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Feeding habits of two shark species: velvet belly, *Etmopterus spinax* (Linnaeus, 1758) and blackmouth catshark, *Galeus melastomus* (Rafinesque, 1810), present in fishing discards in the Gulf of Cádiz

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Abstract In many fisheries, such as trawl fisheries, sharks appear among the catches as bycatch or discards, and these species include velvet belly (*Etmopterus spinax*) and blackmouth catshark (*Galeus melastomus*). The objective of this study was to research the feeding habits of both species in the Gulf of Cádiz and to identify possible differences in diet depending on size and time of day. The most frequent sizes were 12–16 cm for *E. spinax* and 14–20 cm for *G. melastomus.* Both species preyed mainly on euphausiaceans and teleosts; their Index of Relative Importance (IRI) per species were as follows: *E. spinax* 42.30% IRI, 21.66% IRI; *G. melastomus* 52.33% IRI, 27.26% IRI, respectively. Only *Etmopterus spinax* showed significant variation in diet as a function of the time of day ($p < 0.05$), although both species showed similar patterns of feeding throughout the day. With respect to size, *E. spinax* consumes more cephalopods and teleosts as its size increases, while *G. melastomus* increases its consumption of decapods.

Keywords Elasmobranchs · Trawl fishery · Deep-water shark · Diet · Bycatch

Highlights
The most abundant sizes were 12–16 cm for *Etmopterus spinax* and 14–20 cm for *Galeus melastomus*. Both species have specimens caught below the first mature size.
The most consumed prey by both *Etmopterus spinax* and *Galeus melastomus* were crustaceans (euphausiaceans), teleosts, and cephalopods.
The diet of *Etmopterus spinax* shows significant variations throughout the day.
Although there is evidence of niche overlap, food availability may be a factor that allows the concurrence of the two species.

Introduction

Sharks are considered a key player in the regulation of marine ecosystems (Estes et al. 2011). Knowledge about the trophic relationships of many sharks in ecosystems, especially deep-water species, was sparse until very recently (Martin and Mallefet 2023). Despite this, due to the apparent abundance

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of some species in catches in some regions, various studies have been carried out on their feeding behavior (Dulvy et al. 2016). Among these species are velvet belly *Etmopterus spinax* (Linnaeus, 1758) and blackmouth catshark *Galeus melastomus* (Rafinesque, 1810). Despite being commonly caught by trawlers in the Northeast Atlantic near the Canary Islands, Southern Portugal, and Spain (Costa 2014; Blanco et al. 2023), these species have been considered bycatch and, in many cases, discarded from trawl fisheries targeting Norway lobster *Nephrops norvegicus* (Linnaeus, 1758), deepwater pink shrimp *Parapenaeus longirostris* (Lucas, 1846), and hake *Merluccius merluccius* (Linneaus, 1758) (Torres et al. 2013) due to their limited commercial value (Moranta et al. 2000; Carbonell et al. 2003, Besnard et al. 2022). One of the biggest ecological problems caused by this type of fishery worldwide is discards, as well as their economic implications (Bellido et al. 2011). Discarded fish are the part of the catch that are not retained on board during a fishing operation and are discarded at sea, dead or alive (Tsagarakis et al. 2014).

The need for an ecosystem-based analysis of the marine environment and existing trophic relationships has led to many studies on discarded species (e.g. Pennino et al. 2014). Although these shark species have been studied regarding various aspects of their biology, such as bioaccumulation, reproduction, and feeding (Coelho and Erzini 2005; Rodrigues et al. 2022; Zicarelli et al. 2023), studies on the trophic interaction between species whose habitats overlap are particularly rare (Fanelli et al. 2009).

Etmopterus spinax and *G. melastomus* share similar habitats (Fanelli et al. 2009). They can be found on island platforms and upper slopes, at depths of 70 to 2000 m and 150 and to 1200 m, respectively (Froese and Pauly 2005; Coelho and Erzini 2008a), mainly in sandy and muddy bottoms of the continental and insular shelf (Moreno García, 2004). These species prefer to inhabit bottom areas, feeding on small teleosts, crustaceans, and mollusks (Barría et al. 2018). *Etmopterus spinax* feed mainly on decapods, cephalopods, and mesopelagic fish (Macpherson 1981). They have a generalized benthopelagic foraging behavior, mainly targeting pelagic macroplankton/micronekton of appropriate size (Neiva et al. 2006). *Galeus melastomus* has a very diverse diet, although with a generalist niche, with individual specialization in food items of high specific abundance and low occurrence (Barría et al. 2018). In the mid-continental slope zone, the main diet is benthic invertebrates, such as decapods and cephalopods, as well as small pelagic fish and other elasmobranchs; in the upper continental slope zone, they feed mainly on euphausiids and decapods (Fanelli et al. 2009; D'Iglio et al. 2021). This species has been shown to exhibit ontogenetic feeding differences, with *E. spinax* feeding on small crustaceans and cephalopods at smaller sizes and shifting to larger prey such as fish at larger sizes. In contrast, *G. melastomus* feeds on cephalopods at sizes up to 30 cm, increases its preference for cephalopods at medium sizes, and becomes a generalist predator at sizes above 45 cm (Macpherson 1981; Fanelli et al. 2009).

The ecological interaction between these species is still a knowledge gap in areas such as the Gulf of Cádiz, where fishing activity is intense. Understanding aspects of feeding habits can provide useful information about the role of the species in the ecosystem (Wetherbee et al. 1990, 2012).

Due to the fact that they are commonly found in discards and are species with many gaps in the knowledge of their trophic relationships, the object of this study was (1) to characterize the feeding habits of *Etmopterus spinax* and *Galeus melastomus*, (2) to compare their differences with respect to body size and time of day, and (3) to test the overlap of their diet in order to identify the presence or absence of competition for habitat between these two species.

Material and methods

Study area and sampling

The Gulf of Cádiz is a marine ecosystem located in the southwest of the Iberian Peninsula (Atlantic Ocean) (36° 51′ N, 06° 55′ W) (Fig. 1). This ecosystem has several characteristics that make it oceanographically dynamic and unique, such as the existing wind patterns and, above all, the exchange of water through the Strait of Gibraltar (Vargas et al. 2003; Navarro and Ruiz 2006), which, together with the nutrient inputs from the rivers that flow into it, make it a highly productive region (García Lafuente and Ruiz 2007).

Samples of both species were obtained through the ECOFISH + project after processing the discards and performing identification and quantification by

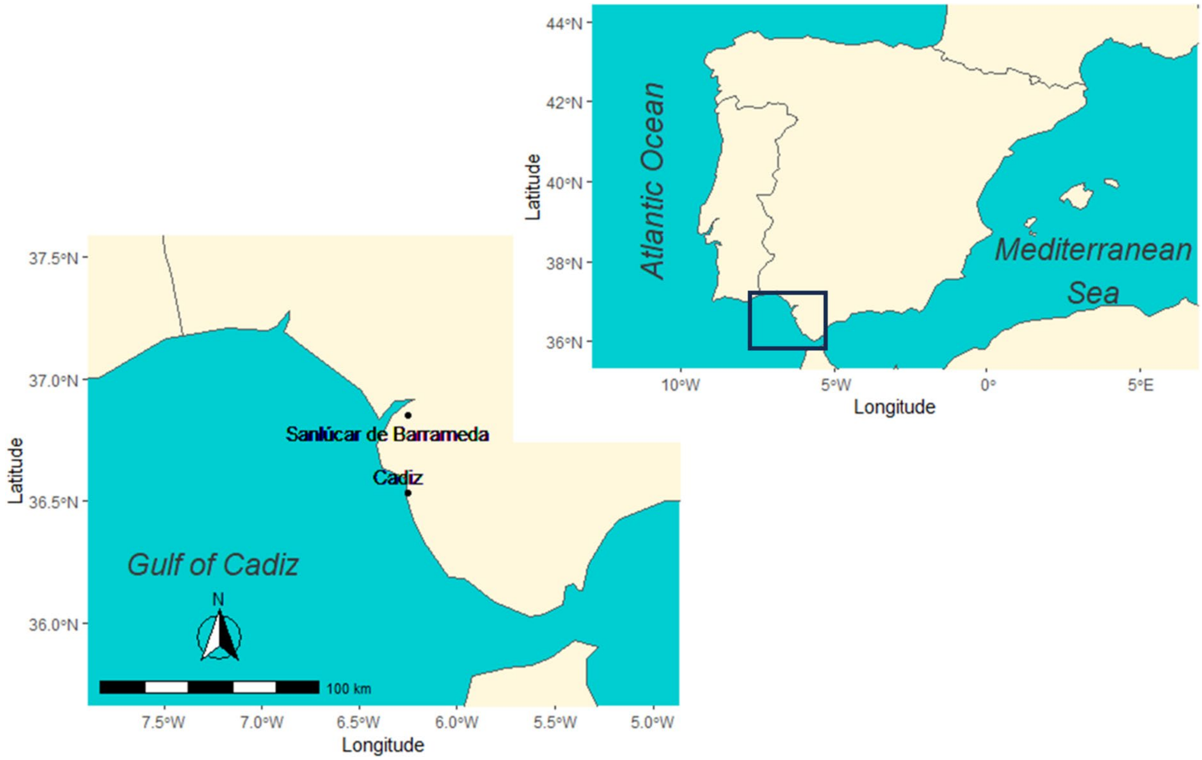

Fig. 1 Geographical location of the study area (Gulf of Cádiz, SW Spain)

species. Sampling occurred alongside the professional trawl fishing fleet's daily operations in the Gulf of Cadiz, conducted without disrupting their routine activities. We analyzed a total of 21 hauls spanning from June to September 2021. For each fishing day, a total of 3 hauls were made with their occurrences distributed across three distinct temporal intervals: night haul, 5 a.m.–9 a.m.; morning haul, 9 a.m.–1 p.m.; afternoon haul, 1 p.m.–5 p.m. The depth at which haul operations are conducted in fishing activities fluctuates within a spectrum from 9 to 300 fathoms (1 fathom = 1.829 m). The different species were separated, identified, and labeled in the laboratory for subsequent analysis.

Morphometric measurements

The collected biometric measurements were essential for observing the catch size and characterizing the species according to size. Total length (TL) of each individual was measured (±0.1 cm), as well as total weight (TW) (±0.01 g).

The stomach contents of each specimen were preserved in 70% alcohol for subsequent identification and quantification of prey. Items were identified to the lowest possible taxonomic classification level using the manual of Hayward and Ryland (2017). The stomach contents found with a very high level of digestion were considered unidentified contents.

The indices analyzed were the Vacuity index for stomach without contents:

$$Vi = \frac{n^{\underline{o}}\ of\ empty\ stomachs}{n^{\underline{o}}\ of\ total\ stomachs} \times 100$$

The proportion of individuals using each resource is expressed as the frequency of occurrence (%F):

$$\%\mathrm{F} = \frac{\mathrm{n^{\underline{o}}\ of\ stomachs\ containing\ aresource}}{\mathrm{total\ n^{\underline{o}}\ of\ total\ stomachs}} \times 100$$

The numerical percentage is the percentage of the total number of prey items of a resource found in each stomach (%Cn):

$$\%\mathrm{Cn} = \frac{\text{n}^{\underline{\text{o}}}\text{. of items of a resource}}{\text{total n}^{\underline{\text{o}}}\text{.of items}} \times 100$$

We calculated a resource's percentage of the total weight of the stomach contents or gravimetric percentage (%Cw) as follows:

$$\%\mathrm{Cw} = \frac{\text{Wet weight of the items of } a \text{ resource}}{\text{total weight of the stomach contents}} \times 100$$

Finally, we calculated the importance of each prey item using the Index of Relative Importance (I.R.I.), based on %F, %Cn, and %Cw:

$$\mathrm{IRI} = \%\mathrm{F} \times (\%\mathrm{Cn} + \%\mathrm{Cw})$$

The diet breadth was calculated using the Standardized Levins Index (Best), which is generated (Krebs 1988) based on the Levins index (B) (Levins 1968).

$$B = \frac{1}{\left(\sum jp^2 i\right)}$$

$$Best = \frac{(B-1)}{(n-1)}$$

where pi = proportion of a predator's diet j that is made up of prey i; and n = number of prey categories, this index varies from 0 to 1, where low values signify a specialist species (diet dominated by few items) while values close to 1 indicate that the species is a generalist (Gibson and Ezzi 1987; Krebs 1988).

The Trophic Diversity Index (D) is complementary to the Levins index:

$$D = -\sum log\mathrm{pi}$$

And finally, to study the possible overlap between the diets of both shark species, the Overlap Schoener Index was calculated as:

$$Schoener\ Index = 1 - 0.5 \times \left(\sum |pji - pki|\right)$$

where p_{ji} and p_{ki} are the estimated proportions of prey i in the diets of species j and k, respectively. This index has a range of values from 0 (no overlap) to 1 (complete overlap), with values greater than 0.6 being considered biologically significant (Macpherson 1981; Wallace 1981).

Data analysis

A numerical summary was made of the biometric measurements of both species, thus obtaining sample means ($\overline{X}$), median (Med.), standard deviations (sd), maximum (Max.), minimum (Min.), and range.

The size of the individuals and the significant differences in feeding as a function of individual size was also studied. For all tests, a significance level (α) of 0.05 was used.

For an in-depth understanding of the *E. spinax* and *G. melastomus* diet, it is vital to establish the minimum amount of stomachs required for analysis (Ferry 1996; Matić-Skoko et al. 2014). In this research, the sufficiency of the gathered shark samples was evaluated by comparing the cumulative count of prey taxa with the cumulative count of stomachs chosen randomly. To neutralize any bias from the sampling order, the stomachs investigated were randomized 500 times. The surfacing of an asymptotic curve implies that we had collected an adequate volume of samples to reliably represent the diet of these species (Ferry et al. 1996; Scenna et al. 2006).

In this study, we employed one-way analysis of similarities (ANOSIM) to statistically discern disparities in diet composition, taking into account variations in time of day and size range. ANOSIM, a nonparametric method used to test differences between groups, is particularly powerful when combined with the Bray–Curtis dissimilarity matrix, a tool robust for comparing dietary compositions across different individuals or populations. This metric, extensively utilized in ecological studies, quantifies the dissimilarity between two communities based on species abundance, effectively accounting for both the presence and abundance of various prey items without giving undue weight to rare species, thus being especially suitable for dietary studies where certain prey might be ecologically significant despite their low abundance (Somerfield et al. 2021; Kendrick and Hyndes 2005; Sampson et al. 2009; Whitley and Bollens 2014).

By contrasting the average distances within groups to those between groups, ANOSIM provides insights into compositional dissimilarities. The Bray–Curtis measure, with values ranging from 0 to 1, offers a comprehensive view of community composition: a score of 0 indicates equal sharing of all species between two samples, whereas a score of 1 suggests no shared species. After constructing the Bray–Curtis distance matrix, we performed the ANOSIM, yielding two primary outputs: a *p*-value indicating the statistical significance of the test's results and the "R" statistic, comparing the mean of ranked dissimilarities between groups to those within groups. An *R* value close to 1 indicates dissimilarity between groups, while an *R* close to 0 suggests an even distribution of high and low ranks within and between groups (Clarke 1993; Warton et al. 2011).

The *p*-value, derived from permutations of the data, communicates the probability of observing the calculated *R* statistic (or a more extreme value) under the null hypothesis of no difference between groups. A small *p*-value (typically ≤ 0.05) suggests that the observed group differences are statistically significant and not just due to chance, whereas a large *p*-value indicates a lack of significant differences. The choice of the Bray–Curtis distance for ANOSIM is further justified by its widespread acceptance and success in similar ecological studies (Clarke et al. 2014).

All statistical analyses were carried out using the *R* software (version 4.1.3; R Core Team, 2022) with a significance level (α) set at 0.05. Additional packages used include "tidyverse" (Wickham et al. 2019) (includes "dplyr" (Wickham 2023a) and "ggplot2" (Wickham 2009)), "lubridate" (Grolemund and Wickham 2011), "vegan" (Oksanen et al. 2022), "reshape2" (Wickham 2007), and "forcats" (Wickham 2023b).

Given that the lengths at first maturity (L_{50}) for *E. spinax* are set at 25 cm for males and 31 cm for females (Coelho and Erzini 2005), and for *G. melastomus*, it is 48.8 cm for females and 44.3 cm for males (de Sola and Massutí, 2005), and acknowledging that both species exhibit ontogenetic dietary changes with size as shown in Neiva et al. (2006) and Fanelli et al. (2009), we have established specific size ranges: range 1, <15 cm; range 2, 15.1–25 cm; range 3, >25.1 cm.

Results

Distribution

The size distribution for both species showed a normal distribution shifted to the left; the most abundant size class for *E. spinax* was between 12 and 16 cm (Fig. 2A), while for *G. melastomus*, the overall catch size was wider, with the most abundant being between 14–20 cm and 22–26 cm (Fig. 2B).

The highest abundances for both *E. spinax* and *G. melastomus* occurred during the night, with 215 *E. spinax* captured and 66 *G. melastomus*, while

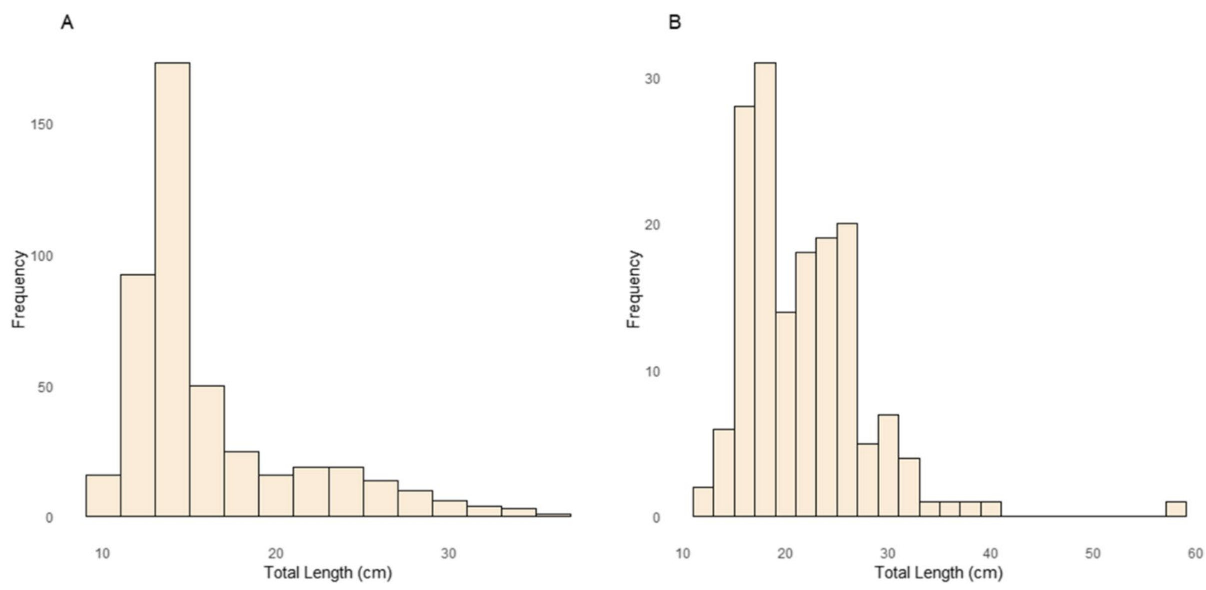

Fig. 2 Length—frequency distribution of **A** *Etmopterus spinax* and **B** *Galeus melastomus* in this work

during the afternoon, both species showed the lowest captures. All size ranges had the highest abundances during the night, declining during the day, except for *G. melastomus* range 3 specimens, which showed their highest abundance during the morning with 20 specimens captured during that time (Table 1).

Figure 3 illustrates the cumulative prey curves for *E. spinax* and *G. melastomus*, based on the total number of stomachs analyzed. Two distinct trends were observed in the analysis: one that includes all identified prey (blue line) and another that accounts for only those prey with an Index of Relative Importance (IRI) of at least 1% (red line). For *E. spinax* (Fig. 3A), the curve excluding prey with an IRI of less than 1% shows stabilization (asymptotic) upon analyzing approximately 100 stomachs, and the same stabilization for *G. melastomus* (Fig. 3B) would require the analysis of about 140 specimens.

The total stomachs sampled were 607. Of these, for 448 stomachs of *E. spinax*, it was possible to identify 10 items, while for 159 *G. melastomus* stomachs, 9 items were identified. The vacuity index for *E. spinax* was 51.12%, and for *G. melastomus*, a lower percentage of 45.92% was obtained.

Diet composition

The diet of *E. spinax* consists mainly of four groups: Order Euphausiacea (42.30% IRI), Subclass Teleostei (21.66% IRI), Order Decapoda (20.47% IRI), and Subclass Coleoidea (15.52% IRI) (Table 2), while *G. melastomus* (Table 3) shows a diet with two main groups: Order Euphausiacea (52.33% IRI) and Subclass Teleostei (27.26% IRI).

The values of the main indexes evaluated were as follows: Levins standardized index 0.36 was obtained for *E. spinax* and 0.28 for *G. melastomus*. The

Table 1 Number of individuals of *Etmopterus spinax* and *Galeus melastomus* as a function of size range and time of day

	Etmopterus spinax			*Galeus melastomus*		
	Night	Day	Afternoon	Night	Day	Afternoon
Range 1	155	111	15	6	2	0
Range 2	48	51	30	51	45	14
Range 3	12	17	9	9	20	12

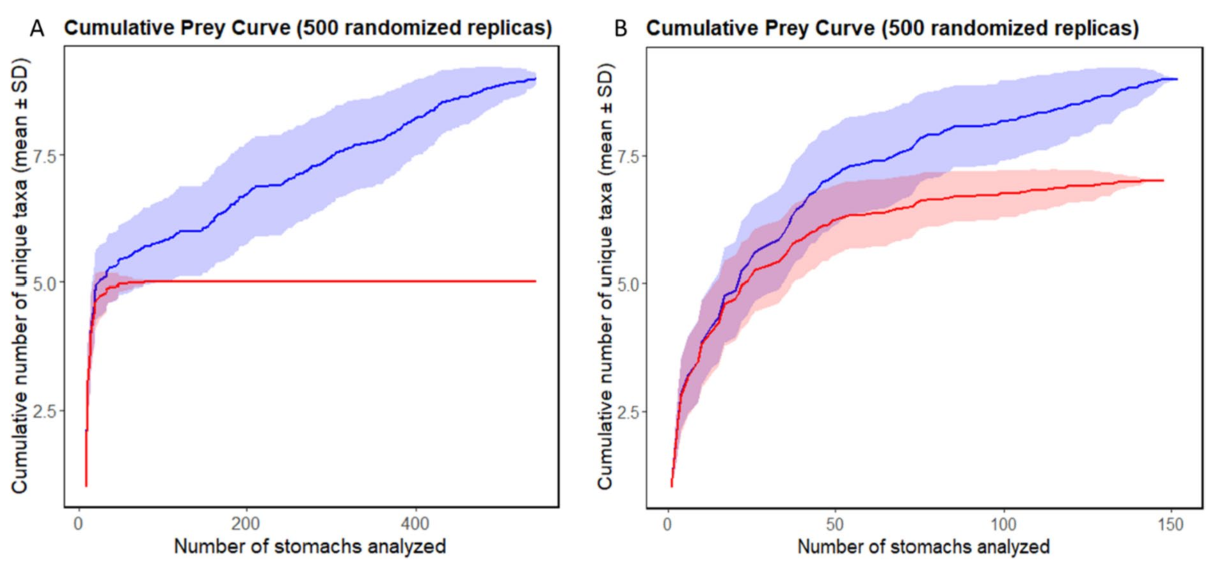

Fig. 3 Cumulative prey curves for the total number of stomachs analyzed. Blue line represents the cumulative prey curve using all different taxa found in *E. spinax* and *G. melastomus* stomachs, and red line represent the cumulative prey curve performed using only prey with an Index of Relative Importance of at least 1%. **A** *Etmopterus spinax*. **B** *Galeus melastomus*

Table 2 Frequency of occurrence (%F), numerical percentage (%Cn), gravimetric percentage (%Cw), and Index of Relative Importance (%IRI) of prey found in the gastrointestinal contents of velvet belly (*Etmopterus spinax*). The different taxonomic categories identified are highlighted in bold. Unid., unidentified

Prey items	%F	%Cn	%Cw	%IRI
Cephalopoda				
Coleoidea unid	16.872	10.926	32.796	15.520
Annelida				
Polychaeta unid	0.412	0.238	0.001	0.002
Crustacea				
Euphausiacea				
Euphausiacea unid	37.860	41.093	12.018	42.303
Decapoda				
Decapoda unid	15.638	11.164	9.532	6.809
Nephrops norvegicus	0.412	0.238	0.372	0.005
Caridea unid	18.519	19.002	15.974	13.626
Parapenaeus longirostris	0.823	0.475	1.415	0.033
Chordata				
Elasmobranchs				
Elasmobranchs unid	0.823	0.713	1.646	0.041
Teleosts				
Teleosts unid	25.103	16.152	24.837	21.647
Myctophidae unid	0.412	0.238	1.408	0.014

Table 3 Frequency of occurrence (%F), numerical percentage (%Cn), gravimetric percentage (%Cw), and Index of Relative Importance (%IRI) of prey found in the gastrointestinal contents of blackmouth catshark (*Galeus melastomus*). The different taxonomic categories identified are highlighted in bold. Unid., unidentified

Prey items	%F	%Cn	%Cw	%IRI
Cephalopoda				
Coleoidea unid	20.652	9.434	8.696	6.900
Echinodermata				
Echonodermata unid	1.087	0.472	2.466	0.059
Crustacea				
Euphausiacea				
Euphausiacea unid	46.739	50.000	17.727	58.332
Decapoda				
Decapoda unid	14.130	13.208	5.216	4.797
Nephrops norvegicus	1.087	0.472	0.649	0.022
Caridea unid	6.522	2.830	2.567	0.649
Plesionika heterocarpus	2.174	0.943	1.107	0.082
Parapenaeus longirostris	2.174	1.887	45.545	1.900
Chordata				
Teleosts unid	40.217	20.755	16.026	27.259

Trophic Diversity Index obtained for both species was 5.73 for *E. spinax* and 7.30 for *G. melastomus*. To measure the dietary overlap of both species, Schoener's index was calculated, which revealed a value of 0.81 (Table 4).

Depending on the time of the day, the diets of both species show differences (Fig. 4). In *E. spinax*, during the night, teleosts are the most important prey, with a % IRI of 40.44%, as are teleosts (27.20% IRI) and decapods (20.32% IRI). During the morning, the prey consumed are mostly decapods (52.66% IRI) and euphausiaceans (30.31% IRI), while during the afternoon, the diet is more like that produced during the night, with teleosts (36.91% IRI), euphausiaceans (35.51% IRI), and decapods (17.60% IRI) dominating.

In the case of *G. melastomus*, it is observed that, both during the night and morning, euphausiaceans are the predominant prey (50.30 and 54.75% IRI, respectively), although it also preys on decapods (21.98 and 25.69% IRI) and teleosts (20.18 and 16.99% IRI). In the afternoon, however, the most abundant prey was teleosts (50.98% IRI).

ANOSIM results as a function of the time of day indicate significant differences for *E. spinax* ($R = 0.015$, $p < 0.05$), while for *G. melastomus*, there were none ($R = 0.005$, $p > 0.05$).

Etmopterus spinax in small size (range 1) fed practically on arthropods (82.77% of IRI), mainly of euphausiaceans (43.24% IRI); in medium size (range 2), cephalopods increased with a presence of 15.54% and the consumption of teleosts with an IRI value of 24.65%; for the larger size range (range 3), an increase in the consumption of cephalopods was observed, with a value of 25.28%; however, the most consumed prey in this range was decapods (31.55% IRI) (Fig. 5).

Galeus melastomus behaved differently with respect to size (Fig. 5), with euphausiaceans being the most important prey (IRI of 84.12%) for the

Table 4 Results of Levins Standardized Index, Trophic Diversity, and Schoener's Index for *E. spinax* and *G. melastomus*

Index	Species	
	E. spinax	*G. melastomus*
Levins Standardized	0.36	0.28
Trophic Diversity	5.73	7.30
Schoener's index	0.81	0.81

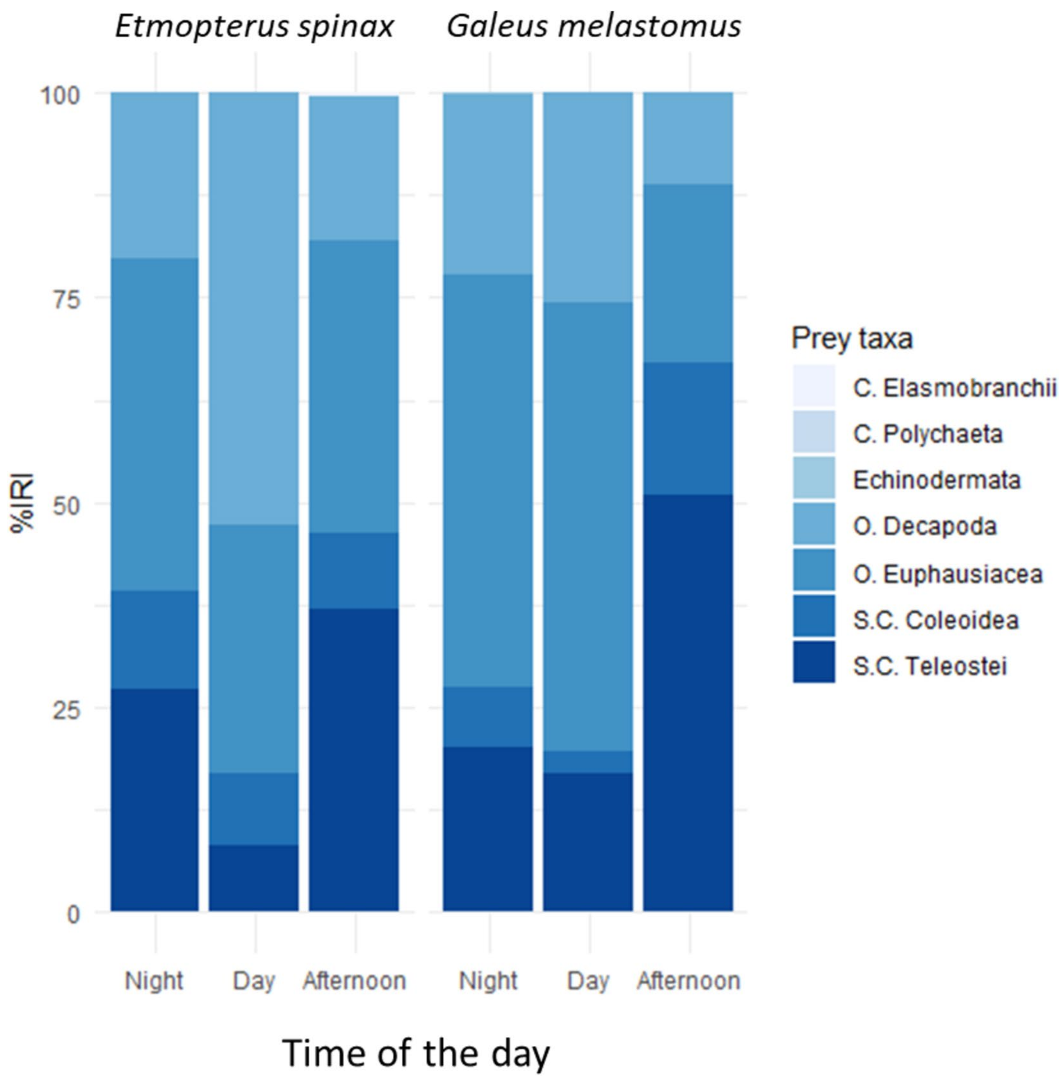

Fig. 4 Diet variation of *E. spinax* and *G. melastomus* in relation to the time of day

small size (range 1), while in medium size (range 2), there is a greater presence of teleosts (30.68% of the IRI) and euphausiaceans, although important, lowers its presence in the diet to 52.97% IRI. In larger size (range 3), the diet was based on decapods, with 50.90% of relative importance at that size.

ANOSIM showed that there were no significant differences for either species by size (*E. spinax*: $R = 0.007$, $p > 0.05$; *G. melastomus*: $R = 0.013$, $p > 0.05$).

Discussion

Regarding the length classes, most of the specimens caught are below the size of first maturity. This may be related to the depth involved in the fishery which is between 400 and 500 m where there is a greater presence of juveniles compared to deeper areas (Fanelli et al. 2009). It could also be related to the fishing gear used, since Coelho and Erzini (2008b) observed that, in the waters of southern Portugal, trawls caught mostly immature individuals of both *E. spinax* and *G.*

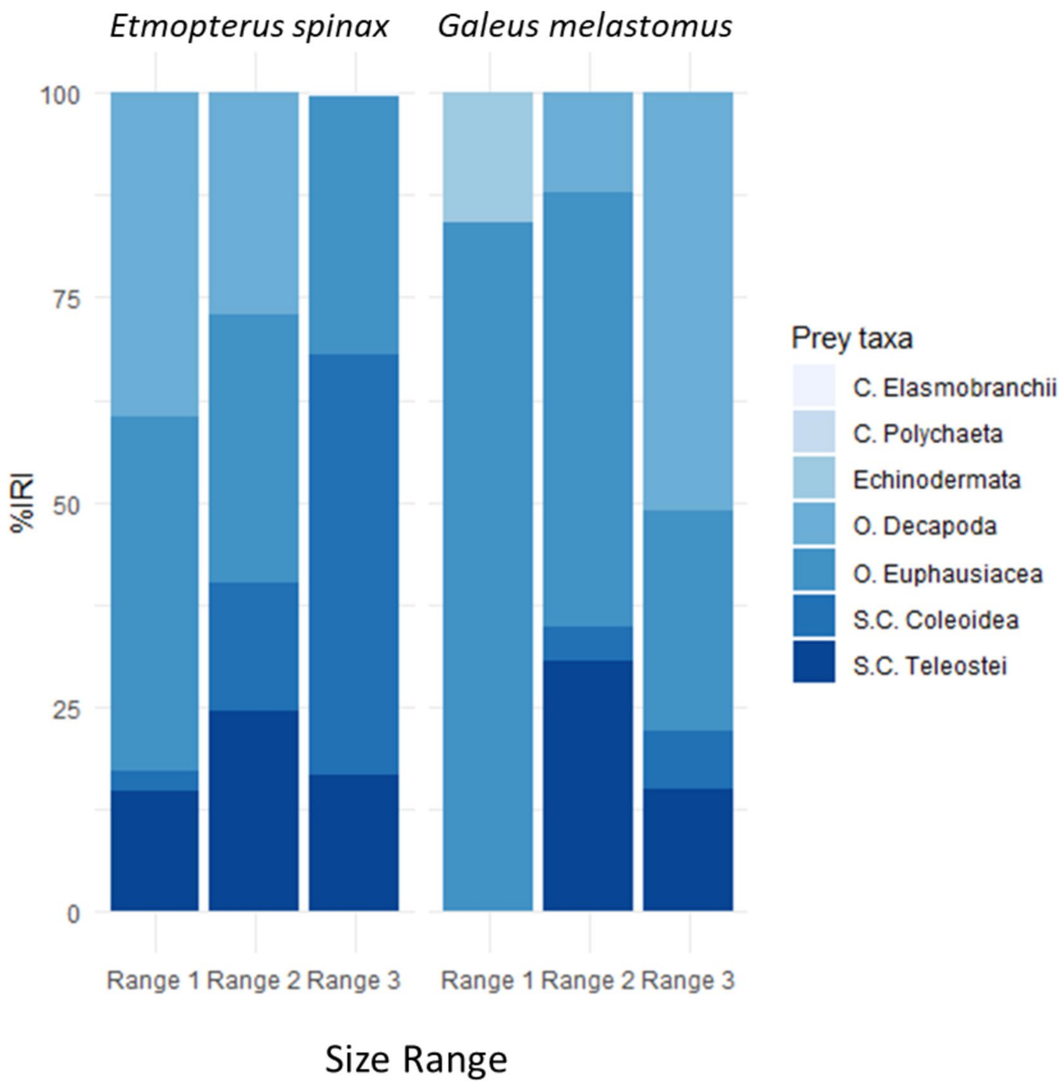

Fig. 5 Diet variation of *E. spinax* and *G. melastomus* in relation to the size range. Range 1, < 15 cm; range 2, 15.1–25 cm; range 3, > 25.1 cm

melastomus, while the opposite was true for longline catches, where most were mature specimens.

Higher vacuity percentages were observed in both species compared to the studies conducted both in the Gulf of Cádiz and off the south of Portugal (Torres 2013; Muñoz 2015; Riesgo et al. 2021). The observed differences in stomach contents compared to other studies could be due to the extended fishing duration in our study, which lasted about 12 h daily. This prolonged period may result in significant digestion or complete consumption of stomach contents before capture, leading to findings of partially or entirely empty stomachs. Additionally, similar to other species caught through trawling, individuals might regurgitate food due to the stress and pressure changes associated with this fishing method (Labropoulou et al. 1998; Madera-Santana et al. 2023).

The diet of both species was similar. A clear preference for crustaceans (decapods and euphausiaceans), teleosts, and cephalopods was observed. These results align with those found in the literature (Fanelli et al. 2009; Anastasopoulou et al. 2013; Torres 2013; Albo-Puigserver et al. 2015; Bengil et al. 2019; Zicarelli et al. 2023). The occurrence of crustaceans, such as specimens of Infraorder Caridea and euphausiaceans, in the diet of *E. spinax* suggests that this species performs migrations in the water column. In addition, it suggests a high degree of dependence of demersal elasmobranchs for resources typical of the pelagic ecosystem (Mauchline and Gordon 1991), associated to the Benthic Boundary Layer (BBL). This hypothesis is reinforced by the low occurrence of benthic prey such as polychaetes or echinoderms (Torres 2013). In the case of *G. melastomus*, the importance of crustaceans and cephalopods in their diet is also described in the Mediterranean Sea (Macpherson 1981; Carrassón et al. 1992; Fanelli et al. 2009; Valls et al. 2011), in the Cantabrian Sea (Preciado et al. 2009), and in nearby waters off the Portuguese coast (Saldanha et al. 1995; Santos and Borges 2001; Neves et al. 2007). The occasional occurrence of benthic prey in our observations might indicate that *G. melastomus* engage in benthic feeding activity, a behavior that tends to be more pronounced in adulthood than in juveniles (Belluscio et al. 2000).

As for the cephalopods identified in this study, the importance of these seems minor with respect to that reported in the Cantabrian Sea and the Mediterranean, where this group reaches greater prominence in these species' diets (Macpherson 1981; Mauchline and Gordon 1991; Fanelli et al. 2009; Valls et al. 2011). Cephalopods are known to have high nutritional value and few inedible remains (Boyle and Rodhouse 2005); this fact could explain their high vacuity rate and the large presence of beaks found in several stomachs, as these hard parts can remain in the stomachs for long periods of time (Anastasopoulou et al. 2013).

Etmopterus spinax and *G. melastomus* are two sharks that share similar distribution and trophic characteristics and can coexist in the same place. The results of the Levins index are in agreement with those found by Fanelli et al. (2009) in Atlantic waters, as well as Bengil et al. (2019) for both species and Anastasopoulou et al. (2013) for *G. melastomus*, in the Mediterranean (Fanelli et al. 2009; Anastasopoulou et al. 2013; Bengil et al. 2019). These results indicate that both species have specialized diets, as reflected in a relatively narrow feeding niche. However, the lower index for *G. melastomus* suggests a more marked specialization in its diet compared to *E. spinax*.

The niche overlap between the two species showed in this work was significant (0.81). Valls et al. (2011), in the Mediterranean, also showed an overlap between these species with a value of 0.67, unlike Fanelli et al. (2009) in Mediterranean Sea whose Schoener's index was 0.47. Species with similar feeding habits and trophic niches can coexist, and these index values do not necessarily imply competition except in cases of food scarcity (Collwell and Futuyma 1971; Macpherson 1977; Valls et al. 2011). The coexistence of these species in the Gulf of Cádiz may therefore be due to the high productivity of the area (García Lafuente and Ruiz 2007), which makes it a resource-rich area (Baldó et al. 2006) that both species can exploit without intense competition.

This diet overlap without competition is observed in the feeding behavior of both species at certain times of day, for example, at night both *E. spinax* and *G. melastomus* prey mainly on euphausiaceans (40.44% IRI and 50.30% IRI, respectively). *Etmopterus spinax* is a species that shows pelagic behavior, performing vertical migrations in search of food, which can happen during the night (Claes et al. 2010; Torres 2013). In the case of *G. melastomus*, it has been observed that small and juvenile specimens feed in both mesopelagic and demersal environments (Fanelli et al. 2009; Valls et al. 2011; D'Iglio et al. 2021). This would explain the high presence of euphausiaceans in the diet of the specimens captured during the night and morning, as this is when the catches of range 1 (<15 cm) and range 2 (15.1–25 cm) specimens were higher. In the afternoon, the absence of range 1 specimens and the decrease in range 2 catches may suggest an increased proportion of larger specimens, possibly in range 3. This is inferred from the dietary shift towards more cephalopods and fish as *G. melastomus* grows. Moreover, this dietary pattern correlates with observations by Kabasakal (2002), who reports that cephalopods stay near the ocean floor before initiating their vertical migration at night.

Differences in diet are observed for both species according to size. In the case of *E. spinax*, changes in their diet are observed at key moments such as between range 1 and range 2 (Neiva et al. 2006), where the juveniles, being larger, begin to consume a greater quantity of larger fish and decapods, and between range 2 and 3, with the latter range seeing a change towards a diet based on cephalopods and larger fish. For *G. melastomus*, the change is that juveniles usually live below 500-m depth; at this size, the proportion of small crustaceans such as mysidaceans and euphausiaceans is greater, and as they increase in size, they increase the depth where they live, changing their diet more towards decapods and large cephalopods, besides showing more scavenging behavior or hunting in groups (Carrassón et al. 1992; Belluscio et al. 2000).

The dietary analysis of these two small sharks in the Gulf of Cádiz reveals that, although both species capitalize on the same resources, they employ distinct adaptive strategies (such as vertical migrations or benthic behaviors) that enable them to coexist without direct competition, thereby maximizing the abundant resources available in the region. Additionally, the observed variations in dietary preferences correlated with both size and diurnal patterns indicate significant ecological flexibility within these species. This flexibility manifests in their ability to diversify food resources in response to individual size or to prey on specific organisms based on the time of day. Notably, the majority of the captured specimens from both species were below the size of first maturity, potentially signalling the presence of a breeding ground within the depths frequented by the trawl fishery in the Gulf of Cádiz. Pursuing further research in this direction is crucial for the effective conservation and management of these species, emphasizing the need to understand not just their dietary habits but also their reproductive and growth environments.

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Data availability Data will be available on reasonable request.

Declarations

Ethics approval and consent to participate The specimens used in this work have never been subjected to animal experimentation. These specimens come from catches made by professional fishermen and are subject to European regulations on Fish Discards.

Competing interests The authors declare no competing interests.

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