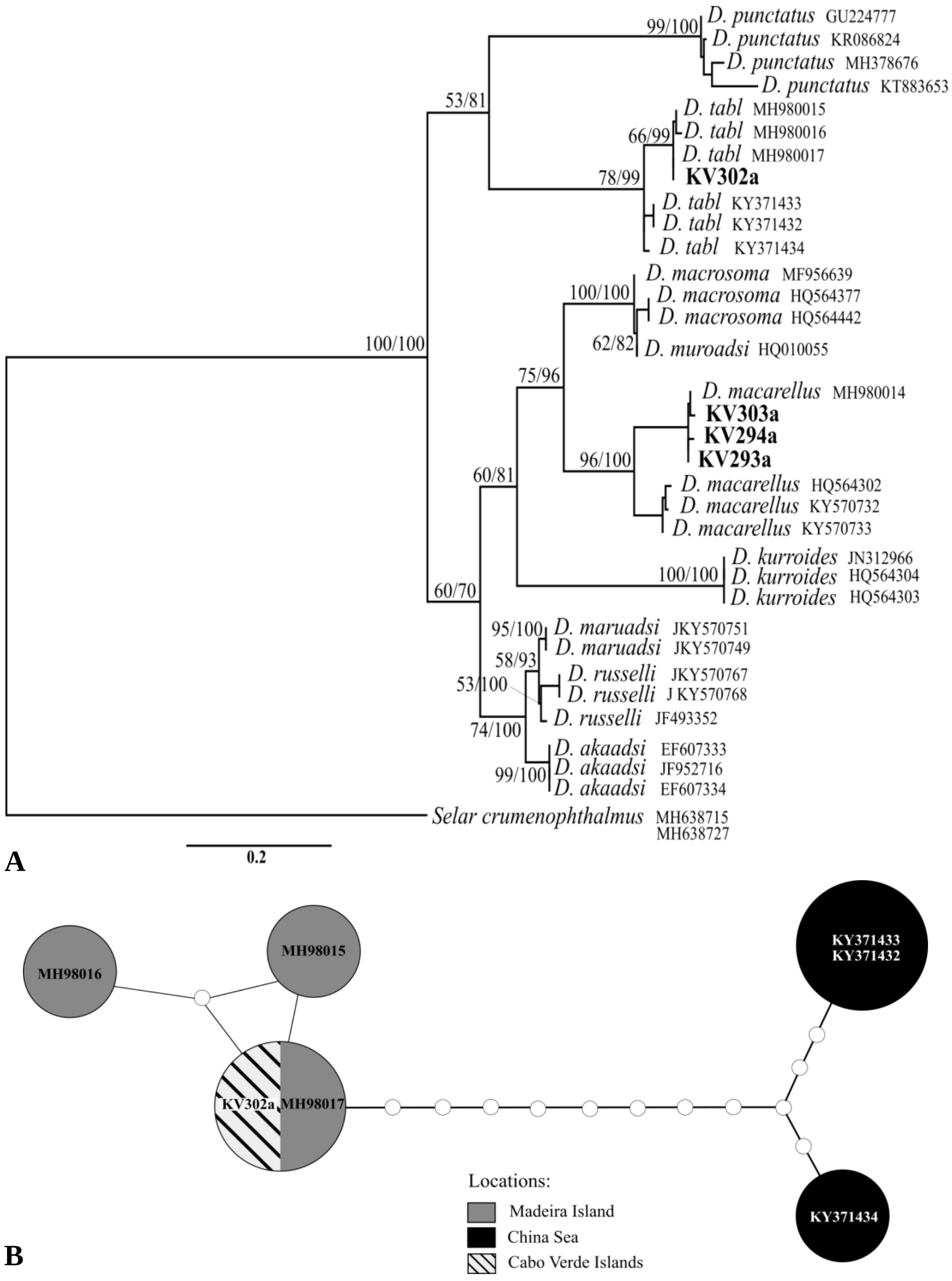

Fig.3. Phylogenetic relationships between the sequences obtained in this study and sequences retrieved from GenBank. **A)** Maximum Likelihood (ML) consensus tree for the 648 bp COI sequences of the genus *Decapterus.* Numbers at nodes are statistical support values for ML (bootstrap)/ BI (Bayesian posterior probabilities). *Decapterus* samples collected on São Vicente, Cabo Verde are shown in bold. Scale bar indicates substitutions per site. The GenBank accession codes or sample codes are also given. **B)** Haplotype networks of *D. tabl* for the COI marker. Lines represent mutational steps and circles haplotypes. The size of circles is proportional to the number of individuals.

DISCUSSION

The morphological characters provided in the diagnosis and the molecular data showed that the specimens found near São Nicolau and São Vicente belong to *Decapterus tabl*, a species now formally confirmed for Cabo Verde waters. The Cabo Verde Archipelago is the second northeastern Atlantic insular habitat for which the presence of the species was confirmed. Recently, Bañón *et al*. (2019) reported the occurrence of the species around Madeira, confirmed by morphological and DNA barcoding (COI) data. This new record for Cabo Verde is important, as it supports the possibility of a more widely distribution of the species in the Northeastern Atlantic, potentially from Madeira in the north and Saint Helena in the south. It is also important economically, as the species is used locally for human consumption and has increased its economic value considerably due to the decreasing of *D. macarellus* catches and landings (Santos, 2018).

Records of new and rare fish species especially around oceanic islands are often considered occasional events (Afonso *et al*. 2013). However, in the nearby Canary Islands, tropicalization processes have recently been described as important driving forces increasing fish diversity (Brito *et al*. 2017). Natural immigration mediated by climate change (Morley *et al*. 2018) is therefore also a possible explanation for recent records of *D. tabl* around Madeira and Cabo Verde islands. An alternative hypothesis is given by Heithaus *et al.* (2008) and Baum & Worm (2009) who explained increased transatlantic migration of schools of small pelagic fish like scads and mackerels as a result of overfishing of oceanic predators (sharks and/or tunas), triggering shifts in the oceanic top-down control. However, it seems equally likely that transatlantic migration is an ocean current driven process, affecting early larval stages of fish (Rocha *et al*. 2008). The permanent occurrence of the roughear scad around Bermuda could be a steppingstone for the eastward transport of patches of larval scad with the North Atlantic gyre.

Cabo Verde has been repeatedly mentioned in the context of pan-Atlantic marine connectivity (van der Land 1993, Morri *et al*. 2000), largely due to a distinct American (mainly Caribbean) imprint, expressed by the occurrence of predominantly Western Atlantic seaweeds (Prud’homme van Reine *et al.* 2002), but also by fish species like moray eels (Muraenidae), damselfishes (Pomacentridae), wrasses (Labridae), and triggerfishes (Balistidae) (Floeter *et al*. 2008). Future phylogeographic and population genetic studies are needed to reveal the origin of this species and the establishment of a population in Cabo Verde, and the consequences of the latter for native species. New records of *D. tabl* can thus be traced back to a founding population in the southeast Atlantic and link genetic data by trans-oceanic processes.

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