


# First record of the opal chimaera, *Chimaera opalescens* (Holocephali: Chimaeridae) and revision of the occurrence of the rabbitfish *Chimaera monstrosa* in the Azores waters

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## Abstract

The presence of the opal chimaera, *Chimaera opalescens*, is reported for the first time in the deep waters of the Azores, with the capture of four specimens by fishermen and the video recording of an additional five individuals. Species identification was supported by the 646 bp sequenced fragment of the mitochondrial gene cytochrome oxidase subunit I. Because *C. opalescens* is a recently recognised species that had been recurrently misidentified as rabbitfish, *Chimaera monstrosa*, the historical data of *C. monstrosa* in the Azores were reviewed to assess the possible presence of both *Chimaera* species in the region. Although several authors have reported the occurrence of *C. monstrosa* in the Azorean waters since the 1800s, the majority of these are based on only three specimens caught during the late 1800s. The investigation performed using literature and examination of the museum specimens still available concluded that the most likely scenario is that *C. monstrosa* is absent from the Azores and past records of that species in the region are most likely misidentifications of *C. opalescens*.

## KEYWORDS

deep sea, first record, mtDNA, museum specimens, north-eastern Atlantic, video imaging

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## 1 | INTRODUCTION

Chimaeras (Holocephali) are represented by only three families worldwide: Callorhynchidae, Rhinochimaeridae and Chimaeridae which comprise 51 valid species (Weigmann, 2016). The family Chimaeridae includes the genus *Chimaera* Linnaeus 1758 with 16 valid species and the genus *Hydrolagus* Gill 1862 with 24 valid species worldwide (Weigmann, 2016). The two genera are distinguishable by the presence of an anal fin in *Chimaera*, which is absent in *Hydrolagus* (Didier *et al.*, 2012). Until recently, *Chimaera monstrosa* was the only *Chimaera* species reported for the north-eastern Atlantic, but in 2011 a new species, *Chimaera opalescens*, was described from deep-water assemblages (Luchetti *et al.*, 2011). There are currently six Chimaeridae species reported for the north-eastern Atlantic, four belonging to the genus *Hydrolagus* and two belonging to the genus *Chimaera* (Weigmann, 2016). Chimaeras are by-catch of deep-water fisheries and are usually discarded as they have no commercial value (Blasdale & Newton, 1998; Moura *et al.*, 2004). Not much is known about the groups' ecology and behaviour, except for *C. monstrosa*, one of the most studied chimerids, with several studies on its reproductive biology, age and population structure (Calis *et al.*, 2005; Catarino *et al.*, 2017; Holt *et al.*, 2013; Moura *et al.*, 2004; Sion *et al.*, 2004). *C. monstrosa* is commonly reported along the continental slopes of the north-eastern Atlantic (from Norway to Morocco), including Greenland, Iceland, Azores and Madeira archipelagos (*e.g.*, Ebert & Stehmann, 2013), and in the Mediterranean Sea (*e.g.*, Ragonese *et al.*, 2013). The species is considered "near threatened" by IUCN because of its biological characteristics, such as its long life span and late maturation (Calis *et al.*, 2005; Dagit *et al.*, 2007), and the high levels of by-catch by trawling in certain areas of the north-eastern Atlantic. This species feeds mainly on bottom invertebrates; nonetheless, the diet can vary according to food availability (Macpherson, 1980; Moura *et al.*, 2005). In contrast, *C. opalescens* was first described as a new species in 2011, along the slope off the British Isles and France (Luchetti *et al.*, 2011). Additional records were obtained from Greenland, Goringe and Galicia banks (Bañon *et al.*, 2016; Luchetti *et al.*, 2011; Vieira & Cunha, 2014), and more recently from Madeira and the north-west African slopes (Freitas *et al.*, 2017). The two species are distinguished by body colour, iris, unpaired fins and digestive canal. Adult males may also be distinguished by the morphology of the claspers, dorsal and prepelvic tenacula (Luchetti *et al.*, 2011). Moreover, *C. opalescens* seems to occur in deeper waters than *C. monstrosa* (Holt *et al.*, 2013; Luchetti *et al.*, 2011).

The Azores are a remote archipelago located in the North Atlantic on the Mid-Atlantic Ridge consisting of nine volcanic islands and several seamounts (Morato *et al.*, 2008), all surrounded by great depths. The first records of *C. monstrosa* in the Azores refer to specimens captured during the late 1800s by the *Talisman* (Vaillant, 1888) and by the *Principe Albert I of Monaco* Expeditions (PAM; Roule, 1919). Since then, *C. monstrosa* has been consistently included in several species' checklists for the Azores region (*e.g.*, Porteiro *et al.*, 2010; Santos *et al.*, 1997).

This is the first study to report the occurrence of *C. opalescens* in the Azores. Furthermore, because *C. opalescens* has been repeatedly misidentified as *C. monstrosa* (Luchetti *et al.*, 2011), the *C. monstrosa* specimens previously captured in the Azores were re-examined to determine whether the two *Chimaera* species co-exist in this oceanic region, part of the Mid-Atlantic Ridge.

## 2 | MATERIALS AND METHODS

### 2.1 | Ethical statement

No specific permits were required to perform this work. The fresh specimens used were caught as by-catch in the commercial bottom longline fishery. All fresh specimens were dead upon arrival on board because they were fished from great depths.

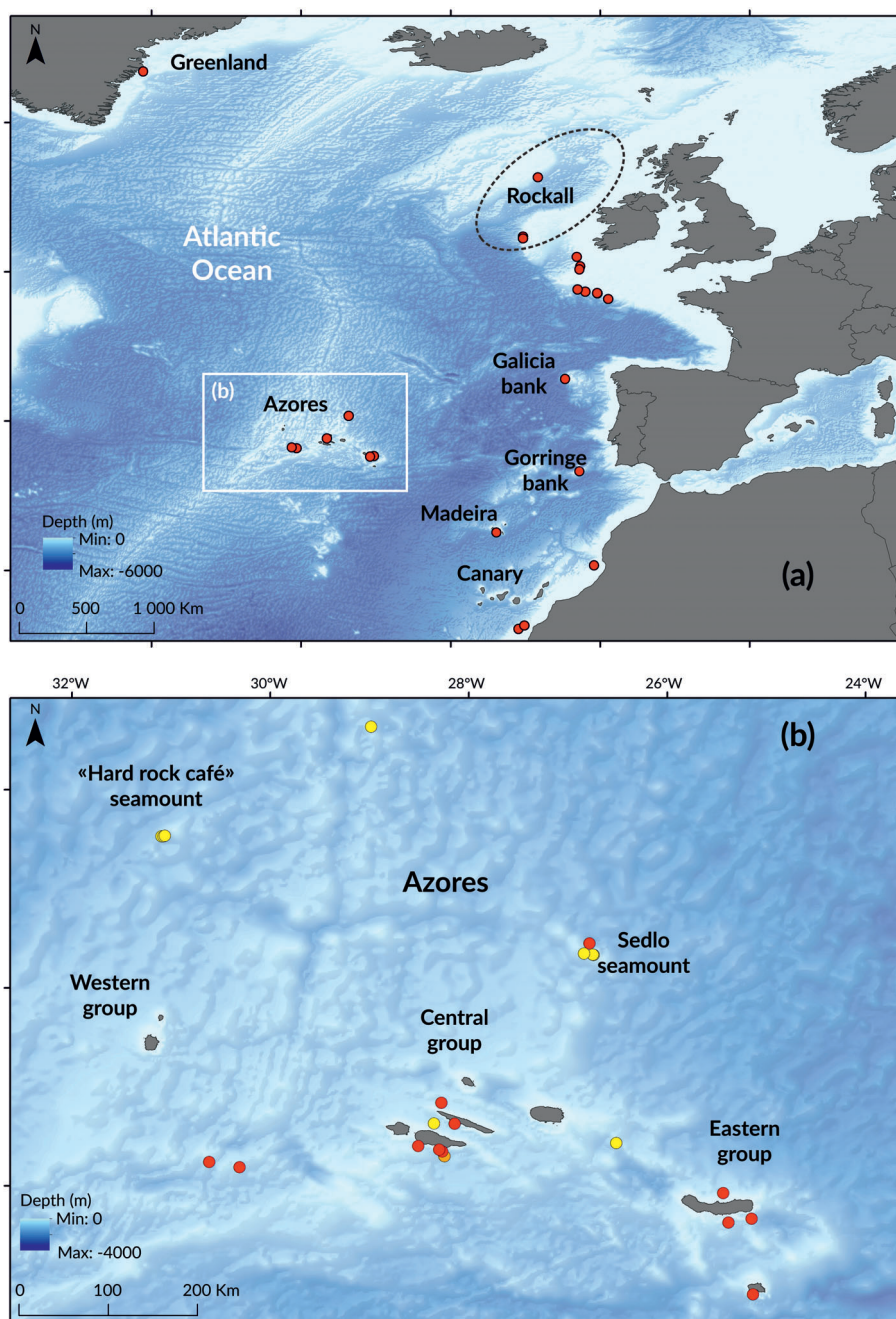
### 2.2 | Sampling and molecular analyses on the collected specimens

Four specimens of *C. opalescens* were caught in the central and eastern groups of the Azores archipelago by commercial fishing vessels (Figure 1; Table 1). The vessels used drift bottom longlines (*e.g.*, Machete *et al.*, 2011) to target the black scabbardfish (*Aphanopus* spp.) and other deep-water fishes, such as the common mora, *Mora moro*. Specimens captured off Faial Island were initially examined fresh, whereas specimens from São Miguel Island were transported frozen to the Department of Oceanography and Fisheries (DOP) at Faial, stored at  $-20^{\circ}\text{C}$  and thawed before examination. A small piece of muscle tissue was collected from each specimen and preserved in 96% ethanol for genetic analyses.

The specimens were photographed, measured, weighed and sexed. After thawing, all measurements were taken at the laboratory according to Luchetti *et al.* (2011): total length (TL) — snout tip to tip of caudal-fin filament; pre-caudal length (LPC) — snout tip to origin of upper caudal lobe; pre-second dorsal fin length — snout tip to origin of second dorsal fin; pre-first dorsal fin length — snout tip to origin of first dorsal fin; head length — snout tip to dorsal edge of gill opening; dorsal spine length along anterior margin — first dorsal-fin origin to tip of spine; first dorsal-fin base length — fin origin to insertion; inter-dorsal space — distance between insertion of first dorsal fin and origin of second dorsal fin; second dorsal-fin base length — fin origin to insertion; caudal-filament length — insertion of dorsal lobe of caudal fin to tip of caudal filament; pectoral-fin anterior margin length — pectoral-fin origin to apex; pelvic-fin anterior margin length — pelvic-fin origin to apex; eye length — horizontal orbital diameter; eye height — vertical orbital diameter; total length of clasper — from insertion of pelvic fin to tip of clasper.

Total genomic DNA was extracted from the four specimens using the Mag-Bind Tissue DNA kit (OMEGA bio-tek, Norcross, GA, USA) according to the manufacturer's instructions and using the autonomous extractor KingFisher mL (Thermo Electron Corporation, Waltham, MA, USA). A portion of the cytochrome *c* oxidase subunit I (COI)

**FIGURE 1** Locations of *Chimaera* specimens collected. (a) Known distribution to date of *Chimaera opalescens*. Red dots report on confirmed specimens from: Luchetti *et al.* (2011), Vieira and Cunha (2014), Møller *et al.* (2004), Bañon *et al.* (2016), Freitas *et al.* (2017) and this study (Azores). The dashed area in Rockall represents several specimens reported by Holt *et al.* (2013) not illustrated. (b) Details of the *Chimaera* specimens' collection sites in the Azores region. Red dots indicate confirmed *C. opalescens* specimens (the location of samples without coordinates in Table 1 is approximate); yellow dots indicate dubious *Chimaera* specimens (eight from FISHOR) or classified as *C. cf. opalescens*; orange dot corresponds to the *Hydrolagus pallidus* specimen. Specimen AZO6 was not represented in the map because no location information was available



region of the mitochondrial DNA was amplified by PCR using the FishF2 and FishR2 primers (Ward *et al.*, 2005). The thermal cycle parameters started with an initial denaturation of 2 min at 94°C, followed by 35 cycles of denaturation of 30 s at 94°C, annealing for 1 min at 50°C, extension for 1 min 35 s at 72°C, with a final extension of 7 min at 72°C. Template-free mix controls were included in each PCR to detect possible DNA contamination. Electrophoresis of PCR products on a 1% agarose gel was performed to evaluate the integrity of the products. Finally, all amplified products were purified using ExoSAP-IT (ThermoFisher Scientific, Santa Clara, CA, USA) and sequenced commercially at BMR Genomics (www.bmr-genomics.it, Padua, Italy).

Sequences of PCR products were compared with those deposited at the National Center for Biotechnology Information database using the BLAST tool (Altschul *et al.*, 1990; Zhang *et al.*, 2000). Four sequences from *C. opalescens* were available in GenBank (accession numbers: GU244531–GU244534; Luchetti *et al.*, 2011) and were used as reference for all downstream analyses. All sequences were aligned using SEAVIEW (Galtier *et al.*, 1996) and CLUSTAL\_X (version 1.8.3; Thompson *et al.*, 1997).

After completing the identification, the four specimens were fixed in 10% formalin solution and then transferred to 80% ethanol for long-term storage. Specimens are deposited at the reference

**TABLE 1** Capture details of all *Chimaera* specimens analysed

Specimen code	Museum code	Capture date	Depth (m)	Source	Capture site	Fishing gear	Latitude	Longitude
Fresh <i>Chimaera opalescens</i> specimens								
AZ01	COLETA 9915	28 October 2011	1193	Local fisheries	Off Faial	Longline	38,839	-28,274
AZ02	COLETA 9916	24 April 2013	1280–1463	Local fisheries	Off Faial	Longline	–	–
AZ03	COLETA 9917	24 March 2015	>800	Local fisheries	Off São Miguel	Longline	–	–
AZ04	COLETA 9918	17 May 2016	823–914	Local fisheries	Off Faial da Terra (São Miguel)	Longline	–	–
<i>Chimaera monstrosa</i> specimens								
PAM01 <sup>a</sup>	MOM-900373	14 July 1895	1165	PAM	Southeast Terceira Island	Trawl nets	38,433	-26,513
PAM02	MOM-POI-4205	31 July 1896	1692	PAM	South of Pico Island	Longline	38,300	-28,246
TAL01	MNHN-IC-1884-0395	1883	1257	Talisman	São Jorge/Pico channel	Trawl nets	38,633	-28,350
FIS01	COLETA 9913	30 May 2001	853–1136	FISHOR	Southwest Faial Island	Trawl nets	38,243	-30,616
FIS02	COLETA 9914	3 June 2001	1134–1141	FISHOR	Sedlo seamount	Trawl nets	40,354	-26,823
FIS03 <sup>b</sup>	–	4 June 2001	1138–1160	FISHOR	“Hard Rock Café” seamount	Trawl nets	41,531	-31,098
FIS04 <sup>b</sup>	–	7 June 2001	1258–1394	FISHOR	DMA seamount	Trawl nets	42,639	-28,984
FIS05 <sup>b</sup>	–	20 June 2001	906–1302	FISHOR	Sedlo seamount	Trawl nets	40,334	-26,740
FIS06 <sup>b</sup>	–	20 June 2001	906–1302	FISHOR	Sedlo seamount	Trawl nets	40,336	-26,748
FIS07 <sup>b</sup>	–	22 June 2001	950–1248	FISHOR	Sedlo seamount	Trawl nets	40,336	-26,748
FIS08 <sup>b</sup>	–	23 June 2001	1129–1142	FISHOR	Hard Rock Café seamount	Trawl nets	41,531	-31,078
FIS09 <sup>b</sup>	–	5 December 2001	1113–1136	FISHOR	Hard Rock Café seamount	Trawl nets	41,538	-31,065
FIS10 <sup>b</sup>	–	10 January 2002	1050–1145	FISHOR	Sedlo seamount	Trawl nets	40,348	-26,837
AZ05	COLETA 10586	8 December 2004	841,25	Local fisheries	Off Porto Formoso (São Miguel)	Longline	–	–
AZ06	COLETA 10587	–	–	Local fisheries	–	Likely longline	–	–

Note: Coordinates are in decimal degrees, COLETA: reference collection at DOP, University of the Azores; MOM: Museum Oceanographic of Monaco; MNHN: Muséum National D'Histoire Naturelle, Paris,

<sup>a</sup>Denotes no specimen available, only aquarelle illustration,

<sup>b</sup>Specimens from FISHOR survey discarded at sea unavailable to be revised,

collection at DOP, University of the Azores (COLETA, 2015), with the catalogue numbers reported in Table 1.

## 2.3 | Video imaging

Bathyal *in situ* observations and image collection were performed by the manned submersible *LULA 1000* (Rebikoff-Niggeler Foundation), which is certified and rated for diving operations at 1000 m depth with a three-membered crew. The *LULA 1000* submersible has been in service in the Azores since 2013. High-quality video was captured by several on-board 4K video cameras. The main camera (Sony Alpha 7SII/R11) was mounted in the focal centre of the 150° spherical front viewport (1400 mm diameter). The lighting system consisted of several strategically positioned HMI lights (400 and 200 W). Positioning

was obtained via an USBL tracking system mounted on the submersible and the support catamaran *Ada Rebikoff*. The latter was also equipped with a CodaOctopus F180 Motion Sensor for ship motion correction and higher accuracy of the tracking data. Species identification for filmed specimens was based on the presence of an anal fin (to separate *Chimaera* from *Hydrolagus*) and on the colouration characters which distinguish *C. opalescens* from *C. monstrosa*, such as body and iris colouration (Luchetti *et al.*, 2011).

## 2.4 | Occurrence of *C. monstrosa* in the Azores

To confirm the possible co-occurrence of the two *Chimaera* species in the Azores region, past records of *C. monstrosa* were re-analysed. For this, an exhaustive bibliographic review of studies reporting *C.*



**TABLE 2** Summary of the biological and morphological details of *Chimaera* specimens analysed, with a revised identification (ID)

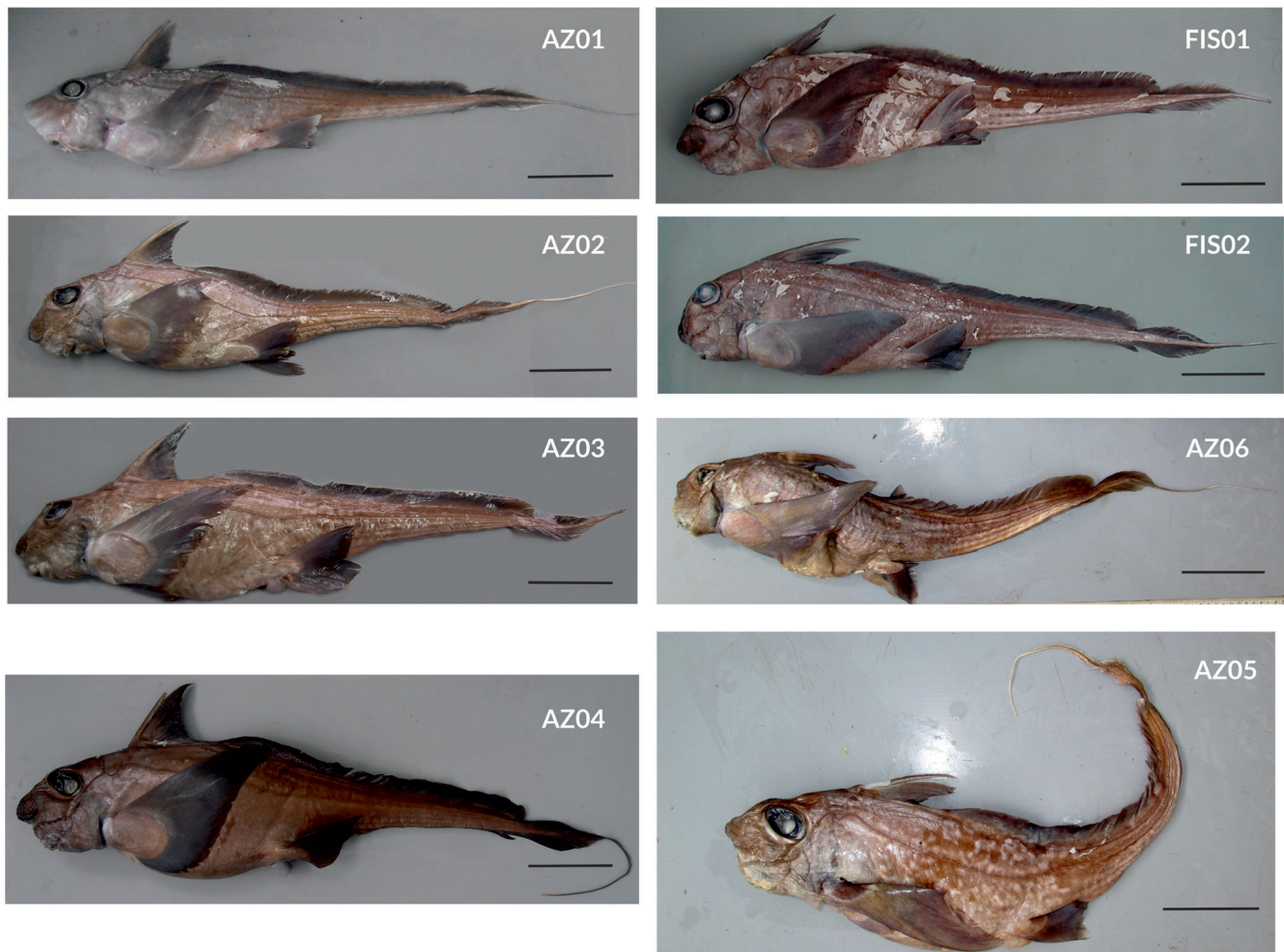
Code	TL	LPC	CFI	%CFI/LPC	PD2	PD1	HDL	DSA	D1B	IDS	D2B	P1A	P2A	EYL	EYH	CLT <sup>a</sup>	TW (g)	Sex	Mat	Iris colour	Gut colour	Anal fin	Original ID	Revised ID
AZ01	770	525	146	27,8	195	108	107	Broken	62	25	357	163	86	41	23	59	1150	M	Adult	Black	Pink	Present	<i>Chimaera opalescens</i>	–
AZ02	740	520	141	27,1	192	116	100	96	73	15	320	129	78	37	24	55	960	M	Adult	Black	Pink	Present	<i>C. opalescens</i>	–
AZ03	740 <sup>b</sup>	596	Cut	–	212	122	112	Broken	69	20	360	193	98	41	28	–	1560	F	Adult	Black	Pink	Present	<i>C. opalescens</i>	–
AZ04	860	580	162	27,9	218	137	114	Broken	80	15	368	197	105	39	29	–	1940	F	Adult	Black	Pink	Present	<i>C. opalescens</i>	–
PAM01 <sup>c</sup>	230	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	Black	–	Present	<i>Chimaera monstrosa</i>	<i>C. cf. opalescens</i>
PAM02	1030	885	23	2,6	347	212	226	Broken	60	52	520	285	150	46	47	115	–	M	Adult	–	–	Absent	<i>C. monstrosa</i>	<i>Hydrolagus pallidus</i>
TAL01	226	137	61	44,5	–	–	–	–	–	–	–	–	–	–	–	–	–	F	Juvenile	Black	–	Present	<i>C. monstrosa</i>	<i>C. cf. opalescens</i>
FIS01	551	430	39	9,1	149	77	72	Broken	25	49	285	143	75	35	24	18	520	M	Juvenile	Black	Pink	Present	<i>C. monstrosa</i>	<i>C. opalescens</i>
FIS02	762	560	87	15,5	211	115	109	129	57	33	355	188	95	34	30	–	1570	F	Adult	Black	Pink	Present	<i>C. monstrosa</i>	<i>C. opalescens</i>
AZ05	795	585	121	20,7	195	130	110	104	61	16	382	191	96	42	28	–	1480	F	Adult	Black	Pink	Present	<i>C. monstrosa</i>	<i>C. opalescens</i>
AZ06	765	525	151	28,8	208	156	92	Broken	60	30	334	187	86	37	28	–	1110	F	Adult	Black	Pink	Present	<i>C. monstrosa</i>	<i>C. opalescens</i>

Note: Measurements are in millimetres. Caudal-filament length (CFI): insertion of dorsal lobe of caudal fin to tip of caudal filament; dorsal spine length along anterior margin (DSA); first dorsal-fin origin to tip of spine; eye height (EYH); vertical orbital diameter; eye length (EYL); horizontal orbital diameter; first dorsal fin base length (D1B); fin origin to insertion; head length (HDL); snout tip to dorsal edge of gill opening; inter-dorsal space (IDS); distance between insertion of first dorsal fin and origin of second dorsal fin; Mat: maturation; pectoral-fin anterior margin length (P1A); pectoral-fin origin to apex; pelvic-fin anterior margin length (P2A); pelvic-fin origin to apex; %CFI/LPC: percentage of the CFI–LPC ratio; pre-caudal length (LPC); snout tip to origin of upper caudal lobe; pre-first dorsal-fin length (PD1); snout tip to origin of first dorsal fin; pre-second dorsal-fin length (PD2); snout tip to origin of second dorsal fin; second dorsal-fin base length (D2B); fin origin to insertion; total length (TL); snout tip to tip of caudal-fin filament; total length of clasper (CLT): from insertion of pelvic fin to tip of clasper; TW: total weight.

<sup>a</sup>Present only in males.

<sup>b</sup>TL measured but with cut caudal filament.

<sup>c</sup>Denotes no specimens available, only aquarelle illustration.



**FIGURE 2** *Chimaera opalescens* specimens collected in the Azores region. Scale bar = 10 cm. Photos taken after thawing

**TABLE 3** Summary of *Chimaera opalescens* specimens filmed with LULA 1000 submersible

Dive	Date	Depth (m)	Location	Area	Latitude	Longitude
2016-075	13 July 2016	1000	Off Lajes	South Pico	38,348	-28,267
2016-082	1 August 2016	1000	Off Urzelina	South São Jorge	38,629	-28,141
2016-090	29 August 2016	1000	Off Vila do Porto	South Santa Maria	36,905	-25,133
2017-105	20 July 2017	1000	Off Lajes	South Pico	38,368	-28,298
2018-157	1 September 2018	855	Off São Mateus	Southwest of Pico	38,404	-28,508

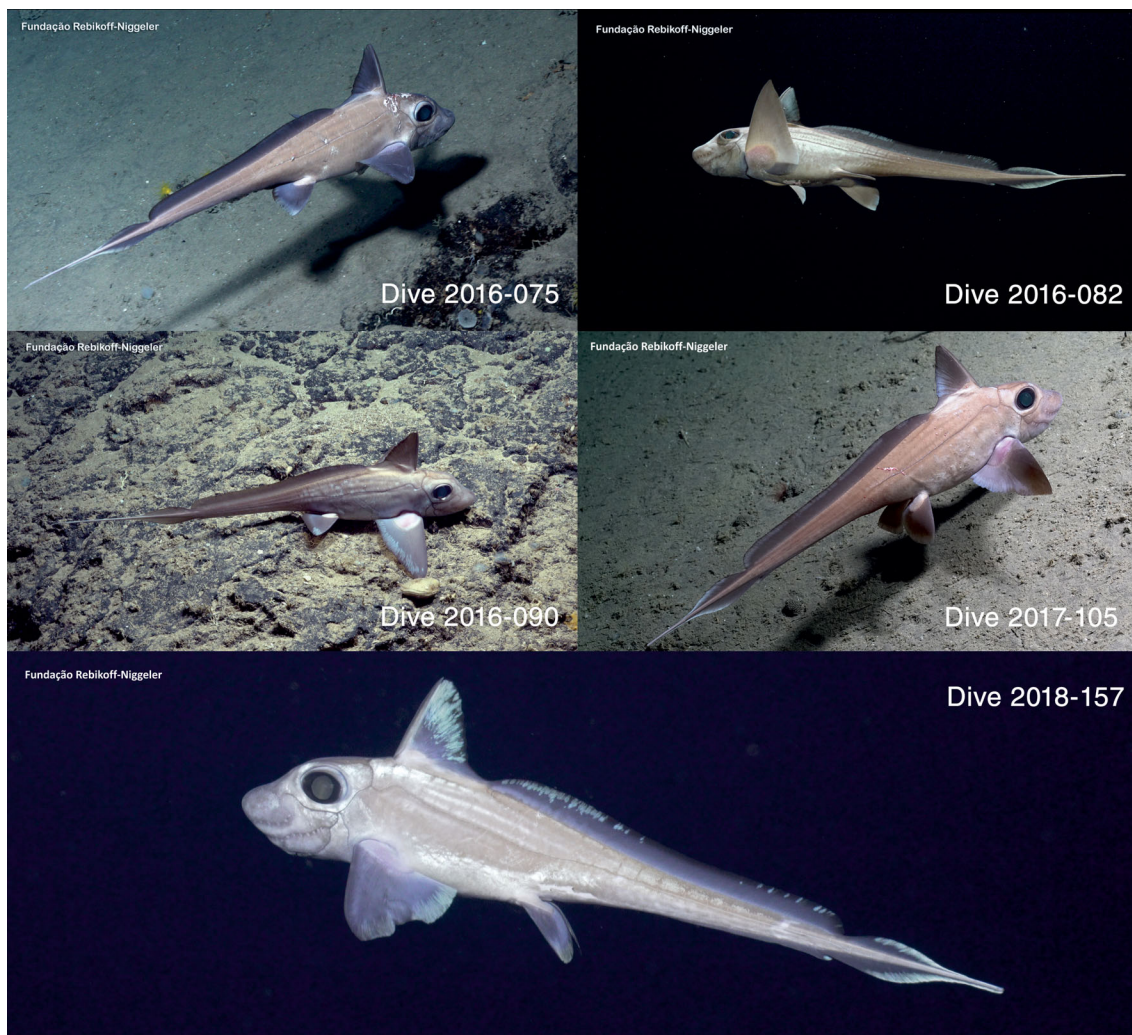
Note: Coordinates are in decimal degrees,

*monstrosa* specimens for the Azores region was performed. The search for former records of the species started with the checklist for marine fishes of the Azores (Santos *et al.*, 1997), in which the authors compile all studies reporting the occurrence of *C. monstrosa* for the region up to the date of publication. All studies reporting *C. monstrosa* records after Santos *et al.* (1997) to the present date were also screened separately. Each publication was then classified as either (a) first-hand record (those that actually collected *C. monstrosa* specimens in the Azores) or (b) second-hand record (those that refer to first-hand records).

Where possible, all specimens of *C. monstrosa* captured in the Azores region that featured in first-hand records were re-examined to validate the taxonomic identification (Table 1). These specimens were as follows:

- Three specimens collected during the late 1800s during PAM or *Talisman* expeditions:

One specimen, MOM-POI-4205 (91-0309; PAM02), is deposited at the Oceanographic Museum of Monaco (MOM). The illustration of



**FIGURE 3** Observations of *Chimaera opalescens* in the Azores archipelago, using the LULA 1000 submersible. Specimens show the presence of an anal fin and a black iris [Correction added on 20 July 2020, after first online publication: Figure 3 has been updated.]

a second specimen (90-0373; PAM01), captured during the PAM expeditions but not kept, is in the exhibition at MOM. And the third specimen, MNHN-IC-1884-0395 (TAL01), is deposited at the Muséum National D'Histoire Naturelle, Paris (MNHN).

- Two of 10 specimens identified as *C. monstrosa* were caught during an exploratory deep-water trawl fishing cruise in the Azores (FISHOR project 2001/2002; Melo & Menezes, 2002; Menezes *et al.*, 2012). These two specimens were photographed, preserved and deposited at the COLETA repository (Table 1), whereas the other eight were discarded at sea.

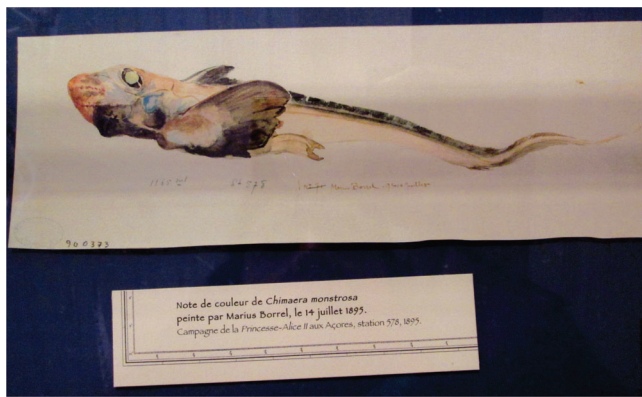
- Two specimens of *C. monstrosa* (AZ05 and AZ06) were obtained from the local fishery and preserved at  $-20^{\circ}\text{C}$  at DOP for several years. Specimen AZ05 (COLETA 10586) was collected in 2004 off São Miguel island. No information on collection site or date was available for specimen AZ06 (COLETA 10587). DNA extraction and amplification were performed following the same protocol used for the freshly collected specimens.

### 3 | RESULTS

#### 3.1 | Biological and molecular data on the freshly collected specimens

The four specimens, collected at more than 800 m depth by commercial fisheries, consisted of two males and two females with total lengths varying between 74 and 86 cm (Tables 1 and 2). Specimens presented evenly coloured and iridescent bodies while fresh, black irises, unpaired brown to purple fins (uniformly coloured or with pale/whitish edges) and pinkish walls of the digestive canals (Table 2; see Figure 2, Supporting Information Figures S1 and S2). These characteristics are consistent with the description of *C. opalescens* by Luchetti *et al.* (2011). Morphological measurements are also in accordance to those reported for the species (Table 2), namely the caudal filament varying from 141 to 162 mm, corresponding to *ca.* 27% of the LPC. As further confirmation to the identification of these specimens, the 646 bp of the mitochondrial gene cytochrome oxidase subunit I (mtDNA COI) sequences resulted in greater than or equal to 99%





**FIGURE 4** Illustration of *Chimaera* in the exhibition at the Oceanographic Museum of Monaco (MOM), painted during *Principe Albert I of Monaco* expeditions. PAM01 (MOM-900373) showing a black iris characteristic of *Chimaera opalescens*

similarity to the *C. opalescens* sequences deposited in GenBank by Luchetti *et al.* (2011). The four new COI sequences consisted of three distinct haplotypes characterised by four polymorphic sites (four transitions at positions 64, 190, 571 and 586). From the three haplotypes found in the Azores, two are identical to those found in Western Ireland (AZ01 and AZ03), and one is a new distinct haplotype (found in AZ02 and AZ04). All sequences that resulted from this study were deposited in GenBank (accession numbers: MN996713–MN996718).

### 3.2 | Image analyses

The *LULA 1000* submersible performed 61 dives with observations of the seabed at depths between 855 and 1000 m. *C. opalescens* was identified on five separate occasions (8.20% of the dives). On each occasion, a single female was observed, and three of the observed fish had abrasions on their skin (Table 3; Figure 3; Supplementary Video <https://doi.org/10.6084/m9.figshare.12453299.v1>). All *C. opalescens* were found swimming near the bottom and, on one occasion, resting on the seabed (dive 2016-090). Some fish were found over sediments mixed with hard substrate (dives 2016-075, 2016-090, 2018-157), whereas others were found over a sandy bottom (dive 2017-105) or near a vertical rocky wall (dive 2016-082).

### 3.3 | Historical records of *C. monstrosa* in the Azores

The checklist from Santos *et al.* (1997) presented only four first-hand records out of the 18 reported references (Supporting Information Table S1). Three of these (Neuville, 1900; Roule, 1912, 1919) referred to two specimens captured during the *PAM* expeditions. One of the references (Vaillant, 1888) referred to one specimen collected during the *Talisman* expedition. Therefore, until recently, these three specimens captured in the late 1800s represented the only records of

*C. monstrosa* in the Azores. All three specimens were captured at depths between 1165 and 1692 m (Table 1). Two of these specimens are still deposited in natural museums today (MOM and MNHN), and therefore, diagnostic characters could be further investigated. Although the specimen PAM01 was not deposited in any natural history museum, an examination of the illustration exhibited in the MOM museum shows a specimen with short caudal filament, beige body coloration without any marked pattern and a clear black iris (Figure 4), which are all diagnostic characters of *C. opalescens*.

The specimen PAM02 deposited in MOM is a large male measuring 103 cm TL (after preservation; Table 2), with a very short caudal filament (2.6% of LPC; Figure 5). The examination of the specimen revealed the existence of a slight cut in the caudal fin. Although this cut had been interpreted as the presence of an anal fin, a careful examination revealed the existence of tissue connecting the two overlapping parts; thus, it does not represent a true and full separation of the fin (see Figure 5b,c). The lack of an anal fin suggests the specimen is a *Hydrolagus*, and other characteristics such as a very short caudal filament, the heavy built body and the shape of the male appendices (claspers, frontal and prepelvic tenacula; see Figure 5d–g) further support this revised classification. A more thorough observation of the shape of the distal edge of the prepelvic tenacula shows a straight margin (Figure 5f,g), suggesting that this specimen is *Hydrolagus pallidus*, a species known to occur in the north-eastern Atlantic, including the Azores region (Ebert & Stehmann, 2013).

The specimen TAL01 deposited in MNHN appears to have a black iris, which may suggest a *C. opalescens* specimen (Figure 6). Nonetheless, it is not certain how the years and preservation technique may have influenced the iris colouration. This specimen also exhibits a very long caudal filament (44.5% of LPC; Table 2), a characteristic typical of *C. monstrosa*. This is a very small female, and because of the fragile condition, it was possible to take only a few measurements (Table 2), and it was not possible to dissect it to observe the colouration of the wall of the digestive canal.

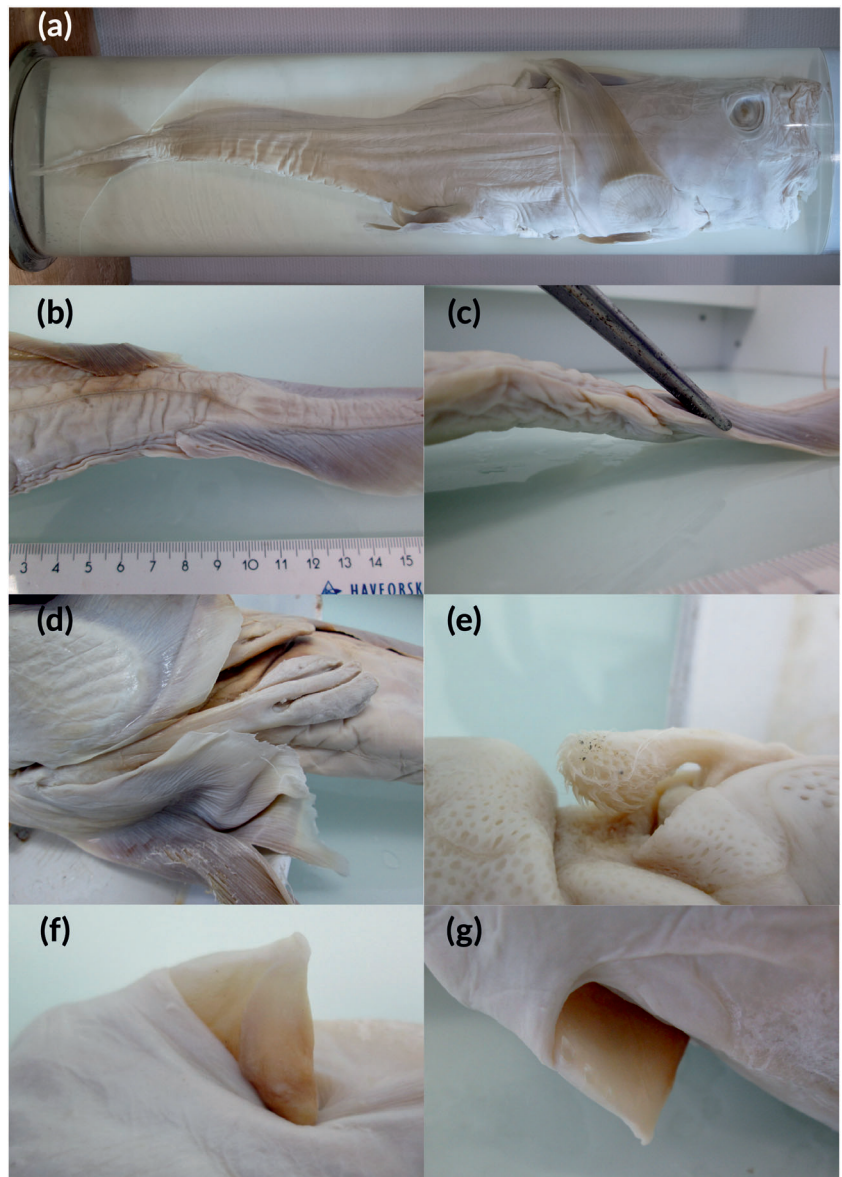
The two specimens caught during the FISHOR cruise show the diagnostic features of *C. opalescens* as described by Luchetti *et al.* (2011), including the black iris and pinkish digestive canal (Table 2; see Figure 2 and Supporting Information Figures S1 and S2). For the other eight specimens discarded at sea, there is no information or images to allow the validation of the previous taxonomic identification. All 10 specimens from the FISHOR expedition were caught at depths between 853 and 1394 m (see Table 1).

All attempts of PCR amplifications for both the 1800s specimens and the available FISHOR specimens were negative.

The re-examination of the two frozen specimens (AZ05 and AZ06) showed characteristics of *C. opalescens* (Table 2; Figure 2 and Supporting Information Figures S1 and S2). This identification was further supported by genetic analysis in which both specimens matched 100% in similarity with *C. opalescens* COI sequences. The AZ05 specimen had the same haplotype as AZ02 and AZ04, whereas AZ06 was genetically identical to the AZ03 haplotype.



**FIGURE 5** *Hydrolagus pallidus* deposited at the Oceanographic Museum of Monaco (MOM), PAM02 (MOM-POI-4205). (a) Full specimen, credit MOM; (b, c) details of the cut in the caudal peduncle showing the overlapping tissue; (d) detail of claspers, (e) details of the male frontal tenaculum; details of male prepelvic tenaculum in (f) dorsal and (g) ventral views, showing a straight distal margin



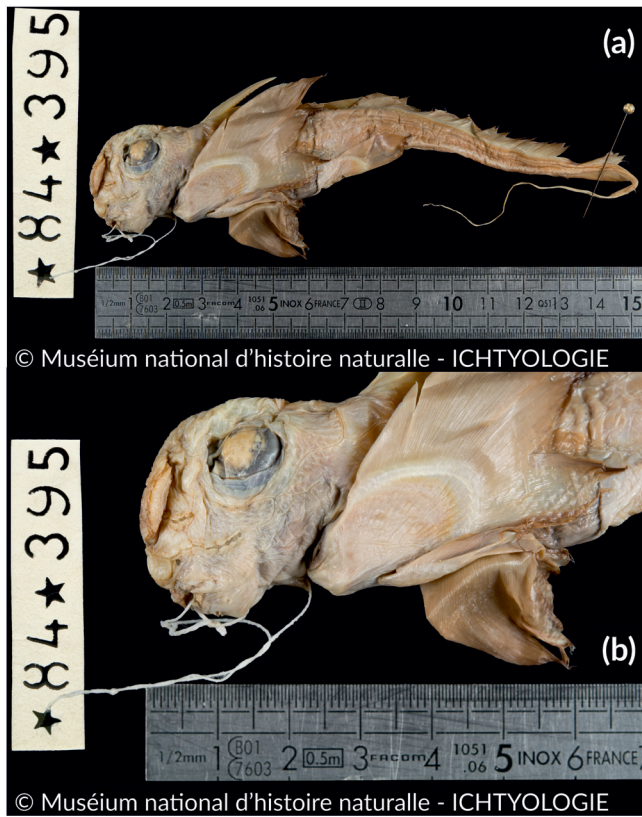
## 4 | DISCUSSION

This is the first study to report the occurrence of *C. opalescens* in the Azores region, identified after the thorough examination of 16 individuals (4 fresh, 6 preserved, 1 illustration and 5 from underwater video), thus extending the known geographic range of the species. Because some of these fish were found at seamounts, the potential presence of *C. opalescens* in other areas along the northern Mid-Atlantic Ridge can be anticipated. The description of these specimens is consistent with the morphological description of *C. opalescens* (Luchetti *et al.*, 2011), and the mtDNA COI sequences of some of the specimens further confirm their identification. Genetically, three of the Azorean specimens shared haplotypes with individuals captured off Ireland (Luchetti *et al.*, 2011), whereas the other three shared a new haplotype. Where depth was recorded (*i.e.*, for all but one specimen), the *C. opalescens* specimens were captured at depths >800 m, which is

within the reported depth range for the species (Freitas *et al.*, 2017; Holt *et al.*, 2013).

### 4.1 | Co-occurrence of *C. opalescens* and *C. monstrosa* in the Azores

Despite *C. opalescens* being common in offshore waters of the British Islands and frequently recorded in French landings (Holt *et al.*, 2013; Luchetti *et al.*, 2011), before being officially recognised as a species in 2011, individuals were recurrently misidentified as *C. monstrosa*. This confusion is likely related to the close resemblance between the two species (Luchetti *et al.*, 2011), and those similarities are also accountable for the misidentification found during this study for the Azores region (*e.g.*, Melo & Menezes, 2002; Menezes *et al.*, 2012), where the species had been misidentified for nearly 140 years.



**FIGURE 6** Specimen TAL01 (MNHN-IC-1884-0395) deposited at Muséum National D'Histoire Naturelle (MNHN) in Paris; photographs taken by L. Randrihasipara (MNHN). (a) Full specimen showing a long caudal filament; (b) details of the head showing what appears to be a black iris

Although *C. monstrosa* is mentioned in several Azorean species checklists (see Supporting Information Table S1), before the beginning of the 21st century, the records of its occurrence in the region were entirely based on only three specimens captured during the late 1800s (Roule, 1919; Vaillant, 1888). A re-examination of the morphological characteristics of these individuals suggests that they were likely misidentified. The conclusions about the specimen PAM01 (MOM-900373) are based only on an illustration; nonetheless, the depiction of a black iris is so apparent that it is hard to reject. This feature, together with the short caudal filament and body colouration, strongly suggests that this is indeed *C. opalescens*. In other illustrations from the same period (e.g., Bloch, 1796; Donovan, 1803; Philibert, 1806; Robert, 1851), the *C. monstrosa* specimens are shown with a light-colour iris and mottled body pattern, true characteristics of *C. monstrosa*.

The examination of the specimen PAM02 (MOM-POI-4205) concluded that it is *H. pallidus*, a species that was only described nearly 100 years later (Hardy & Stehmann, 1990). Characteristics such as the lack of an anal fin and the shape and length of the male claspers clearly dismiss the identification as *C. monstrosa* (see Luchetti *et al.*, 2011, for a description of the male appendices of *C. monstrosa*). Unique features, such as the shape of the male prepelvic tenacula, provide other important diagnostic characters in chimaeras: a straight

margin at the distal edge, as shown in this study's specimen (Figure 5f, g), clearly indicates *H. pallidus* (Hardy & Stehmann, 1990), whereas an indented margin points to *Hydrolagus affinis* or *C. opalescens* (Hardy & Stehmann, 1990; Luchetti *et al.*, 2011), and a rounded margin identifies *C. monstrosa* (Luchetti *et al.*, 2011). The identification of the specimen collected by Vaillant, 1888 (TAL01), and deposited at MNHN in Paris was the most challenging case mainly due to its poor condition. This specimen is a very small female, and therefore, some of the diagnostic features are absent compared with adult males. Because of its age and preservation method, many of the colour-based characteristics have faded away or are difficult to interpret. Furthermore, likely due to the age of the specimen, none of the attempts at DNA extraction and amplification provided positive results. Nevertheless, the examination of the specimen revealed that although the black iris suggested *C. opalescens*, the long caudal filament (44.5% of LPC) could also indicate *C. monstrosa*. According to Luchetti *et al.* (2011), although usually *C. opalescens* have shorter caudal filaments compared to that of *C. monstrosa*, their length ranges between 2.7% and 50.7% of the LPC. Therefore, although this specimen shows a longer filament compared with the other specimens found in the region, its proportions are within the range described for *C. opalescens* in other locations. Given these characteristics, together with the depth of capture (1257 m; see more about depth later), it is likely that this specimen is *C. opalescens*.

The more-recent checklists (e.g., Barreiros & Gadig, 2011; Ebert & Stehmann, 2013; Menezes *et al.*, 2012; Porteiro *et al.*, 2010) use the identification of *C. monstrosa* specimens captured during the FISHOR exploratory fishing campaign (Melo & Menezes, 2002). Nonetheless, the examination of the two specimens still available concluded that these were *C. opalescens*.

Besides the morphological characteristics that separate the two species, *C. opalescens* is generally found in deeper waters compared to *C. monstrosa* (Holt *et al.*, 2013; Luchetti *et al.*, 2011). The reported vertical distribution of *C. monstrosa* in the north-eastern Atlantic is relatively well known. Along Continental Europe and the British islands, the species is most abundant between the 300 and 500 m depth range (Holt *et al.*, 2013; Lorance *et al.*, 2000; Luchetti *et al.*, 2011; Moura *et al.*, 2005), whereas in the Mediterranean Sea the highest abundances are reported to be deeper, between 500 and 600 m depth (Mytilineou *et al.*, 2005; Ragonese *et al.*, 2013; Relini *et al.*, 2000), noting that the Mediterranean population is likely to be isolated from other populations (Catarino *et al.*, 2017). Although there is not a defined depth boundary that separates the two species, *C. monstrosa* seems to be mainly an upper-slope dweller (Gordon & Bergstad, 1992; Lorance *et al.*, 2000), and deeper records of the species may partly consist of misidentifications of *C. opalescens* (Holt *et al.*, 2013). All records of *C. monstrosa* from the Azores consisted of specimens captured deeper than 800 m. Although an examination of the eight specimens discarded at sea during the FISHOR campaign is not possible, all were captured at depths within the *C. opalescens* preferred range (see Table 1). Evidence from the demersal fishery data, scientific fishing surveys and underwater videos suggests that *C. monstrosa* is absent in shallower waters in the Azores. Despite decades of

monitoring fishing (*i.e.*, landings, on-board observers and logbooks), one of the main economic activities in the Azores (Carvalho *et al.*, 2011; Diogo *et al.*, 2015; Menezes *et al.*, 2013; Pham *et al.*, 2013), the capture of *Chimaera* specimens in the region is rare, and there are no records of chimerids captured shallower than 800 m depth. The main fishery in the Azores uses handlines and bottom longlines to catch demersal species (Menezes *et al.*, 2006, 2013). The bottom longline fishery is well established and operates down to 600–800 m or deeper (Diogo *et al.*, 2015). Recently, drift bottom longlines were used for a brief period to target the black scabbardfish, with fishing operation usually between 1000 and 1990 m depth (Machete *et al.*, 2011). No trawl nets are allowed in the Azorean Exclusive Economic Zone (European Commission Council Regulation number 1568/2005). Furthermore, in the 25 years of the scientific *Demersais* monitoring programme (Menezes, 2014) in the region, which operates bottom longlines down to 800 m (sometimes to 1200 m depth; Menezes *et al.*, 2006), no *Chimaera* have been captured. Although bottom longlines may not be the optimal gear to capture *C. monstrosa* because of species feeding habits (Mauchline & Gordon, 1983; Moura *et al.*, 2005), it has been shown that the species gets attracted to bait and capture is possible (*e.g.*, Kutti *et al.*, 2014). In addition, no *Chimaeras* were observed during the several hours of video footage from ROVs operating within the preferred depth range of *C. monstrosa* (300–500 m depth; *e.g.*, Gomes-Pereira, 2016, 2017) or during the 67 dives performed with the Rebikoff-Niggeler Foundation's previous manned submersible, *LULA500*, at depths between 200 and 500 m on the islands' slopes (Faial, Pico and São Jorge islands). Only when the submersible started to perform deeper dives was *C. opalescens* observed. Based on these evidences, *C. monstrosa* appears to be absent from the shallower habitats of the Azores.

This study suggests two possible scenarios regarding the presence of *Chimaera* in the Azores region: either *C. monstrosa* cohabits with *C. opalescens* in much deeper water than its Atlantic conspecifics, or *C. monstrosa* is absent and past records of this species are *C. opalescens*. Given the remoteness of the Azores archipelago, the great depths that surround it, the fact that *C. monstrosa* primarily occupies the upper slope and the high degree of misidentification in past records leads to the conclusion that the second scenario is more plausible. This study therefore suggests the replacement of *C. monstrosa* with *C. opalescens* in the checklist of elasmobranchs for Azores given by Das and Afonso (2017), with a total number of four confirmed *Chimaera* species reported for the region. In the Azores, because of the ban on trawling and low capture of chimerids using baited hooks, the populations of these vulnerable species (*i.e.*, long life span and late maturation) are less susceptible to fishing, an important aspect for the conservation of these species in the region.

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## AUTHOR CONTRIBUTIONS

D.C., E.G. and S.S. conceived the study. D.C., E.G., S.S., F.M.P., K.J. and J.J. designed the study. D.C., H.D., A.C. and O.M. collected and/or sampled the specimens. K.J. and J.J. collected the video data. D.C. prepared the manuscript with contribution from all authors.

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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