ICCAT Manual
ICCAT CICTA CICAA
INTERNATIONAL COMMISSION FOR THE CONSERVATION OF ATLANTIC TUNAS

CHAPTER 2.2.1.12: CROCODILE SHARK	AUTHORS: MILLER P., DOMINGO A., FORSELLEDO R. AND MAS F.	LAST UPDATE: August 2022 Original: Spanish

2.2.1.12 Description of crocodile shark (PSK)

1. Names

1.a. Classification and taxonomy

Species name: *Pseudocarcharias kamoharai* (Matsubara, 1936)
Synonyms: *Carcharias kamoharai* (Matsubara, 1936), *Carcharias yangi* (Teng, 1959), *Pseudocarcharias pelagicus* (Cadenat, 1963)
Etymology: According to Castro (2011), *Pseudocarcharias* is derived from the Greek, *psudes*, false and *karcharios*, the name for man eating sharks. For its part, *kamo harai* is derived from the latinisation of the surname of Professor Toshiji Kamohara, who obtained the type specimen from the Kôti Fish Market and passed it on to Matsubara for its formal description.
ICCAT Species Code: PSK
ICCAT names: crocodile shark (English), requin crocodile (French), tiburón cocodrilo (Spanish).

According to the ITIS (Integrated Taxonomy Information System), the crocodile shark is classified as follows:

- Phylum: Chordata
- Subphylum: Vertebrata
- Superclass: Gnathostomata
- Class: Chondrichtyes
- Sub-class: Elasmobranchii
- Superorder: Euselachii
- Order: Lamniformes
- Family: Pseudocarchariidae
- Genus: *Pseudocarcharias*

1.b. Common names

List of vernacular names in use according to ICCAT, FAO and Fishbase (www.fishbase.org). The list is not exhaustive and some local names might not be included.

Australia: Crocodile shark
Brazil: Tubarão-crocodilo
China: 大洋拟锥齿鲨, 大洋擬錐齒鯊, 杨氏锥齿鲨, 楊氏錐齒鯊, 蒲原拟锥齿鲨
Chinese Taipei: 蒲原氏擬錐齒鯊
Comoros: N'ganu
Costa Rica: Tiburón cocodrilo
Denmark: Krokodillehaj
Ecuador: Tiburón cocodrilo
Estonia: Krokodillhai
France: Requin crocodile
French Polynesia: Requin crocodile
Germany: Krokodilhai
Hawaii: Crocodile shark

Indonesia: Hiu buaya, Hiu tongar, Japanese ragged-tooth shark, Kamohara´s sand-shark
Japan: Mizuwani, ミズワニ
Korea: 강남상어
Mexico: Tiburón cocodrilo
Mozambique: Tubarão-crocodilo
Netherlands: Krokodilhaai
Portugal: Tubarão-crocodilo
Saint Helena: Crocodile shark
South Africa: Krokodilhaai, Grootoog-skeurtandhaai, Crocodile shark, Bigeye ragged-tooth shark
Spain: Tiburón cocodrilo
United Staes: Crocodile shark
Uruguay: Tiburón cocodrilo
Venezuela: Tiburón cocodrilo, Tiburón tártaro

2. Identification

Characteristics of *Pseudocarcharias kamoharai* (see Figure 1).

Figure 1. Crocodile shark (*Pseudocarcharias kamoharai*) (Matsubara, 1936). Photo: Tassapon Krajangdara.

Lengths

References to size throughout this document consistently relate to total length (TL), unless otherwise specified (e.g. fork length: FL).

The largest known individual is a female of 117 cm (FL) caught in the Atlantic Ocean, reported by Coelho *et al.* (2012). Other studies carried out on individuals caught in the Atlantic report considerably smaller maximum sizes, in all cases corresponding to females; 122 cm (Oliveira *et al.*, 2010), 101 cm FL (Kindong *et al.*, 2020), 99 cm FL (Wu *et al.*, 2020), 112 cm (Vieira and Lessa, 2010), and 97 cm FL (Gao *et al.*, 2013). The maximum size reported for individuals caught in the Indian Ocean is 106 cm FL, corresponding to a female caught in the eastern Indian Ocean (Novianto *et al.*, 2014). The maximum reported size in the Pacific is 117 cm (Tiban-Vivar, 2013), corresponding to a female caught in Ecuador.

Colouring

Brownish light grey to dark grey colour in the dorsal area and upper flanks, which becomes gradually lighter towards the ventral area. They have a whiteish underside and sometimes have small darker patches that can reach the lower part of the flanks. The dorsal surface of the pectoral fins is dark, while the ventral surface is light. In some cases, the trailing edge of the pectoral fins are light-coloured. Some individuals have a round light-coloured (almost white) patch on either side of their head, located in front of the gill slits (Intriago ,2013, Rodríguez-Acosta *et al.,* 2016).

External characteristics

It is the smallest of the species in the order Lamniformes. Its eyes are very large and lack a nictating membrane. The gill slits are long and its body is slender and elongated. The anterior teeth are elongated and prominent and do not have lateral cusps. It has small pectoral fins and two dorsal fins without spines, in addition to an anal fin behind the second dorsal fin. There are weak keels on caudal peduncle, as well as upper and lower precaudal pits. The caudal fin is asymmetrical (non-lunar) with a relatively large ventral lobe. Some studies report that the caudal peduncle keels are missing, such as an individual caught in Chile (Meléndez *et al.*, 2006), an individual caught in the NW Pacific (Dolganov and Ginanova, 2016), and three individuals caught in the South Caribbean (Rodríguez-Acosta *et al.*, 2016).

Internal characteristics

Very long teeth. The anterior teeth have no lateral cusp and protrude from the mouth. The lateral teeth have a wide base and exhibit traces of small lateral cusps. Soto (2000) mentions variations in the dentary formula (12-1-2/2-1-12, 11-2/2-11, 9-1-2/2-1-9, 9-2/2-9), while Stewart (2001) reports (from right to left) 10-1-2-2-1-10 (upper jaw) and 9-2-2-9 (lower jaw). Meléndez (2006) indicates 24 teeth in the upper jaw of a female with the dentary formula of 9-1-2-2-1-9 from left to right, and 20 teeth in the lower jaw with a dentary formula of 8-2-2-8. Stewart (2001) analysed an adult male of 110 cm TL and found that its spinal column consisted of 131 vertebrae (mentioning 54 monospondylous vertebrae and 32 precaudal dispondylous vertebrae).

3. Distribution and population ecology

3.a. Geographic distribution

P. kamoharai has a cosmopolitan distribution in tropical and subtropical regions, mainly in oceanic waters. It is known to be present in the Atlantic, Indian and Pacific Oceans, but there are no records of its presence in the Mediterranean Sea, or in the Red Sea. Most documented records in the Atlantic Ocean correspond to catches by fisheries targeting pelagic fish that operate with pelagic longlines, in areas far off the continental shelf including both international waters (Castro and Mejuto, 1995; Martínez and Correia, 2010; Oliveira *et al.*, 2010 ; Pacheco *et al.*, 2011; Andrade *et al.*, 2012; Coelho *et al.*, 2012; Gao *et al.*, 2013 ; da Silva Ferrette *et al.*, 2015; Lessa *et al.*, 2016, Wu *et al.*, 2020, Kindong *et al.*, 2020) and waters within the EEZ of several countries such as Venezuela (Rodríguez-Acosta *et al.*, 2016), Brazil (Amorim *et al.*, 1998; Gadig, 2000; Soto, 2000; Vieira and Lessa, 2010; Lessa *et al.*, 2016), Saint Helena (Edwards, 1993), Angola (Cadenat and Blache, 1981), and South Africa (Petersen *et al.*, 2009). This species' presence in the Indian Ocean has been documented in several studies, including the SW Indian Ocean (Moon *et al.*, 2007; Petersen *et al.*, 2009; Coelho *et al.*, 2011), shallow waters in Kenya (Kiilu *et al.*, 2016), Pakistan (Moazzam, 2021), the SE Indian Ocean (Novianto *et al.*, 2014), and Australia (Stevens and Wayte, 2008). Occurrence of this species has also been documented in the East Pacific (Bearez *et al.*, 2001; Meléndez *et al.*, 2006; Ruiz-Campos *et al.*, 2010; Dai *et al.*, 2012; Intriago, 2013; Estupiñán-Montaño and Galván-Magaña, 2020), and West Pacific (Stewart, 2001, Moon *et al.*, 2007, Curran and Bigelow, 2011, Dolganov and Ginanova, 2016).

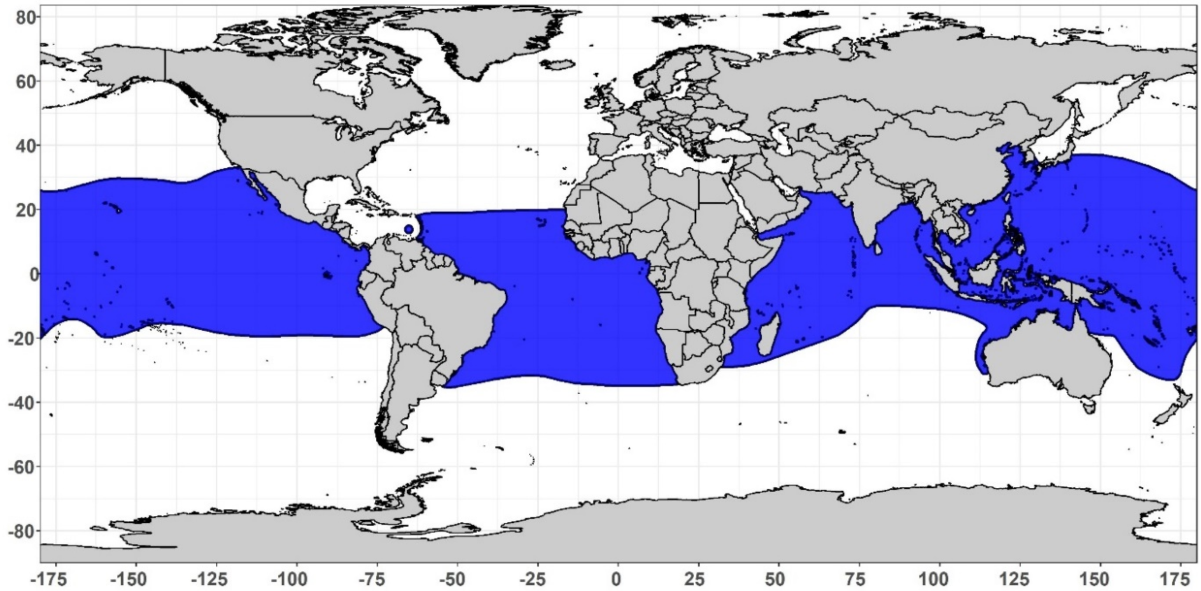

Figure 2. Map of distribution of crocodile shark (*Pseudocarcharias kamoharai*). Taken from International Union for Conservation of Nature (IUCN) (IUCN SSC Shark Specialist Group 2018. *Pseudocarcharias kamoharai*. The IUCN Red List of Threatened Species. Version 2021-1).

3.b. Habitat preferences

Knowledge on the habitat preferences of *P. kamoharai* is practically limited to data originating from catch distribution analysis. Compagno (2001) indicates that it is a rare to locally abundant oceanic species, epipelagic and possibly mesopelagic, usually found far from the shore at depths of at least 590 m below the surface. Fujita (1981) reports that individuals were caught at around 180 metres below the surface by longline vessels. Walsh *et al*. (2009) found that for the longline fleets operating around Hawaii, the frequency of occurrence and relative abundance of *P. kamoharai* were greater in the catches obtained with deep longline as compared with longlines operating closer to the surface. Li *et al.* (2013) analysed the data obtained during a research cruise in the Central Indian Ocean, where the gear depth was measured. All *P. kamoharai* (n=21) were caught on hooks operating at depths of between 200–320 metres, and no catches of this species were recorded in more superficial layers. The same study indicated that fishing sets where *P. kamoharai* catches were recorded took place in waters with an Sea Surface Temperature (SST) of between 28.1–30.5°C. Referring to the conclusions of Xu *et al.* (2012), Li *et al.* (2013) expressed that *P. kamoharai* was caught by pelagic longline vessels at an average depth of 169–191 metres. Most occurrences of this species were recorded during fishing operations in waters with a surface temperature of over 22°C.

3.c. Migrations

There is no knowledge about the migrations of this species. Very few individuals have been tagged, and there have been no reported recaptures. In the latest National Marine Fisheries Service (NMFS) Cooperative Shark Tagging Program report, Kohler and Turner (2019) reported that a mere 20 individuals had been tagged, all in the equatorial zone of the Atlantic from Brazil to Ghana (between latitudes 2°S and 4°N and longitudes 0° and 35°W), and none of them were recaptured.

4. Biology

4.a. Growth

There are limited studies on age and growth of *P. kamoharai* (**Table 1**). In general, these works were mainly based on individuals with a size range strongly biased towards longer individuals, possibly due to the selective nature of the fishing gears used to catch them. The work carried out by Gago (2014) is mainly based on individuals of over 70 cm FL. A similar situation occurs in the work carried out by Lessa *et al.* (2016), which only includes one individual of under 70 cm TL, and in the work of Kindong *et al.* (2020), where more than 90% of the individuals analysed have a length of above 65 cm FL.

The maximum age determined by Lessa *et al*. (2016) reached 8 and 13 years, for males and females, respectively, caught in the equatorial and tropical West Atlantic. In a later study, Kindong *et al.* (2020) found that the maximum ages observed were 11 and 10 years, for males and females, respectively. The longest living individuals were reported by Rosa *et al.* (2017), informing of maximum ages of 13 and 14 years for males and females, respectively. These authors underlined that the differences in maximum ages estimated could be related to differences in populations, areas and sizes sampled, as well as to differences in processing methodology and vertebrae staining. In relation to the growth parameters, Rosa *et al.* (2017) assessed various models, and indicated that all produced similar curves and that statistically there is not much difference between them.

Table 1. Growth parameters for *Pseudocarcharias kamoharai* according to the Von-Bertalanffy growth model (L_{oo}: asymptotic maximum length (cm), k: growth rate ($years^{-1}$), t_o: theoretical age at size 0 (years).

Growth Parameter						
L_{oo}	k	t_o	Area	Reference	Sex	Method
123.6 (FL)	0.067	35 (FL)[a]	Atlantic Ocean	Gago (2014)	Males	Vertebrae
152.0 (FL)	0.049	35 (FL)[a]	Atlantic Ocean	Gago (2014)	Females	Vertebrae
139.6 (FL)	0.055	35 (FL)[a]	Atlantic Ocean	Gago (2014)	Both	Vertebrae
115.9 (FL)	0.081	-3.9	Atlantic Ocean	Gago (2014) [b]	Males	Vertebrae
168.5 (FL)	0.039	-6.4	Atlantic Ocean	Gago (2014) [b]	Females	Vertebrae
141.5 (FL)	0.053	-5.4	Atlantic Ocean	Gago (2014) [b]	Both	Vertebrae
129.2 (TL)	0.137	-3.9	Western Atlantic	Lessa *et al.* (2016)	Both	Vertebrae
107.8 (FL)	0.18	41.34 (FL)[c]	Central Atlantic	Kindong *et al.* (2020)	Both	Vertebrae
94.55 (FL)	0.18	32 (FL)[d]	Eastern Atlantic	Rosa *et al.* (2021)	Males	Vertebrae
105.6 (FL)	0.14	32 (FL)[d]	Eastern Atlantic	Rosa *et al.* (2021)	Females	Vertebrae

TL: total length (cm); FL: fork length (cm); BRC: Bomb Radiocarbon. **a**: A modified version of Von-Bertalanffy was used with a fixed size at birth of 35 cm FL. **b:** According to the authors, the Von-Bertalanffy model with a fixed size at birth exhibited slightly greater adjustment than the traditional Von-Bertalanffy model, but the latter is presented in the table for the purpose of comparison against other published models. **c:** A reparametrized version of Von-Bertalanffy was used to estimate L_0 instead of t_0. **d**: A modified version of Von-Bertalanffy was used with the size of birth established at 32 cm FL.

4.b. Length-weight relationship

Published length-weight relationships for several geographic areas in the Atlantic are shown in **Table 2**.

Table 2. Published length-weight relationships for *Pseudocarcharias kamoharai*. TW: total weight (kg), TL: total length (cm), FL: fork length (cm).

Equation	N	Length range	R^2	Area	Reference
$TW = 2x10^{-5} x (FL)^{2.7614}$	238 (females)	56-99	0.836	Tropical North Atlantic	Gao *et al.* (2013)
$TW = 2x10^{-6} x (FL)^{3.3287}$	89 (males)	48-97	0.853	Tropical North Atlantic	Gao *et al.* (2013)
$TW = 3.3532x10^{-4} x (FL)^{2.1156}$	319	69-102	0.43	SW Indian Ocean	Ariz *et al.* (2007)
$TW = 9.0843x10^{-3} x (TL)^{1.3455}$	377	78-118	0.27	SW Indian Ocean	Ariz *et al.* (2007)
$TW = 4.2536x10^{-6} x (FL)^{3.07}$	385	44.2-101.5	0.84	East Atlantic	Rosa *et al.* (2021)
$TW = 7.1546x10^{-6} x (FL)^{2.94}$	169 (males)	44.2-92.8	0.88	East Atlantic	Rosa *et al.* (2021)
$TW = 3.9265x10^{-6} x (FL)^{3.09}$	216 (females)	57-101.5	0.82	East Atlantic	Rosa *et al.* (2021)

4.c. Conversion factors

Table 3. Published length-length relations for *Pseudocarcharias kamoharai*. TL: total length (cm), FL: fork length (cm). PCL: Precaudal length (cm).

Equation	N	Length range	R^2	Area	Reference
FL = 0.7516 x (TL) + 11.33	238	-	0.856	-	Romanov *et al.* (2008)
FL = 0.8325 x (TL) + 1.7341	27	81.5 – 112 (TL)	0.91	West Equatorial Atlantic	Vieira & Lesa (2010)
TL = 1.1513 x (LH) – 0.3496	248	-	0.94	Tropical North Atlantic	Gao *et al.* (2013)
FL = 0.8083 x (TL) + 7.1478	407	68 – 118 (TL)	0.85	SW Indian	Ariz *et al.* (2007)
TL = 1.11 x (FL) + 5.18	380	44.2–101.5 (FL)	0.96	East Atlantic	Rosa *et al.* (2021)
TL = 1.21 x (PCL) + 6.81	380	42.2–91.5 (PCL)	0.95	East Atlantic	Rosa *et al.* (2021)

4.d. Reproduction

While there are several studies that provide information on different aspects of the reproductive biology of *P. kamoharai*, these are based on the analysis of specimens captured in different regions and in some cases show bias in terms of lengths, and space and time coverage of the sampling.

Gestation and pupping

Like all the species belonging to the order Lamniformes, *P. kamoharai* has aplacental viviparous reproduction, and the embryos of this species are oophageous, i.e. they actively feed on unfertilised eggs during part of their development. This has been evidenced based on analysis of embryo stomach contents, in which the presence of yolk remains was observed (Fujita, 1981; White, 2007; Oliveira *et al*., 2010). Unlike other viviparous shark species, the embryos of *P. kamoharai* absorb the yolk sac and the umbilical cord disappears when they are still very small (Fujita, 1981). From then onwards, the embryos nourish themselves by feeding on the oocytes rich in yolk that are released by their mother during gestation. Fujita (1981) observed that in the smallest embryos (38-41 mm) egg capsules are attached to the abdomen, and while the spiral valve contained yolk material, the empty stomach did not appear to be used during this stage of development. In the case of larger embryos (410-428 mm), these had an extended abdomen, and the stomach contained a considerable amount of yolk material, representing around 25% of body weight. They did not present umbilical scarring. White (2007) observed that the functional ovary of three gravid females analysed, contained numerous eggs with yolk, signaling this to be an indication of oophagy. The same author indicated that although according to Compagno *et al.* (2005) adelphophagy (or intrauterine cannibalism) may occur in this species, each uterus usually contains 2 embryos, which is consistent with later studies using larger samples, and is a strong indication that embryos of *P. kamoharai* do not practice adelphophagy. Oliveira *et al*. (2010) observed intense vitellogenesis activity during early stages of pregnancy, with a relatively high number of unfertilised eggs present in each uterus, decreasing during the intermediary stages of pregnancy. These disappeared completely in at term females, presumably having been eaten by the embryos.

As regards the temporality of the reproductive cycle, Fujita (1981) indicated that the marked size difference between the embryos of two gravid females caught at the same time suggests that the copulation period in the Central Pacific could be extensive in time. White (2007) made a similar observation for individuals analysed in Indonesia, indicating that reproductive seasonality could not be determined as embryos in late stages of development were recorded in March, April and October, and neonates mainly in July and December. Similarly, according to Oliveira *et al*. (2010) variation in morphology and gonad weight, as well as embryos at different developmental stages throughout the year, suggest that the reproductive seasonality of *P. kamoharai* is not well defined in the Tropical Atlantic, where copulation and pupping possibly occur over a prolonged period of the year. The same authors observed towards the end of the pregnancy, a decrease in the gonadosomatic index, apparently linked to oophagy as the reproductive strategy. They indicate that in late pregnancy, the embryos will have received all the energy that they require to complete their development and that production of oocytes in the ovary therefore decreases. They indicate that this could imply that females require a relatively long resting phase in which to gather enough energy to carry out the next reproductive cycle, possibly resulting in a cycle that is longer than one year.

As regards length at birth, several works report on this aspect. White (2007) found that the largest near-term embryos measured between 298-450 mm, and that the smallest neonate measured 363 mm, indicating that the length at birth would be between 360-450 mm. Shimada (2002) found that the largest embryo measured 43 cm, and that the smallest free swimmer measured 59 cm. Oliveira *et al*. (2010) reported that the estimated length at birth is 41.5 cm. Dai *et al*. (2012) reported that the maximum sizes of the embryos reached 36 cm FL for females and 34 cm FL for males. Coelho *et al*. (2012) reported on neonates with a minimum length of 38 cm FL. Wu *et al*. (2020) analysed a total of 146 embryos and established that the maximum size was 39.5 cm FL for females and 36.5 cm FL for males.

Maturity

A variety of studies conclude that females have a greater size at maturity than males in the Atlantic (Oliveira *et al.* 2010; Gao *et al.*, 2013; Wu *et al.*, 2020; Kindong *et al.*, 2020; Rosa *et al*., 2021), Indian (White, 2007) and Pacific Oceans (Intriago, 2013). Based on 490 specimens caught in the Tropical West Atlantic, Oliveira *et al.* (2010) found that males reached sexual maturity at between 760–810 mm TL (TL_{50} = 800 mm) and females at 870–980 mm TL (TL_{50} = 916 mm). Gao *et al.* (2013) found that length at 50%-maturity was 84.6 cm FL for females and 78.96 cm FL for males caught in the North Atlantic. A more recent study of 383 individuals caught in international waters in the tropical North Atlantic determined that 50% of individuals reach maturity at 84.9 cm FL in the case of females and 78.5 cm FL in the case of males (Wu *et al.*, 2020). Also, for Atlantic individuals, Kindong *et al.* (2020) indicated that most females over 86 cm were pregnant and males above 72 cm FL had claspers of over 9 cm and sperm in the sperm duct, while most males over 77 cm FL had articulated claspers and were able to rotate anteriorly. In the same study, considering the sizes at maturity established by Wu *et al.* (2020), the authors established an age at 50%-maturity of 4.55 years for males and 5.91 years for females using the best fitting growth model. Rosa *et al.* (2021) analized 387 individuals caught in the East Atlantic, determining sizes of medium maturity (L50) of 67.2 FL for males and 81.57 cm FL for females, corresponding to estimated ages of 4.85 and 8.21 years, respectively. The same study reports that the size of the largest immature male reached 77.6 cm FL, while the smallest mature male measured 62.2 cm FL. For females, the largest immature individual measured 93.7 cm FL, and the smallest mature individual measured 75.5 cm FL. For the Indian Ocean, White (2007) reported that males reach maturity at a size of approximately 72.5 cm, while he reported a size at maturity of between 87 and 103 cm for females, and the smallest gravid female was 103.2 cm TL. For the Pacific, Fujita (1981) and Dai *et al.* (2012) reported the minimum size of gravid females to be 98.2 cm TL and 80 cm FL, respectively. A study carried out on individuals caught by the medium-scale fleet in Ecuador determined that females reach sexual maturity at 88 cm TL and males at 84 cm TL (Intriago, 2013). Also regarding individuals caught in Ecuadorian waters, Estupiñán-Montaño and Galván-Magaña (2020) determined an average size at maturity of 78.9 cm for males based on a clasper calcification analysis.

Sex ratio

Several studies provide information on sex ratios and indicate heterogeneity, possibly related to time-area segregation patterns.

Castro and Mejuto (1995) analysed 113 individuals caught in the eastern equatorial Atlantic, finding 83 males and 30 females. Amorim *et al.* (1998) reported a sex ratio of 37 males and 15 females in a group of 52 individuals examined in Brazil from April to October 1990. Subsequently, Oliveira *et al.* (2010) reported that the sex ratio was biased towards females (1:1.8) in a group of 490 individuals caught in the tropical West Atlantic, finding 177 males and 313 females. Based on an analysis of 383 individuals caught between November 2011 and March 2012 in international waters of the Tropical North Atlantic, Wu *et al.* (2020) found a sex ratio of 1F:2.79M (101 males and 282 females). Kindong *et al.* (2020) found a sex ratio biased towards males of 1F:1.91M. With regard to embryos, in a sample from the tropical West Atlantic, Oliveira *et al.* (2010) found a sex ratio of close to 1:1, slightly biased towards females (53.7%F *vs* 46.3%M), although no significant statistical differences were detected. Rosa *et al.* (2021) found practically an identical result to Oliveira *et al.* (2021), with a proportion of embryo sexes of 53.2% F *vs* 46.8% M. For the SE Indian Ocean, Novianto *et al.* (2014) found a male-to-female sex ratio of 1M:0.67F (169 males, 114 females). Information has also been generated for the Pacific Ocean. Dai *et al.* (2012) found that for a total of 142 individuals analysed during a 5-month fishing trip in the East Pacific, the sex ratio was not significantly different from 1:1 in any single month, except one. The sex ratio over the entire sample period was significantly different from 1:1, with a much larger number of females than males (88 females, 54 males). Based on samples of landings between June 2012 and May 2013 in the port of Santa Rosa (Ecuador), Intriago (2013) found a sex ratio of 1F: 0.89M in a total sample of 146 individuals (77 females and 69 males). Also in the East Pacific, for a total of 59 individuals caught between 2003 and 2009 by the artisanal longline fleet in Ecuadorian waters, Estupiñán-Montaño and Galván-Magaña (2020) found a sex ratio of 1.9F:1M.

Fecundity

As in other oophagous species, litter size is small. Most studies agree that gravid females most frequently have 4 embryos, 2 in each uterus (Fujita, 1981; Amorim *et al.*, 1998; Soto, 2000; White, 2007; Oliveira *et al.*, 2010; Dai *et al.*, 2012; Wu *et al.*, 2020; Rosa *et al.*, 2021). In a study performed on individuals caught in the western Atlantic, Oliveira *et al.* (2010) reported that most of the females contained two embryos in each uterus, also reporting that 12.3% of the uteri analysed had only one embryo, and in one case only a uterus with three embryos. This study also calculated an average fecundity of 3.9 ± 0.6 in each reproductive cycle, based on the number of completely developed, almost at-term embryos. In a study performed on females caught in the South Caribbean, Rodríguez-Acosta *et al.* (2016) reported finding two gravid females, one of which was carrying five embryos and the other four. Wu *et al.* (2020) analysed females caught in the tropical North Atlantic and found that the majority had two embryos in each uterus. However, they also indicated that some females had one embryo in each uterus and seven only had embryos in one uterus, three of which had 4 embryos in the same uterus. Based on the assessment of 34 gravid females caught in the East Atlantic, Rosa *et al.* (2021) found an average fecundity of 3.7 embryos per litter. In a study performed on females caught in the East Pacific, Dai *et al.* (2012) found that, although almost 90% of females had two embryos in each uterus, some females had a total of 3 or 2 embryos.

4.e. Diet

Information on the diet of *P. kamoharai* is relatively scarce. Very few works address this subject; three works are based on analysis of the stomach contents of individuals caught in the western Pacific Ocean, while the other provides an approximation of the trophic position of *P. kamoharai* based on analysis of stable isotopes in individuals caught in the southwestern Indian Ocean.

Compagno (1984) indicates that there is little knowledge regarding this species' eating habits, but that its long, curved teeth suggest that it may prey on moderately large and active oceanic species. Of the five individuals analysed, four had empty stomachs while the fifth contained some small fish (Gonostomatidae and possibly Myctophids), in addition to small shrimps and squid beaks, including Onychoteuthidae, Mastigoteuthidae and Pholidoteuthidae. Compagno (2001) subsequently reported that two individuals were analysed and had the same food items in their stomachs as those analysed previously.

Tibán-Vivar (2013) analysed 146 individuals caught and landed in the East Pacific (Santa Rosa, Ecuador) and found that 64% had an empty stomach, while a total of 12 different preys were identified in the 52 stomachs that did have contents, including at least 7 species of cephalopods and three species of Osteichthyes. The analysis showed that cephalopods were the most significant item, mainly *Ancistrocheirus lessuerii* (%IIR = 58.8), *Histioteuthis* sp. (%IIR = 28.2) and *Sthenoteuthis oualaniensis* (%IIR = 5.9). Less importantly, the fish *Auxis thazard*, *Sarda sarda,* and *Scarus ghobban* were found. This study also evaluated dietary breadth and used the Levin Index to determine that it is low (Bi: 0.22), which would indicate that *P. kamoharai* could be considered a specialist predator as it only consumes specific prey. This differs from the results of Compagno (2001), who reported finding small mesopelagic fish (Gonostomatidae and Myctophids) and small shrimp, none of which were present in the stomachs analysed by Tibán-Vivar (2013). In a later study, also carried out in Ecuador, Estupiñán-Montaño and Galván-Magaña (2020) analysed the stomach contents of 59 individuals caught by the artisanal fishing fleet that operates in the ports of Manta and Puerto López, observing that just two of the individuals had food items in their stomachs. In both cases, the only species found was the mesopelagic squid (*Ancistrocheirus lesueuri*). Calle-Morán *et al.* (2022) analyzed the stomach contents of 401 individuals caught in the SE Pacific obtained from landings and artisanal fisheries in the port of Santa Rosa (Ecuador), reporting that 62.8% of the stomachs were empty, and that those that contained food items at least ten species of cephalopods and five fish could be identified. Cephalopods, *Histioteuthis heteropsis*, *A. lesueurii*, and *S. oualaniensis*, were the three most abundant prey, without significant differences in diet composition for males and females. Fish represented less than 3% of the total weight of the items found in their stomachs. These results confirm previous reports by Tibán-Vivar (2013) and suggest that *P. kamoharai* is a specialist predator.

In a study performed on individuals caught in the SW Indian Ocean based on isotopes of nitrogen, Kiszka *et al.* (2015) determined that *P. kamoharai* had a relatively high trophic position taking into account its small size compared to other pelagic shark species included in the same analysis, and indicated that high levels of δ15N could be due to a greater nitrogen baseline at the depths where this species feeds. The mercury concentration found in *P. kamoharai* was also much higher than in other species. This result was not expected, as the species appears to feed in a similar trophic position to other species. Considering that some large predator species which feed on mesopelagic species have exhibited significantly higher mercury concentrations than epipelagic predators, Kiszka *et al.* (2015) suggest that the high mercury concentrations found in *P. kamoharai* are possibly due to the fact that this species feeds in a significantly deeper habitat than the other species analysed (including, among others, *Isurus oxyrinchus*, *Prionace glauca* and *Carcharhinus longimanus*), which are more superficial.

4.f. Physiology

There is no information on the physiology of *P. kamoharai*.

4.g. Mortality

There is no information on natural mortality of *P. kamoharai.*

As regards catching mortality, Coelho *et al.* (2012) reported that mortality reached 13.3% of a total of 1,621 of individuals caught by longline operating the Atlantic. Later, Jordaan *et al.* (2020) found that, in 11 of the fishing trips (71,102 hooks observed), 10 were found alive and discarded in good conditions. Gilman *et al*. (2016) carried out a meta-analysis on works aiming to assess the effects of bycatch mitigation measures in longline fisheries, and found that average mortality of *P. kamoharai* individuals was 26.24%.

5. Fisheries biology

5.a. Populations/Stock structure

Based on a mitochondrial DNA control region analysis involving 255 individuals, da Silva Ferrette *et al*. (2015) determined that there are no differences in the population structure of areas sampled in the Atlantic or between the Atlantic and the Western Indian Ocean. The results show a high degree of gene flow between the studied areas, which determines the existence of a single genetic stock with low population variability. The two most common haplotypes were found in all of the sampled regions, representing 74.5% of the analysed specimens.

When potential differences between the various areas sampled in the Atlantic were considered, the results indicated a lack of structure and non-significant differences. These non-significant differences were observed when testing several hypotheses, including structure between the Northern and Southern Hemispheres and the East and West Atlantic. Similarly, the analysis used to test the hypothesis of structure between the Atlantic and Western Indian Ocean also showed that the population displayed no genetic differentiation. When indices of structure between regions were compared, no evidence of population differentiation was found in any case, even when comparing pairs between the Atlantic and Western Indian Ocean. The authors indicate that it can be assumed that *P. kamoharai* constitutes a single genetic stock with a high degree of genetic flow throughout its distribution in the Atlantic Ocean, and that there is no differentiation in the genetic structure between the individuals analysed from the Western Indian Ocean and those from the Atlantic, specifying that it may be the same genetic stock distributed in both ocean basins, constituting a single population. That said, it is important to bear in mind that the samples from the Indian Ocean that were analysed in the work of da Silva Ferrette *et al*. (2015) are from individuals mostly caught in South African waters, and that samples obtained from other regions of the Indian Ocean were not included in the analysis. This absence of samples from other regions of the Indian Ocean could be the reason why a difference in genetic structure between the two basins was not observed, as suggested by Kindong *et al*. (2021).

5.b. Description of fisheries: catches and effort

Although *P. kamoharai* is not a target species of any fishery, it is taken as bycatch by several fleets operating in different regions. Although the statistical information on catches and landings of this species is practically inexistent, several works report that they are caught by different fleets, especially those targeting tropical tunas and swordfish using pelagic longline.

There are also a few records of occasional *P. kamoharai* catches using other fishing gears, including pelagic trawling (Dolganov and Ginanova, 2016), driftnets (Moazzam, 2012; Rodríguez-Acosta *et al*., 2016), and bottom trawling (Kiilu *et al*., 2019).

Available information on the occurrence of *P. kamoharai* in catches of longline fleets operating in the Atlantic Ocean indicates that it is a relatively frequent species, although its catches reflect a low relative abundance in comparison with other species. Castro and Mejuto (1995) reported that 113 individuals were caught during a longliner fishing trip targeting swordfish in the Gulf of Guinea from May to September 1993. A total of 77 sets were performed (242,200 hooks), which implies a CPUE of 0.47 inds./1,000 hooks. On this fishing trip, *P. kamoharai* was the fourth most caught shark species (by number of individuals). Joung *et al.* (2005) provided information on the catch of 242 individuals in 401 sets (1,142,300 hooks) carried out between 1999 and 2003 by Chinese Taipei longliners targeting BET in the Atlantic between 5ºN and 15ºS, during which *P. kamoharai* represented 11.9% of total shark catch and was the second most frequently caught species (by number of individuals). Pacheco *et al*. (2011) reported the catch of 25 specimens, in a total catch of 2,292 individuals, which were caught in 81 sets (50,170 hooks) made by Brazilian longlines operating in the western equatorial Atlantic from 2006 to 2007, in the area between 5ºN – 5ºS and 27ºW – 32ºW. Andrade *et al.* (2012) reports the catch of 7 individuals in 827 sets made in 2010 by 4 Spanish vessels targeting swordfish in the West Atlantic off Brazil. Amorim *et al.* (2015) recorded the catch of 219 *P. kamoharai* in 310 sets made by Portuguese longliners targeting swordfish in the South Atlantic from 2008 to 2012, with a CPUE=0.49 inds./1,000 hooks. Frédou *et al.* (2015) analysed catch and effort data of the chartered Brazilian fleet that operated mainly in the western equatorial and tropical SW Atlantic from 2004-2010, and found that *P. kamoharai* accounted for 1.97% of the total of individuals caught. Nunes *et al*. (2019) reported that *P. kamoharai* represented 1.2% (23 individuals) of the total catch during 53 fishing sets that were monitored to investigate the variables that potentially affect post-capture mortality in the Brazilian fleet in the western equatorial Atlantic. Coelho *et al*. (2012) reported the capture of 1,621 individuals, representing 5% of the sharks caught by 5 Portuguese longlines in 834 sets (1,078,200 hooks) during 18 trips covering a large area of the Atlantic Ocean between 2008 and 2011. In this study, *P. kamoharai* was the second most frequently caught shark species, reaching a CPUE of 1.5 individuals for every 1,000 hooks. Fernandez-Carvalho *et al.* (2015) reported the capture of 664 individuals in a total of 202 by pelagic longline experimental fishing sets (254,520 hooks), mainly conducted between October and January within and in the proximity of Cabo

Verde's EEZ. Muñoz-Lechuga and Coelho (2018) reported that 1,250 *P. kamoharai* were caught in 787 sets carried out by the Portuguese longline fleet in the Atlantic Ocean between 2011 and 2016. It was the second most frequently caught shark species, representing 2.3% of the total catch. This study also analysed data on the fleet operating in the South Indian Ocean which performed 903 sets in the same period. Fewer individuals of *P. kamoharai* were caught i.e. 41, which represented 0.1% of the total catch.

Petersen *et al*. (2009) reported that, although *P. kamoharai* is rarely caught, this species accounted for 4.2% of all the sharks caught by longline fleets operating in South Africa between 1998 and 2005, with a maximum of 81 individuals caught in a set off the east coast of South Africa in February 2002. The same paper reported a CPUE of 0.12 inds./1,000 hooks for the Asian fleet operating in South Africa, and a CPUE of 0.64 inds./1,000 hooks for the domestic fleet. Based on an analysis of observer data, Foulis (2013) mentioned that *P. kamoharai* was the shark most frequently caught by the South African fleet targeting SWO (22.5% of total shark catch) in fishing trips off the East coast of South Africa between 2002 and 2010. The crocodile shark was the fourth most frequently caught species by the tuna fleet, representing 2.1% of total shark catch. Li *et al.* (2013) reported that 21 individuals were caught in a fishing trip by a Chinese longliner in the central equatorial Indian Ocean from November 2012 to March 2013.

Based on information obtained by observers on board six Indonesian longliners operating in a relatively small area of the Western Indian Ocean (to the South of Java) between 2010 and 2011, Setyadji and Nugraha (2013) determined that 191 *P. kamoharai* were caught with an effort of 262,527 hooks, which gives a CPUE of 0.73 individuals for every 1,000 hooks. Subsequently, Novianto *et al.* (2014) analysed another set of data obtained by observers on board the Indonesian longline fleet, relating to 2,268 sets during 94 fishing trips carried out in the SE Indian Ocean (East of 75°E) between 2013 and 2015, during which 1,099 *P. kamoharai* were caught, accounting for 32.1% of the total number of sharks caught.

As in the case of the Atlantic, *P. kamoharai* is also caught by different fisheries in the Pacific Ocean. Moon *et al*. (2007) reported the catch of *P. kamoharai* in 4 of 6 trips carried out by Korean longliners between 2004-2007 in the central and western equatorial Pacific, indicating that all the individuals were discarded, and that the species represented 15.3% of the total sharks caught (second in number of individuals). Stevens and Wayte (2008) reported that *P. kamoharai* accounted for 2.1% (in number) of the total 44,306 sharks caught by Japanese longliners operating in Australian waters between 1992 and 1996. The species is also caught off Hawaii. Walsh *et al*. (2008) reported the capture of 1,927 individuals in a total of 26,507 fishing sets made by the Hawaii based fleet between 1995-2006, having been caught in 4.8% of the sets, with a total CPUE of 0.037 inds/1,000 hooks. Later, in a study carried out in the same area, Curran and Bigelow (2011) reported that 66 individuals were caught in a total of 1,393 sets (2,773,427 hooks) made by 16 vessels. Dai *et al*. (2012) reported that at least 142 individuals were caught in a fishing trip by a Chinese longliner targeting BET in the East Pacific from July to November 2003.

P. kamoharai is currently classified at global level as a species of Least Concern in the IUCN red list (Kyne *et al*. 2019).

6. Bibliography

Amorim, A.F., Arfelli, C.A., Fagundes, L. 1998. Pelagic elasmobranchs caught by longliners off southern Brazil during 1974 - 97: an overview. Marine and Freshwater Research 49: 621.

Amorim, S., Santos, M.N., Coelho, R., Fernandez-Carvalho, J. 2015. Effects of 17/0 circle hooks and bait on fish catches in a Southern Atlantic swordfish longline fishery. Aquatic Conservation: Marine and Freshwater Ecosystems 25: 518–533.

Andrade, H.A., Simoni, M.E.R. 2012. Discards of sharks by the Brazilian leased fleet in 2010. Collective Volumes of Scientific Papers ICCAT 68: 1938–1948.

Ariz, J., Delgado de Molina, A., Ramos, M.L., Santana, J.C. 2007. Length-weight relationships, conversion factors and analyses of sex-ratio, by length-range, for several species of pelagic sharks caught in experimental cruises on board Spanish longliners in the southwestern Indian Ocean during 2005. IOTC-2007-WPEB-04. Presented at the Indian Ocean Tuna Commission.

Bearez, P., Zambrano, M., Treviño, H. 2001. Premier signalement pour le Pérou de trois poissons océaniques: *Pseudocarcharias kamoharai* (Chondrichthyes, Pseudocarchariidae), *Alepisaurus ferox* (Osteichthyes, Alepisauridae) et *Pteraclis velifera* (Osteichthyes, Bramidae). Cybium 25: 181–184.

Cadenat, J., Blache, J. 1981. Requins de Méditerranée et d'Atlantique (plus particulièrement de la côte occidentale d'Afrique). Faune Tropicale 21: 1–330.

Calle-Morán, M.D., Hernández-Téllez, A.R., Tibán-Vivar, E.R., Intriago-Vera, Y.E., Del Valle-Coello, I.G., Loor-Jama, B.C., Ganchozo-López, Á.R. 2022. Diet composition and feeding habits of the crocodile shark, *Pseudocarcharias kamoharai*. Environmental Biology of Fishes 105: 685–697.

Camhi, M.D., Pikitch, E.K., Babcock, E.A. (Eds.) 2008. Sharks of the Open Ocean. Blackwell Publishing Ltd., Oxford, UK.

Castro, J., Mejuto, J. 1995. Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. Marine and Freshwater Research 46(6): 967.

Castro, J.I. 2011. The sharks of North America. New York: Oxford University Press. 613 pp.

Coelho, R., Fernandez-Carvalho, J., Lino, P.G., Santos, M.N. 2012. An overview of the hooking mortality of elasmobranchs caught in a swordfish pelagic longline fishery in the Atlantic Ocean. Aquatic Living Resources 25: 311–319.

Coelho, R., Lino, P.G., Santos, M.N. 2011. At-haulback mortality of elasmobranchs caught on the Portuguese longline swordfish fishery in the Indian Ocean. IOTC-2011-WPEB07- 31. Presented at the Indian Ocean Tuna Commission, Mahe, Seychelles, p. 9.

Compagno, L.J.V. 1984. Sharks of the world: an annotated and illustrated catalogue of shark species known to date, FAO fisheries synopsis. United Nations Development Program, Rome.

Compagno, L.J.V. 2001. Bullhead, mackerel and carpet sharks: Heterodontiformes, Lamniformes and Orectolobiformes, Sharks of the world. Food and Agriculture Organization of the United Nations, Rome.

Curran, D., Bigelow, K. 2011. Effects of circle hooks on pelagic catches in the Hawaii-based tuna longline fishery. Fisheries Research 109: 265–275.

Da Silva Ferrette, B.L., Mendonça, F.F., Coelho, R., de Oliveira, P.G.V., Hazin, F.H.V., Romanov, E.V., Oliveira, C., Santos, M.N., Foresti, F. 2015. High Connectivity of the Crocodile Shark between the Atlantic and Southwest Indian Oceans: Highlights for Conservation. PLoS ONE 10, e0117549.

Dai, X.J., Zhu, J.F., Chen, X.J., Xu, L.X., Chen, Y. 2012. Biological observations on the crocodile shark *Pseudocarcharias kamoharai*. Journal of Fish Biology 80: 1207–1212.

Dolganov, V.N., Ginanova, T.T. 2016. Pseudocarchariidae, a family of lamnoid sharks that are new to the fauna of Russia. Russian Journal of Marine Biology 42: 100–101.

Edwards, A.J. 1993. New records of fishes from the Bonaparte Seamount and Saint Helena Island, South Atlantic. Journal of Natural History 27: 493–503.

Estupiñán-Montaño, C., Galván-Magaña, F. 2020. First Insight into the Biological Aspects of the Crocodile Shark *Pseudocarcharias kamoharai* in the Eastern Pacific Ocean. Thalassas: An International Journal of Marine Sciences 37: 229–233.

Fernandez-Carvalho, J., Coelho, R., Santos, M.N., Amorim, S. 2015. Effects of hook and bait in a tropical Northeast Atlantic pelagic longline fishery: Part II—Target, bycatch and discard fishes. Fisheries Research 164: 312–321.

Foulis, A. 2013. A retrospective analysis of shark catches made by pelagic longliners off the east coast of South Africa and biology and life history of shortfin mako shark, *Isurus oxyrinchus* (Master's Thesis). University of Kwazulu-Natal, Durban, South Africa.

Fujita, K. 1981. Oviphagous Embryos of the Pseudocarchariid Shark, *Pseudocarcharias kamoharai*, from the Central Pacific. Japanese Journal of Ichthyology 28: 37–44.

Gadig, O.B.F. 2001. Tubarões da costa brasileira (PhD Thesis). Universidade Estadual Paulista, Rio Claro, SP, Brasil.

Gadig, O.B.F., Bezerra, M.A., Feitosa, R.D., Furtado-Neto, M.A.A. 2000. Ictiofauna marinha do estado do Ceará, Brasil: I. Elasmobranchii. Arquivos de Ciências do Mar 33: 127–132.

Gago, M. 2014. Idade e crescimento do tubarão-crocodilo, *Pseudocarcharias kamoharai*, no Oceano Atlântico (Master's Thesis). Universidade do Algarve, Faro, Portugal.

Gao, C.X., Tian, S.Q., Dai, X.J., Wu, F., Xu, Y.W. 2013. Preliminary analysis of the biology of the crocodile shark, *Pseudocarcharias kamoharai* in the tropical Eastern-central Atlantic Ocean. Journal of Shanghai Ocean University 22: 289–294.

Gilman, E., Chaloupka, M., Swimmer, Y., Piovano, S. 2016. A cross-taxa assessment of pelagic longline by-catch mitigation measures: conflicts and mutual benefits to elasmobranchs. Fish and Fisheries 17(3): 748–784.

Intriago, Y.E. 2013. Aspectos reproductivos del tiburón cocodrilo (*Pseudocarcharias kamoharai*) desembarcados en el puerto Santa Rosa, Salinas, provincia de Santa Elena, junio 2012 a mayo 2013 (tesis de grado). Universidad de Guayaquil, Guayaquil, Ecuador.

IUCN SSC Shark Specialist Group. 2018. *Pseudocarcharias kamoharai*. The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org. Downloaded on 20 May 2021.

Jordaan, G.L., Santos, J., Groeneveld, J.C. 2020. Shark discards in selective and mixed-species pelagic longline fisheries. PLoS ONE 15: e0238595.

Joung, S.J., Liu, K.M., Liao, Y.Y., Hsu, H.H. 2005. Observed By-catch of Taiwanese Tuna Longline Fishery in the South Atlantic Ocean. Journal of the Fishery Society of Taiwan 32: 69–77.

Kiilu, B., Kaunda-Arara, B., Oddenyo, R., Thoya, P., Njiru, J. 2019. Spatial distribution, seasonal abundance and exploitation status of shark species in Kenyan coastal waters. African Journal of Marine Science 41: 191–201.

Kindong, R., Wang, H., Wu, F., Dai, X., Tian, S. 2020. Age, Growth, and Sexual Maturity of the Crocodile Shark, *Pseudocarcharias kamoharai*, From the Eastern Atlantic Ocean. Frontiers in Marine Science 7: 586024.

Kindong, R., Xia, M., Pandong, N.A., Sarr, O., Wu, F., Tian, S., Dai, X. 2021. All we know about the crocodile shark (*Pseudocarcharias kamoharai*): Providing information to improve knowledge of this species. Journal for Nature Conservation 63: 126039.

Kiszka, J.J., Aubail, A., Hussey, N.E., Heithaus, M.R., Caurant, F., Bustamante, P. 2015. Plasticity of trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by stable isotope and mercury analyses. Deep Sea Research Part I: Oceanographic Research Papers 96: 49–58.

Kohler, N.E., Turner, P.A. 2020. Distributions and Movements of Atlantic Shark Species: A 52-Year Retrospective Atlas of Mark and Recapture Data. Marine Fisheries Review 81: 1–93.

Kyne, P.M., Romanov, E., Barreto, R., Carlson, J., Fernando, D., Fordham, S., Francis, M.P., Jabado, R.W., Liu, K.M., Marshall, A., Pacoureau, N., Sherley, R.B. 2019. *Pseudocarcharias kamoharai* (errata version published in 2020). The IUCN Red List of Threatened Species 2019: e.T39337A171964644. https://dx.doi.org/10.2305/IUCN.UK.2019-1.RLTS.T39337A171964644.en. Downloaded on 08 June 2021.

Lessa, R., Andrade, H.A., de Lima, K.L., Santana, F.M. 2016. Age and growth of the midwater crocodile shark *Pseudocarcharias kamoharai*. Journal of Fish Biology 89(1): 371–385.

LI, J., Song, L., Li, D. 2013. The capture depth of the dominant bycatch species and the relationship between their catch rates and the sea surface temperature. IOTC-2013-WPEB09-39. Presented at the Indian Ocean Tuna Commission, Mahe, Seychelles, p. 18.

Lucena Frédou, F., Tolotti, M.T., Frédou, T., Carvalho, F., Hazin, H., Burgess, G., Coelho, R., Waters, J.D., Travassos, P., Hazin, F.H.V. 2015. Sharks caught by the Brazilian tuna longline fleet: an overview. Reviews in Fish Biology and Fisheries 25: 365–377.

Martínez, J., Correia, M. 2010. Reporte de tiburón cocodrilo o tártaro, *Pseudocarcharias kamoharai* (Matsubara, 1936). Boletín Cofa: Convivencia Pesquera 8: 12–24.

Meléndez, R., Lopez, S., Yáñez, E. 2006. Nuevos antecedentes de *Pseudocarcharias kamoharai* (Matsubara, 1936) (Chondrichthyes: Lamniformes: Pseudocarchariidae), frente al norte de Chile. Investigaciones Marinas 34(2): 223–226.

Moazzam, M., 2012. Status report on bycatch of tuna gillnet operations in Pakistan. Presented at the IOTC 8th Session of The Working Party on Ecosystems and Bycatch (WPEB), Cape Town, p. 12.

Moon, D.Y., Hwang, S.J., An, D.H., Kim, S.S. 2007. Bycatch of sharks in Korean tuna longline fishery. Bulletin of the Korean society of Fisheries Technology 43: 329–338.

Muñoz-Lechuga, R., Coelho, R. 2018. Depredation in pelagic surface longlines in the Atlantic and Indian Oceans. Fisheries Management and Ecology 25(6): 429–440.

Novianto, D., Rochman, F., Nugraha, B. 2014. Species composition, CPUE and length frequency of oceanic sharks based on observer data from the Indonesian longline fishery in the Indian Ocean. IOTC–2014–WPEB10–13 Rev_1. Presented at the Indian Ocean Tuna Commission, Mahe, Seychelles, p. 12.

Nunes, D., Hazin, F., Branco, I., Hazin, H., Pacheco, J., Afonso, A., Mourato, B., Carvalho, F. 2019. Survivorship of species caught in a longline tuna fishery in the western equatorial Atlantic Ocean. Latin American Journal of Aquatic Research 47(5): 798–807.

Oliveira, P., Hazin, F.H.V., Carvalho, F., Rego, M., Coelho, R., Piercy, A., Burgess, G. 2010. Reproductive biology of the crocodile shark *Pseudocarcharias kamoharai*. Journal of Fish Biology 76: 1655–1670.

Pacheco, J.C., Kerstetter, D.W., Hazin, F.H., Hazin, H., Segundo, R.S.S.L., Graves, J.E., Carvalho, F., Travassos, P.E. 2011. A comparison of circle hook and J hook performance in a western equatorial Atlantic Ocean pelagic longline fishery. Fisheries Research 107: 39–45.

Petersen, S.L., Honig, M.B., Ryan, P.G., Underhill, L.G., Compagno, L.J. 2009. Pelagic shark bycatch in the tuna and swordfish directed longline fishery off Southern Africa. African Journal of Marine Science 31: 215–225.

Rodríguez-Acosta, E.D.V., Figueredo Rodríguez, A.J., Espinoza Moya, H.L., Ron Esteves, E.J. 2016. Acerca de la presencia de *Pseudocarcharias kamoharai* (Matsubara) (Lamniformes: Pseudocarchariidae) en aguas al suroeste de la isla de Margarita, Estado Nueva Esparta, Venezuela. Boletín de Investigaciones Marinas y Costeras 45: 335–344.

Romanov, E.V., Ward, P., Levesque, J.C., Lawrence, E. 2008. Preliminary analysis of crocodile shark (*Pseudocarcharias kamoharai*) distribution and abundance trends in pelagic longline fisheries. IOTC-2008-WPEB-09. Presented at the Indian Ocean Tuna Commission, Bangkok, Thailand, p. 29.

Rosa, D., Gago, M., Fernandez-Carvalho, J., Coelho, R. 2021. Life history parameters of the crocodile shark, *Pseudocarcharias kamoharai*, in the tropical Atlantic Ocean. Journal of the Marine Biological Association of the United Kingdom 101(4): 753-763.

Ruiz-Campos, G., Castro-Aguirre, J.L., Balart, E.F., Campos-Dávila, L., Vélez-Marín, R. 2010. Nuevos ejemplares y nuevos registros de peces cartilaginosos (*Vertebrata: Chondrichthyes*) de la costa del Pacífico mexicano. Revista Mexicana de Biodiversidad 81: 363–371.

Setyadji, B., Nugraha, B. 2013. Discards of the Indonesian tuna longline fishery in Indian Ocean. Indonesian Fisheries Research Journal 19: 25-32.

Shimada, K. 2002. Teeth of Embryos in Lamniform Sharks (Chondrichthyes: Elasmobranchii). Environmental Biology of Fishes 63: 309-319.

Soto, J.M.A. 2000. Sobre a presença do tubarão-crocodilo *Pseudocarcharias kamoharai* (Matsubara, 1936) (Condrichthyes, Pseudocarchariidae) no Sudoeste do Atlantico. Estudos de Biologia 46: 59–70.

Stewart, A.L. 2001. First record of the crocodile shark, *Pseudocarcharias kamoharai* (Chondrichthyes: Lamniformes), from New Zealand waters. New Zealand Journal of Marine and Freshwater Research 35: 1001–1006.

Tibán-Vivar, E. del R. 2013. Hábitos alimenticios del tiburón cocodrilo (*Pseudocarcharias kamoharai*) desembarcados en el puerto pesquero Santa Rosa, Salinas, provincia de Santa Elena (tesis de grado). Universidad de Guayaquil, Guayaquil, Ecuador.

Vieira, R.S., Lessa, R.P. 2010. Morfometria do tubarão crocodilo, *Pseudocarcharias kamoharai* (Matsubara, 1936) capturado na Zona Econômica Exclusiva - ZEE. Presented at the X Jornada de Ensino, Pesquisa e Extensão – Jepex 2010 - UFRPE, Recife, p. 3.

Walsh, W.A., Bigelow, K.A., Sender, K.L. 2009. Decreases in Shark Catches and Mortality in the Hawaii-Based Longline Fishery as Documented by Fishery Observers. Marine and Coastal Fisheries 1: 270–282.

White, W.T. 2007. Biological observations on lamnoid sharks (Lamniformes) caught by fisheries in eastern Indonesia. Journal of the Marine Biological Association of the United Kingdom 87(3): 781–788.

Wu, F., Kindong, R., Dai, X., Sarr, O., Zhu, J., Tian, S., Li, Y., Nsangue, B.T.N. 2020. Aspects of the reproductive biology of two pelagic sharks in the eastern Atlantic Ocean. Journal of Fish Biology 97(6): 1651–1661.

Xu, Y., Dai, X., Zhuang, Z., Zhu, J., Chen, Y. 2012. Vertical distribution of bycatch species captured by tuna longline fishery in the Atlantic Ocean. Transaction of Oceanology and Limnology 4: 55–63.