Fisheries Research 269 (2024) 106876

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Feeding ecology of the African cuttlefish *Sepia bertheloti* (Cephalopoda: Sepiidae) in western Africa

Airam Guerra-Marrero *, Ana Espino-Ruano, Lorena Couce-Montero, David Jiménez-Alvarado, José J. Castro

IU-ECOAQUA, University of Las Palmas de Gran Canaria, Edf. Ciencias Básicas, Campus de Tafira, Las Palmas de Gran Canaria, 35017 Las Palmas, Spain

ARTICLE INFO

Handling by B. Morales-Nin

Keywords:
Cephalopods
Diet
Trophic ecology
Niche breadth
Morocco
Guinea-Bissau

ABSTRACT

The African cuttlefish, *Sepia bertheloti*, is a commercially exploited cephalopod in two productive system areas off West Africa. However, there is a lack of information on its feeding ecology, making it difficult to describe its ecological role (Morocco and Guinea-Bissau). In the present study, we analyse the gastric contents of 1.114 individuals, collected between July 2018 and January 2020 using the traditional analysis of stomach contents. A total of 65 and 49 prey items were identified as part of the diet of Moroccan and Guinean African cuttlefish, respectively. The sample size was evaluated using species cumulative curves and the methods used to describe the diet were the frequency of occurrence, number, and weight. Our results suggest that *S. bertheloti* does not present differences in diet between sexes or areas, although significant differences were observed in terms of prey abundance, richness, and diversity of species. According to the taxonomic groups, crustaceans were the most abundant prey taxa, followed by fish and cephalopods. Amphipods (*Gammarus* sp.) were the prey that showed the greater importance of occurrence in the diet at both study areas, showing a strictly benthic feeding behaviour. Niche breadth was evaluated using Levin's index, indicating that *S. bertheloti* is an omnivorous species (Trophic level ~3.6) with a heterogeneous diet and without a marked generalist or specialist feeding strategy.

1. Introduction

The Atlantic coast of North and West–Central Africa hosts one of the world's most productive areas, the Canary Current Large Marine Ecosystem (CCLME) (Valdés and Déniz-González, 2015). Due to encompassing several upwelling systems in Morocco, West Sahara, Mauritania, and Senegal that support a high diversity and abundance of marine species, the CCLME is a very important system for fisheries, particularly for pelagic species like *Sardinella aurita, Engraulis encrasicolus,* or *Sardina pilchardus,* among others (Bas, 1995; Valdés and Déniz-González, 2015; Rocha and Cheikh-Abdellahi, 2015; Failler, 2020; Luna et al., 2021). Fishing in the area indeed represents an important economic activity from Morocco to the Gulf of Guinea, whether performed with artisanal boats or large industrial fleets. Valdes and Déniz-González (2015) have highlighted the importance of such fishing grounds in the CCLME, given its annual estimated production of 2–3 million tons and the most important cephalopod fishery in the Atlantic Ocean. However, according to Gascuel et al. (2007), the overfishing of an important part of the area has reduced biological productivity (particularly evident in the higher trophic levels). In the case of Mauritania's shelf, for example, the biomass of target demersal species has shrunk by 75% in the past 25 years, and the trophic structure has been significantly altered.

In 2019, a total catch of 158,494 t of cephalopods was recorded in Area 34 by the Food and Agriculture Organization of the United Nations (56.08% octopi, 16.87% squids, and 27.05% cuttlefish) (FAO, 2021); however, according to Belhabib et al. (2012) the actual catches were likely far higher due to unreported catches and illegal fishing activities described in the area. Those underestimated official catches, the lack of transparency in extractive activities, and the lack of biological information about the exploited species make Africa's Atlantic coast an endangered system, one where overexploitation has been reported for years (Balguerías et al., 2000; Alder and Sumaila, 2004; Gascuel et al., 2007).

Although statistics indicate a decrease in cephalopod catches since 1980 (Balguerías et al., 2000; Gascuel et al., 2007), the oceanographic conditions in West Africa still show high productivity levels thanks to the combination of upwelling systems (Arístegui et al., 2009; Pelegrí

* Corresponding author.
E-mail address: airam.guerra@ulpgc.es (A. Guerra-Marrero).

https://doi.org/10.1016/j.fishres.2023.106876
Received 3 November 2022; Received in revised form 3 October 2023; Accepted 4 October 2023
Available online 17 October 2023

et al., 2017). According to Bas (1995), such upwelling productivity systems are rather heterogeneous along the Atlantic coast of North and West–Central Africa, where the greatest upwelling activity, given its intensity and permanence, occurs in the area around Mauritania. By contrast, the northern zone (i.e. from the Gulf of Cádiz to Mauritania) and the southern zone (i.e. from Mauritania to Guinea-Bissau) are characterised by weaker seasonal upwellings (Bas, 1995; Arístegui et al., 2009; Pelegrí et al., 2017).

Many studies have shown that those primary characteristics of production generate large exploitable stocks (Cury et al., 2000; Rocha and Cheikh-Abdellahi, 2015), particularly of small pelagic species (Bas, 1995; Gascuel et al., 2007). Even so, understanding the ecology of exploited species is a less studied subject, one that typically focuses on target species with high economic yield. The productivity and variability of those systems amid uncontrolled extractive activity induces changes in the population dynamics of such species, not only in their growth and reproduction, but also in the system's ecological role (Gascuel et al., 2007). All of that productivity makes the trophic connectivity of ecosystems more complex than in other less productive or oligotrophic systems, where an increase or reduction of species in each area can significantly impact potential prey communities and alter trophic relationships (Gascuel et al., 2007; Butler et al., 2010). Concerning the marine trophic structure of Mauritanian waters in particular, Gascuel et al. (2007) reported its significant modification and a declining mean trophic level (TL) of catchable biomass, from more than 3.7 to less than 3.5 since 1980.

Demonstrating opportunistic predatory behaviour, cephalopods feed primarily on crustaceans, fish, and other cephalopods (Rocha et al., 1994; Rodhouse and Nigmatullin, 1996). In studies on cephalopod dietary changes (Castro and Guerra, 1990; Markaida and Sosa-Nishizaki, 2003), juvenile diets consisted primarily of crustaceans, and incorporated fish and other cephalopods with ontogeny (Guerra-Marrero et al., 2020). In West Africa, however, studies on cephalopods' feeding behaviours have been typically focused on octopus and squid (Hernández-García, 1992, 2003; Villanueva, 1993; Piatkowski et al., 1998; Smith, 2003; Idrissi et al., 2016, among others). Regarding *Sepia* species, by contrast, only a few publications describe the feeding of *S. officinalis* and *S. australis*, the two most commercial species in the genus (Mqoqi et al., 2007; Mzaki et al., 2017; Oluboba and Lawal-Are, 2022).

Sepia bertheloti is distributed from northern Morocco to Guinea-Bissau, for which there are no separate statistics regarding catches and landings because it is marketed with other cuttlefish such as *S. hierredda* (Joufre and Inejih, 2005) and *Sepia* spp (42.514 t for 2019; FAO, 2021). According to Jereb and Roper's (2005) estimate, *S. bertheloti* represent between 11% and 35% of the catches of both species. Although *S. bertheloti* is a rare species in catches due to its low abundance and being mislabelled or discarded among other target species, this short-lived species is key to understanding the role it fills in the food-web, and is essential for understanding the impact of human activities, the energy flow through a system, and the factors affecting the productivity of higher trophic levels.

Studies of feeding ecology are traditionally based on the analysis and identification of each prey found in the stomach contents, although in recent years analyses through stable isotopes have been incorporated (Ibáñez et al., 2021). This technique is useful to evaluate the structures of trophic chains through elements such as carbon and nitrogen, which are useful in estimating the trophic level of the analysed organisms (Layman et al., 2012), but it does not provide specific information on the prey consumed.

Therefore, in the present study, we focused on gathering information about the feeding ecology of the African cuttlefish, *Sepia bertheloti,* using the traditional analysis of stomach content (Hyslop, 1980), analysing prey by prey in two West African areas. So, we aim to identify how the species interacts in these highly productive ecosystems, providing information on its feeding strategy and giving new insights into the ecological role of *S. bertheloti* in two important fishing areas of West Africa. Our study provides a detailed description of the prey consumed by this cuttlefish, which is useful to increase the knowledge of the general hypothesis that cephalopods feed on fish, crustaceans, and cephalopods, establishing the current interaction of these populations in food webs.

2. Materials and methods

Biological samples of *Sepia bertheloti* were collected from commercial captures in Morocco and Guinea-Bissau (i.e. North and West–Central Africa, Fig. 1.) and caught with bottom trawl nets between July 2018 and January 2020. Specimens were not available every month due to the seasonality of the fishery and the mandatory biological stoppages of the fleet. Because its capture is obtained as a by-catch of *Sepia officinalis* and because it is not always separated well in commercial captures, samples of the African cuttlefish are quite difficult to obtain. Data sampling is summarised in Table 1.

After being caught, all specimens were immediately frozen for further analysis. The cuttlefish were sorted, and *Sepia bertheloti* individuals were identified taxonomically using the key developed by Nesis (1987). In the laboratory, the sex of the samples was determined, and the dorsal mantle length (DML) and total wet weight (TW) were recorded to the nearest 1 mm and 0.01 g, respectively.

Digestive tracts were extracted and fixed in 70% ethyl alcohol. In all analyses, the normality and homoscedasticity of the data were calculated; to that end, differences in the distribution of DML and TW, according to the areas studied, were compared using the t-test. Since all cuttlefish caught were found in a mature/spawning or post-spawning stage, an analysis of ontogenetic changes based on diet was not carried out to avoid misinterpretations of the results.

All stomach contents were weighed to the nearest 0.0001 g. Each item in the stomach contents was analysed with an Olympus SZ-40 stereoscopic microscope, and prey items were identified to the lowest taxonomic level possible. Prey items were identified using species identification guides by Estrada and Genicio (1970), Newell and Newell (1970), Manning and Holthuis (1981), Zariquiey (1968), and Burukovskii (1992) to identify Decapoda crustaceans; guides by Härkönen (1986), Campana (2004), Tuset et al. (2008), and Lombarte et al. (2006) to identify sagittal otoliths in fish; Clarke's (1986) guide to identify cephalopod beaks; and Hernández et al. (2011) guide to classify gastropods, bivalves, and other molluscs.

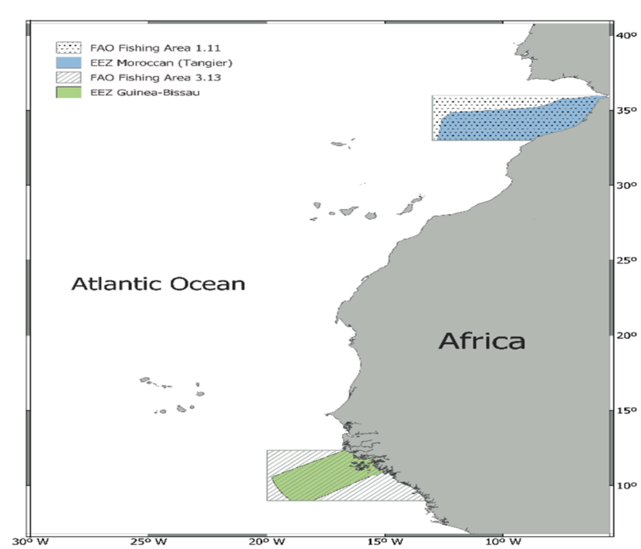

Fig. 1. Sampling areas (FAO Fishing Area 34) where the commercial trawlers caught *Sepia bertheloti* in Morocco (FAO 34.1.11) and Guinea-Bissau (FAO 34.3.13). Exclusive Economic Zone (EZZ) for Morocco and Guinea-Bissau where these trawlers can operate in the FAO Fishing Area 34 are shaded.

Table 1
Number of stomachs analysed as well as empty stomachs of Sepia bertheloti in two areas of West Africa from July 2018 to January 2020.

Date	Morocco		Guinea-Bissau	
	Stomachs	Empty	Stomachs	Empty
July 2018	234	83		
August 2018	43	24		
September 2018	44	9		
July 2019			42	17
August 2019			36	18
September 2019			97	43
October 2019			78	35
November 2019			157	86
December 2019			155	72
January 2020	168	90	60	16
Total	489	206	625	287

To establish the number of stomachs suitable for diet characterisation, we created a randomised cumulative prey curve using the vegan package (Oksanen et al., 2012) based on identified prey. The vegan package allowed calculating the cumulative curve ($\pm$ 2 *SD*) by plotting 500 random permutations of the data. The number of stomachs needed to describe the diet was determined when the last four points approached the asymptote (Hurtubia, 1973), and the trend line did not differ significantly (Bizzarro et al., 2007).

For each prey taxa, the frequency of occurrence (%FO), numerical frequency (%N), and weight percentage (%W) of the prey items were calculated according to Hyslop (1980). The Relative Importance Index (IRI) were not calculated to avoid greater uncertainty in the data, as recommended by Ibáñez et al. (2021). To pinpoint significant differences, we compared the frequency at which the prey categories occurred between sexes using the distribution of χ^2 (observed vs. expected).

Prey abundance, Brillouin's richness and diversity indices, and Berger–Parker dominance indices were also calculated according to Ibáñez et al. (2021) recommendations using the vegan package (Oksanen et al., 2012). The t-test was performed to identify differences between the areas under study (i.e. Morocco and Guinea-Bissau).

To characterise the feeding strategy of *Sepia bertheloti* in both areas, we used the SPAA package (Zhang et al., 2016) to calculate the standardised Levin's index (B_{sta}), which specifies the width of the trophic niche:

$$Bsta = (B - 1)/(n - 1)$$

in which B is Levin's index (calculated according to Levins, 1968) and n is the number of prey species. B_{sta} values ranged from 0 (minimum niche breadth and maximum selectivity: specialist predator) and 1 (maximum niche breadth and minimum selectivity: generalist predator).

The results of the stomach content analysis were grouped into six categories of prey (crustaceans, cephalopods, fish, bivalves, gastropods, and echinoderms) to calculate the TL of *Sepia bertheloti* in each area under study. The analysis was performed only with data obtained in our study, mainly because no other diet studies have been performed for the species.

To calculate the TL we needed to know the proportion of each category of prey (P_j) in the diet (Cortés, 1999), calculated as:

$$P_j = \frac{\sum_{i=1}^{n} P_{ij} N_i}{\sum_{j=1}^{6} \left(\sum_{i=1}^{n} P_{ij} N_i \right)}$$

in which P_{ij} is the proportion of category of prey j in study i, N_i is the number of stomachs with food used to calculate P_{ij} in study i, n is the number of studies, j is the number of categories of prey (6), and $\Sigma P_j = 1$. In our study, P_{ij} values were calculated using %FO.

Meanwhile, TL was calculated by following Cortés (1999) formula:

$$TL = 1 + \left(\sum_{j=1}^{6} P_j \quad x \quad TL_j \right)$$

in which TL_j is the TL of each category of prey j. According to Cortés (1999), the TL of each category of prey was obtained from the literature, especially from Pauly and Christensen (1995), Pauly et al. (1998), and Hobson and Welch (1992). The standard values for TL used are shown in Table 2. All statistical analyses were performed in R software (version 4.2.1, R Development Core Team, 2022).

3. Results

A total of 1114 individuals of *Sepia bertheloti* were analysed: 489 from Morocco and 625 from Guinea-Bissau (Table 1). Males in both areas were more abundant with a sex ratio of 1:0.27 and 1:0.45 for Morocco (DML range = 6.0–17.6 cm) and Guinea-Bissau (DML range = 6.0–13.8 cm), respectively. DML and TW showed significant differences between the sexes and areas (t-test, $p < 0.001$), including that males were larger and heavier than females in both areas, and individuals from Guinea-Bissau were larger and heavier than those from Morocco (Fig. 2). Although all stomachs were considered in the analysis, only 57.87% and 54.08% of African cuttlefish from Morocco and Guinea-Bissau, respectively, had stomach contents (Table 1). The absence of juveniles in the catches (i.e. DML<60 mm) did not allow for assessing ontogenetic changes of the species or diet according to length, which could have helped prevent erroneous conclusions due to the sample size.

The cumulative prey curves revealed that the number of individuals subjected to stomach content analysis was adequate for characterising the African cuttlefish diet for the accumulation prey curve representing Morocco ($n = 283$, $p = 0.31$) and Guinea-Bissau ($n = 338$, $p = 0.22$), as shown in Fig. 3.

As shown in Table 3, 76 prey items were recorded from the stomach content analysis for both areas: 65 from Morocco and 49 from Guinea-Bissau. The prey species identified were categorised as bivalves, cephalopods, echinoderms, gastropods, crustaceans, or fish. No significant differences surfaced between the areas studied concerning bivalves ($\chi^2 = 1.41$, $p = 0.23$), cephalopods ($\chi^2 = 3.43$, $p = 0.06$), echinoderms ($\chi^2 = 0.35$, $p = 0.55$), and gastropods ($\chi^2 = 3.09$, $p = 0.07$), whereas crustaceans ($\chi^2 = 5.96$, $p = 0.01$) and fish ($\chi^2 = 4.97$, $p = 0.026$) did show significant differences. They were also more representative in the diet of individuals from Morocco.

Although no significant differences emerged in %FO of all categories of prey and sexes (i.e. chi-square observed vs. expected, $p > 0.09$), abundance of prey showed significant differences between areas (t-test, $p < 0.001$). The mean number of prey species per stomach was 3.19 for individuals from Morocco and 1.43 for those from Guinea-Bissau (Table 4). Along similar lines, richness (t-test, $p < 0.001$) and diversity (t-test, $p < 0.001$) differed between the areas, although no differences emerged in dominant categories of prey (t-test, $p > 0.05$), as shown in Table 4.

One (58.88%) or two (16.27%) prey species dominated in the stomach contents of African cuttlefish from Morocco, whereas in those from Guinea-Bissau the proportion of individuals with only one prey species was slightly less (33.92%); however, 19.08% contained two prey

Table 2
Standardised trophic level (TL) by category of prey (modified from Cortés, 1999).

Code	Category of prey	TL
FISH	Teleost fishes	3.24
CEPH	Cephalopods (i.e. squids and octopi)	3.20
MOL	Molluscs, excluding cephalopods	2.10
CR	Decapod crustaceans (i.e. shrimp, crabs, prawns, and lobsters)	2.52
INV	Other invertebrates (i.e. all invertebrates except molluscs, crustaceans, and zooplankton)	2.50

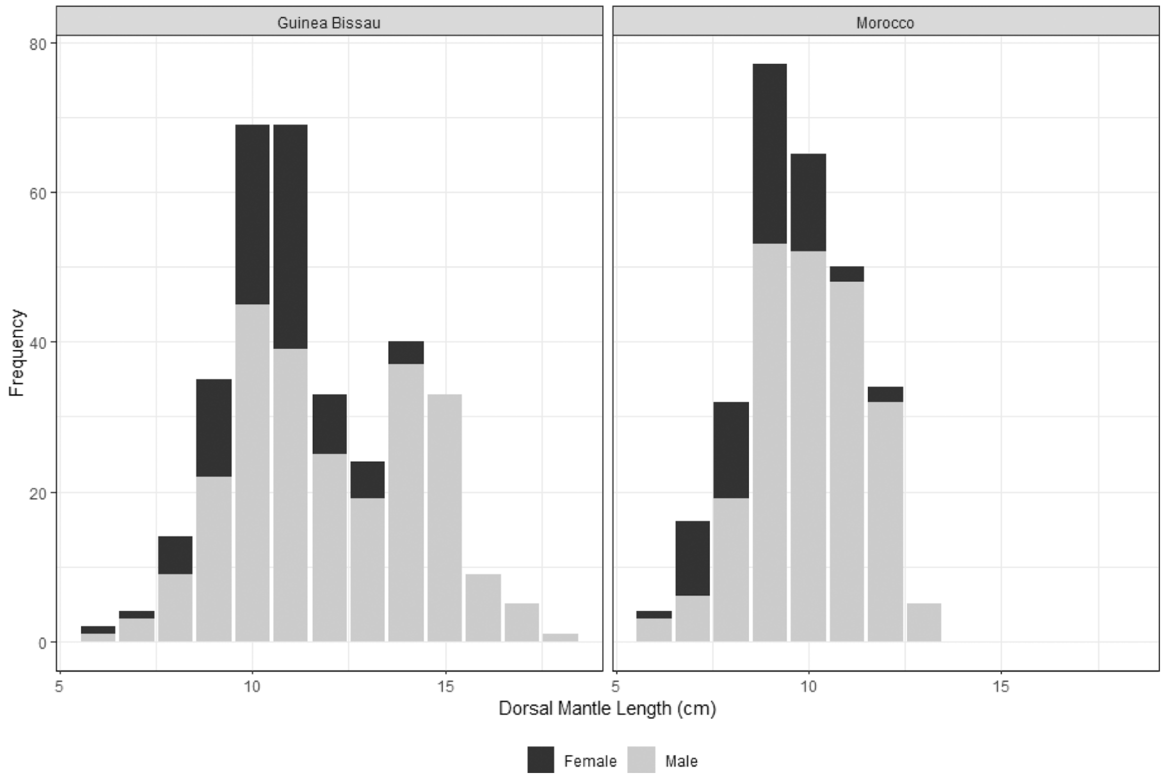

Fig. 2. Size–frequency distribution of female and male *Sepia bertheloti* in each area studied.

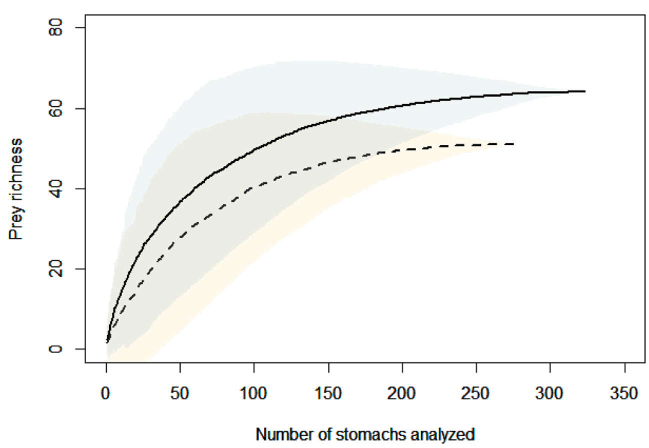

Fig. 3. Cumulative prey curve of the *Sepia bertheloti* stomachs analysed from Guinea-Bissau (dashed line) and Morocco (continuous line).

species and 12.72% had three. More than three prey species were present in 34.28% and 18.34% of the stomachs from Morocco and Guinea-Bissau, respectively, normally in larger individuals. Fish was the category of prey with the greatest diversity of species—29 from Morocco and 25 from Guinea-Bissau—followed by crustaceans, with 22 and 15 species present in the stomachs of individuals from Morocco and Guinea-Bissau, respectively. Even so, crustaceans were the most abundant category of prey in both areas in terms of weight, followed by fish and cephalopods, whereas bivalves, echinoderms, and gastropods were far less represented. *Sepia bertheloti* from Morocco fed more on amphipods, which were the most significant kind of prey in terms of weight (%W = 7.89), whereas those from Guinea-Bissau fed more on pandalids (%W = 2.79). Nevertheless, amphipods were the more frequent and numerous prey items identified in both areas. Species of amphipods could not be established due to their degree of digestion, but given their morphological characteristics these were primarily classified as *Gammarus* spp., except for *Orchestia* sp. (Tralitridae) and *Rachotropsis* sp. (Eusiridae). At the same time, it should be highlighted that the presence of body parts of conspecifics indicates the cannibalistic behaviour of *S. bertheloti*.

The niche breadth was very wide, and, as shown in Table 4, B_{sta} values of approximately 0.50 confirmed a heterogeneous diet among African cuttlefish in both areas, without any clear specialist or generalist feeding behaviour. Although a greater diversity and richness of species was observed among cuttlefish from Morocco, TL analysis showed that *Sepia bertheloti* from both Morocco and Guinea-Bissau are secondary consumers ($TL_k < 4$, Table 4) with great similarity in the %FO of prey items, among which crustaceans and fish dominated in the stomach contents.

4. Discussion

Despite many studies conducted to understand the biology and ecology of cephalopods (e.g. Clarke, 1966; Boyle and Rodhouse, 2008; Piatkowski et al., 2003) - particularly their trophic spectrum as a means to know their function within the trophic web (e.g. Summers, 1983; Castro and Guerra, 1990; Rasero et al., 1996; Pinczon du Sel et al., 2000; Markaida and Sosa-Nishizaki, 2003; Coll et al., 2013; Hernández-Urcera et al., 2014; Hoving and Robison, 2016; Villanueva et al., 2017) - the Sepiidae family has rarely been studied and, in those rare cases, typically with a focus on *Sepia officinalis* (Mzaki et al., 2017; Oluboba and Lawal-Are, 2022). In this study, the feeding habits of the African cuttlefish in two areas of great fishing interest were evaluated, trying to assess the differences in its feeding ecology between areas. A preliminary vision of the diet of *S. bertheloti* is provided for both areas, but the results should be taken with caution since the sampling time did not cover the entire year. This handicap was due to the seasonality of the fishery, which made continuous sampling impossible, a factor that has been reflected in previous studies that describe the diet of *Illex coindetii, Todaropsis eblanae, Todarodes sagittatus, Octopus magnificus* or

Table 3
Diet composition of the African cuttlefish *Sepia bertheloti* from Morocco and Guinea-Bissau. %FO = frequency of occurrence in percentage, %N = numerical frequency in percentage, %W = weight percentage.

Prey categories	Morocco			Guinea-Bissau		
	%FO	%N	%W	%FO	%N	%W
BIVALVIA	**7.07**	**1.48**	**1.57**	**3.25**	**1.61**	**0.49**
Cardiidae	0.35	0.06	0.02	0.00	0.00	0.00
Donax sp.	0.71	0.11	0.07	0.00	0.00	0.00
Moerella sp.	2.83	0.51	0.53	0.29	0.12	0.02
Unidentified bivalvia	3.53	0.63	0.67	2.96	1.36	0.39
Venerupis sp.	1.06	0.17	0.27	0.30	0.12	0.07
CEPHALOPODA	**13.78**	**4.34**	**5.41**	**5.62**	**2.85**	**1.28**
Octopus vulgaris	1.77	0.29	0.24	0.00	0.00	0.00
Sepia bertheloti	8.13	1.31	1.35	1.18	0.50	0.35
Sepia sp.	2.82	0.46	0.30	0.59	0.25	0.05
Unidentified cephalopods	13.22	2.28	3.52	5.03	2.11	0.88
CRUSTACEA	**96.81**	**74.77**	**56.77**	**65.68**	**79.93**	**67.20**
Amphipoda						
Orchestia sp.	8.12	13.47	3.40	0.00	0.00	0.00
Rhachotropis sp.	1.06	0.17	0.12	0.00	0.00	0.00
Gammarus spp.	30.87	38.64	7.89	6.50	32.96	2.46
Isopoda	6.36	1.83	0.57	2.37	3.59	0.89
Decapoda						
Bathynectes maravigna	2.12	0.34	0.97	0.00	0.00	0.00
Cryptosoma cristatum	1.06	0.17	0.45	0.30	0.12	0.12
Euchirograpsus liguricus	0.35	0.06	0.02	0.00	0.00	0.00
Inachus nanus	2.47	0.40	0.36	0.00	0.00	0.00
Maja sp.	0.71	0.17	0.27	0.00	0.00	0.00
Munida sp.	0.00	0.00	0.00	0.89	0.37	0.86
Oplophoridae	0.00	0.00	0.00	0.30	0.12	0.02
Paguridae	0.35	0.06	0.15	1.18	0.50	0.28
Palinuridae	1.77	0.57	0.26	0.30	0.12	0.64
Pandalidae	0.35	0.06	0.89	1.48	0.62	2.79
Penaeidae	0.71	0.11	0.25	0.89	0.62	0.17
Polycheles typhlops	3.53	0.57	1.01	0.30	0.12	0.08
Porcellanidae	0.71	0.11	0.23	1.18	0.50	1.87
Portunidae	4.24	0.68	1.24	0.00	0.00	0.00
Thranita sp.	6.00	1.03	2.12	0.30	0.12	0.77
Richardina spinicincta	0.71	0.11	0.47	0.00	0.00	0.00
Scyllaridae	0.35	0.06	0.09	0.59	0.25	0.17
Upogebia pusilla	2.47	0.40	0.18	0.00	0.00	0.00
Unidentified decapods	21.55	4.05	6.54	5.03	2.97	3.51
Unidentified crustacea	57.95	11.70	29.29	51.18	36.93	52.57
ECHINODERMATA	**0.35**	**0.11**	**0.13**	**0.00**	**0.00**	**0.00**
Ophiura sp.	0.35	0.06	0.07	0.00	0.00	0.00
Unidentified Echinodermata	0.35	0.06	0.07	0.00	0.00	0.00
GASTROPODA	**9.54**	**2.68**	**1.50**	**3.25**	**1.86**	**0.35**
Nayticidae	0.71	0.11	0.17	0.00	0.00	0.00
Tona sp.	6.36	1.03	0.87	0.59	0.25	0.08
Unidentified Gastropoda	6.71	1.54	0.46	2.96	1.61	0.27
FISHES	**44.81**	**16.61**	**33.49**	**26.04**	**13.75**	**28.01**
Argyropelecus hemigymnus	0.00	0.00	0.00	0.30	0.12	0.10
Arnoglossus imperialis	0.00	0.00	0.00	0.30	0.12	0.55
Arnoglossus sp.	0.71	0.11	1.80	1.48	0.62	1.41
Bathysolea profundicola	1.06	0.17	0.13	0.30	0.12	0.07
Bothus podas	1.77	0.29	0.78	1.48	0.62	2.14
Derichthys serpentinus	0.35	0.11	0.03	0.00	0.00	0.00
Dicoglossa cuneata	2.12	0.63	0.48	0.30	0.12	0.85
Dicologlossa hexopthalma	0.00	0.00	0.00	0.59	0.25	0.19
Gobius cruentatus	0.35	0.06	0.02	0.00	0.00	0.00
Gobius sp.	0.35	0.06	0.37	0.89	0.37	0.91
Gymnothorax maderensis	0.00	0.00	0.00	0.59	0.25	0.61
Halobatrachus sp.	0.71	0.11	2.06	0.30	0.12	0.02
Hippocampus hippocampus	0.35	0.06	0.71	0.00	0.00	0.00
Lepidorhombus boscii	0.35	0.17	0.08	0.59	0.25	1.15
Lesueurigobius sanzi	0.71	0.11	0.04	0.00	0.00	0.00
Lesueurigobius sp.	0.35	0.06	0.08	0.00	0.00	0.00
Melanostigma atlanticum	3.89	0.80	0.91	0.59	0.25	0.31
Microchirus azevia	0.00	0.00	0.00	0.59	0.25	0.22
Microchirus boscanion	4.59	1.48	1.88	0.89	0.50	0.57
Microchirus ocellatus	6.71	1.14	0.96	0.89	0.37	0.13
Monochirus hispidus	1.41	0.23	0.72	0.00	0.00	0.00

Table 3 (*continued*)

Prey categories	Morocco			Guinea-Bissau		
	%FO	%N	%W	%FO	%N	%W
Myctophum sp.	1.07	0.17	0.39	1.18	0.50	0.74
Parapistipoma octolineatum	0.35	0.06	0.71	0.00	0.00	0.00
Pegusa sp.	0.35	0.06	0.52	0.89	0.37	1.29
Scorpaena sp.	0.70	0.11	1.30	0.30	0.12	0.36
Serranus cabrilla	1.77	0.29	2.14	1.18	0.50	0.98
Serranus sp.	4.59	0.74	0.74	1.48	0.62	0.97
Solea solea	0.35	0.06	0.05	0.30	0.12	0.22
Stomias boa	0.00	0.00	0.00	0.30	0.12	0.15
Sygnathus sp.	1.77	0.29	0.10	0.00	0.00	0.00
Sygnathus typhle	0.71	0.11	0.04	0.00	0.00	0.00
Symphurus lugulatus	0.00	0.00	0.00	0.30	0.12	0.58
Symphurus nigrescens	1.06	0.63	0.10	0.00	0.00	0.00
Synodus saurus	0.35	0.06	0.46	0.00	0.00	0.00
Trachurus sp.	0.00	0.00	0.00	0.30	0.12	0.29
Trisopterus sp.	0.35	0.06	0.52	0.89	0.37	1.29
Unidentified fishes	38.86	8.39	15.37	14.79	6.44	11.90
Unidentified organic matter	0.00	0.00	1.13	0.00	0.00	2.67

Table 4
Prey abundance, richness, diversity, and dominance of prey taxa in the stomach contents of *Sepia bertheloti* in each area studied.

	Morocco		Guinea-Bissau	
	Mean	SD	*Mean*	*SD*
Abundance	3.19	6.48	1.43	3.89
Richness	2.46	1.63	1.44	0.88
Diversity	0.38	0.37	0.13	0.23
Dominance	0.31	0.55	0.23	0.39
Bsta	0.51		0.54	
TL	3.63		3.60	

S. officinalis, among others species (Hernández-García, 1992; Villanueva, 1993; Piatkowski et al., 1998; Hernández-García, 2003; Mzaki et al., 2017). Even knowing these handicaps, our study seeks to elucidate for the first time the feeding habits of *S. bertheloti* in the waters of Morocco and Guinea-Bissau, since it is a species of fishing interest whose contribution to the food web is unknown and could be a key point in evaluating and understanding in the future the potential interactions between commercially exploited species.

Males of the African cuttlefish predominated in the catches we assessed and had a larger DML than females. Sexual dimorphism has also been observed for other species, such as *Sepia latimanus* (Dan et al., 2012), *S. koilados, S. sulcata*, and *S. subplana.* Even so, it is not particular to the Sepiidae family, within which Jereb and Roper (2005) described the condition for most cuttlefish species (i.e. *S. acuminata*, *S. australis*, *S. bidhaia*, *S. braggi*, *S. elegans*, *S. filibranchia*, *S. sulcata*, *S. latimanus*, *S. limata*, *S. mestus*, *S. orbignyana*, *S. plana*, *S. senta*, *S. smithi*, *Sepiella inermis*, and *S. weberi*). However, in all those cases, females were larger than males.

Sepia bertheloti from the Atlantic coast of North and West–Central Africa showed a similar diet based on six prey categories: fish, cephalopods, bivalves, gastropods, echinoderms, and crustaceans, particularly decapods. The high relative importance of crustacean decapods in the diet of *S. bertheloti* has been observed in other species of the Sepiidae family (Castro and Guerra, 1990; Pinczon du Sel et al., 2000; Mzaki et al., 2017), for which fish and cephalopods also have dietary importance. Fish was the second most important group in the diet of *S. bertheloti,* coinciding with previous studies for other cuttlefish. Since the first contributions by Najai and Ktari (1974) for *Sepia officinalis*, the importance of bony fish is well known, reporting as 31% of %FO. Although at first glance this value could be considered average for this study (44.81% FO for Morocco and 26.04% FO for Guinea-Bissau), and similar to that obtained in other Sepia studies (Scalera Liaci and

Piscitelli, 1982; Guerra, 1985; Le Mao, 1985; Castro and Guerra, 1990; Mzaki et al., 2017), this value should be interpreted in the context of the temporal limitations in the sampling procedure of the present study, such as mandatory biological stoppages of the fleets that did not coincide at the same time in both areas. Thus, a robust assertion of dietary differences and potential seasonal or ontogenetic changes could not be assessed. Nevertheless, the analysis of stomach contents revealed that amphipods were the most common prey in the diet of the African cuttlefish on the central and north coast of West Africa. Pinczon du Sel et al. (2000) also highlighted the importance of amphipods in the diet of *S. officinalis*, considering that amphipods represented 30% of the prey items found in its stomach contents. However, these crustaceans become less important as cuttlefish increase in size and eventually become substituted for crustacean decapods and fish (Pinczon du Sel et al., 2000).

The marked presence of amphipods in the diet of Sepiidae species may be due to the strictly benthic habit of the Sepiidae family, although we can consider that *Sepia bertheloti* may have a more benthic feeding habit than other cuttlefish. Castro and Guerra (1990) defined *Palaemon* sp. as the highest value in %FO for *S. officinalis* and *S. elegans* from Ría de Vigo (Castro and Guerra, 1990). Conversely, in the description of the diet of *S. officinalis* for the Moroccan Atlantic waters, Mzaki et al. (2017) observed that the %FO of the Portunidae family is much higher (26.15%) than that of amphipods (1.06%). In these comparisons it is observed that *S. bertheloti* consume similar prey but in different proportions, which may indicate there is a high trophic competition between these species of cuttlefish. However and despite that, our work should be taken as a preliminary approximation to the feeding habits of *S. bertheloti*. The importance of gammarids should not be a surprise, since the nutritional contribution of these amphipods is greater than other species of this group (Baeza-Rojano et al., 2010).

Cannibalism is a common behaviour among cephalopods (Markaida and Sosa-Nishizaki (2003); Hernández-Urcera et al. (2014); Hoving and Robison (2016), and is associated with environmental variations, population density, the availability of food, and body size, among other factors (Villanueva et al., 2017). In our study, we documented such cannibalism among *Sepia bertheloti*, but as Markaida and Sosa-Nishizaki (2003) indicated, we cannot rule out that the cannibalism observed was motivated and produced once in the fishing gear (i.e. bottom trawl), because the *Sepia* spp. preyed upon were fresh and in a very low degree of digestion.

Differences in the abundance, richness, and diversity of species between the areas studied were expected due to different oceanographic conditions. The coast of Morocco is influenced by continuous upwelling (i.e. weak from winter to spring and more intense between summer and autumn, Arístegui et al., 2009), while Guinea-Bissau plays host to seasonal upwelling between winter and spring (Arístegui et al., 2009). High productivity in the Guinea-Bissau area also needs to be considered, because it is conditioned by the contribution of organic matter from rivers and lagoons (Fransen, 2014).

The African cuttlefish is an euryphagic feeder (standardised Levin's index, B_{sta} ~0.5), where the high diversity of prey and the abundance of sporadic prey species (with low %FO) characterise it as an opportunistic feeder, with a wide and varied feeding strategy. According to Stergiou and Karpouzi's (2002) classification of Mediterranean species, *Sepia bertheloti* is an omnivorous feeder with a preference for animals (TL = 2.9–3.7) and feeds on a variety of prey, including fish, crustaceans, and cephalopods. However, according to our results, the African cuttlefish can be classified as an entirely carnivorous species and the possibility of its herbivority discarded, given the great predominance of amphipods in their diet, with very low TLs that would include it in the category of omnivores. Moreover, *S. bertheloti* individuals from Northwest Africa showed a TL slightly higher than that reported by Cortés (1999) for cuttlefish, thereby characterising them as secondary consumers.

Funding

Guerra-Marrero was supported by a PhD-fellowship (PIFULPGC-2017-CIENCIAS-2) from the University of Las Palmas de Gran Canaria (Canary Islands, Spain).

CRediT authorship contribution statement

Airam Guerra-Marrero: Conceptualization, Methodology, Software, Data curation, Investigation, Writing – original draft. **Ana Espino-Ruano**: Methodology, Investigation, Data curation, Writing – review & editing. **Lorena Couce-Montero**: Methodology, Investigation, Data curation, Writing – review & editing. **David Jiménez-Alvarado**: Methodology, Investigation, Data curation, Writing – review & editing. **José J. Castro**: Supervision, Methodology, Investigation, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests. Guerra-Marrero, Airam reports a relationship with University of Las Palmas de Gran Canaria that includes: funding grants.

Data Availability

The data that has been used is confidential.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106876.

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