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Advancing the understanding of the trophic ecology of *Scyliorhinus canicula* in the Mediterranean Sea: Insights from a Tyrrhenian case study and a review of current knowledge

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ABSTRACT

Sharks are cartilaginous fishes that serve as both meso- and top predators in marine ecosystems. Globally, they are targeted by commercial and recreational fisheries and represent a significant portion of fishery bycatch. Among mesopredatory sharks, the small-spotted catshark (*Scyliorhinus canicula*) is one of the most common and widely distributed species in the Mediterranean Sea. This study investigates the diet and trophic position of *S. canicula* from the Tyrrhenian Sea using an integrated approach by combining stomach content analysis (SCA) and stable isotope analysis (SIA). Bayesian mixing models were applied to isotope data and suggested an ontogenetic dietary shift in the species. Additionally, we analyzed Mediterranean landings data of *S. canicula*, finding a consistent increase in catches up to 2019. A literature review of previous SCA studies across the Mediterranean confirmed that *S. canicula* is a generalist mesopredator, feeding primarily on crustaceans and teleosts—the latter becoming increasingly dominant from the Balearic to the Aegean Sea. Overall, these findings confirm the important mesopredatory role of *S. canicula* in Mediterranean benthic food webs and underscore the need for further investigation into the consequences of mesopredator release on the ecosystems, particularly in the context of increasing anthropogenic pressures.

1. Introduction

Depending on the species and ecosystem, sharks can be found at both mid-level and apex positions within marine food webs. They are often typified as opportunistic predators, with a wide diet that includes items ranging from planktonic organisms to marine mammals (Compagno, 1990; Ferretti et al., 2010). As top or meso- predators, they can modulate the community structure, the habitat use of prey organisms, and consequently the ecosystem functioning (Baum and Worm, 2009; Ferretti et al., 2008; Heupel et al., 2014). Worldwide, they are overfished as commercial and recreational fishing targets and constitute one of the largest portions of the fishery by-catch, together with seabirds, marine mammals and turtles (Lewison et al., 2014; Oliver et al., 2015). The removal of top predators has negative and direct cascading effects on the entire food web (Ferretti et al., 2010) and could also cause the so-called "mesopredator release" phenomenon, which leads to an increase in mesopredators abundance with a consequent change in the ecosystem energetic balance (Ritchie and Johnson, 2009; Baum and Worm, 2009).

Despite the important ecological role of elasmobranchs as both top- and meso- predators, information on the trophic ecology of some species is limited because of their intrinsic biological characteristics such as low population densities, high mobility, elusive behavior, and large-distances migrations (Hussey et al., 2011; Heupel et al., 2014). One of the most common mesopredator species that inhabits the Mediterranean Sea, whose ecology and behavior are yet partially unknown, is the small-spotted catshark *Scyliorhinus canicula* (Navarro et al., 2016). It is found in the Northeast and Eastern Central Atlantic Ocean (from Norway and the Shetland Islands to Senegal) and in the Mediterranean Sea (Lyle, 1983; Compagno et al., 2005; Martinho et al., 2012; Šantić et al., 2012). It is mainly a nocturnal species and a generalist predator (Olaso et al., 2005) that feeds on diverse benthic prey with a wide range of sizes and morphologies (Karachle and Stergiou, 2010; Kousteni et al., 2017) and is predated by larger fish, including other elasmobranchs (Šantić et al., 2012). Both the Global and European IUCN assessments indicated its

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population status as "Least Concern" (LC, Serena et al., 2015). Nevertheless, recent studies revealed that *S. canicula* represented a significant portion of European bycatch (especially trawls and gillnets) (Carpentieri et al., 2021). Under scenarios involving cumulative stressors (e.g., increased fishing pressure, prey depletion, competition with other mesopredators, and climate-related changes), local populations of *S. canicula* could experience declines. For example, reductions in abundance have already been documented in the Adriatic Sea (Barausse et al., 2014), where intense fishing pressure has negatively affected local stocks (Gubili et al., 2014). Thus, information on the composition of its diet is essential for conservation, and can be obtained through different approaches, such as Stomach Content Analysis (SCA) (Hyslop, 1980) and Stable Isotope Analysis (SIA) among the most common methods (MacNeil et al., 2005). SCA provides instant information on a consumer's diet in a specific interval of time and space (i.e., quantification and identification of the ingested food) (Hyslop, 1980), however, results could be biased by the difficulty to recognize the di*gested* species, as well as the number of digested prey, leading to a possible over or underestimation of prey number (Amundsen and Sanchez-Hernandez, 2019). Furthermore, the identification of the items in the stomach is time-consuming, and requires extensive taxonomic knowledge (Baker et al., 2014). SIA is less subjected to temporal bias, so it provides time-integrated information on the contribution of a food item to the diet of the studied species (Domi et al., 2005; Fanelli et al., 2010, 2023a, 2023b). This approach is useful to obtain an indication of the origin and transformations of organic matter (i.e., assimilated food) (Layman et al., 2007a) but it cannot be used to identify specific ingested prey (Shiffman et al., 2012). The ratios among stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) allow to obtain information on the foraging ecology, whether the carbon source is more planktonic or more benthic (Jennings et al., 1997), or marine vs. continental, thus providing indications of a movement/migration patterns (Hobson, 1999; Fry, 2006; Rabehagasoa et al., 2012) and estimate the trophic position (Owens, 1988), as $\delta^{15}N$ increases with increasing trophic level (Fry, 2006). Integrating multiple methods in trophic ecology research using various approaches, like SIA and SCA together, resulted to be particularly useful (Amundsen and Sanchez-Hernandez, 2019). In fact, SCA provides information on the diets of animals that feed on different items that may be difficult to identify with SIA alone (Layman et al., 2005), such as for gelatinous prey (Cardona et al., 2012).

The aim of the current study is to analyze the diet and the trophic position of one of the most common mesopredator species that inhabits the Mediterranean Sea, *S. canicula,* by i) considering a case study on the Tyrrhenian Sea (Central Mediterranean Sea) in which SIA was used together with SCA, and *ii*) comparing its results with those gathered by conducting a qualitative literature search on already published results dealing with *S. canicula*'s diet in the Mediterranean Sea. Besides, a qualitative evaluation of its population trends across the last decade has been obtained by analyzing landing data to make inferences about how fishery could affect the conservation status of the species.

2. Materials and methods

2.1. Case study

2.1.1. Study area and sampling process

The study area is in the Tuscan archipelago, South of Elba Island, and the northern Tyrrhenian Sea (Fig. 1).

Specimens of *S. canicula* were collected at the end of November 2017 by a week of commercial trawling along a stretch A-B with coordinates N 42° 28′ 3 E 10° 34′ 32 and N 42° 29′ 48 E 10° 27′ 36, respectively. Specimens used in this study were randomly selected out of the overall catch and the individuals were frozen at −20 °C and taken to the laboratories of Polytechnic University of Marche. Depth of collection ranged from 255 to 330 m. The type of trawl used in the GSA9 (Geographical Sub-area 9 - General Fisheries Commission for the Mediterranean Sea) is single, 4-faces trawl, with a total length of 76.4 m. Once caught and pulled into the boat, dead sharks were collected for the study, measured (Total Length or TL, in cm) and weighed (Wet Weight or WW, in g). Sex was then assessed based on the occurrence of claspers.

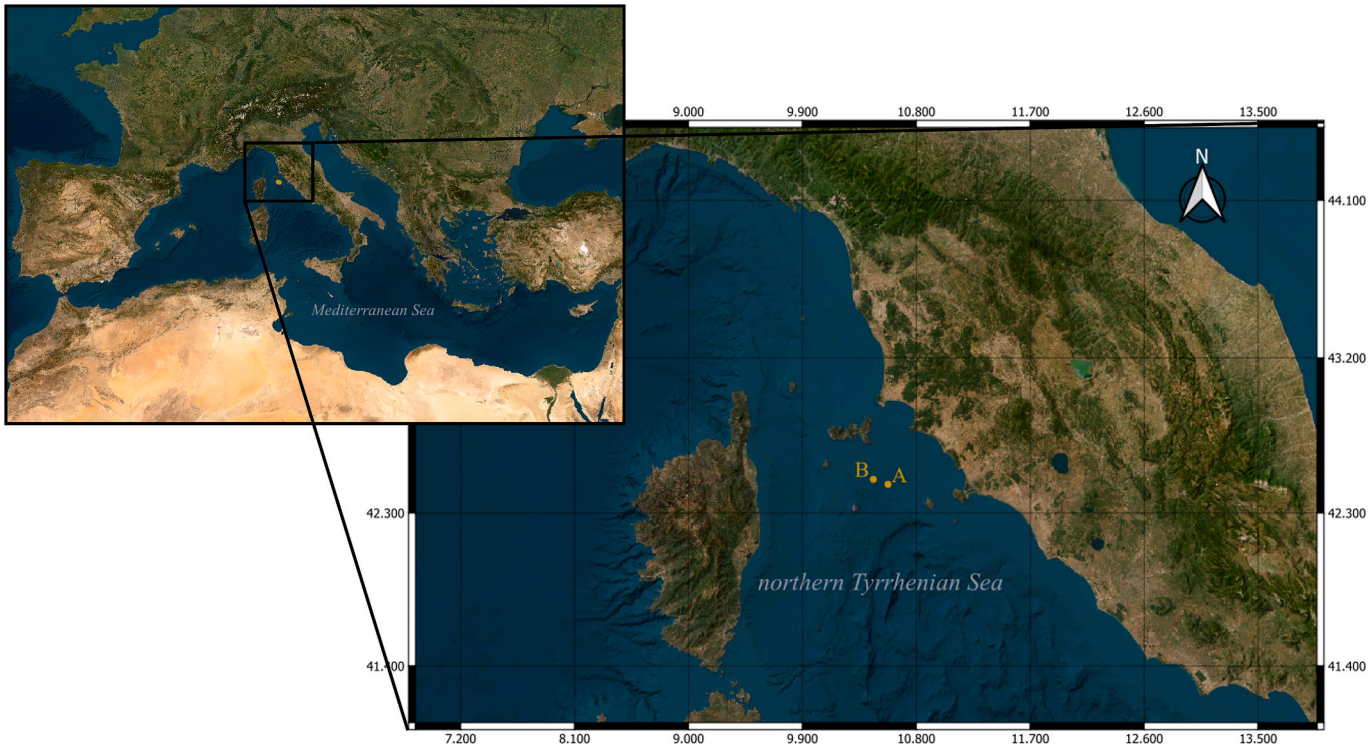

Fig. 1. Study area. Sampling location in the northern Tyrrhenian Sea (QGIS version 3.30.2 + ESRI World Imagery map). A and B are the beginning and ending points, respectively, of the stretch followed by the trawler that collected *S. canicula* specimens used for this study.

According to the length-frequency distribution and the mean length at which 50% of the population is sexually mature (TL ~ 40–41 cm), as reported in literature (Leloup and Olivereau, 1951; Capapé et al., 2008; Kousteni et al., 2017; Higueruelo et al., 2025), collected specimens were separated into two categories: Size1 (TL < 40 cm), and Size2 (TL ≥ 40 cm; see Results section).

2.1.2. Stomach content analysis (SCA)

A total of 41 specimens were analyzed for SCA, and all stomachs contained prey items (no empty stomachs were recorded). Each stomach was removed from animals and weighed with all stomach contents (stomach weight or SW, expressed in g). Then, each stomach was carefully emptied, and the contents were collected in Petri dishes. Subsequently, each stomach wall was weighed, and the wet weight of the stomach contents (expressed in g) was obtained by subtracting the weight of the stomach wall from SW (Fanelli and Cartes, 2010). Stomach contents were analyzed under a light microscope (Leica ICC50) and the ingested items were identified at the lowest taxonomic level possible. The weight contribution of each item was obtained using the points' method (Swynnerton and Worthington, 1940): a rank was assigned to each item found (very common', 'common', 'frequent', 'rare', etc.), based on rough counts and judgement by eye. These categories are selected based on the estimation of the contribution of each prey (expressed as percentage) to the total stomach content weight.

Then, the stomach fullness percentage (% stomach fullness) was calculated for each specimen (stomach content weight/body weight × 100) as it is considered a proxy of feeding intensity. Traditional trophic indices were also estimated: percentage of frequency of occurrence (%F) and percentage of weight (%W) (Hyslop, 1980). An Index of Relative Importance (IRI):

$$\%IRI = \%F \times (\%N + \%W)$$

was used to determine the importance of prey items in catsharks' diet.

To determine whether enough stomachs were analyzed, the cumulative number of pooled stomachs was plotted against the mean cumulative number of prey species (Ferry and Cailliet, 1996). This was done by using the "species-accumulation" plot in PRIMER6 & PERMANOVA+, under 9999 permutations and using bootstrapping. Sample size was considered sufficient when the cumulative prey species curve reached an asymptote with changes in the number of species observed for additional sample < 0.1 (Fanelli et al., 2023b).

2.1.3. Stable isotope analysis (SIA)

A piece of muscle close to the dorsal fin was taken from 19 specimens and stored in a freezer at −20 °C until the successive analyses. Then, samples were oven-dried at 60 °C for 24 h. Each dried sample was grinded using a mortar and a small pestle, and ca. 1–1.2 mg was placed into tin capsules (Elemental Microanalysis Tin Capsules Pressed, Standard Weight 5 × 3.5 mm), and these were inserted in an elemental analyzer (Thermo Flash EA 1112) used to determine total carbon and nitrogen contents (%). The elemental analyzer was coupled through a continuous-flow with an isotope-ratio mass spectrometer (IRMS, Thermo Delta Plus XP) for the determination of $\delta^{13}C$ and $\delta^{15}N$ contents, at the Laboratory of Stable Isotope Ecology of the University of Palermo (Italy). A stable isotope ratio was expressed, in relation to international standards (Vienna Pee Dee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively), as:

$$\delta^{13}C \text{ or } \delta^{15}N : \left[\left(R_{sample}/R_{standard}\right)^{-1}\right] \times 10^3$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. Analytical precision based on standard deviations of internal standards (International Atomic Energy Agency IAEA-CH-6; IAEA-NO-3; IAEA-N-2) ranged from 0.10 to 0.19 ‰ for $\delta^{13}C$ and 0.02 to 0.08 ‰ for $\delta^{15}N$.

Total mass percentage proportion of C and N were used to calculate C:N ratios. Lipid extraction is important as high storage quantities of squalene in sharks could affect the $\delta^{13}C$ values and thus the results of the analysis (Hussey et al., 2012). In this study, lipids were not extracted from samples, but the arithmetical equation proposed by Post et al. (2007) was taken into consideration to correct $\delta^{13}C$ values if C/N ratio was >3.5:

$$\delta^{13}C_{corrected} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C : N_{bulk}$$

2.1.4. Data treatment for SCA and SIA

With the aim of determining whereas the significance of any dietary changes was based on differences inferred by total length, a multivariate PERMANOVA (Permutational Multivariate Analysis of Variance) main test was also performed on a modified Gower resemblance matrix of fourth root transformed prey biomass data (%W). As stomach content data was generally deficient and contained many zeros, Gower resemblance matrix is considered the most suitable for this kind of data (Clarke and Warwick, 2001; Anderson et al., 2008). A one-way design was used, with "Total Length" as a fixed factor with two levels (Size1 and Size2). SIMPER (Similarity Percentage) analysis was applied on stomach contents data to determine the most important food sources in the diet of *S. canicula* specimens (Clarke and Warwick, 2001).

For stable isotope analysis, differences among $\delta^{13}C$ and $\delta^{15}N$ values driven by the considered factor were tested by univariate and multivariate PERMANOVA main tests, carried out on the two Euclidean resemblance matrices of untransformed $\delta^{13}C$ and $\delta^{15}N$ values, respectively.

For all PERMANOVA tests, the significance value was set at $p < 0.05$ and tests were carried out with permutation of residuals under the reduced model. A total of 9999 permutations was used to generate the empirical null distribution of the statistic test. The Monte-Carlo test was applied because of the low sample size. In addition, if the main test of PERMANOVA highlighted significant differences, a pair-wise test was performed to identify the source of variation. Multivariate and univariate statistical analyses on the obtained results were conducted using PRIMER6 and PERMANOVA+ (Clarke and Warwick, 2001; Anderson et al., 2008). The linear correlation between $\delta^{13}C$ or $\delta^{15}N$ and the total length was calculated with the software PAST (version 4.0.9) (Hammer et al., 2001).

2.1.5. Mixing models and standard ellipse area

A Bayesian model *simmr* (Stable Isotope Mixing Models in R; Parnell, 2021) was run to estimate the contribution of the different food sources to the diet with the software R 4.0.5 (R Core Team, 2021). The variability in the isotope values (mean and standard deviation) of prey species can be incorporated into the model (Parnell et al., 2013). The list of potential prey living in the same study area was taken from the results of SCA, and their isotopic content values were taken from existing literature (**Supplementary Table S1**). Before running *simmr*, the isotopic values of the potential sources and of the catsharks were plotted together, applying the correct trophic enrichment factors – TEFs – to the sources to determine the best mixing polygon (Smith et al., 2013; Phillips et al., 2014). TEFs used for $\delta^{13}C$ and $\delta^{15}N$ were 0.9 ± 0.33 ‰ and 2.29 ± 0.22 ‰, respectively, according to Hussey et al. (2010).

The SIBER package (Stable Isotope Bayesian Ellipses in R 3.5.3) (Jackson et al., 2011) was used to compare isotopic niche widths among Size1 and Size2 specimens and within communities (sensu SIBER). It was also used to calculate TA (Total Convex Hull Area) and SEA_C (Standard Ellipse Area corrected), with p-interval = 0.40 to encompass the 40% of our data (Layman et al., 2007b) for the different communities. SEA_C is used because of small sample size. Only one model was run with TLs as groups and a unique community (sensu SIBER).

2.2. Literature review of the diet of S. canicula in the Mediterranean Sea

To shed light on the trophic ecology of *S. canicula*, a literature search

was conducted considering published articles from 1972 to 2024. Existing studies were found through "Scopus", "Research Gate" and "Google Scholar" research operators, following keywords: "Diet AND catsharks AND Mediterranean Sea"; "*Scyliorhinus canicula* AND diet"; "*Scyliorhinus canicula* AND trophic ecology"; "Feeding ecology AND small-spotted catshark", and using the previous keywords by adding "AND stable isotopes". Articles reporting Index of Relative Importance (IRI, which reflects the importance of prey items in catsharks' diet - see 2.1.2) values for each of the main food items found were retrieved; together with articles reporting stomach contents and stable isotope values. Data on the total length and depth where each individual was collected was also extracted from the articles selected when possible. The %IRI values were then used to highlight the possible differences in the diet of the small-spotted catshark throughout the Mediterranean Sea. Further differences were highlighted according to the total length of each individual. Information regarding the stomach content and the stable isotope composition was summarized.

2.3. Analysis of Mediterranean landing data of catsharks

Official landings data of the species *S. canicula* from Mediterranean fishery fleet were retrieved from STECF (Scientific, Technical and Economic Committee for Fisheries of the European Commission) landings database (https://stecf.jrc.ec.europa.eu/dd/fdi last accessed on 03 January 2024). GFCM – FAO (https://www.fao.org/gfcm/data/capture-production/en/) database is not used in the present study because it points out landings data from only five European Countries (Croatia, France, Italy, Malta and Spain). Data (live landed catches in tons) from STECF database are available yearly from 2013 to 2022. Landings were analyzed according to the 30 GSAs (STECF landings database) in which the Mediterranean Sea and the Black Sea are divided by GFCM classification (https://www.fao.org/gfcm/data/maps/gsas/en/). Landings data were included to provide a broad-scale, independent context of fishing pressure and population trends of *S. canicula* in the Mediterranean Sea. This information supports the interpretation of trophic ecology results by framing the ecological role of this mesopredator within a system experiencing long-term exploitation and changes in predator assemblages.

3. Results

3.1. Case study (northern Tyrrhenian Sea)

A total of 41 individuals were caught during a week of commercial trawling. Specimens were assigned to two size classes according to total length (TL): Size1 (< 40 cm; $N = 20$), and Size2 (≥ 40 cm; $N = 21$) individuals (Fig. 2).

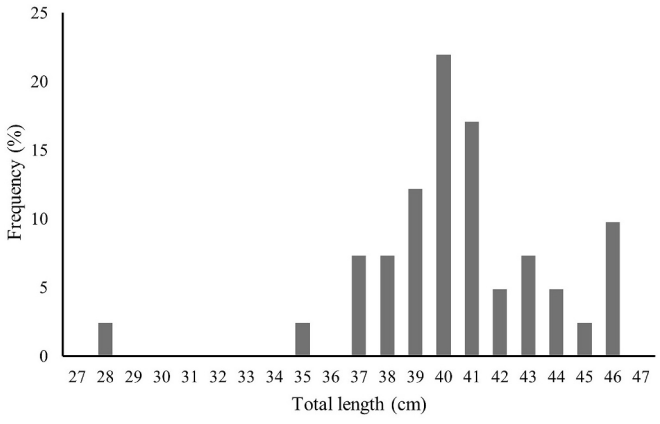

Fig. 2. Length-frequency distribution. Length-frequency distribution for catsharks collected in the northern Tyrrhenian Sea; $N = 41$.

3.1.1. SCA results

Forty-one ($n = 41$) full stomachs were analyzed, this sample size was considered sufficient to represent the diet of the species, as 93% of the trophic diversity is already shown by analyzing only 23 stomachs, according to the cumulative prey type curve and the bootstrapping (**Supplementary Fig. S1**). The identified stomach contents belonged to 29 species that were grouped into 4 main taxa (**Supplementary Table S2**), for further analyses. Some of the main abundant taxa were the decapod crustaceans *Alpheus glaber*, *Dardanus arrosor*, *Diogenes pugilator*, *Polybius navigator*, *Parapenaeus longirostris* and *Xantho* sp. In terms of %IRI (**Supplementary Fig. S2**), Crustacea was the most abundant taxon in the stomach contents and Brachyura represents the most important infraorder. Many remains of Osteichthyes were found representing the second most abundant taxa. Seven families of Polychaeta were found accounting for the 9% (%IRI) of stomach contents in which individuals of the family Flabelligeridae were the most abundant. Cephalopod represented only 4% (%IRI) of the ingested prey. Such composition slightly differed between Size1 and Size2 specimens (Fig. 3).

The SIMPER analysis showed a low similarity in the diet according to the total length, with a high contribution of Osteichthyes to Size1, and a high contribution of Crustacea to Size2 specimens. 91.29% of this dissimilarity is explained by the contribution of Osteichthyes, Crustacea and Cephalopoda (Table 1).

3.1.2. SIA results

Nineteen specimens were analyzed for SIA. Since C/N ratio was <3.5 in all analyzed samples, no extraction or mathematical normalization was applied as it would have a little influence on the $\delta^{13}C$ values (Post et al., 2007).

$\delta^{13}C$ values were on average − 18.3 ± 0.6 ‰ while $\delta^{15}N$ mean values were 9.5 ± 0.7 ‰. Mean $\delta^{13}C$ contents were − 18.5 ± 0.6 ‰ and − 18.1 ± 0.6 ‰ for Size1 and Size2 specimens, respectively. Similarly, small variations were observed in mean $\delta^{15}N$ content between these groups (9.6 ± 0.8 ‰ and 9.4 ± 0.7 ‰ for Size1 and Size2 specimens, respectively).

The correlation between $\delta^{13}C$ and $\delta^{15}N$ vs. TL resulted to be

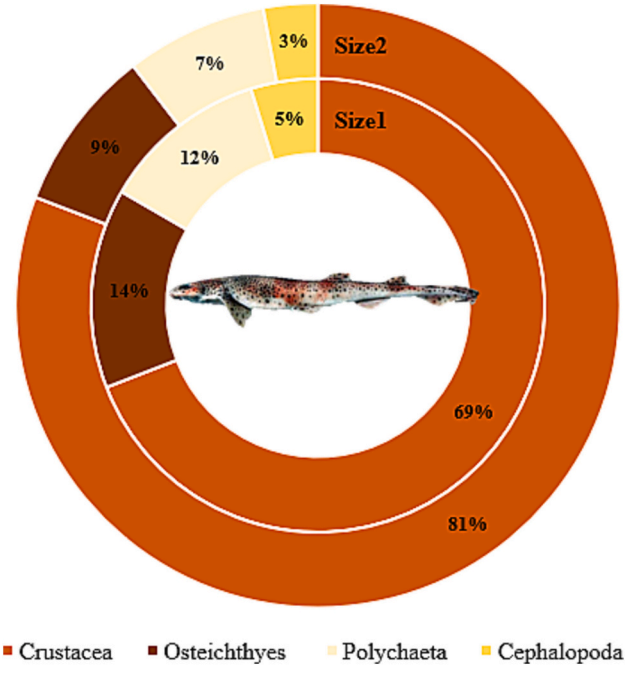

Fig. 3. Diet composition. Composition in terms of % IRI of catsharks categorized as Size1 (N = 20) and Size2 (N = 21) collected in the northern Tyrrhenian Sea.

Table 1
Percentage of prey similarity and dissimilarity between Size1 and Size2 catsharks collected in the northern Tyrrhenian Sea. Cut-off for low contribution at 60%. Av.Abund = average abundance; Av.Sim = average similarity; Contrib % = percentage of variance explained by explanatory variables; Cum % = cumulative percentage of variance explained by the explanatory variables.

Group Size1		Average similarity: 7.61		
Species	Av.Abund	Av.Sim	Contrib%	Cum. %
Osteichthyes	0.37	3.87	50.81	50.81
Crustacea	0.18	1	13.13	63.95
Group Size2		**Average similarity: 9.66**		
Species	**Av.Abund**	**Av.Sim**	**Contrib%**	**Cum. %**
Crustacea	0.19	2.45	25.39	25.39
Brachyura	0.24	2.43	25.2	50.59
Osteichthyes	0.25	1.93	20.03	70.62
Groups Size1 & Size2		**Average dissimilarity = 91.29**		
	Group Size1	Group Size2		
Species	**Av.Abund**	**Av.Abund**	**Contrib%**	**Cum. %**
Osteichthyes	0.37	0.25	12.59	12.59
Crustacea	0.18	0.19	11.26	23.85
Cephalopoda	0.15	0.14	6.42	30.27
Brachyura	0.06	0.24	6.19	36.46
Paguridae	0.12	0.12	4.89	41.35
Flabelligeridae	0.1	0.13	4.8	46.15

significant only for $\delta^{13}C$ ($\delta^{15}N$: $R = 0.09$, $p > 0.05$; $\delta^{13}C$: $R = 0.9$, $p < 0.001$) (**Supplementary Fig. S3**). Univariate PERMANOVA test carried out on $\delta^{13}C$ and $\delta^{15}N$ values showed no significant differences for the factor "TL" (**Supplementary Table S3**).

3.1.3. Mixing models and standard ellipse area

The construction of the mixing polygon (**Supplementary Fig. S4**) allowed to select *Capros aper*, *Goneplax rhomboides*, *Loligo vulgaris*, *Alpheus glaber* and *Diogenes pugilator* as potential food sources to be used for the Bayesian mixing model run with *simmr*. The two groups are homogeneously distributed, confirming the results reported by PERMANOVA analysis. *Capros aper* and *D. pugilator* contributed the most to Size1 and Size2 specimens' assimilated food, respectively, providing more accurate information on their diet (Fig. 4).

Standard ellipses obtained by running SIBER showed the isotopic niche widths of the groups. Size1 and Size2 catsharks had similar niche widths (in terms of both TA and SEA_C) and similar values of Layman metrics, as confirmed also by calculating SEA_C (p-interval = 40%) values and Layman metrics (**Supplementary Fig. S5** and **Supplementary Table S4**).

3.2. Literature search

3.2.1. On the diet of S. canicula in the Mediterranean Sea

The diet of *S. canicula* in the Mediterranean Sea reported in previous literature studies was investigated and summarized. The Mediterranean basin was divided into 6 main geographical sub-areas, as reported in the studies analyzed: Balearic Sea, Tyrrhenian Sea (Sardinia), Central Mediterranean Sea, Adriatic Sea, Aegean Sea and Sea of Marmara (Fig. 5). Pie charts were used to represent the most abundant taxa in the diet along the basin.

For each sub-area, the main prey (in order of importance), the range size of the specimens analyzed, the depth range and the year of sampling, are reported in **Supplementary Table S5**.

Previous studies from the western Mediterranean Sea (Balearic Sea) show that the most important prey are crustaceans, followed by teleosts, and polychaetes, with some differences between the different bathymetric strata (Valls et al., 2011). In the continental shelf, the main prey are benthic decapods followed by polychaetes and teleosts while in the deeper waters euphausiids represent the largest portion of the diet (Valls et al., 2011). Juveniles feed on amphipods, mysids and, mainly, euphausiids while adults prefer cephalopods and teleosts (Valls et al., 2011). A similar diet occurs in the Tyrrhenian Sea (Sardinia) where crustaceans are the most important prey followed by osteichthyes and cephalopods. Among crustaceans, decapods are the most abundant, followed by mysids and euphausiids (Mulas et al., 2010). Juveniles feed mainly on euphausiids while decapods increase as total length of *S. canicula* increase (Mulas et al., 2010). On the contrary, in the central Mediterranean Sea (around Malta) and in the northern coast of Tunisia, teleosts are the main prey (Gravino et al., 2010; Mnasri et al., 2012). Among the most common species are, respectively, *Trachurus trachurus* and *Macroramphosus scolopax* (Gravino et al., 2010) and *Ophisurus serpens*, *Sardinia pilchardus* and *Sardinella aurita* (Mnasri et al., 2012).

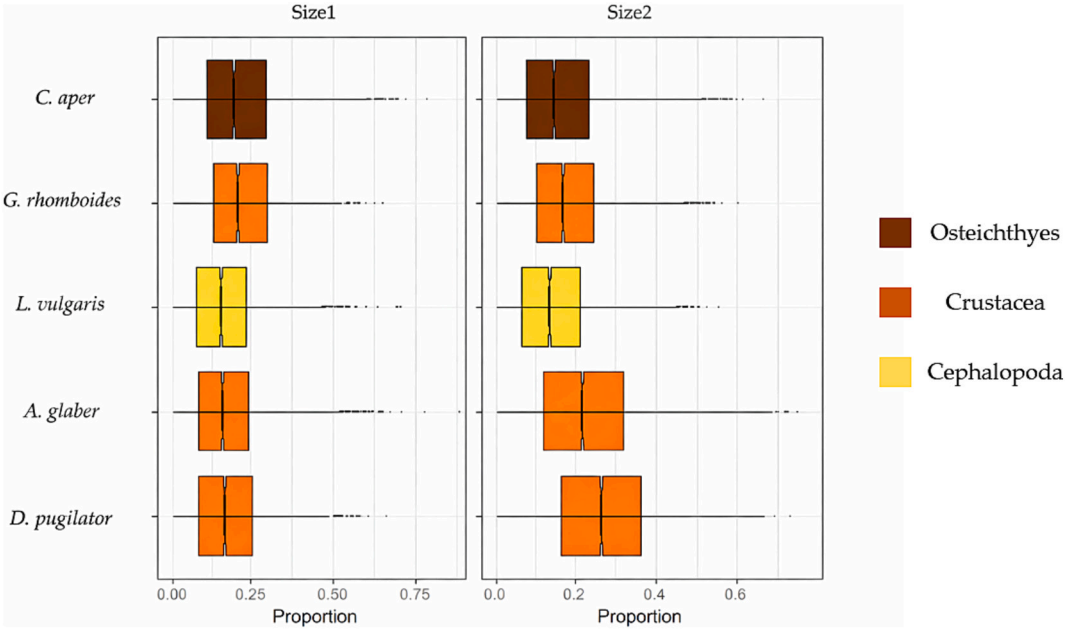

Fig. 4. Output of simmr models. Proportional contribution of each food source in the diet of the catsharks categorized as Size1 and Size2 collected in the northern Tyrrhenian Sea. Boxplots were obtained with stable isotope mixing models. Each plot shows proportions for each food source in the specific TL. Boxes indicate 50%, 75% and 95% Bayesian confidence intervals.

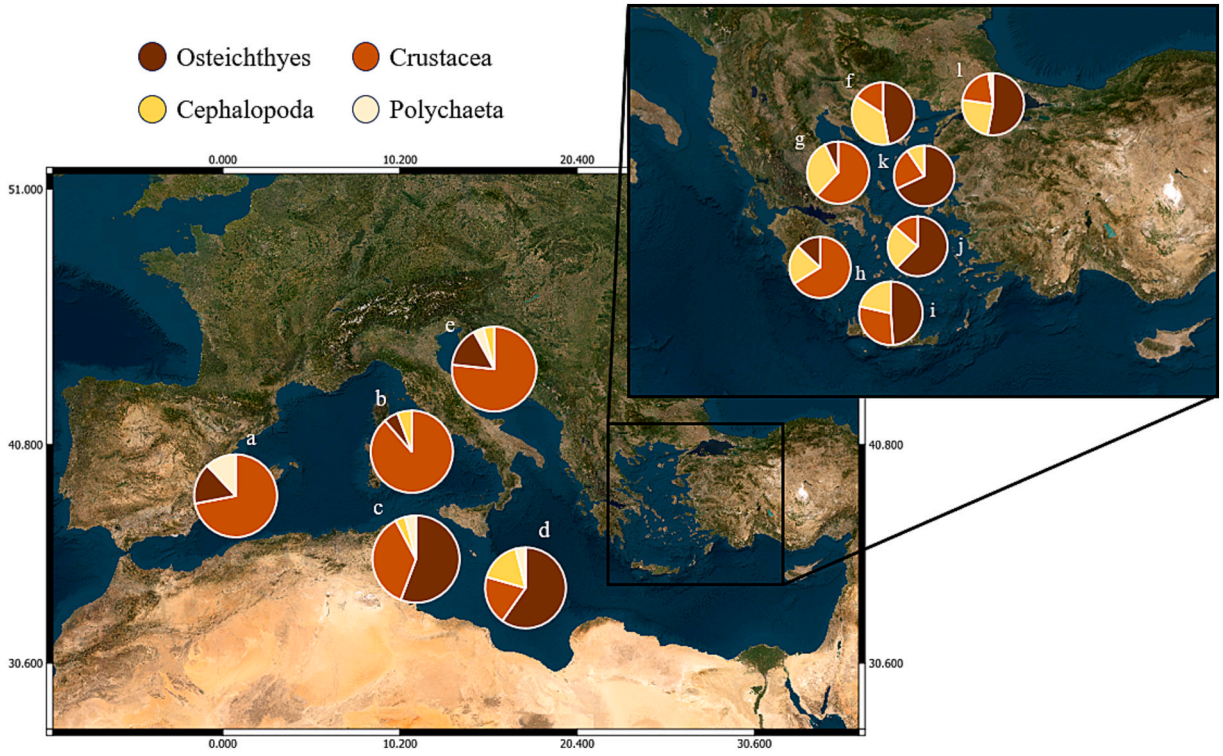

Fig. 5. Existing literature data on the diet of Mediterranean *S. canicula*. Representation of the diet of *S. canicula* in the Mediterranean Sea based on the IRI indexes found. a) Valls et al., 2011; b) Mulas et al., 2010; c) Gravino et al., 2010; d) Mnasri et al., 2012; e) Jardas, 1972; Šantić et al., 2012; Finotto et al., 2023; f) Kabasakal, 2001; Türker Çakir et al., 2005; Kousteni et al., 2017; g) Kousteni et al., 2017; h) Kousteni et al., 2017; i) Kousteni et al., 2017; j) Kousteni et al., 2017; k) Kabasakal, 2001; Türker Çakir et al., 2005; Bengil et al., 2019; l) Gül and Demirel, 2021.

The second abundant prey are crustaceans, especially, *Alpheus glaber* and *Parapeneaus longirostris*, followed by cephalopods (Gravino et al., 2010; Mnasri et al., 2012). A small percentage of the diet consists of polychaetes, represented by the family Aphroditidae (Gravino et al., 2010). Juveniles feed mainly on crustaceans, while adults prefer fish and cephalopods. Cannibalism was also reported (Gravino et al., 2010; Mnasri et al., 2012).

In the Adriatic Sea the most abundant prey are benthic decapods, followed by teleosts (Jardas, 1972; Šantić et al., 2012; Finotto et al., 2023). Amphipods, polychaetes and mysids represent the least abundant part. As the total length of the small-spotted catshark increases, the presence of mysids and euphausiids decreases and the amount of decapods, teleosts and cephalopods increases (Jardas, 1972; Šantić et al., 2012; Finotto et al., 2023). Compared to the Adriatic Sea, in the Northern, Southern and Eastern Aegean Sea teleosts represent the most important prey, followed by cephalopods and crustaceans (Kabasakal, 2001; Türker Çakir et al., 2005; Kousteni et al., 2017; Bengil et al., 2019). On the contrary, in the Western Aegean Sea (North Evoikos Gulf and Saronikos Gulf) crustaceans are the most abundant prey, followed by cephalopods and teleosts (Kousteni et al., 2017). In the last sub-area

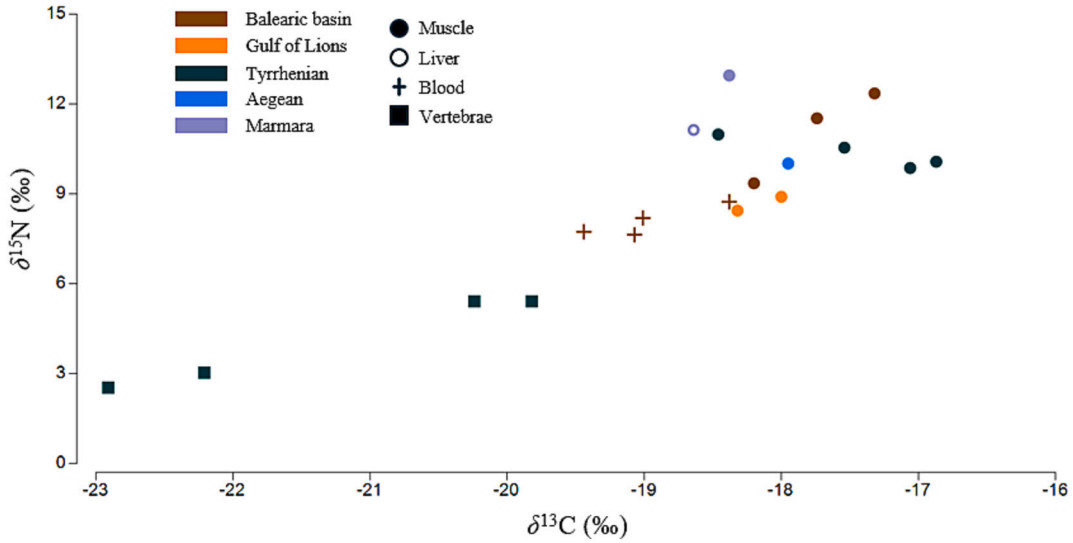

Fig. 6. Biplot of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values of *S. canicula* collected in different Mediterranean areas. Colors indicate the sampling area (Balearic basin, Gulf of Lions, Tyrrhenian, Aegean, and Marmara), while symbols represent the tissue type analyzed (muscle, liver, blood, and vertebrae).

(Sea of Marmara) teleosts represent the most important prey, followed by cephalopods, shrimps and polychaetes (Gül and Demirel, 2021).

3.2.2. On the isotopic composition of S. canicula in the Mediterranean Sea

A total of 9 papers containing 20 mean isotopic data of *S. canicula* were analyzed (Fig. 6 and Supplementary Table S6). Of these, 11 corresponded to muscle tissue signatures, four to vertebrae, four to blood, and one to liver. Most papers regard specimens collected in the western Mediterranean and only two studies are inherent to samples from the eastern Mediterranean. Size and weight are reported for only a few specimens, and even fewer have data on sex and maturity, preventing any analysis by length or sex. Muscle samples showed average values of -17.80 ± 0.55 ‰ for $\delta^{13}C$ and 10.45 ± 1.40 ‰ for $\delta^{15}N$. Vertebrae exhibited lower isotopic signatures (-21.30 ± 1.30 ‰ and 4.10 ± 1.41 ‰, respectively), while blood samples showed intermediate values (-18.98 ± 0.95 ‰ and 8.07 ± 0.43 ‰). The single liver signature reported in literature showed values of $\delta^{13}C$ and $\delta^{15}N$ of -18.64 ± 0.55 ‰ and 11.13 ± 0.54 ‰, respectively.

3.3. Landings analysis of catsharks

Landings data (tons of live catches) of catsharks in the Mediterranean Sea between 2013 and 2022 from STECF database were used to calculate the percentage of specimens of *S. canicula* landed in the considered period (Fig. 7). The area represents percentage on total landings in the 24 sub-regions (GSA1, GSA2, and GSA4 to GSA25).

The STECF data shows an important decrease in catches landed in 2017 (4.3% of total tons), and after a peak in 2019 (more than 10% of total tons), a constant decrease is reported until 2022. The same trend is reported for the Italian waters (GSA8, GSA9, GSA10, GSA11, GSA15, GSA16, GSA17, GSA18, GSA19) represented by the area under the red line. There is an important decrease in catches landed in 2017 (1.4% of total tons) and a peak in 2019 (4.8% of total tons). As for the total Mediterranean Sea, a constant decrease is reported until 2022 when the catches landed do not exceed 1.8% of total tons.

4. Discussion

4.1. Case study (northern Tyrrhenian Sea)

In this case study, the few collected samples were captured during a week of commercial trawling. The absence of seasonality and the low number of individuals hinders the definition of the diet using only SCA. Therefore, stable isotope analysis (SIA) was used to provide an integrated, time-averaged perspective of assimilated diet, while SCA offered taxonomic resolution of recently ingested prey. SCA showed that decapod crustaceans were the most represented food items along with fish, in agreement with a previous study conducted in the same area (Mulas et al., 2010). Some of the crabs found in the stomachs were found intact, bitten or not digested, likely due to "net feeding" phenomenon (Park et al., 2020; Fanelli et al., 2023a, 2023b).

Bayesian mixing models carried out on SIA results allowed to highlight a preference of smaller individuals for demersal species that live over muddy-sandy bottoms like the boarfish *C. aper,* while the larger ones prefer benthic crustaceans such as the hermit crabs *D. pugilator*, suggested a specialization of larger individuals for the selection of benthic prey (Gravino et al., 2010; Mulas et al., 2010; Šantić et al., 2012; Mnasri et al., 2012; Barría et al., 2018).

Usually, in sharks, the $\delta^{15}N$ content increases with animals' size (Kim et al., 2012). This means that as the shark grows, it feeds on larger prey positioned at a higher trophic level. However, in our case study, probably due to the small size range (37–43 cm) of the specimens analyzed, it was not possible to confirm or not the existence of this correlation in specimens collected in this area. Considering that other studies conducted in the Mediterranean Sea report an ontogenetic diet shift in this species at 37 cm (Barría et al., 2018), further investigations with a broader number of specimens are needed to confirm with SIA the possible existing ontogenetic shift also the Tyrrhenian Sea.

Usually, higher $\delta^{13}C$ values (from -13 to -17 ‰) indicate that a species is relying on a benthic food web, while lower $\delta^{13}C$ values pointed out to a greater dependance on a pelagic food web (Jennings et al., 1997). The positive relationship between $\delta^{13}C$ and total length observed in this case study can suggest an ontogenetic dietary shift associated with changes in morphology, physiology, or lifestyle. Probably, smaller individuals feed more on benthopelagic prey caught in the water column

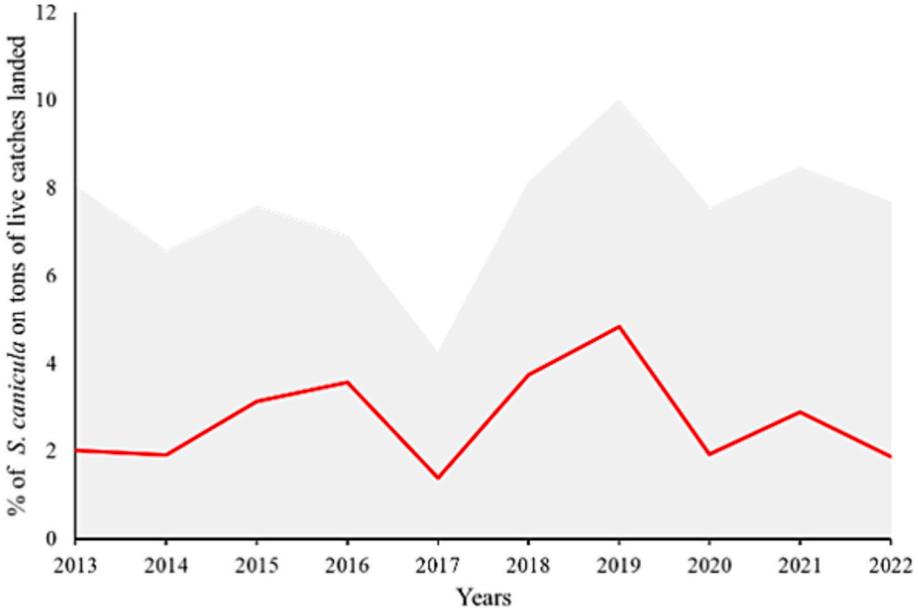

Fig. 7. Trend of the landings of *S. canicula* in the Mediterranean Sea. % of *S. canicula* on tons of live catches landed from 2013 to 2022 in the Mediterranean Sea (data obtained from STECF database, accessed on 03 January 2024). The red line indicates the trend reported for Italian waters (GSA8–11, GSA15–19). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

or others approaching to the bottom, and larger individuals preferably live closer to the seabed, feeding on benthic items (Lyle, 1983; Šantić et al., 2012; Barría et al., 2018). In fact, it is known that in larger individuals, the well-developed olfactory sense facilitates the catch of benthic items (Kimber et al., 2009). Furthermore, it was already demonstrated that in the Mediterranean Sea, smaller catsharks are mainly found in areas below 100–200 m, while shallower waters are mainly inhabited by largest (D'Onghia et al., 1996; Massutí and Moranta, 2003), thus supporting our finding on the correlation between $\delta^{13}C$ and total length.

4.2. The diet and stable isotope composition of S. canicula in the Mediterranean Sea

Scyliorhinus canicula is a generalist mesopredator that feeds mainly on crustaceans and teleosts. Moving from the Balearic to the Aegean Sea, we have shown that these two prey groups provide a different contribution to its diet. The variation of the prey's importance in different parts of the Mediterranean Sea could be related to the different benthic assemblage composition and/or to the different depth range where the specimens were collected among the areas (Šantić et al., 2012).

Crustaceans represent the most abundant prey in the western Mediterranean Sea and are replaced by teleosts in the Central Mediterranean and Aegean Sea, although with some exceptions (Valls et al., 2011; Mulas et al., 2010; Gravino et al., 2010; Mnasri et al., 2012; Kousteni et al., 2017; Bengil et al., 2019). However, this outcome contrasts with the results of a study conducted 46 years ago in the western Mediterranean slope from Alicante to Cape Creus, that indicated that fish were the main prey for small-spotted catshark (Macpherson, 1981). In both studies conducted in the western Mediterranean Sea, samplings were carried out along the slope between 200 and 800 m depth and the specimens analyzed are within the same size range (10–49 cm). Macpherson (1981) showed that this catshark fed mainly on teleosts (%W = 41.1) (*Micromesistius poutassou, Gadiculus argenteus* and *Engraulis encrasicolus*), followed by crustaceans (%W = 25.5) (*Alpheus glaber, Meganyctiphanes norvegica* and *Pasiphaea sivado*) and cephalopods (%W = 6.5) (*Sepietta oweniana*) while recent outcomes reported that crustaceans represent the most abundant part of the diet (%IRI = 77.64), followed by teleosts (%IRI = 16.68) (Valls et al., 2011). This difference could be due to a decrease in fish abundance because of increasing fishing pressure during recent decades (Cartes et al., 2013) and to an increase in crustaceans' abundance thanks to their resilience to trawling disturbance (de Juan et al., 2007). Therefore, the diet of *S. canicula* seems to differ among different areas according to prey availability. Prey availability, environmental factors, and human variables such as fishing activity can affect the abundance, biomass, and occurrence rate of small-spotted catshark (Navarro et al., 2016). From the Balearic to the Adriatic Sea, a difference between juveniles' and adults' diet is demonstrated. Juveniles seem to prefer small benthopelagic crustaceans, such as mysids and euphausiids, while adults prefer benthic crustacean decapods, teleosts and cephalopods. Furthermore, this species probably occupies different areas during its life history moving from the slope to the continental shelf (D'Onghia et al., 1996; Massutí and Moranta, 2003) feeding on benthopelagic and benthic prey, respectively. These results may confirm an ontogenetic shift in the diet of this catshark.

The literature review on the stable isotope composition of *S. canicula* in the Mediterranean Sea highlighted a strong variability of $\delta^{15}N$ and $\delta^{15}C$ values across the examined studies that considered different tissues. Particularly, the signatures obtained in the vertebrae of specimens inhabiting the same study area study area are depleted with respect to our results (Reinero et al., 2023). Despite a discrepancy between the isotopic signal reported for vertebrae birth mark and that of our samples was expected, the large difference observed with the values of the outer ring reported in the cited study was instead a surprise, especially for the $\delta^{15}N$ ($\Delta\delta^{15}N$ our sample-vertebrae = 4.1). The birth mark is the first part of the vertebra deposited during the animal's life and, in an oviparous species that feeds on the egg yolk, it essentially reflects the egg's signal. The outer ring should instead correspond to the last year of the animal's life, and its signal should be similar to that of the muscle. Apart from this, the mean values of muscles and vertebra from all over the Mediterranean basin are quite comparable with ours, being the mean $\delta^{15}N$ and $\delta^{13}C$ values of the firsts equal to 10.5 ± 1.4 ‰ and − 17.8 ± 0.5 ‰, respectively, and the $\delta^{15}N$ and $\delta^{13}C$ values of our samples equal to 9.5 ± 0.7 ‰ and −18.3 ± 0.6 ‰, respectively).

4.3. Landings data analysis

The Mediterranean Sea's elasmobranchs are under threat due to lack of detailed fishery catch statistics (Cashion et al., 2019; Giovos et al., 2020). Large predators have declined due to direct fishing and overfishing (Bearzi et al., 2006; Lotze et al., 2011), leading to a decrease in elasmobranch abundance and competition pressure on mesopredators (Dell'Apa et al., 2012). This could lead other species to modify their trophic niches and habitats, potentially extincting sensitive prey (Ritchie and Johnson, 2009; Elmhagen et al., 2010). The Mediterranean Sea also shows an increase in mesopredators as apical predators decrease (Ferretti et al., 2010).

In the Mediterranean Sea, *S. canicula* accounts for ca. 21.6% of the total catch of elasmobranchs, but this percentage could be underestimated since different national authorities register elasmobranchs in aggregate-landing categories (Giovos et al., 2021). Here, its population is not considered in decline, rather the species has shown an increase in both density and biomass over the past 10 years even if the high level of trawl fishing exploitation led to a decreasing trend in length at first maturity (Ramírez-Amaro et al., 2020). This catshark manages to resist on account of its higher recovery capacities, different life strategy than other viviparous elasmobranch mesopredators, and habitat use. This is reflected by increasing trend of the tons of live catches landed from 2013 to 2019 (STECF data), despite a constant decrease reported until 2022. This reduction in the last years follow the continuous reduction in overall fishing pressure, which has fallen the percentage of overexploited stocks from 73% in 2020 to 58% in 2021 (FAO, 2023) and the shift of the fleet towards deep waters (Ramírez-Amaro et al., 2020). Compared to the biennium (2018–2019), last annual landings and, therefore, the catches, showed a decline in most countries (28,7% decrease in Italy) also probably due to the impact of the COVID-19 pandemic on fleet dynamics (FAO, 2023).

4.4. The trophic role of Scyliorhinus canicula in the Mediterranean Sea

Scyliorhinus canicula shares the same position in the isospace with other marine benthic taxa like batoids (i.e., *Raja asterias*, *Raja clavata*) (Fanelli et al., 2023a, 2023b). These taxa cluster within a $\delta^{15}N$ range of approximately 9–12 ‰, which supports their classification as mesopredators (Fig. 8).

At this trophic level, *S. canicula* plays a key role in mediating energy transfer between lower trophic levels and higher predators by preying predominantly on benthic invertebrates, particularly crustaceans, many of which include commercially important species that are either overexploited or frequently caught as bycatch.

Stable isotope results from the present study, together with literature data, highlight a clear functional overlap among benthic mesopredators within the Mediterranean Sea, suggesting potential trophic redundancy but also emphasizing the importance of *S. canicula* in maintaining benthic food-web structure. Similar to other demersal elasmobranchs, the species exhibits an ontogenetic dietary shift, with juveniles relying mainly on small benthic crustaceans and adults progressively incorporating larger decapod crustaceans (e.g. crabs and shrimps) and teleost fishes into their diet (Mulas et al., 2010; Šantić et al., 2012; Barría et al., 2018).

From a food-web perspective, the trophic plasticity of *S. canicula* appears to be a key factor underlying its resilience to anthropogenic

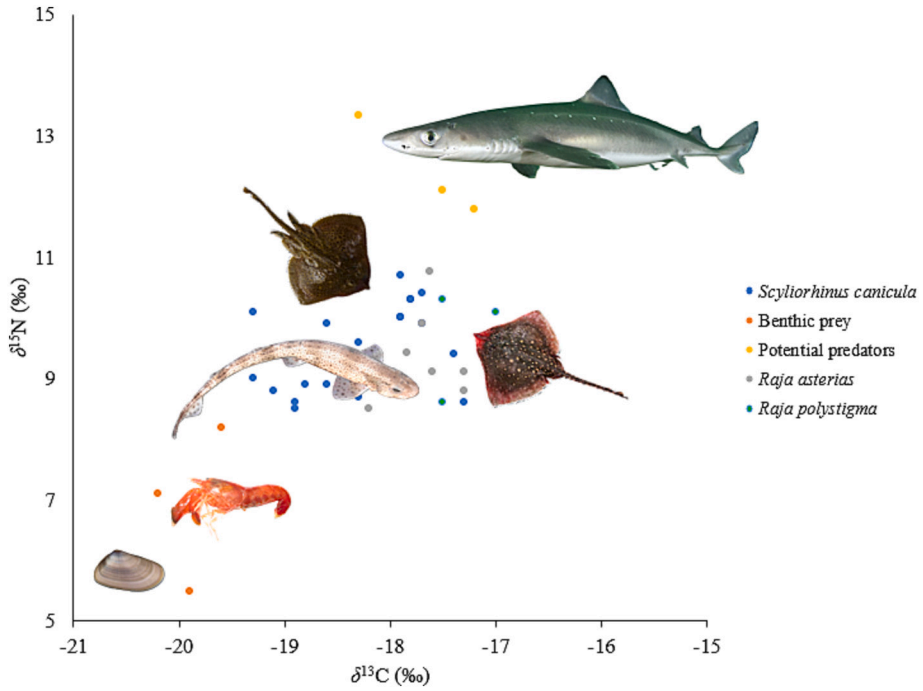

Fig. 8. Mediterranean benthic trophic web investigated through stable isotope analysis. Stable isotopes content data were taken from the present study for *S. canicula*, from Fanelli et al., 2023a, 2023b for *R. asterias* and from ISOMED database for the other species.

pressures. In contrast to other mesopredators such as *Raja asterias*, whose Mediterranean populations show declining trends (Serena et al., 2016), the small-spotted catshark displays stable or even increasing population trends in several Mediterranean areas. This pattern has been attributed to life-history traits such as early sexual maturity, relatively rapid turnover rates, and continuous reproductive cycles, as documented in the Gulf of Lions (NW Mediterranean Sea; Navarro et al., 2016). In heavily trawled areas, *S. canicula* was reported as the last predator to disappear under intense fishing pressure, highlighting its high trophic adaptability and survivorship in disturbed benthic systems (Navarro et al., 2016).

Overall, these characteristics suggest that *S. canicula* represents a resilient mesopredator capable of persisting in simplified or altered food webs, where it may partially compensate for the decline of more vulnerable elasmobranch species. Its increasing abundance in some regions (Ramírez-Amaro et al., 2020; Finucci et al., 2021) may therefore have important implications for benthic community dynamics, particularly through top-down control on invertebrate prey assemblages. In this context, the species should be considered not only in terms of conservation status, but also for its functional role within Mediterranean benthic food webs.

5. Conclusions

In conclusion, the present case study confirmed the role of the small-spotted catshark as a mesopredator in the Mediterranean benthic food web. Further studies in other areas of the Mediterranean Sea characterized by increasing fishing pressure are needed to define the consequences of the release of this mesopredator, caused by the removal of its predators together with the reduction of potential competitors due to their moderate commercial interest (Fanelli et al., 2023a, 2023b). These studies could help to define management measures that could better conserve not only this specific consumer but also the lower part of the marine food web it controls.

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CRediT authorship contribution statement

Luca Caracausi: Visualization, Formal analysis, Writing – review & editing, Writing – original draft. **Zaira Da Ros:** Visualization, Validation, Writing – review & editing, Writing – original draft. **Paula Masia Lillo:** Visualization, Data curation, Writing – review & editing. **Alessandro Ligas:** Validation, Supervision, Conceptualization, Writing – review & editing. **Emanuela Fanelli:** Validation, Supervision, Funding acquisition, Conceptualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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