Diet of the leaf scale gulper shark (*Centrophorus squamosus*) in the North Atlantic off Morocco

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Abstract. Squaliform sharks are a relatively vulnerable bycatch in many deep-water fisheries. Diets of the leafscale gulper shark (*Centrophorus squamosus*) on the continental slope and continental shelf (200–1600 m) of Moroccan coasts (north-east Atlantic) were studied based on samples landed by 11 longliners in 8 Moroccan fishing ports. The samples were collected every month between February 2018 to March 2021. The diet of 713 individuals with sizes from 60 to 138 cm (total length), 362 females and 351 males, were determined by the examination of the stomach content. Macroscopic and microscopic observations were carried out and we found that the diet of *C. squamosus* consists of five groups of prey: teleostei, cephalopods, crustaceans, nematodes and chondrichthyes. The main species of prey consumed by the leafscale gulper shark are: *Alepocephalus* sp. and *Aphanopus carbo* (Teleostei), *Sepia* sp. and *Octopus vulgaris* (cephalopods), *Aristeus antennatus* and *Nephrops norvegicus* (crustaceans). In the diet of *C. squamosus*, chondrichthyes (*Chimaera monstrosa* and *Dalatias licha*). The Teleostei group comprised the preferential prey for leafscale gulper shark, with an index of relative importance of 174.18.
Key Words: North-East Atlantic, prey, squaliform, stomach.

Introduction. The trophic ecology of marine predators and adequate dietary information for deep-water shark species is essential to understand their ecological role in marine ecosystem. Currently, the International Council for the Exploration of the Sea (ICES) defines deep-water fisheries as those taking place in waters deeper than 400 m (Clarke et al 2003), while the Food and Agriculture Organization of the United Nations (FAO) defines them as those that take place beyond and below the continental-shelf break (FAO 2011).

The population sustainability of deep-water sharks can be provided by two factors. Firstly, there are the by-catches of unquantified sharks discarded at sea, or those landed and quantified, as well as mortality caused by accidental fishing. Secondly, overexploitation of certain shark stocks have affected the productivity of their populations and destroyed their ecosystems by promoting natural mortality (Rayer 2004; Dunn et al 2013). Many chondrichthyes are the top predators in their marine environment, occupying an important ecological niche. Feeding trends of fish species are crucial in classical ecological theory, mainly in the identification of food competition (Bacheler et al 2004), structure and stability of the food chain (Post et al 2000) and evaluation of the functional responses of prey and predators (Dörner & Wagner 2003). The objective of any biological and ecological study, in this case, the determination of the diet of deep-sea sharks, is essential for good fisheries management. Over the past decade, scientists have used the trophic level to predict the impact of fishing effort on the sustainability of a particular species (Pauly et al 1998). Deep-sea sharks are abundant and distributed on Moroccan coasts, where they are a bycatch in trawl fisheries and a catch of longline fisheries (INRH 2002). The trawler ships considered this group of sharks as bycatch, but the longliner ships target them for the liver. The squaliformes are an abundant order. However, little is known about the behavior of deep-water shark populations on the continental slope and the continental shelf of Morocco (north-east Atlantic). To date, the diet of deep-water sharks in Moroccan coasts is unknown. In order to provide more reliable information for the conservation of the leaf scale gulper shark, this work aims to study its diet in the North Moroccan Atlantic, by using the stomach content analysis (SCA), and to determine its preferential, occasional and accidental preys.

Material and Method

Sampling. 713 specimens of *C. squamosus* (Centrophoridae) were collected from landed catches of long-line fishing vessels between February 2018 and March 2021, from the continental slope and the continental shelf waters exceeding (200-1600 m depth) around the coasts of Morocco (north east Atlantic). Sampling was done in eight Moroccan fishing ports: Larache, Casablanca, El Jadida, Safi, Agadir, Laayoune, Boujdour and Dakhla. Samples were collected from 11 longliners by conducting surveys with the fishing captain during each sampling operation. The longliners operated in the area between 20°55′N and 35°30′N. The sample unit consists of a standardized plastic case (56x37x16 cm). For each sample batch, sharks were identified to species level and sex was determined. The total weight, gutted weight and liver weight (nearest to 1 g), total length (TL) (nearest to 1 cm) and maturity stages were recorded. All stomachs were removed and fixed immediately, individually, in a 70% ethanol solution in order to analyzed the contents based on a monthly period. From each stomach, food items were separated and identified to the lowest possible taxonomic level, and then the percentage of each prey in the stomach was estimated. All dissections and identifications of stomach contents were done in a laboratory of Chouaib Doukkali University, El Jadida, Morocco. Fish bait used to attract bottom sharks to the hook were excluded from the analyses. Big preys were identified to the lowest taxonomic level possible, counted, and weighted (nearest 0.1 g). Small preys were observed under a binocular microscope and using various identification references (Richardson et al 2013). Preys in an advanced state of digestion were recognized by their undigested remains, such as the appendages of crustaceans. Empty stomachs were also counted during the identification process. The following indices were used to quantify the importance of different preys in the diet of these deep-water sharks. Specimens with regurgitated stomach contents or inverted stomachs were excluded from the sample population.

Stomach content analysis. The performed stomach content analysis followed the fullness rating scale (0–3, where 0 is empty and 3 is completely full) and the level of digestion scale (0–3, where 0 indicates prey is newly eaten, and 3 indicates prey items at an advanced level of digestion and cannot be identified) (Pethybridge et al 2011). Before dissection, each stomach was weighed (nearest 0.1 g) then everted. Contents were discarded, sieved, recorded and prey items were identified as much as possible. Taxonomic resolution was achieved where possible, with the aid of identification keys (Keable & Bruce 1997; Reiss et al 2009; Marceniuk et al 2017; Luna et al 2021) and local reference collections (Lloris & Rucabado 1998). After identification, prey items were classified in groups and families: Cephalopods, Crustaceans, Elasmobranchs, Chimeras and Teleost.

Vacuity index (Vi). The vacuity index (Vi%) represent the percentage of the number of empty stomachs (NEs) compared to the total number of stomachs examined (TNs) (Hureau 1970; Geistdörfer 1975). The coefficient is inversely proportional to the power supply intensity, and it is calculated according to the following equation:

$$Vi\% = NEs / TNs \times 100$$

Frequency of occurrence (Fo). The frequency of occurrence (Fo%) represents the percentage of the number of stomachs that contain at least one identified individual prey (Nsi) compared to the total number of non-empty stomachs (Nsp). To calculate Fo, we used the following equation (Hureau 1970; Labourg & Stequert 1973):

$$Fo = Nsi / Nsp \times 100$$

The Fo expresses the importance of a given prey in relation to the number of stomachs examined and makes it possible to know the dietary differences of the species studied according to the following scale: Fo>50%, qualified as preferential prey; 10<Fo<50%, qualified as secondary prey; Fo<10%, occasional prey.

Total fullness index (TFI). The total stomach fullness index (TFI) was calculated for each individual stomach containing at least one prey (Bowering & Lilly 1992). This index, used to assess stomach filling from a quantitative point of view, was calculated as follows (Bozzano et al 1997):

$$TFI = Wsc \times 10^4 / TW_i$$

Where: Wsc is the weight of stomach contents; TWi is the total weight of the individual.

Index of relative importance (IRI). The ratio for each prey group in the diet was expressed in terms of three parameters: percentage of Fo, percentage of abundance in number (N) and percentage of abundance by weight (P) (Hyslop 1980). A modification of the version of IRI described by Pinkas et al (1971) was used. Hence, the following equation was used to determine the index of relative importance (IRI):

$$IRI = Fo \times (N + P)$$

Where: IRI>50% for preferential prey; 10<IRI<50% for secondary prey; 1<IRI<10% for complementary prey and IRI<1% for accidental prey.

Statistical analysis. To calculate the degree of similarity of food preferences in different seasons as well as between different size groups of deep-water sharks, we used the Ascending Hierarchical Classification (AHC) using the Primer 6 software, with the Jump Minimum as an aggregation method and Euclidean distance for distance measurement, this method being the most used for this type of analysis. The dendrograms obtained showed the composition of different classes and seasons, as well as the order in which they were formed. It also showed, on the horizontal axis, what the value of the index between the two classes that were aggregated at a given stage or both seasons was. The analysis of variance (ANOVA) was used to test the variability of the different indices according to size classes and seasons. The estimation of the degree of similarity of food preferences between the different size groups of this species using the Bray-Curtis similarity index.

Results and Discussion. Stomach content examinations showed 4 types of content: empty stomach, content with identified undigested preys at the genus and family taxonomic level and unidentified content in tow forms, unidentified biotic material (UBM) and unidentified abiotic material (UAM). Content analysis confirms that this species has exclusively a carnivorous diet. Some preys were recognized by components such as: otoliths, scales, and vertebras for Teleostei; antennas, shells and appendages for crustaceans; beaks, mantles, suckers and tentacles for cephalopods. Table 1 presents the prey items identified based on stomach content analysis. Identification of all prey ingested, identified abiotic material (IAM) and unidentified abiotic material were recorded (Table 1). The effective sample sizes for examining the diet were reduced, because many stomachs were empty (between 29 and 46%) (Table 2). According to this study, the diet of *C. squamosus* was composed by 30 prey taxa in total, including 18 teleost, 4 cephalopods, 4 crustaceans, 3 elasmobranchs, and 1 annelid. The prey of *C. squamosus* was dominated by teleost fishes, with an Fo of 52.34% (Table 3).

Table 1

Diet composition of *Centrophorus squamosus*

Prey group	*Prey family*	*Prey identification*
Cephalopodae	Ommastrephidae	*Illex coindetii*
	Loliginidae	*Loligo vulgaris*
	Octopodidae	*Octopus vulgaris*
	Sepiidae	*Sepia* sp.
	Ommastrephidae	Unidentified
	Unidentified	Unidentified
Crustaceae	Aristeidae	*Aristeus antennatus*
	Nephropidae	*Nephrops norvegicus*
	Penaeidae	*Penaeopsis serrata*
	Aristeidae	*Plesiopenaeus* sp.
	Unidentified	Unidentified crustaceae
Chondrichtyes	Dalatidae	*Dalatias licha*
	Chimaerae	*Chimaera monstrosa*
		Chimaera sp.
	Unidentified	Unidentified
Teleostei	Macrouridae	*Malacocephalus* sp.
		Nezumia aequalis
		Trachyrhynchus trachyrhynchus
	Gadidae	*Diretmichthys parini*
		Gadidae
		Unidentified (otoliths, bones, eyes, others)
	Congridae	*Bassanago* sp.
		Gnathophis sp.
	Alepocephalidae	*Alepocephalus rostratus*
		Alepocephalus sp.
	Trichiuridae	*Aphanopus carbo*
		Lepidopus caudatus
	Scombridae (bait)	*Scomber* sp.
	Clupeidae (bait)	*Sardina pilchardus*
	Bramidae	*Brama brama*
	Merluciidae	*Merluccius* sp.
	Ophichthidae	*Pisodonophis* sp.
	Phycidae	*Phycis* sp.
	Nematodes	Unidentified nematodes
IAM	Abiotic material	Fish hook
IAM	Abiotic material	Monofilament hook line
UAM	UAM	Unidentified abiotic material
UBM	UBM	Unidentified biotic material

Note: IAM - identified abiotic material; UAM - unidentified abiotic material; UBM - unidentified biotic material.

Table 2

Qualitative stomach fullness and prey diversity

		Number of stomachs
Stomach fullness	% Empty stomach (0)	34
	% 1/3 full	13
	% 2/3 full	26
	% 3/3 full	27
Prey diversity	Empty or digestive fluid	242
	1 IP	392
	2 IP	39
	3 IP	8
	4 IP	5
	5 IP	3
	6 IP	2
Stomachs rejected (regurgitated)		22

Note: IP - identified prey.

Table 3

Frequency of occurrence (Fo) of prey groups in the diet of *Centrophorus squamosus*

Prey group	Nei	Nep	Fo (%)	Classification prey
Cephalopodae	118	449	26.28	Secondary
Crustaceae	49		10.91	Secondary
Teleostei	235		52.34	Preferential
Chondrichtyes	11		2.45	Occasional
Annelida	9		2	Occasional

Note: Nei - number of stomachs containing at least 1 prey of the group; Nep - number of stomachs containing at least one prey.

The fullness of the *C. squamosus* stomachs that were examined consisted of 27% full stomachs, 26% medium full, 13% at one third of the capacity, and 34% empty. In general, stomachs were rarely full. We have recorded a diversity of prey per stomach varying from 1 to 6. However, those containing 3 or more types of prey did not exceeding 18 samples in total (Table 2). About half of the stomachs examined contained a single prey. On the other hand, less than 1% of the samples present 3 to 6 prey per stomach (Table 2). For stomachs with well-digested contents, we found only bones and scales, making it difficult to identify prey from these pieces. These prey items remained unidentified, being well-digested fish remains. The existence of teleost flesh in the stomach contents suggests that the prey had been scavenged or that live prey had been attacked, and not fully ingested.

The seasonal evolution of the Vi of the two sexes shows a variation along the seasons, and from year to year, except in autumn 2019 and autumn 2020, when the Vi of the males and the females were almost the same, 40 to 20%, respectively. The Vi varied in males from 0% in spring 2018 to 70% in tow times, autumn 2018 and spring 2019. For females, the Vi varied between 15% in spring 2019 and 63% recorded in tow times, winter 2019 and spring 2020. There is no difference between males and females' vacuity index ($p>0.05$), and there is no difference between seasons variations and Vi variations ($p>0.05$). The Vi is influenced by season, depth or the marine environment. We conclude that during the 2018-2021 sampling period, the Vi did not have the same rate of variation (Figure 1). As a result, we recorded that the Vi for small size classes [95-99 cm] of *C. squamosus* is more than 40%, which means that probably the small sized fish have a specific more rapid digestion or they have not yet developed a good predation practice. From the size group [100-104 cm], the Vi starts to decrease with the increasing class sizes (Figure 2).

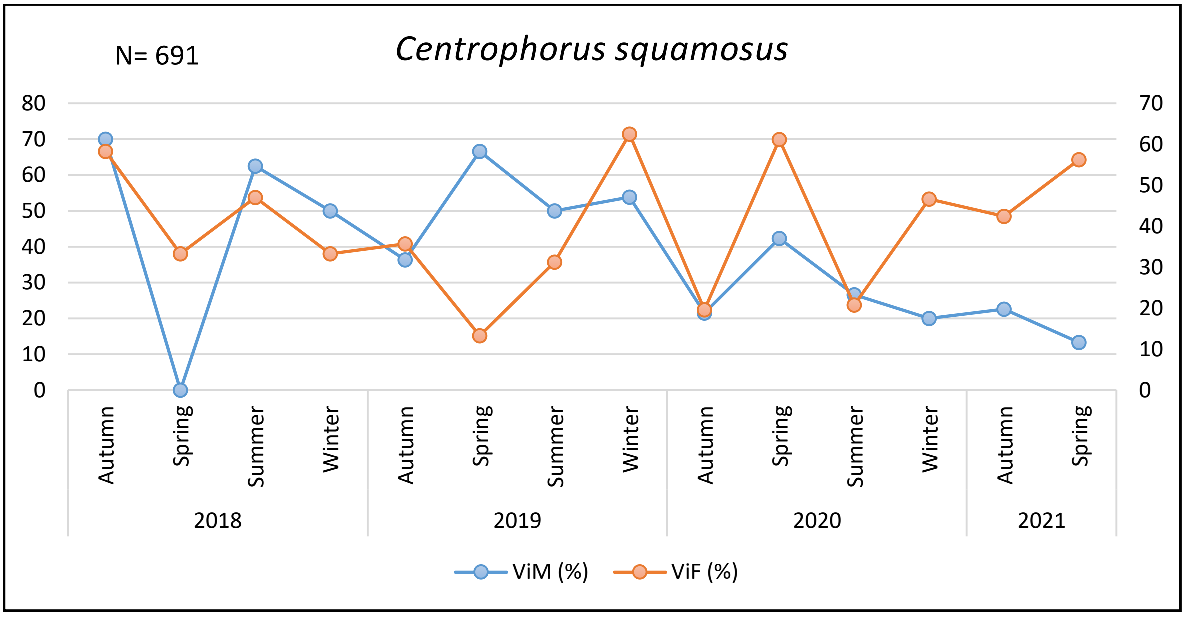

Figure 1. Evolution of the Vacuity index (Vi) per seasons from 2018 to 2021 of *Centrophorus squamosus* males (M) and females (F).

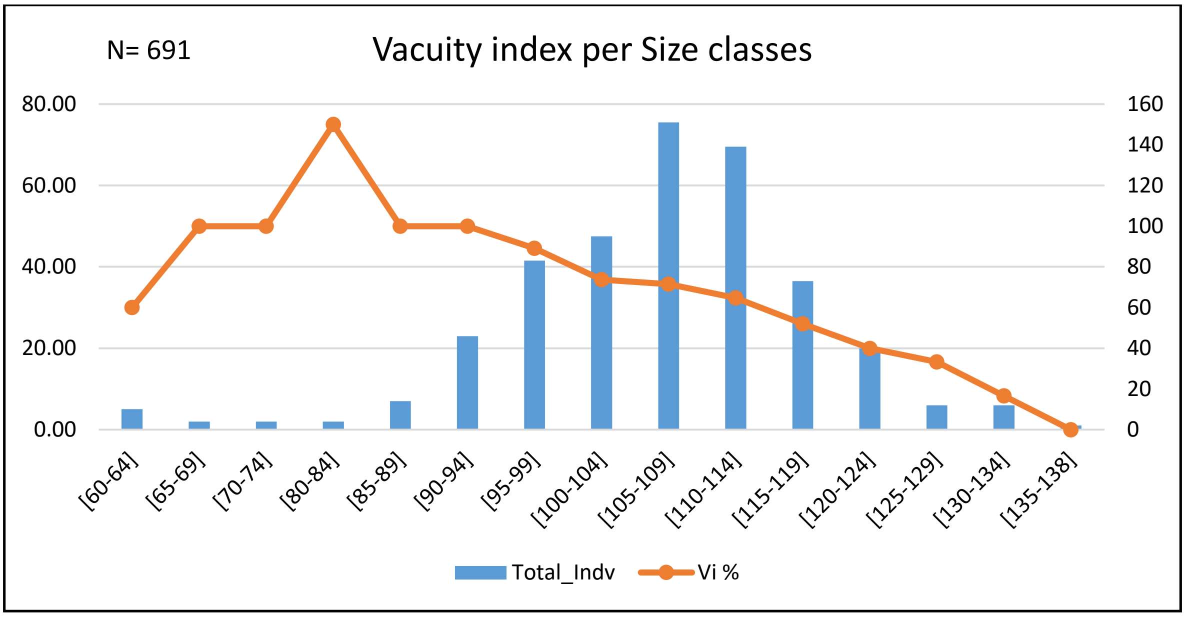

Figure 2. Evolution of the Vacuity index (Vi) per size classes (cm) of *C. squamosus*.

The results of the Fo calculated for *C. squamosus* show that the Teleostei group have a large Fo, exceeding 52%. As a result, this group is classified as preferential prey. Cephalopods group have a Fo of 26.28%, which allows it to be classified as secondary prey. The crustaceans group are also classified as a secondary prey, with a Fo of 10.91%. The chondrichthyes and annelid groups are classified as occasional prey in diet of *C. squamosus*. The shark prefers to feed on Teleostei, and in the absence of fish in their search for prey, they eat secondarily or occasionally the other groups recorded, namely cephalopods, crustaceans and annelids.

The Teleostei group have a large IRI, exceeding 174 for *C. squamosus*. As a result, this group is classified as preferential prey. Cephalopods group have an IRI of less than 50%, which allows it to be classified as secondary prey. The crustaceans group is classified as a complementary prey for *C. squamosus* (9.94%). The Chondrichthyes group are classified as an accidental prey in diet of *C. squamosus*. The annelids group was also qualified as accidental prey (Table 4).

Table 4
Index of Relative Importance (IRI) of the diet composition of the leaf scale gulper shark (*Centrophorus squamosus*)

Prey group	*Fo (%)*	*N*	*P (kg)*	*IRI (%)*	*Prey classification*
Cephalopodae	26.28	138	16.42	40.58	Secondary
Crustaceae	10.91	87	4.05	9.94	Complementary
Teleostei	52.34	305	27.8	174.18	Preferential
Chondrichtyes	2.45	11	3.87	0.36	Accidental
Annelida	2	21	0.018	0.42	Accidental

Note: Fo - frequency of occurrence; N - number of stomachs; P - weight of total preys; IRI - index of relative importance.

The Total Fullness Index (TFI) calculated shows that the *C. squamosus* stomach contents comprised of crustacean prey group has a ratio that exceeds 387, followed by cephalopods and chondrichthyes with a value of approximately 200, and a value of 0.69 for annelids (Table 5). As a result of the TFI analysis, crustaceans and cephalopods have the highest ratio, eventhough they are classified by the other indices (Fo and IRI) as secondary prey for *C. squamosus*. The Teleostei group, which has been classified as preferential prey for this species, has a TFI value of 131.04, almost 1/3 of the value for crustaceans.

Table 5
Total stomach Fullness Index for the diet composition of *Centrophorus squamosus*

Group	*Wsc (g)*	*Twi (g)*	*TFI*
Cephalopodae	16419.82	805873.4	203.75
Crustaceae	3861.36	99525.9	387.98
Teleostei	4046.17	308779.2	131.04
Chondrichtyens	27765.21	1408612.9	197.11
Annelida	1.75	25278.9	0.69

Note: Wsc - weight of stomach contents; Twi - total weight of the individual; TFI - total fullness index.

By analyzing the composition of the stomach content of the *C. squamosus* by size classes, we observed that sizes less than [80-84 cm] have food composed only of nematodes and small-sized fish. From sizes [85-89 cm], this species began to diversify their diet by adding fish of different sizes, cephalopods, crustaceans and unidentified biotic material (UBM) with the absence of nematodes. For this species, from sizes of [100-104 cm], we recorded the appearance of traces of the Chondrichthyes group in the stomach contents. The fish are present almost for all size classes, with a different percentage varying from 30 to 75% (Figure 3).

The estimation of the degree of similarity of food preferences between the different size groups of *C. squamosus* using HAC shows that the population can be divided into three groups with a degree of similarity of 20%: the first group size has a diet composed by cephalopods and chimaerids; the second one prefers teleost and nematodes; the third has a diet composed by teleost, cephalopods, crustaceans and Chondrichthyes. The first group is composed of individuals belonging to the 135-138 cm size range. The second group is composed of individuals of sizes between 60-84 cm and the third group is composed of individuals of sizes between 85-134 cm (Figure 4).

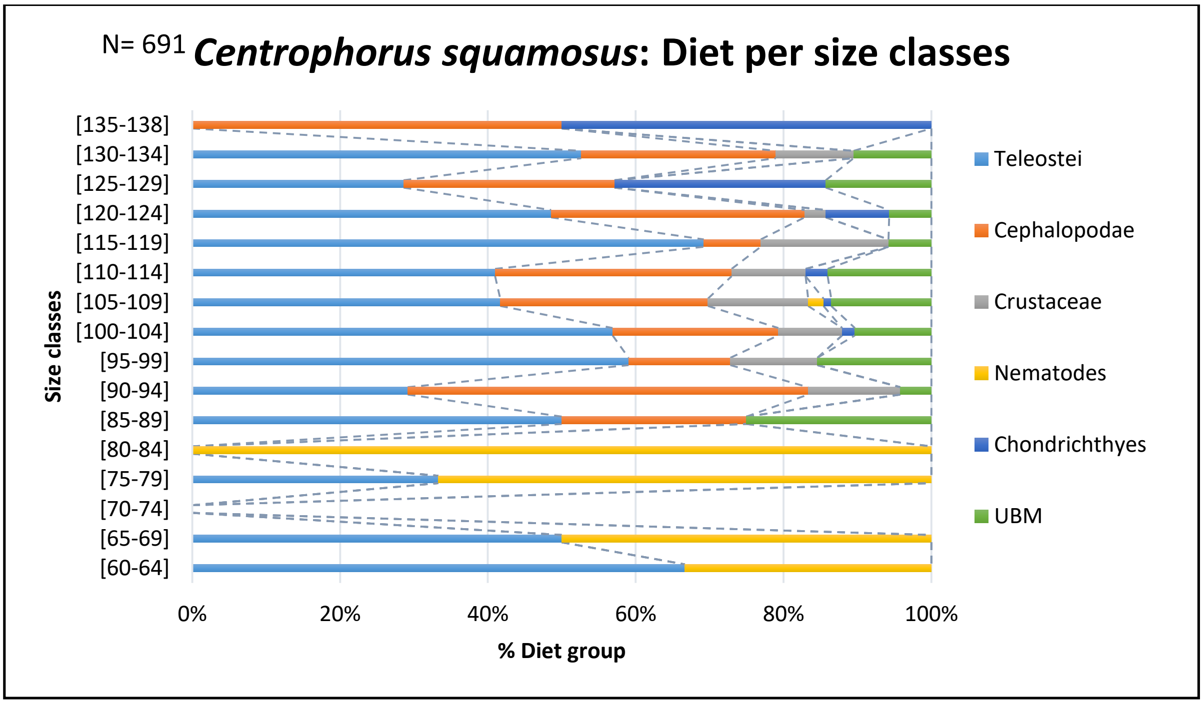

Figure 3. Diet composition per size classes of *Centrophorus squamosus* (UBM - unidentified biotic material).

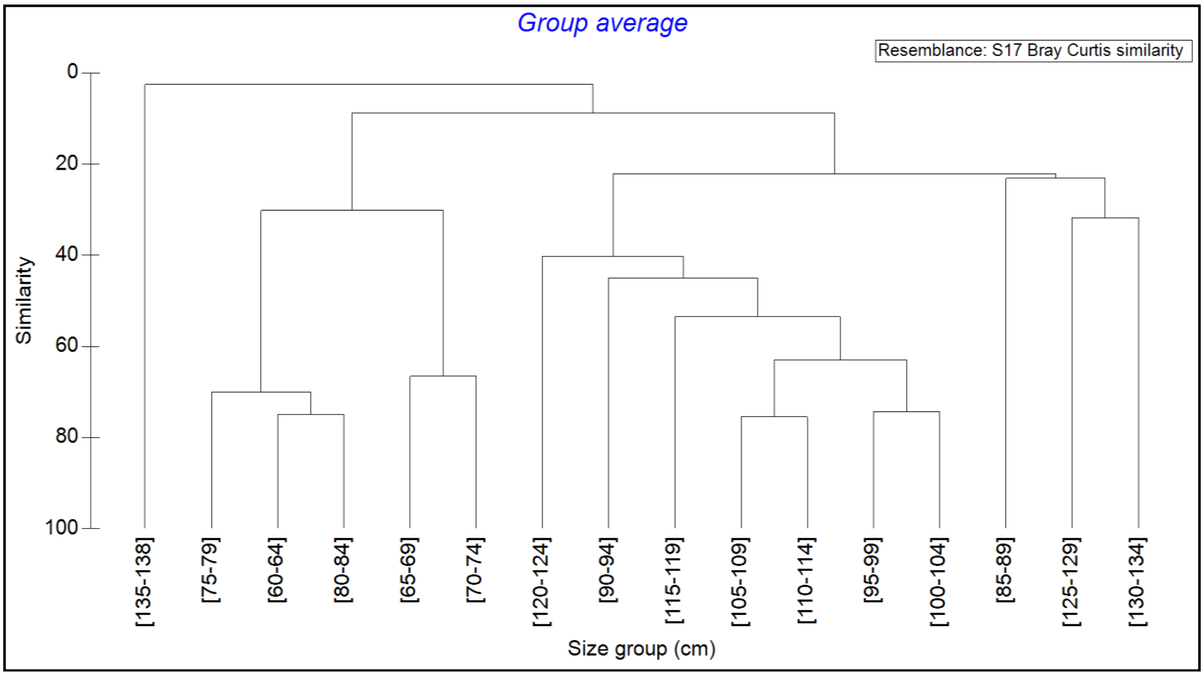

Figure 4. Dendrogram showing the food similarity of size classes of *Centrophorus squamosus*.

According to classical ecological theory, the food preference characterizing certain species of fish is an important factor in the identification and estimation of food competition, the structure and stability of the marine trophic chain and the evaluation of functional responses of prey and predators (Post et al 2000; Bacheler et al 2004). Whether a sample is considered large enough to adequately describe the diet depends on the level of taxonomic detail to which the prey species are identified, and the statistics used to measure diet breadth, which may be the number of prey species, individuals, or prey diversity.

Although as few as 15-30 non-empty stomach samples may be considered adequate to describe prey diversity for some shark species (Alonso et al 2002; Lucifora et al 2006), we consider the sample sizes achieved in this study to better indicate prey and feeding behavior. The deep-water shark *C. squamosus* was found to have eaten primarily Teleostei composed by 13 families in total. *C. squamosus* eat cephalopods as a second prey, crustaceans as a complement one and they consumed Chondrichthyes and annelids accidentally. The parts of some species were found in the stomach content, like heads or flesh. These occurrences indicate incomplete ingestion, or perhaps scavenging. Jack mackerel heads and/or tails were found in the stomachs of *C. squamosus*, and were almost certainly scavenged discards from commercial fishing vessels. In 449 *C. squamosus*, we found predominantly demersal and benthic teleost prey, dominated by Trichiuridae, Alepocephalidae and Macrouridae, seconded by cephalopods and crustaceans and some Chondrichthyes dominated by Chimaera. Dunn et al (2010) found that the diet of *C. squamosus* was composed by demersal and benthic teleost prey, of which hoki (*Macruronus novaezelandiae*) was the predominant species, followed by some elasmobranchs. In the North Atlantic Sea, Mauchline & Gordon (1983) found that the diet of this species was composed predominantly by fishes, including Chondrichthyes. Ebert et al (1992) fond that cephalopods were the dominant prey group in diet of *C. squamosus* from South Africa coasts, unidentified teleost and *Merluccius paradoxus* were the second and third most important prey items, respectively.

The Teleost group constitute the dominant prey of the studied shark's diet. The abundance of prey, the size of individuals and their biological parameters have an influence on its diet composition. These results, and others like them, are of great importance for making a good decision by ensuring good fisheries governance that aims for sustainable management, economically profitable and socially equitable exploitation.

Conclusions. The examination and analysis of stomach contents of the deep-water shark, *C. squamosus*, reveals their very diverse diet, this species being opportunist. The diet is essentially composed by teleosts (Myctophidae, Trichiuridae, Merluciidae, Phycidae and Scombridae), cephalopods (Octopodae and Ommastrephidae) crustaceans (Penaeidae, Aristeidae and Nephropidae) and annelids (nematodes). In addition, *C. squamosus* feeds on a few Chondrichthyes (Dalatidae and Chimaerae).

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Conflict of Interest. The authors declare that there is no conflict of interest.

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