

New insights on the ecology and biology of the rare shark species *Oxynotus paradoxus* from recent records

by

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Abstract. – *Oxynotus paradoxus*, documented in the Eastern Atlantic Ocean from Senegal to Scotland at depths ranging between 92 and 1044 m, has been a subject of limited scientific attention in Portugal. Despite its presence in various Portuguese occurrence checklists, only two scientific studies have reported *O. paradoxus*, one off the mainland and the other off the Azores islands. In this study, conducted during fishing campaigns, four *O. paradoxus* specimens were caught off the southwest coast of Portugal (SW Iberian Peninsula) at depths ranging between 742 and 1238 m. Notably, an adult female achieved a new maximum depth record for this species, measuring 650 mm in total length. By examining this adult female, we provide novel insights into the ecology and biology of *O. paradoxus*. Morphometric measurements are compared with previous studies, revealing some intra-specific variability. The observed low hepato-, gonadosomatic, and ecophysiological indices suggest that the adult female had refrained from feeding for some time before collection. This individual-focused approach contributes significantly to the understanding of this poorly known species, especially considering its rarity. This study marks a noteworthy effort to enhance knowledge and emphasizes the importance of individual-based investigations when targeting rare species.

Résumé. – Nouveaux aperçus sur l'écologie et la biologie de l'espèce rare de requin *Oxynotus paradoxus* à partir de données récentes

Oxynotus paradoxus a été signalé dans l'océan Atlantique Est, du Sénégal à l'Écosse, à des profondeurs de 92 à 1044 mètres. Malgré sa présence dans diverses listes d'occurrences portugaises, seules deux études scientifiques ont signalé *O. paradoxus* au Portugal, l'une au large du continent et l'autre au large des Açores. Au cours de campagnes de pêche à bord d'un chalutier commercial ciblant les crustacés, quatre spécimens de *O. paradoxus* ont été capturés accidentellement au sud-ouest du Portugal (sud-ouest de la péninsule ibérique) à des profondeurs variant entre 742 et 1238 mètres. Cette dernière profondeur constitue un nouveau record pour cette espèce, atteint par une femelle adulte mesurant 650 mm de longueur totale. Grâce à cette femelle adulte, nous apportons de nouvelles perspectives sur l'écologie et la biologie de cette espèce. Des mesures morphométriques sont ici présentées et comparées à des études antérieures révélant une certaine variabilité intra-spécifique. Les faibles indices hépato-gonadosomatiques et écophysologiques suggèrent que la femelle adulte ne se nourrissait pas depuis un certain temps avant d'être collectée. Cette étude contribue à accroître nos connaissances sur cette espèce peu connue, en utilisant une approche individuelle, ce qui est primordial lorsque l'on s'intéresse à des espèces rares.

Key words

Bycatch
SW Iberian Peninsula
Gonadosomatic index
Hepatosomatic index
Morphometry
Ecophysiological index

INTRODUCTION

The Oxynotidae constitute a family of elasmobranchs within the order Squaliformes, exclusively represented by the genus *Oxynotus*. Species in this genus exhibit a compressed body, a triangular cross-section, two high-spined dorsal fins, very rough skin, a small thick-lipped mouth, large closely positioned nostrils, and a flat blunt snout (Ebert *et al.*, 2021).

Out of the five globally occurring species of *Oxynotus*, only two inhabit European waters: the angular roughshark

Oxynotus centrina (Linnaeus, 1758) and the less studied sailfin roughshark *Oxynotus paradoxus* (Frade, 1929). The latter is distributed along the continental slopes of the North-east Atlantic, ranging from Scotland to Senegal, including the Azores and Canary Islands, but is absent in the Mediterranean.

Previous studies have reported *O. paradoxus* at depths varying between 92 and 877 m in the British Isles (*e.g.*, Norman, 1932; Tucker and Palmer, 1949; Rae and Lamont, 1960; Blacker, 1962; Went, 1968; Quigley and Flannery, 1994), along the French Basque coast (*e.g.*, Frade, 1932;

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Harambillet *et al.*, 1976), and in the Galicia Bank seamount (Bañón *et al.*, 2016). Pajuelo *et al.* (2016) captured the species in NW Africa during experimental fishing trips at depths ranging between 803 and 1044 m. In SW Iberian waters, particularly in Portugal, *O. paradoxus* has been reported in areas surrounding the mainland and the islands of Azores and Madeira (Kreff and Tortonese, 1979; Santos *et al.*, 1997; Carneiro *et al.*, 2014; Biscoito *et al.*, 2018). Despite its occurrence in Portuguese waters, the available scientific literature on *O. paradoxus* is scarce. Azevedo *et al.* (2003) described dermal denticles from two specimens caught off the Azores in 1993 and 1995 (one female caught at 600 m depth with a gill net and a male with no depth indication). Moura *et al.* (2015) presented the barcoding of one specimen of *O. paradoxus* caught off the coast of mainland Portugal during a bottom-trawl research survey conducted by the Portuguese Institute for the Sea and Atmosphere (IPMA), reaching a maximum depth of 750 m.

Oxynotus paradoxus individuals are born with a total length (TL) of 25 cm and can attain a maximum TL of 128 cm (O’Riordan, 1984). Males reach maturity at around 75 cm TL, but information on females’ maturity is lacking (Ebert *et al.*, 2021). According to IUCN criteria, *O. para-*

doxus is globally classified as Vulnerable (Finucci *et al.*, 2021), and in Europe, it is classified as Data Deficient (Soldo *et al.*, 2015), signifying insufficient information for a direct or indirect assessment of its risk of extinction based on distribution and/or population status (IUCN, 2022).

In the present study, we describe a new depth record for *O. paradoxus* off the SW Iberian Peninsula slope, including morphometric measurements and new insights into the biology of this poorly understood species.

MATERIAL AND METHODS

Between June 2020 and May 2022, a total of 106 trawling hours were conducted by both a commercial crustacean bottom-trawler and the RV *Mário Ruivo* of the Institute for the Sea and Atmosphere (IPMA) along the southwest coast of Portugal. The fishing operations were carried out at depths ranging from 27 to 1244 m, within the coordinates of 37–39°N and 9–10°W.

During these operations, four specimens of *Oxynotus paradoxus* were collected by the commercial vessel while targeting the giant red shrimp *Aristaeomorpha foliacea*

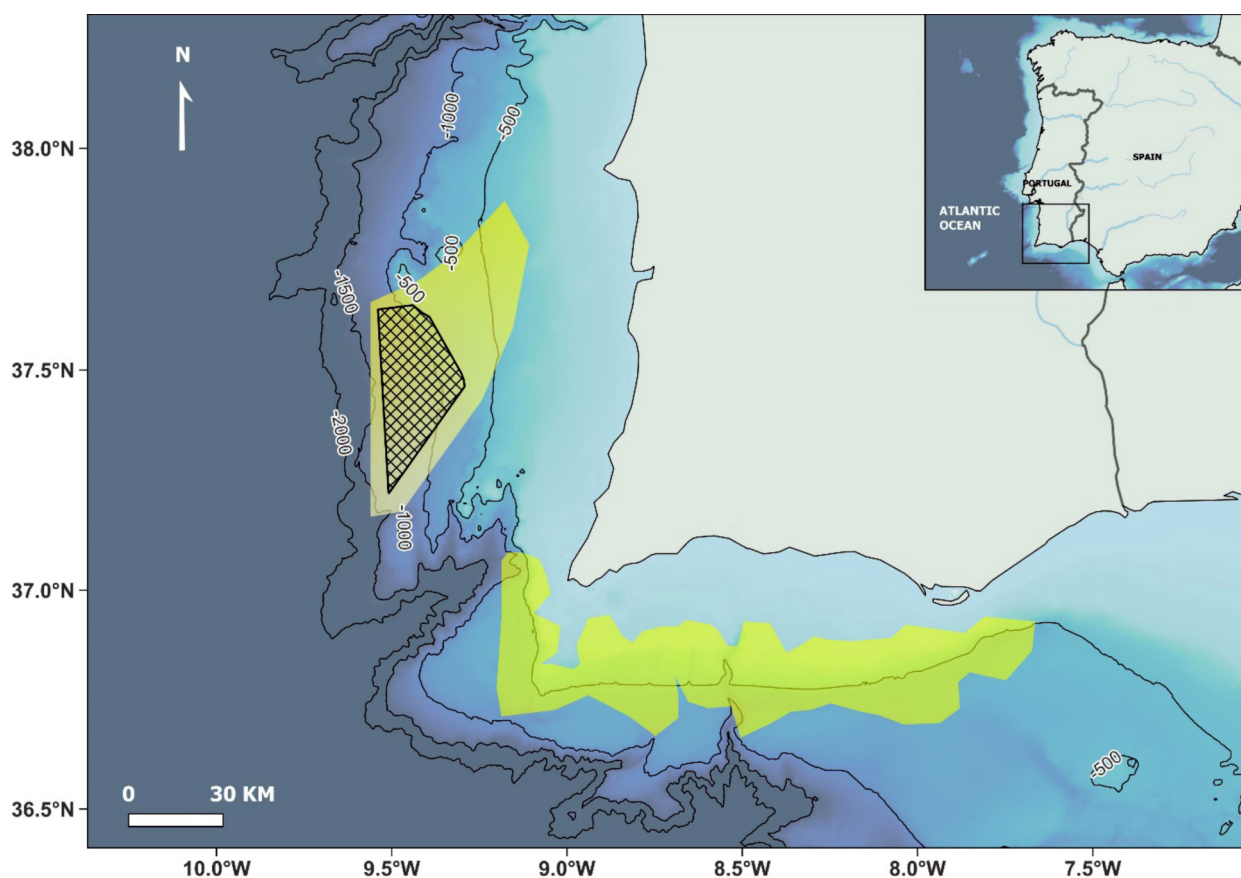


Figure 1. – Study area where the yellow polygons represent the areas where fishing was conducted and the black dashed polygon corresponds to the area where *Oxynotus paradoxus* specimens were caught.

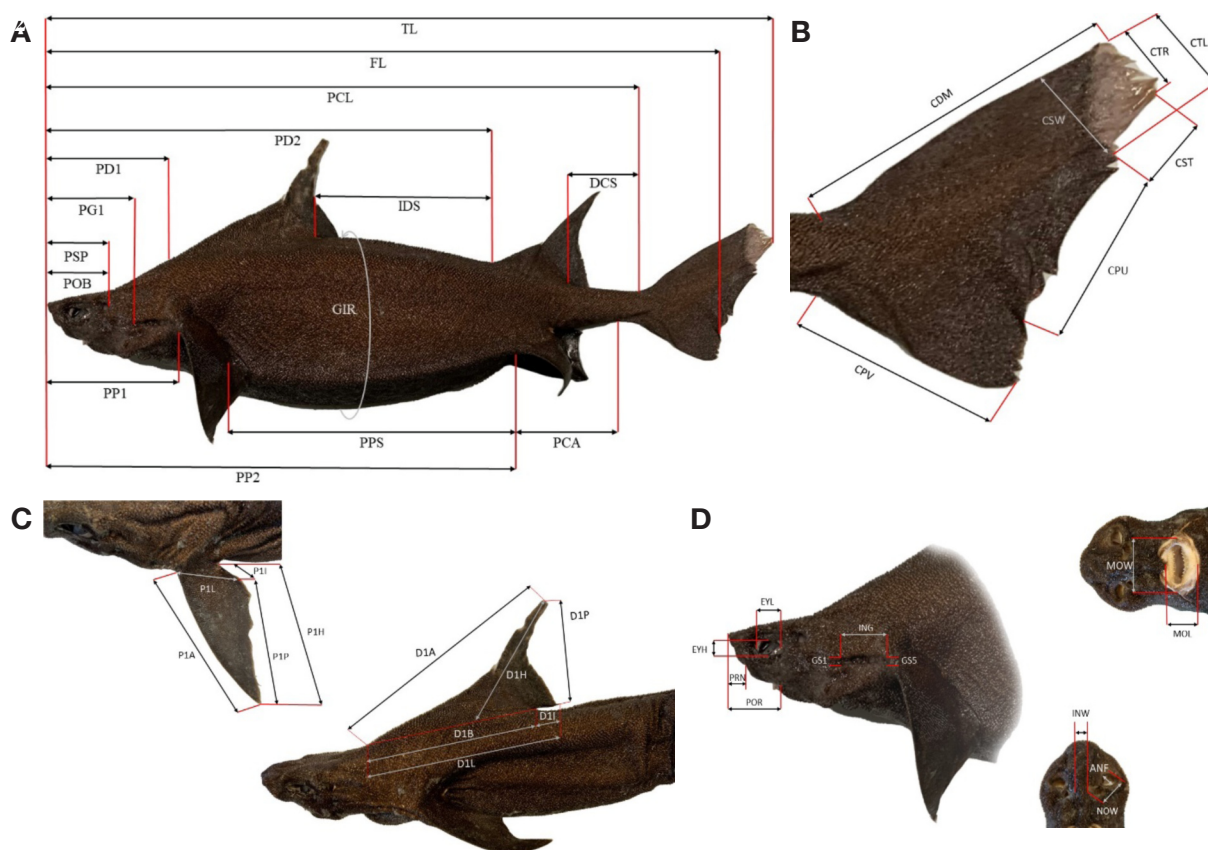


Figure 2. – This figure is not scaled and shows external measurements of the *Oxynotus paradoxus* specimen #4.093 (see Table II for further details). **A:** Full body measurements before dissection and after the first thaw; **B:** Caudal fin measurements; **C:** Pectoral and first dorsal fin measurements after dissection and second thaw; **D:** Eye, gill slits, nostrils, and mouth measurements.

(Risso, 1827) and the scarlet shrimp *Aristaeopsis edwardsiana* (Johnson, 1868). The collection depths varied from 742 to 1238 m and took place during both summer and winter trips in 2021 (Fig. 1).

The fishing depths (m) were recorded using a Star Oddi® mini-CTD. The GPS points, vessel velocity, and vessel track were automatically integrated into the Olrac Dynamic Data Logger (DDL)® software.

Upon collection, the specimens of *O. paradoxus* were frozen onboard and subsequently transported to the Fisheries Biodiversity and Conservation laboratory (CCMAR) at the University of Algarve. Each specimen was weighed unviscerated (g), and its total length (TL) was measured in millimetres. Sex was macroscopically determined, and maturity stages were assigned following Stehmann’s maturity scale (Stehmann, 2002). Recognition of adult females was based on enlarged oocytes and well-rounded ovaries.

For the ecophysiological index, the RNA/DNA standardized ratio (sRD) was determined in accordance with Graça Aranha *et al.* (2023) and references therein. The sRD index is widely employed as a nutritional condition index at the organism level in marine ecology (Chícharo and Chícharo, 2008).

The specimen caught at the greatest depth (Table I, #4.093 Matos *et al.*, 2024) underwent further investigation. After being thawed and frozen twice, external morphometric measurements were taken using a digital calliper (to the nearest 0.5 mm) or a metric tape (for measurements exceeding 120 mm). Given that the morphometry of *Oxynotus* species differs from most sharks due to the unusual shape of their dorsal fins and the absence of anal fins, graphic illustrations depicting the measurements conducted in this study were provided (Fig. 2). These measurements were expressed both in millimetres and as a percentage of total length (% TL) and were compared with the average % TL obtained by Yano and Matura (2002) for a 555 mm TL male and a 508 mm TL female from Western Sahara and Ireland, respectively (Table II).

The liver and gonads were extracted from specimen #4.093. Subsequently, these organs were weighed to the nearest 0.01 g to calculate the hepatosomatic and gonadosomatic indices (Table I).

The hepatosomatic index (HSI) was calculated as:

$$HSI\% = [\text{Liver weight} / \text{Total body weight}] \times 100$$

and the gonadosomatic index (GSI) as:

$$GSI\% = [\text{Gonad weight} / \text{Total body weight}] \times 100$$

RESULTS

Among the collected *Oxynotus paradoxus* specimens, one was identified as a juvenile male (#8.086), while two were juvenile females (#8.085 and 8.087), and one was an adult female (#4.093; Table I).

The adult female exhibited an HSI of 18.6% (liver weight = 374.12 g) and a GSI of 1.33% (gonads weight = 26.87 g). Notably, this adult female displayed the lowest sRD values among all the specimens captured (Table I).

Out of the 65 measurements conducted, only 36 were deemed comparable due to differences in the measurement protocols employed by different authors. The present study adhered to the methodology outlined by Ebert *et al.* (2021), while Yano and Matsura (2002) followed Yano and Tanaka (1983).

Although the measurements conducted in the present study were generally similar to those presented by Yano and Matsura (2002), notable differences were observed. Specifically, the inter-dorsal space (IDS) and spiracle length (SPL) were smaller in the present study, while the pre-orbital length (POB) and pelvic insert to caudal lower origin (PCA) were greater in the present study (Table II).

DISCUSSION

This study presents a noteworthy finding of an *O. paradoxus* specimen captured at 1238 m, marking the highest depth ever reported for this species. This observation supports the hypothesis that the species may occur at greater depths than previously documented (Azevedo *et al.*, 2003; Soldo *et al.*, 2015).

The limited information available on this species in EU waters could be attributed to various factors. Firstly, the rarity of the species, possibly due to its preference for deeper waters, may contribute to the scarcity of sightings. Additionally, areas deeper than 750 m are not covered by the research

Table I. – General information on the *Oxynotus paradoxus* specimens collected off the SW Iberian Peninsula with the code for each specimen, total length (TL) in mm, weight in g, RNA/DNA standardized ratio (sRD), sex (female or male), maturity stage according to Stehmann (2002), mean haul depth in meters, season, latitude, and longitude of the start of the haul.

Code	TL (mm)	Weight (g)	sRD	Sex	Maturity stage	Mean depth (m)	Season	Latitude (°N)	Longitude (°W)
#4.093	650	2015.0	0.08	F	3 (mature)	1238	Winter	37.589884	-9.512294
#8.085	240	62.5	0.62	F	1 (immature)	765	Summer	37.630817	-9.405929
#8.086	285	154.0	0.41	M	1 (immature)	752	Summer	37.49418	-9.298284
#8.087	440	596.0	0.71	F	2 (maturing)	742	Summer	37.622667	-9.39556

Table II. – External morphometric measurements (mm) and percentage of total length (% TL) of a female *Oxynotus paradoxus* (code #4.093) from the SW Iberian Peninsula collected at 1238 m depth, and as a mean of the % TL for a female and male for Yano and Matsura (2002). * Measurements not presented in Fig. 2.

Measurements	Code	#4.093		Yano and Matsura (2002)
		n = 1		n = 2
Sex		F		F-M
Range of TL (mm)		650		508-555
		mm	% TL	% TL
Pre-orbital length	POB	36	5.54	3.8
Pre-narial length	PRN	16	2.46	1.8
Pre-oral length	POR	38.5	5.92	5.8
Pre-spiracular length	PSP	71	10.92	9
Pre-first dorsal length	PD1	92	14.15	16.6
Pre-second dorsal length	PD2	344	52.92	56.4
Pre-pectoral length	PP1	115	17.69	19.6
Pre-pelvic length	PP2	350	53.85	
Inter-dorsal space	IDS	95	14.62	21.9
Dorsal caudal space	DCS	68	10.46	11.4
Pectoral-pelvic space	PPS	222	34.15	37.8
First dorsal anterior margin	D1A	205	31.54	
First dorsal height	D1H	108.5	16.69	16.2
First dorsal posterior margin	D1P	111	17.08	15
First dorsal base	D1B	145	22.31	18.9
Second dorsal anterior margin	D2A*	139	21.38	
Second dorsal height	D2H*	106	16.31	14.6
Second dorsal posterior margin	D2P*	103	15.85	14.4
Second dorsal base	D2B*	82	12.62	12.6
Pelvic anterior margin	P2A*	78.5	12.08	9.9
Pelvic height	P2H*	61	9.38	
Pelvic posterior margin	P2P*	44	6.77	
Pelvic base	P2B*	46	7.08	6.3
Pelvic inner margin	P2I*	35	5.38	
Dorsal caudal margin	CDM	124	19.08	22
Terminal caudal margin	CTR	31	4.77	
Sub-terminal caudal-fin margin	CST	29	4.46	
Upper post-ventral caudal margin	CPU	100	15.38	
Caudal pre-ventral margin	CPV	87	13.38	

surveys carried out in Portuguese waters under the EU Data Framework Collection for Fisheries. Furthermore, the imposition of a total allowable catch of 0 for this species since 2010 by the EU (European Council Regulation n° 2021/91) prohibits its landing. In support of the first hypothesis, it is noteworthy that in NW Africa, 66 specimens were caught at depths ranging between 803 and 1044 m (Pajuelo *et al.*, 2016).

The capture of an adult female *Oxynotus paradoxus* at 1238 m, a depth surpassing that of the three juveniles caught during the summer at shallower depths (742 to 765 m), has led us to hypothesize potential ontogenetic segregation by season, depth, or both. This phenomenon has been reported for other deep-sea sharks such as *Centroscymnus coelolepis*, *Centrophorus squamosus*, and *Deania calceus* (Moura *et al.*, 2014). The relatively small area where the specimens were collected in this study, compared to the total surveyed area, raises the possibility of a sparse distribution, as also previously suggested by Viana and Lisher (2018) for an *Oxynotus* sp. in the western Indian Ocean.

The adult female, measuring 650 mm TL, displayed large well-rounded ovaries at maturity stage III, while the two females were juveniles at maturity stages I and II (Stehmann, 2002). Although no reproductive studies are available for *O. paradoxus*, Capapé *et al.* (1999) observed that the smallest adult females of the congener *O. centrina* in the Mediterranean and East Atlantic had a TL of 640 mm.

For adult females of *O. centrina*, the HSI range is 23.4-42.0% (Capapé *et al.*, 1999), and an immature female of *Oxynotus* sp. caught in the western Indian Ocean presented a 36.6% HSI (Viana and Lisher, 2018). On the other hand, Megalofonou and Damalas (2004) found 18.8% HSI in an *O. centrina* gravid female in the Mediterranean Sea, supporting that HSI decreases sharply in breeding females as liver reserves are used for gonadal products (Capapé *et al.*, 1999; Megalofonou and Damalas, 2004). The adult female captured in this study had an HSI of 18.6%, closer to the value found by Megalofonou and Damalas (2004); however, since the GSI values were 1.33%, it appears that hepatic reserves were not used in gonadal products (Capapé *et al.*, 1999). Since HSI depends on lipid deposition derived from food intake, the low HSI values suggest the use of hepatic reserves due to food scarcity (Craik, 1978). In addition, the sRD of the adult female was also very low compared to the values obtained for the other *O. paradoxus* in this study and also to those reported by Graça Aranha *et al.* (2023) for five deep-sea shark species sampled in the same area. This may indicate reduced

Table II. – Continued.

Measurements	Code	#4.093		Yano and Matsura (2002)
		n = 1		n = 2
Sex		F		F-M
Range of TL (mm)		650		508-555
		mm	% TL	% TL
Head length	HDL*	121	18.62	
Mouth length	MOL	8	1.23	
Mouth width	MOW	31.5	4.85	5.4
First gill slit height	GS1	10	1.54	1.3
Fifth slit height	GS5	8	1.23	1.1
Inter-gill length	ING	28	4.31	
Spiracle length	SPL*	5	0.77	2.2
Nostril width	NOW	16.5	2.54	
Anterior nasal flap length	ANF	11.5	1.77	
Internarial width	INW	9	1.38	1.3
Eye spiracle space	ESL*	12.5	1.92	
Eye length	EYL	28.5	4.38	4.5
Eye height	EYH	9.5	1.46	1.8
Head width	HDW*	51	7.85	
Trunk width	TRW*	74.5	11.46	
Caudal subterminal width	CSW	37	5.69	
Caudal terminal lobe	CTL	39	6.00	
First dorsal inner margin	D1I	29	4.46	
First dorsal length	D1L	175	26.92	23.2
Second dorsal inner margin	D2I*	27.5	4.23	
Second dorsal length	D2L*	107	16.46	14.8
Pelvic length	P2L*	63	9.69	11.4
Fork length	FL	576	88.62	75.7
Precaudal length	PCL	515	79.23	78.6
Snout to vent	SVL*	358	55.08	
Pelvic insert to caudal lower origin	PCA	118	18.15	9.9
Interorbital space	IOS*	39	6.00	8.5
Caudal peduncle width	CPW*	14	2.15	
Lower labial furrow length	LLA	16	2.46	
Girth	GIR	350	53.85	
Pectoral anterior margin	P1A	131	20.15	15
Pectoral radial length	P1R*	50	7.69	7.2
Pectoral inner margin	P1I	24	3.69	
Pectoral posterior margin	P1P	91	14.00	9.9
Pectoral height	P1H	115	17.69	
Pectoral length	P1L	57	8.77	

nutritional condition, suggesting that this female did not feed in the short to medium term prior to collection (Buckley *et al.*, 1999).

Given that deep-sea sharks in this area feed on commercially important crustaceans (Graça Aranha *et al.*, 2023), and that adult females of *O. centrina* are also known to feed on crustaceans (Capapé, 1975; Compagno, 1984; Barrull and Mate, 1996), it is possible that *O. paradoxus* also prey on crustaceans. Since its spatial distribution overlaps with deep-water fisheries for crustaceans (*e.g.*, Borges *et al.*, 2001; Campos *et al.*, 2021), some overlap between their foraging grounds and fishing areas may occur. Unfortunately, dietary information was not available in the present study due to the small number of specimens collected. Given the metabolic rates and feeding habits of deep-sea shark species (*e.g.*, Graça Aranha *et al.*, 2023), a large number of stomachs from specimens that died during fishing procedures should be considered for this purpose. This approach, coupled with stable isotope analysis, would enhance our understanding of *O. paradoxus*' preferred prey and potential interactions with fisheries resources.

Morphometric measurements in this study were generally similar to those presented by Yano and Matsura (2002), with some differences noted in PCA, IDS, SPL, and POB measurements. These variations could be attributed to specimen preservation or divergences in measurement protocols, as highlighted by Viana and Lisher (2018), thus, a standardized approach to *Oxynotus* spp. measurements is recommended for future comparisons.

Despite the limitations imposed by the low number of specimens, our individualized approach contributes to the advancement of knowledge on this rare species.

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Ethical standards. – This study was conducted in accordance with the Guidelines of the European Union Council (86/609/EU) and Portuguese legislation for the use of animals and enforced by

CCMAR. CCMAR staff are certified to house and conduct experiments with live animals, and their facilities are also certified in accordance with the three “R” policy, national and European legislation, and with guidelines defined by the ethical committee ORBEA CCMAR-CBMR.

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