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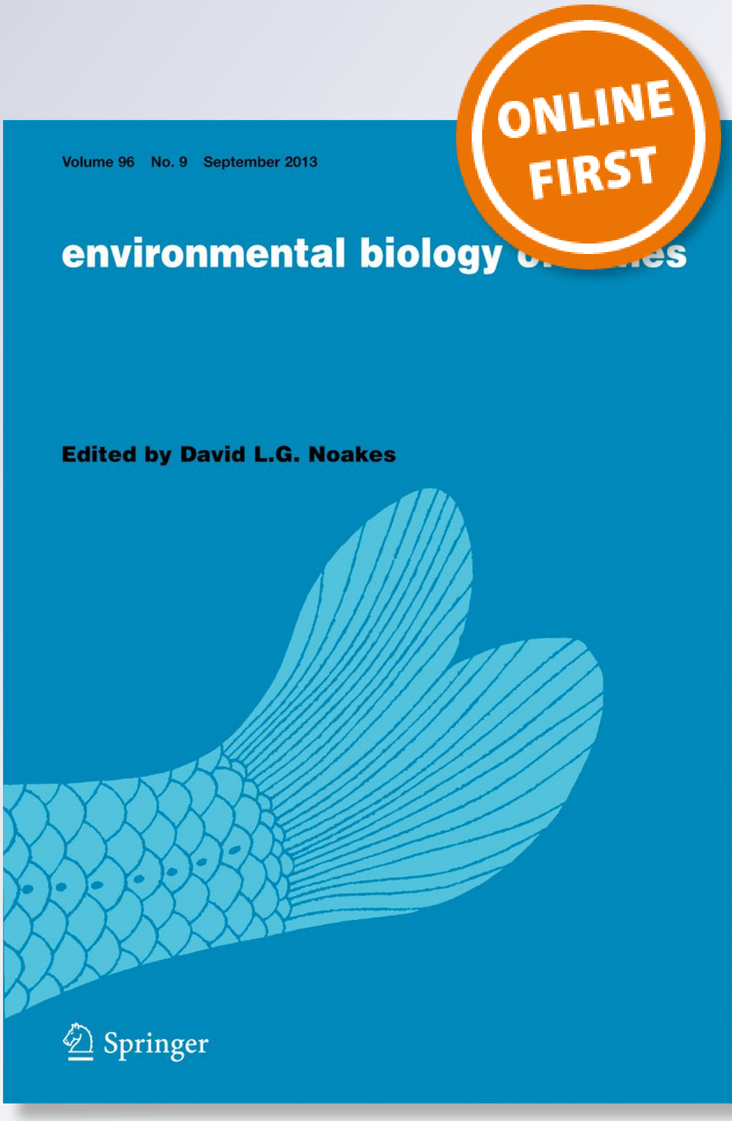

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Ichnology applied to the study of Cookiecutter shark (*Isistius brasiliensis*) biogeography in the Gulf of Guinea

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Abstract Scarce bycatches of Cookiecutter Shark (*Isistius brasiliensis*) is the reason why this species is easier studied through the marks they leave on their prey rather than by direct observation of the shark itself. However, scientific studies that have used ichnology to remedy this lack of knowledge have been probably based on mistaken assumptions transmitted among previous authors without due verification. Despite identifying the problem almost twenty years ago, the authors of this paper were unable to obtain a sufficient number of Cookiecutter Shark specimens until now in order to confirm their hypothesis. This work provides a set of biometrics of Cookiecutter Shark specimens among which worth highlighting is the measure of the lower jaw width (LJW), which was absent in the relevant literature. This parameter is crucial for correcting the linear regression between total length and mouth width on which earlier biogeographical works were based. The new linear regression obtained using LJW was later applied to the bites observed on Swordfish caught in the Gulf of Guinea in 1996. The results show a probability of 0.50 for Cookiecutter Shark attack on Swordfish in the study area (29.4% of Swordfish bitten), and a positive correlation between predator and prey sizes. The lengths of Cookiecutter Shark inferred from bite size on sampled Swordfish revealed a certain geographical disaggregation in the area, with older individuals, probably females, concentrating in waters near the mouth of the Congo River.

Keywords Cookiecutter shark · Swordfish · Longline fleet · Gulf of Guinea

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Introduction

The Cookiecutter Shark (*Isistius brasiliensis*, Quoy & Gaimard, 1824) is an ectoparasite of a wide variety of pelagic fish and marine mammals (Jones 1971; Le Boeuf et al. 1987; Hiruki et al. 1993). The morphology of its mouth enables it to bite portions of flesh from larger animals (Shirai and Nakaya 1992). One of the most commonly used methods to study this species is through analysis of bite marks left on its prey (due to scarcity of this shark in commercial catches).

A pioneering study on this subject was the innovative contribution from Muñoz-Chapuli et al. (1988), who inferred the Cookiecutter Shark's population density and population structure from bites observed on Swordfish (*Xiphias gladius,* Linnaeus, 1758) caught in African NW Atlantic waters. They assumed that this shark's body size is proportional to the size of the bite inflicted. The same method was later used by

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Papastamatiou et al. (2010) for bites observed in different pelagic fish species from the Pacific Ocean, where Swordfish presented the highest percentage of attack by this shark. Both works have applied the same linear regression between total length (TL) and mouth width (MW) of Cookiecutter Shark, calculated by Muñoz-Chapuli et al. (1988) based on biometric data provided by Cadenat and Blache (1981).

The present work was begun almost twenty years ago with the objective of extending the biogeographical study of Muñoz-Chapuli et al. (1988) to other areas of the Atlantic Ocean. The huge delay in performing our analysis was due to an accidental capture of a specimen of Cookiecutter Shark with two "*cookies*" (portions of the prey flesh) in its stomach, the dimensions of which made us rethink some of the basic assumptions of the Muñoz-Chapuli's study. On the other hand, the great bias in the prediction of the total length of our specimen after applying the linear regression provided by Muñoz-Chapuli et al. (1988) led us to conclude that the original biometric data (Cadenat and Blache 1981) had to be revalidated with biometrics of new specimens.

From then on, a long period was spent trying to obtain new specimens of Cookiecutter Shark to contrast measurements and arrive at a new relationship between the total length and the lower jaw width of the Cookiecutter Shark. The collection of a sufficient number of specimens took longer than desired because it is a very rare species in the catches of commercial fleets.

The aim of our work is, firstly, to provide biometric data of Cookiecutter Shark, which can be used to offer a contrasted alternative to the linear regression used until now by the scientific community to infer its total length from bite dimensions on prey. Secondly, we have analysed swordfish bite data from the Gulf of Guinea and have thus increased the information available on Cookiecutter Shark biogeography to other ocean areas. To do this, our methodology was based on the same main assumptions as in previous works (Muñoz-Chapuli et al. 1988; Papastamatiou et al. 2010): 1) all crater wounds were inflicted by Cookiecutter Shark, 2) for fresh bites, the bite was inflicted while the fish was on the long-line, and 3) bite diameter of fresh scars corresponds with shark mouth diameter. However, unlike these authors, we specify the use of the minor axis of the bite as the exact footprint of the shark's lower jaw after incision.

Materials and methods

Nine ($n = 9$) specimens of Cookiecutter Shark were collected on board the Spanish drifting longline fleet (targeting Swordfish and other large pelagic fish) operating in the Atlantic and Pacific oceans, between 1996 and 2015. These specimens were frozen on board, after recording the date and the geographical position of capture. After landing, they were transported and stored frozen in the laboratory, where they are part of a fish collection. In 2016, these specimens were thawed for biometric sampling, and whenever possible, the following characteristics were recorded (Fig. 1): total length (TL), fork length (FL), preorbital length (POB), prespiracular length (PSP), prebranchial length (PG1), head length (HDL), pre-first dorsal-fin length (PD1), pre-second dorsal-fin length (PD2), precaudal-fin length (PCL), interdorsal space (IDS), dorsal caudal-fin space (DCS), prepectoral-fin length (PP1), prepelvic-fin length (PP2), snout-vent length (SVL), prenarial length (PRN), preoral length (POR), eye length (EYL), eye height (EYH), first gill slit height (GS1), intergill length (ING), fifth gill slit height (GS5), pectoral-fin anterior margin (P1A), pectoral-fin posterior margin (P1P) and pectoral-fin height (P1H). All specimens were weighed to record their total weight (TW). In particular, the lower jaw width (LJW) dimensions were collected instead of the mouth width dimensions (Fig. 2). The logarithms of total length (TL) and lower jaw width (LJW) of these nine specimens of Cookiecutter Shark were used to estimate the linear regression between both parameters: $\ln TL = a + b * \ln LJW$.

The presence or absence of fresh crater wounds was also recorded for the 1825 Swordfish caught by a Spanish drifting longline vessel operating in the Gulf of Guinea between August and November 1996. Swordfish size (LJFL: lower jaw-fork length), sex and geographical grid of capture (square of 5° latitude × 5° longitude) were also recorded for all of them. Healed wounds were not taken into account. In like manner, the presence or absence of recent bites in a sub-sample of Swordfish was also recorded by taking into account their condition and whether specimens were hauled dead or alive.

The abundance of Cookiecutter Shark was inferred based on the probability of their attack on Swordfish, following the same methodology proposed by Muñoz-Chapuli et al. (1988) and also used by Papastamatiou et al. (2010). To this end, P is defined as the probability that a single specimen of Swordfish will be attacked and

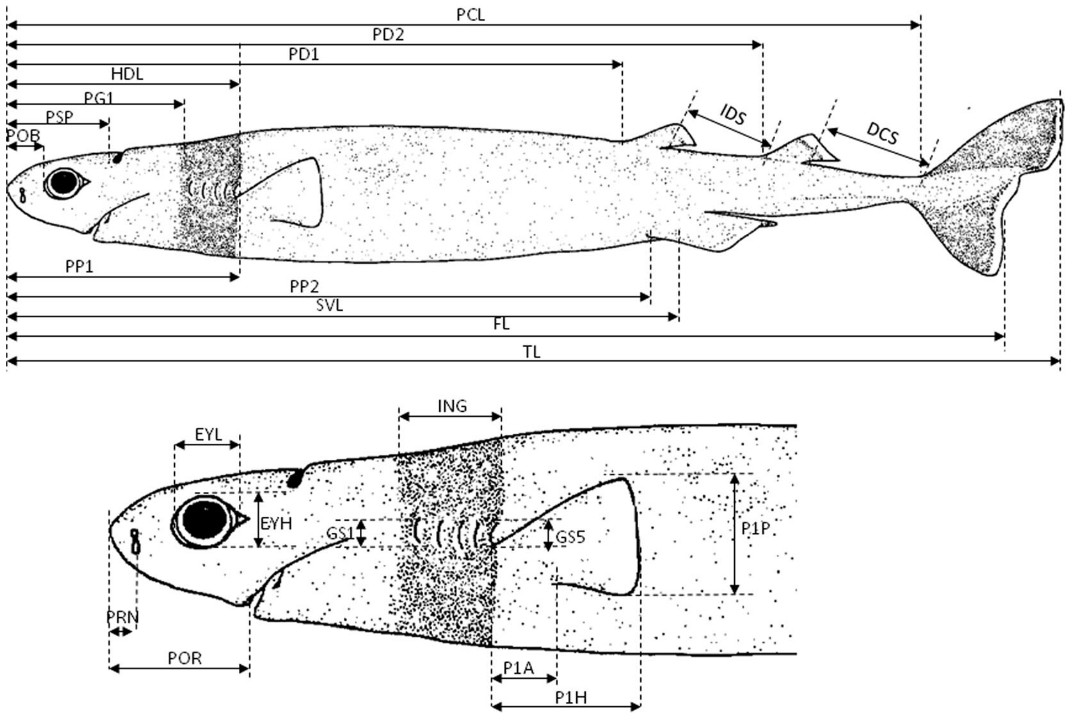

Fig. 1 Diagram showing biometrics performed: total length (TL), fork length (FL), preorbital length (POB), prespiracular length (PSP), prebranchial length (PG1), head length (HDL), pre-first dorsal-fin length (PD1), pre-second dorsal-fin length (PD2), precaudal-fin length (PCL), interdorsal space (IDS), dorsal caudal-fin space (DCS), prepectoral-fin length (PP1), prepelvic-fin length (PP2), snout-vent length (SVL), prenarial length (PRN), preoral length (POR), eye length (EYL), eye height (EYH), first gill slit height (GS1), intergill length (ING), fifth gill slit height (GS5), pectoral-fin anterior margin (P1A), pectoral-fin posterior margin (P1P) and pectoral-fin height (P1H)

bitten one or more times, based on the binomial distribution, $P = 1- (1 - f)^2$, where f is the frequency that a Swordfish will be bitten one or more times. P was analysed for different variables: geographic grid (by applying a one-way ANOVA test), size of Swordfish (linear regression), and the sex and condition of Swordfish (Wilcoxon-Mann-Whitney test).

Fig. 2 Photograph showing the procedure used for measuring the width of the Cookiecutter Shark's lower jaw. Specimen No. 4 in Table 1

The major and minor axes of 829 fresh wounds were recorded. The total length (TL) of the Cookiecutter sharks was estimated from the minor axis of the corresponding bites inflicted on Swordfish using our linear regression TL-JLW. The size of the Cookiecutter Shark could thus be analysed against geographical (grid) and ecological variables (size and sex of prey) by applying a Multivariate Regression Tree (MRT) (Breiman et al. 1984). The final number of clusters is decided by applying the "one standard error" stopping rule (1-SE rule): thus the smallest tree within one standard error of the best is selected as the optimum tree. Computations were performed using the R software (R Core Team 2015).

Results

The accidental capture of a Cookiecutter Shark specimen on board a Spanish longliner in the Gulf of Guinea in November 1996 helped refute one of the main assumptions on which the work of Muñoz-Chapuli et al. (1988) was based. The stomach content of this specimen contained two swordfish meat "cookies" of elliptical shape. Both minor axes coincided exactly with the lower jaw width (35 mm), but this was not the case with their respective major axes (45 mm and 65 mm) (specimen No. 1 in Table 1). This isolated finding was later confirmed in another specimen caught in the central Atlantic in 2009 whose stomach content contained one swordfish meat "cookie" (specimen No. 6 in Table 1; Fig. 3).

Table 1 Biometric data of nine ($n = 9$) specimens of Cookiecutter Shark collected onboard the Spanish surface longlining fleet targeting Swordfish and other large pelagic fish in the Atlantic and Pacific between 1996 and 2015. Sex: male (1), and female (2). Total length (TL), fork length (FL), lower jaw width (LJW), total weight (TW), bite (minor axis of the "cookies" found in the stomach), preorbital length (POB), prespiracular length (PSP), prebranchial length (PG1), head length (HDL), pre-first dorsal-fin length (PD1), pre-second dorsal-fin length (PD2), precaudal-fin length (PCL), interdorsal space (IDS), dorsal caudal-fin space (DCS), prepectoral-fin length (PP1), prepelvic-fin length (PP2), snout-vent length (SVL), prenarial length (PRN), preoral length (POR), eye length (EYL), eye height (EYH), first gill slit height (GS1), intergill length (ING), fifth gill slit height (GS5), pectoral-fin anterior margin (P1A), pectoral-fin posterior margin (P1P) and pectoral-fin height (P1H). All measures in millimetres (mm), except TW in grams (g)

Specimen Year Coordinates	1 1996 02°28'S 08°39'W	2 2005 –	3 2005 –	4 2006 06°20'N 33°05'W	5 2007 29°41'S 93°56'W	6 2009 02°33'N 25°45'W	7 2011 13°05'S 03°24'W	8 2015 03°04'N 33°15'W	9 – –
Sex	1	2	2	1	2	1	2	1	2
TL	400	345	384	154	458	217	471	204	471
LJW	35.0	26.9	26.8	15.0	40.9	20.3	36.1	20.1	42.3
TW (g)	300	139.1	171.1	8.5	434.0	29.8	518.3	28.3	327.1
Bite	35.0/35.0	–	–	–	–	20.2	–	–	–
FL	375	321	351	145	418	203	439	189	440
POB	–	10	6	2	16	5	14	4	14
PSP	–	29	25	13	41	20	33	18	27
PG1	–	60	57	27	80	36	–	33	73
HDL	–	74	70	34	93	46	–	43	95
PD1	–	207	244	95	272	129	282	119	288
PD2	–	247	280	114	319	155	345	142	344
PCL	–	294	388	136	385	187	–	171	412
IDS	–	31	21	13	36	19	48	–	44
DCS	–	36	91	16	54	26	–	–	52
PP1	–	73	72	34	95	46	–	46	–
PP2	–	221	254	99	28	132	306	125	300
SVL	–	228	263	102	293	138	–	135	–
PRN	–	3	2	1	3	2	5	2	4
POR	–	22	17	11	31	13	24	12	23
EYL	–	14.4	–	6.0	12.5	–	–	6.0	–
EYH	–	9.5	–	4.0	9.8	–	–	4.0	–
GS1	–	3.3	3.3	2.0	3.2	–	–	–	3.4
ING	–	15.2	16.8	7.0	19.6	7.8	–	9.0	19.7
GS5	–	3.8	–	–	3.9	–	–	–	–
P1A	–	23.9	23.4	–	33.3	–	–	13.0	–
P1P	–	18.3	14.9	–	20.9	10.5	–	8.0	20.9
P1H	–	20.6	21.5	–	27.7	–	–	13.0	21.0

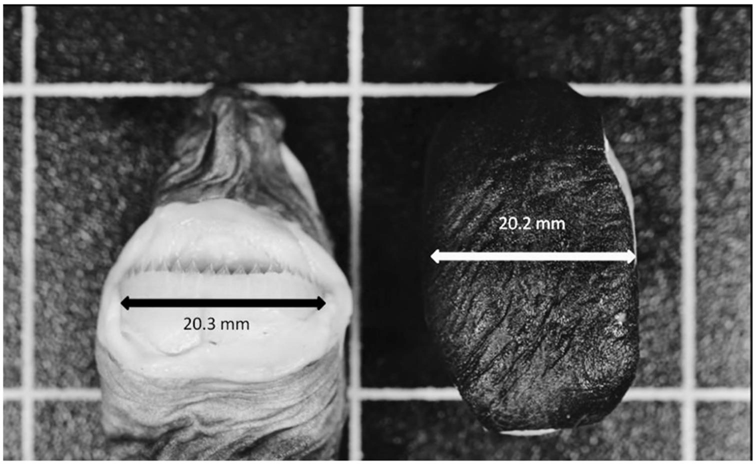

Fig. 3 Ventral view of a specimen of Cookiecutter Shark showing lower jaw beside a plug of swordfish flesh found inside its stomach. Specimen No. 6 in Table 1

Moreover, the finding of our first Cookiecutter Shark specimen in 1996 also enabled us to test the relationship between total length (TL) - mouth width (MW) used by Muñoz-Chapuli et al. (1988): TL = 4.51(MW) + 82.8. According to this formula, a specimen with a mouth width (MW) of 35 mm should have a total length (TL) of 241 mm, which represents 60% of the 400 mm total length of our specimen. In order to verify the correction of this linear regression, we recalculated it using original data provided by Cadenat and Blache (1981), and obtained: ln (TL) = 3.201 + 0.872 * ln (MW) ($r^2 = 0.84$; $\alpha < 0.0001$). This new TL-MW relationship predicts a length of 546 mm for our specimen, and represents 137% of the actual measurement.

The biometric information of the nine ($n = 9$) Cookiecutter Shark specimens collected by us over the last twenty years is shown in Table 1. The total length of the sampled Cookiecutter Shark specimens ranged from 154 mm to 471 mm. The linear regression calculated between total length (TL) and lower jaw width (LJW) ($r^2 = 0.93$; $\alpha < 0.0001$; Fig. 4) provides the following equation:

$$\ln(TL) = 2.034 + 1.126^{*} \ln(LJW)$$

where ln (TL) is the natural logarithm of the total length (mm) of the shark and ln (LJW) is the natural logarithm of its lower jaw width (mm). This TL-LJW relationship was contrasted against the TL-MW relationship of Muñoz-Chapuli et al. (1988), which is still used by the scientific community (Papastamatiou et al. 2010). The predictions obtained with the linear regression of Muñoz-Chapuli et al. (1988) provide a mean deviation of −40%, while the predictions of our TL-LJW relationship present a mean deviation of 0.5% (Table 2).

The probability of a Cookiecutter Shark attack on Swordfish ranges from 0.24 for coastal waters (grid 7) to 0.73 for open waters of the Gulf of Guinea (grid 3) (Table 3, Fig. 5). However, these differences between geographic grids are not statistically significant (ANOVA: $F_{1,5} = 0.55$, $p = 0.5$), which would leave an attack probability of 0.50 for the entire Gulf of Guinea. The percentage of swordfish with fresh wounds presents a mean of 28.8% (±11.8) between grids and of 29.4% for the entire Gulf of Guinea.

The Swordfish sampled have size distribution in the range of 70–260 cm lower jaw-fork length (LJFL), with

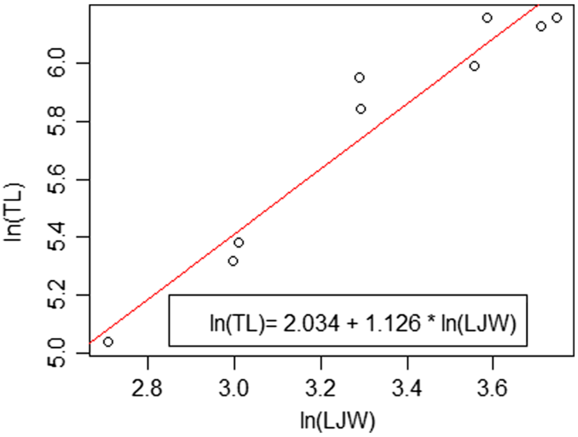

Fig. 4 Scatter diagram with the regression line of total length (TL) versus lower jaw width (LJW), both in mm, in nine ($n = 9$) specimens of Cookiecutter Shark directly compiled between 1996 and 2015 ($r^2 = 0.93$). The variables are significantly correlated ($\alpha < 0.0001$)

Table 2 Prediction of Cookiecutter Shark total length (TL_{pre}) and deviation from observed value (TL_{pre}/TL_{obs}) between the TL-MW regression used by Muñoz-Chapuli et al. (1988) and the TL-LJW regression provided in the present paper. The measurements are presented in millimetres

	Observed data		Muñoz-Chapulí et al. (1988) TL-MW regression		TL-LJW regression presented here	
Specimen	TL_{obs}	LJW_{obs}	TL_{pre}	TL_{pre}/TL_{obs}	TL_{pre}	TL_{pre}/TL_{obs}
1	400	35.0	240.7	0.60	418.7	1.05
2	345	26.9	204.3	0.59	311.9	0.90
3	384	26.8	203.8	0.53	310.3	0.81
4	154	15.0	149.2	0.96	162.3	1.05
5	458	40.9	267.2	0.58	498.9	1.09
6	217	20.3	174.4	0.80	227.0	1.05
7	471	36.1	245.7	0.52	433.9	0.92
8	204	20.1	173.3	0.84	223.8	1.07
9	471	42.3	273.6	0.58	518.5	1.10

a mean LJFL of 139.6 cm (± 34.7). The probability (P) of a Cookiecutter Shark attack shows a positive correlation with Swordfish size ($r^2 = 0.84$; $\alpha < 0.0001$; Fig. 6). However, P does not significantly differ by sex ($P_{male} = 0.52$, $P_{female} = 0.47$) or by Swordfish condition ($P_{alive} = 0.59$, $P_{dead} = 0.59$).

The application of our TL-LJW relationship to the Swordfish bites sampled in the Gulf of Guinea provides a Cookiecutter Shark size distribution within the 84–832 mm range and a mean total length of 319 mm (± 129 mm) (Table 3, Fig. 7). The mean TL by geographic grid varies from 280 mm for waters of Nigeria and Benin (grid 4) to 500 mm for waters of Gabon and Congo (grid 7). The multivariate regression tree for the Cookiecutter Shark size versus geographic grid and size and sex of Swordfish shows that the cross-validated relative error decreases to a minimum for a tree size of two before increasing again (Fig. 8). In this way, a geographic disaggregation could be determined in two areas: grids 1–6 (mean size 314 mm) and grid 7 (mean size 500 mm). This new stratification is confirmed by the ANOVA test ($F_{1,827} = 37.16$, $p < 0.0001$).

Discussion

The finding of two specimens of Cookiecutter Shark with swordfish meat "cookies" in their stomachs enables us to demonstrate that the attack and biting mechanism of the Cookiecutter Shark has probably been misinterpreted by the scientific community. The biogeographical analysis of Muñoz-Chapuli et al. (1988)

Table 3 Frequency and probability of Cookiecutter Shark attack on Swordfish, and mean Cookiecutter Shark total length (mm) by geographical grid (5°×5° square). SWO: FAO code of Swordfish. TL: total length

No.	Position Square 5°×5°	Total number of SWO sampled	Number of SWO wounded	Frequency	P	Cookiecutter Mean TL (mm)
1	0010NW	41	9	0.2195	0.3908	386
2	0005NW	372	84	0.2258	0.4006	310
3	0005SW	212	101	0.4764	0.7259	352
4	0000NE	490	174	0.3551	0.5841	280
5	0000SE	91	34	0.3736	0.6076	290
6	0005SE	480	116	0.2417	0.4249	331
7	0010SE	139	18	0.1295	0.2422	500
TOTAL	Gulf of Guinea	1825	536	0.2937	0.5011	319

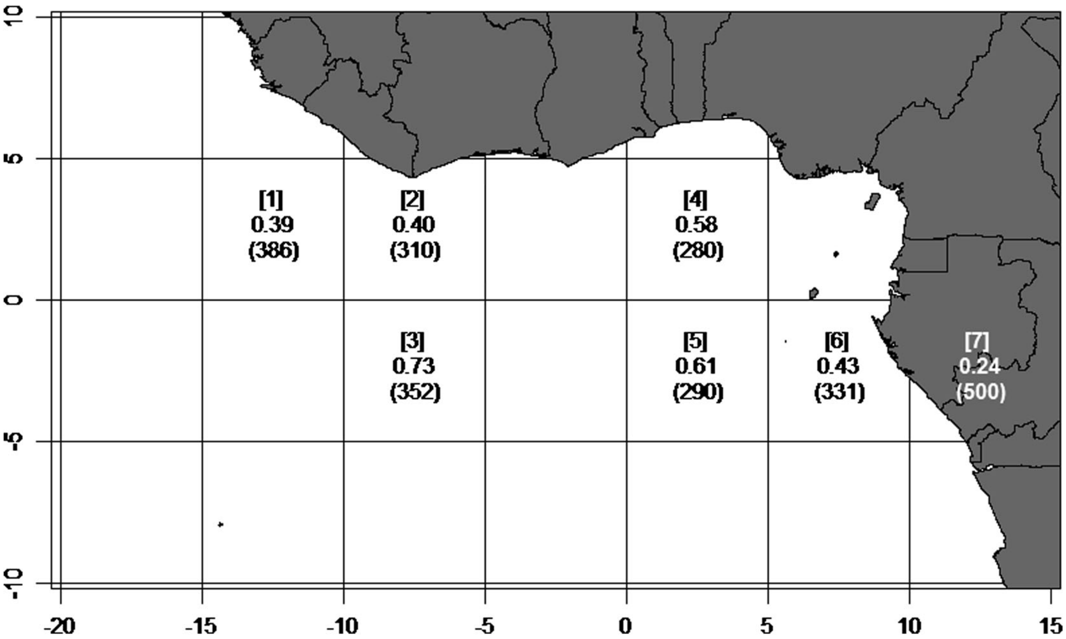

Fig. 5 Area of the Gulf of Guinea covered by sampling in 1996. Probability of Cookiecutter shark bite on Swordfish. Numerical code of geographical grid in square brackets. Mean Cookiecutter shark's total length (mm) in brackets

consisted in the estimation of the total length of the Cookiecutter Shark by applying a total length (TL) - mouth width (MW) relationship where the latter parameter was replaced by the major axis of the crater wounds found in Swordfish. The hypothesis sustaining the second assumption used by these authors, namely; "dimensions of crater wounds are proportional to the body length of the specimen which inflicted the wound" is valid, but it is the minor axis and not the major axis of the bite which needs to be taken into account. This mistake has been observed to survive in subsequent research works. Even though Papastamatiou et al. (2010) do not specify the axis measured when describing their sampling methodology, (they simply mention "bite diameter"), we assume that they have followed the methodology of Muñoz-Chapuli et al. (1988), since they do not contradict it.

On the other hand, the TL-MW relationship provided by Muñoz-Chapuli et al. (1988), and used by other authors in subsequent works (Papastamatiou et al. 2010), underestimates the Cookiecutter Shark total length by about 40%. This bias is not corrected by

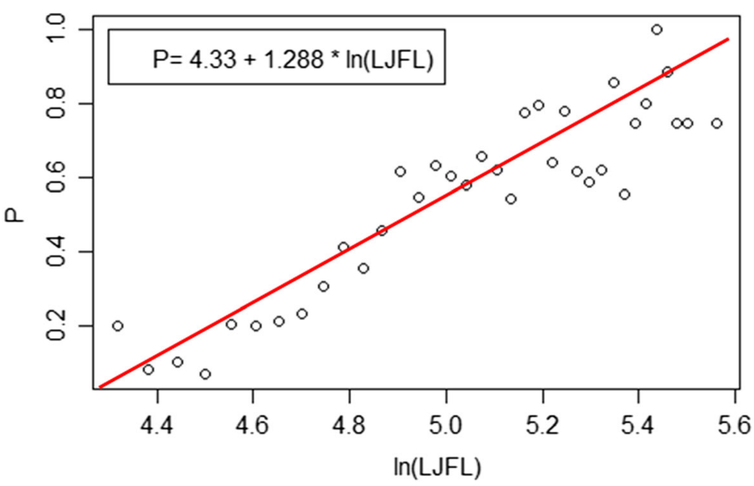

Fig. 6 Probability of Cookiecutter Shark attack (P) versus Swordfish length (LJFL) in cm ($r^2 = 0.84$)

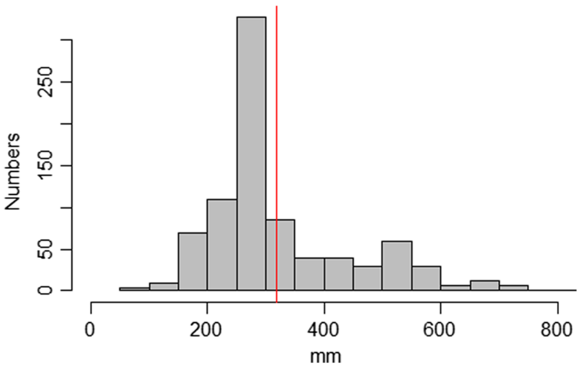

Fig. 7 Length frequency distribution of Cookiecutter shark inferred from fresh wounds sampled on Swordfish in the Gulf of Guinea in 1996. The black line represents the mean length (319 mm)

recalculating the linear regression using the original data provided by Cadenat and Blache (1981), but rather results in an overestimate of 36.5%. Ignoring the TL-MW relationship of Muñoz-Chapuli et al. (1988), whose possible calculation errors are now difficult to ascertain, the bias produced by the new TL-MW relationship recalculated using the data of Cadenat and Blache (1981) appears to originate in a bad interpretation of the selected parameter. These authors describe this parameter as mouth width, "Larg. bouche" in the original French version, and present it as a percentage of the total length. It is entirely plausible that the mouth width measurement of a fish with a unique food strategy such as the Cookiecutter Shark, with sucking lips that facilitate gripping on their prey during attack, deviates significantly from the width of the skeletal part of its lower jaw, which is what really leaves the bite mark.

The relationship between total length (TL) and lower jaw width (LJW) calculated by us using Cookiecutter Shark specimens provide predictions of this shark's total length with a minor bias. The full coincidence between the width of the lower jaw and the dimensions of the minor axis of the "cookies" found in the stomach of two of our specimens supports the hypothesis that the minor axis of the wounds found in Swordfish is the best parameter to replace LJW in our linear regression.

Our geographic analysis extends to the south of the biogeographical study area of Muñoz-Chapuli et al. (1988) in the Atlantic Ocean. These authors observed the maximum probability (0.55) of Cookiecutter Shark attack at latitudes between 10°N and 15°N, in waters of Guinea-Bissau, Senegal and Cape Verde. A decrease in population density of this shark is observed southwards, where the probability of attack is 0.10 in waters at latitude 5°N. This value is much lower than that found by us between 5°N-5°S, where the probability (0.50) of Cookiecutter Shark attack is similar to the maximum probability observed by these authors in 10°N-15°N. Moreover, the oceanographic characteristics of the Gulf of Guinea are different from those in North-Western Atlantic waters (Moroshkin et al. 1970), and 12 years have elapsed between the two samples. It should also be borne in mind that Muñoz-Chapuli et al. (1988) sampled just the one flank of Swordfish

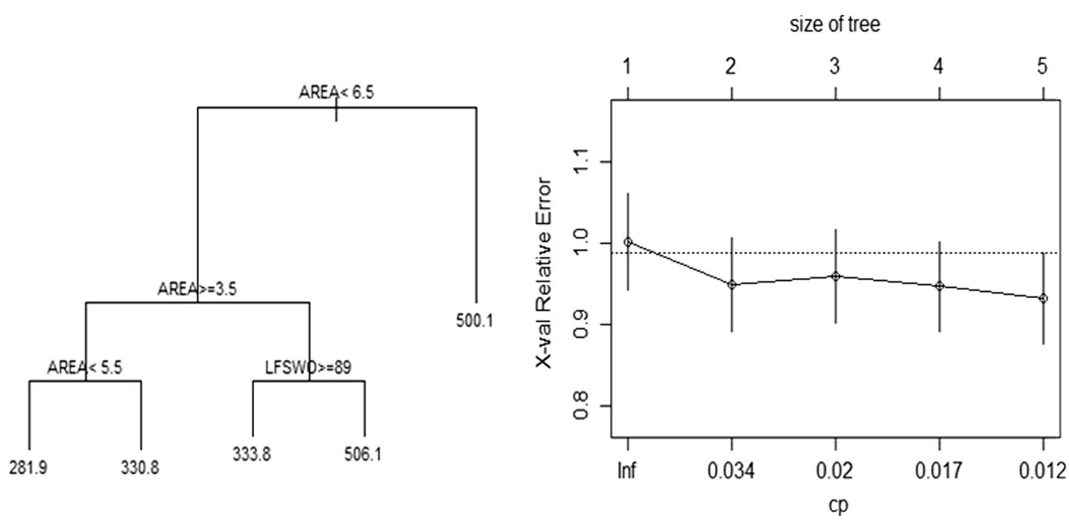

Fig. 8 Multivariate regression tree for Cookiecutter Shark's total length (mm) versus geographical grid, and Swordfish length (cm) and sex. The cross-validated relative error (below) decreases to a minimum for a tree size of two, before increasing slightly

and doubled their estimates assuming a random landing of these specimens at the auction site. The probability of attack observed in the Gulf of Guinea corresponds to 29.4% of Swordfish with bites. This percentage is almost double that found by Papastamatiou et al. (2010) in Swordfish sampled in the Pacific Ocean in 2007 (16.9%).

The similar results observed between Cookiecutter Shark attack on live and dead Swordfish seem to rule out a possible opportunistic behaviour of the predator. However, what is certain though is that a Swordfish hooked on a longline has very limited span of movement.

The range of Cookiecutter Shark sizes inferred from bites measured on Swordfish in the Gulf of Guinea exceeds the maximum size recorded in literature (Ebert 2003; Compagno et al. 2005): 420 mm TL for males and 560 mm TL for females. These ranges are based on a small number of records of Cookiecutter Shark; therefore they do not necessarily invalidate the existence of larger specimens, as indicated by the presence of some large bites within the 829 fresh wounds sampled here.

The mean length differences of Cookiecutter by geographic grid in the Gulf of Guinea might indicate some sort of sexual disaggregation. In particular, the biggest size found in ocean waters near the mouth of the Congo River may indicate a concentration zone of females that sexually mature at size 380–440 mm (Compagno et al. 2005). In the North Atlantic, Muñoz-Chapuli et al. (1988) found a latitudinal gradient with decreasing size of Cookiecutter Shark towards the south. Unfortunately, the results from both studies cannot be integrated due to the use of different formulae in the calculation of total length. The same reason has also prevented any possible comparison of our Atlantic results with those from the Pacific provided by Papastamatiou et al. (2010).

Very little is known about Cookiecutter Shark biology, apart from its unique parasitic foraging strategy. The other species of the Genus, i.e. Largetooth Cookiecutter Shark (*Isistius plutodus*, Garrick and Springer, 1964) seems to be even rarer than Cookiecutter Shark (Wenzel and López 2012) and shows a different biting mechanism (Compagno 1984). There are currently no conservation measures in place for either of these two species, and the IUCN Red List classifies its extinction risk as "Least Concern" (IUCN 2017), mainly due to their low commercial catches. Knowledge of the biogeography of Cookiecutter Shark is interesting not only from an ecological point of view but also in relation to its economic implications, due to depreciation in selling price of their prey when bitten (Papastamatiou et al. 2010). The results of our work provide new data that may help to clarify some aspects of the biology and ecology of this species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. This article does not contain any studies with human participants or animals performed by any of the authors.

References

Breiman L, Friedman JH, Olshen RA, Stone CJ (1984) Classification and regression trees. Chapman & Hall/CRC, Boca Raton

Cadenat J, Blache J (1981) Requin de Mediterranee et d'Atlantique (Plus Particulierement de la Cote Occidentale d'Afrique) (Faune Tropicale, vol. 21). Office de la Recherche Scientifique et Technique Outre-Mer, Paris

Compagno L (1984) FAO species catalogue, Vol. 4, Part 1: Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. FAO, Rome

Compagno L, Dando M, Fowler S (2005) Sharks of the world. Princeton University Press, Princeton

Ebert DA (2003) Sharks, rays and chimaeras of California. California natural history guides no. 71. University of California Press, Berkeley. p e284

Hiruki LM, Gilmartin WG, Becker BL, Stirling I (1993) Wounding in Hawaiian monk seals (*Monachus schauinslandi*). Can J Zool 71(3):458–468. https://doi.org/10.1139/z93-066

IUCN (2017) The IUCN Red List of Threatened Species. Version 2017-2. www.iucnredlist.org. Accessed 28 Sept 2017

Jones EC (1971) *Isistius brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. Fish Bull 69:791–798

Le Boeuf BJ, McCosker JE, Hewitt J (1987) Crater wounds on northern elephant seals: the Cookiecutter shark strikes again. Fish Bull 85(2):387–392

Moroshkin KV, Bunov VA, Bulatov RP (1970) Water circulation in the eastern South Atlantic Ocean. Oceanology 10:27–34

Muñoz-Chapuli R, Rey Salgado JC, De La Serna JM (1988) Biogeography of *Isistius brasiliensis* in the north-eastern Atlantic, inferred from crater wounds on swordfish (*Xiphias gladius*). J Mar Biol Assoc UK 68(02):315–321. https://doi.org/10.1017/S0025315400052218

Papastamatiou YP, Wetherbee BM, O'Sullivan J, Goodmanlowe GD, Lowe CG (2010) Foraging ecology of Cookiecutter sharks (*Isistius brasiliensis*) on pelagic fishes in Hawaii, inferred from prey bite wounds. Environ Biol Fish 88(4): 361–368. https://doi.org/10.1007/s10641-010-9649-2

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org

Shirai S, Nakaya K (1992) Functional morphology of feeding apparatus of the Cookiecutter shark, *Isistius brasiliensis* (Elasmobranchii, Dalatiinae). Zool Sci 9:811–821

Wenzel FW, López P (2012) What is known about cookiecutter shark (Isistius spp.) interactions with cetaceans in Cape Verde seas? Zoologia Caboverdiana 3(2): 57–66