



## Assessing juvenile swordfish (*Xiphias gladius*) diet as an indicator of marine ecosystem changes in the northwestern Mediterranean Sea

Elena Fernández-Corredor<sup>a,\*</sup>, Luca Francotte<sup>a</sup>, Ilaria Martino<sup>a</sup>,  
Fernando Á. Fernández-Álvarez<sup>a</sup>, Salvador García-Barcelona<sup>b</sup>, David Macías<sup>b</sup>, Marta Coll<sup>a,c</sup>,  
Francisco Ramírez<sup>a</sup>, Joan Navarro<sup>a</sup>, Joan Giménez<sup>a</sup>

<sup>a</sup> Institut de Ciències del Mar (ICM), CSIC, Barcelona, Spain

<sup>b</sup> Centro Oceanográfico de Málaga (IEO-CSIC), Fuengirola, Spain

<sup>c</sup> Ecopath International Initiative (EII), Barcelona, Spain

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### ABSTRACT

To preserve marine biodiversity, we need reliable early warning indicators that inform changes in marine ecosystems. As reliable samplers of mid-trophic level communities, studying the trophodynamics of large pelagic fish can contribute to monitoring these changes. Here, we combined stomach content and stable isotope analyses to reconstruct the diet of juvenile swordfish (*Xiphias gladius*) in the northwestern Mediterranean Sea, in a time-lapse of almost a decade (2012 and 2020). Overall, our study showed that swordfish fed on a wide range of fish and cephalopod species from both pelagic and demersal habitats. A dietary shift towards increasing consumption of cephalopods and decreasing consumption of Gadiformes had been observed between 2012 and 2020. Stable isotope approaches revealed that gelatinous organisms were also important prey, particularly for smaller-sized swordfish. We underline the importance of combining multiple and complementary approaches to better reconstruct the diet of generalist species. Our findings highlight the generalist and opportunistic diet of Mediterranean swordfish, which makes them good candidates for monitoring changes in the ecosystem.

### 1. Introduction

Within the current context of global environmental change, there is an urgent need for developing reliable, early warning indicators informing on changes in the structure and functioning of marine ecosystems (Pech et al., 2017). In this context, the use of species as ‘sentinels’ of different processes in the environments they inhabit has gained interest in marine ecosystem monitoring and management (Siddig et al., 2016). Ecosystem sentinel species are defined as “conspicuous, easily accessible, and observable species” that respond to fluctuations within the ecosystem and can serve as indicators of potential shifts in ecosystem function that might otherwise go unnoticed (Hazen et al., 2019). Marine top predators integrate trophic processes and interactions along food webs and can be reliable sentinel species informing on ecosystem changes and cause-effect relationships in a realistic way (Moore et al., 2014). They play an important role in shaping marine food webs, exhibit clear responses to environmental variability, and reflect anthropogenic impacts and pressures on the ecosystem, all in a timely and measurable

way (Hazen et al., 2019), which are key characteristics of a good sentinel species.

The diet of these marine sentinels provides an opportunity to quantitatively monitor marine ecosystems by characterizing the diversity, distribution, and availability of prey species (Duffy et al., 2017; Hazen et al., 2019; Nicol et al., 2013). Large pelagic fish such as tunas or seabirds such as penguins have been proposed as reliable samplers of the mid-trophic level communities (Carpenter-Kling et al., 2019; Olson et al., 2014), as they can collect data on offshore prey, which are usually scarce (Duffy et al., 2017). This is particularly relevant given that human and climate stressors are causing significant shifts in the composition of marine communities, and species with short life cycles and adaptability to temporal and spatial changes, such as cephalopods and gelatinous organisms, may thrive in this changing environment (Doubleday and Connell, 2018; Hoving et al., 2013).

The swordfish (*Xiphias gladius*) is a paradigmatic example of an efficient sampler of pelagic and mesopelagic species (Bello, 1991; Markaida and Hochberg, 2005; Romeo et al., 2011). This widespread

\* Corresponding author. Institut de Ciències del Mar (ICM), CSIC, Passeig Marítim de la Barceloneta, 37-49, 08003, Barcelona, Spain.

E-mail address: [elenafc@icm.csic.es](mailto:elenafc@icm.csic.es) (E. Fernández-Corredor).

species performs vertical migrations (Canese et al., 2008), and contributes to the demersal-pelagic coupling of marine ecosystems (Navarro et al., 2017, 2020). It feeds on a wide range of prey from epipelagic and mesopelagic to benthopelagic and demersal species, showing high trophic plasticity (Abid et al., 2018; Carmona-Antoñanzas et al., 2016; Preti et al., 2023; Rosas-Luis et al., 2017). Despite being currently listed as “Near Threatened” in the Mediterranean Sea by the International Union for the Conservation of Nature (IUCN; Collette et al., 2022), swordfish remain highly overfished (ICCAT, 2020) due to their high commercial interest (Damalas and Megalofonou, 2014; Palko et al., 1981), which also facilitates sample collection.

In the Mediterranean Sea, previous studies have reported information on the diet of swordfish (e.g., Biton-Porsmoguer et al., 2022; Navarro et al., 2017; Romeo et al., 2009). However, differences in the methodology across studies have resulted in contrasting conclusions regarding the relative importance of different prey in its diet; thus, hampering the proper evaluation of swordfish trophodynamics in response to varying environmental conditions. While studies based on stomach content analysis have identified fish and cephalopods as the main prey consumed (Biton-Porsmoguer et al., 2022; Carmona-Antoñanzas et al., 2016), the use of stable isotopes has highlighted the significance of gelatinous organisms as an important part of the assimilated diet of swordfish (Cardona et al., 2012). Both techniques have their own biases (Boecklen et al., 2011; Hyslop, 1980; Young et al., 2015). Stomach content analysis can provide a high-resolution taxonomic description of diet composition, yet it can be biased due to differential digestion rates (Hyslop, 1980). While biochemical tracers such as stable isotopes provide integrated information on the assimilated fraction of the diet, they can be based on untested or unrealistic assumptions such as some parameter selection related to the paucity of experimental studies (Young et al., 2015). The combined use of both approaches has been proposed as a suitable means for providing more realistic dietary estimates (Chiaradia et al., 2016; Giménez et al., 2017; Navarro et al., 2014); particularly when it comes to quantifying the consumption of organisms, such as gelatinous species, that are not usually detected in stomach contents analysis due to fast degradation (Cardona et al., 2012; Chiaradia et al., 2016). Moreover, few studies on swordfish have previously evaluated dietary changes across periods (e.g., Preti et al., 2023); thus, precluding inferences on food web dynamics and changes in the structure and functioning of marine ecosystems.

Here, we provide a diet reconstruction of swordfish inhabiting the highly impacted northwestern Mediterranean Sea, based on the combination of stomach content analyses and stable isotope approaches. Specifically, we aimed to describe the trophodynamics of juvenile swordfish and to compare diet inferences performed with different techniques. We evaluate dietary shifts between two years separated by almost a decade and hypothesize likely responses to changes in the community. This is particularly important in our study area, where climate and human-driven changes (e.g., warming water temperatures) are occurring at a fast rate (Coll et al., 2012; Salat et al., 2019; Tuel and Eltahir, 2020) and several commercial and non-commercial species, including swordfish prey (e.g., European hake, *Merluccius merluccius*), have declined in both abundance and biomass (FAO, 2022; Piroddi et al., 2017). As a reliable sentinel species and a mesopelagic sampler, we expect that the swordfish diet would closely track the reported changes in prey availability and, hence, the structure and functioning of the marine community.

## 2. Materials and methods

### 2.1. Study area and sampling procedures

A total of 100 juvenile swordfish were caught by drifting longline fishing vessels operating in Tarragona (northwestern Mediterranean Sea, Fig. 1) between summer and autumn of two years separated by almost a decade (2012 and 2020). No anomalous environmental

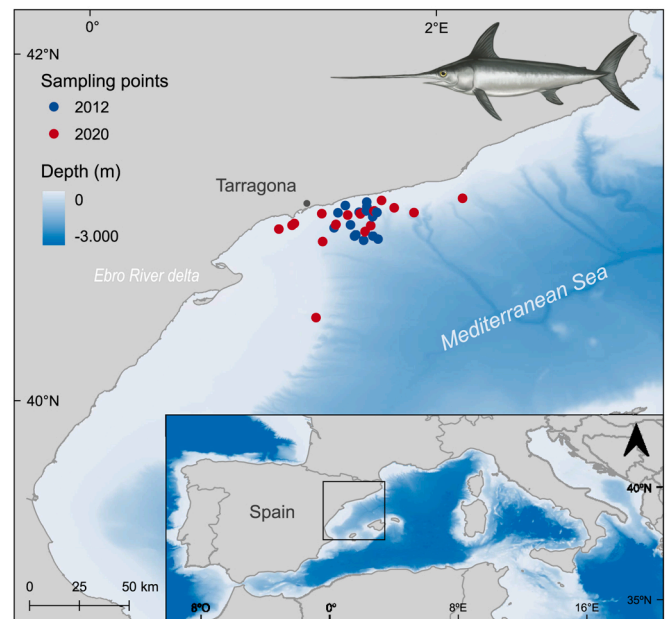


Fig. 1. Sampling area in the northwestern Mediterranean Sea. The geographic position of the studied area in the Mediterranean Basin is also indicated in the bottom right corner. Swordfish illustration by Alex Mascarell.

conditions for sea water potential temperature ( $^{\circ}\text{C}$ ) and net primary productivity ( $\text{mg}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$ ) that could potentially impact individuals' diet or foraging behavior were observed within our study area for the sampling years (see Supplementary Methods in Appendix A). Once on board, the lower jaw fork length (LJFL) was measured, then white muscle samples and the whole stomach were collected and frozen at  $-20^{\circ}\text{C}$  until further analyses were conducted.

### 2.2. Laboratory analyses

The stomach contents were carefully separated by filtering using two different sieves (1 mm and 500  $\mu\text{m}$ ). Prey items retained in the sieves were identified to the lowest possible taxonomic level. Prey otoliths were stored dry and measured using stereomicroscopes and identified using the AFORO database (<http://aforo.cmima.csic.es>, Lombarte et al., 2006). The otolith length (OL) was used to infer individual length and weight using otolith length–fish length and fish length–fish weight published regressions (see Table A1 from the Appendix). Round sardinella (*Sardinella aurita*) individuals with low digestion signs were excluded from the analysis as this species was used as bait by the longliners. Cephalopod beaks were preserved in 70% ethanol and identified using an in-house beak collection (AFOC, ICM-CSIC; Sánchez-Márquez et al., 2023). Lower Rostral Length (LRL) and Crest Length (CL) were measured to estimate the length and weight using published regressions (Table A1; Clarke, 1986).

Muscle samples were dried at  $60^{\circ}\text{C}$  and ground to a fine powder. Before analysis, lipids were extracted with a chloroform/methanol (2:1) solution to correct for the effect of high lipid ratio in the tissue on carbon ( $\delta^{13}\text{C}$ ) levels (Bodin et al., 2009). Analyses of  $\delta^{13}\text{C}$  and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios were carried out at the Laboratory of Stable Isotopes of the Estación Biológica de Doñana - CSIC (Sevilla, Spain). Samples were combusted at  $1020^{\circ}\text{C}$  using a continuous flow isotope-ratio mass spectrometry system (Thermo Electron) using a Flash HT Plus elemental analyser interfaced with a Delta V Advantage mass spectrometer. Based on laboratory standards, the measurement error was  $\pm 0.1$  and  $\pm 0.2$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively. The standards used were EBD-23 (cow horn, internal standard), LIE-BB (whale baleen, internal standard), and LIE-PA (razorbill feathers, internal standard). These laboratory standards were

**Table 1**

Importance of prey species identified in the stomach contents of juvenile swordfish (*Xiphias gladius*) captured in 2012 and 2020 in the northwestern Mediterranean Sea. Prey importance is given as: %N (percentage of individual prey species identified), %F (percentage of stomachs with each prey category), %W (percentage of reconstructed prey weight), %IRI (Index of Relative Importance). Individuals from 2020 were split into two groups: small 2020 individuals (LJFL <75 cm) and large 2020 individuals (LJFL >75 cm) in order to compare only similar body sizes between 2012 and 2020. LJFL: Lower Jaw Fork Length.

	2012				2020							
	n = 41 ( $\bar{x}$ = 92 cm)				LJFL >75 cm ( $\bar{x}$ = 90 cm), n = 16				LJFL <75 cm ( $\bar{x}$ = 66 cm), n = 42			
	N%	F%	W%	IRI%	N%	F%	W%	IRI%	N%	F%	W%	IRI%
<b>ACTINOPTERYGII</b>	94.47	100	82.86	95.83	78.14	87.50	53.91	79.15	41.58	85.71	49.01	38.04
<b>Anguilliformes</b>												
Congridae												
<i>Ariosoma balearicum</i>					0.40	6.25	–	–	0.14	2.38	–	–
<i>Conger conger</i>	0.03	2.38	0.27	0.01								
<i>Gnathophis mystax</i>					0.40	6.25	0.39	0.11	0.27	4.76	0.10	0.04
<b>Atheriniformes</b>												
Atherinidae												
<i>Atherina</i> sp.									0.14	2.38	0.02	0.01
<b>Aulopiformes</b>												
Aulopidae												
<i>Aulopus filamentosus</i>									0.14	2.38	1.06	0.07
Paralepididae												
<i>Arctozenus rissoi</i>	5.53	50.00	12.48	16.89	9.72	37.50	3.66	10.99	3.40	16.67	3.75	2.89
<i>Lestidiops jayakari</i>	7.32	66.67	18.78	32.64	45.75	37.50	27.68	60.38	15.90	40.48	11.37	26.77
<i>Paralepis speciosa</i>									0.41	7.14	–	–
Paralepididae unid.					0.40	6.25	–	–				
Evermannellidae												
<i>Evermannella balbo</i>	0.03	2.38	0.08	<0.01	0.40	6.25	0.31	0.10				
<b>Carangiformes</b>												
Carangidae												
<i>Trachurus mediterraneus</i>									0.14	2.38	0.90	0.06
Carangidae unid.									0.41	4.76	–	–
<b>Clupeiformes</b>												
Clupeidae												
<i>Alosa fallax</i>									0.14	2.38	1.88	0.12
<i>Sardina pilchardus</i>	0.10	7.14	0.59	0.09	0.81	6.25	2.08	0.40				
<i>Sardinella aurita</i>	0.54	21.43	9.69	4.11	1.62	12.50	8.45	2.76	0.68	7.14	9.40	1.75
Engraulidae												
<i>Engraulis encrasicolus</i>	0.47	26.19	1.48	0.96	2.83	12.50	2.99	1.59	0.82	4.76	1.46	0.26
Clupeiformes unid.	0.24	16.67	0.46	0.22								
<b>Gadiformes</b>												
Lotidae												
<i>Molva</i> sp.	0.07	2.38	<0.01	<0.01								
Gadidae												
<i>Micromesistius poutassou</i>	15.63	47.62	26.61	37.72					0.14	2.38	1.65	0.10
<i>Trisopterus capelanus</i>									0.27	4.76	0.40	0.08
<i>Gadiculus argenteus</i>	0.07	4.76	0.06	0.01					0.27	2.38	0.17	0.03
Merlucciidae												
<i>Merluccius merluccius</i>	0.24	9.52	3.09	0.59	0.40	6.25	0.50	0.12				
Macrouridae												
<i>Coelorinchus caelorinchus</i>	0.10	4.76	0.07	0.02								
Gadiforme unid.	0.58	4.76	–	–								
<b>Mugiliformes</b>												
Mugilidae												
<i>Mugil cephalus</i>									0.14	2.38	–	–
<b>Myctophiformes</b>												
Myctophidae												
<i>Benthoema glaciale</i>	0.07	4.76	0.04	0.01	0.40	6.25	0.25	0.09	0.54	7.14	0.07	0.11
<i>Ceratoscopelus maderiensis</i>	0.88	33.33	0.61	0.93					5.43	19.05	0.73	2.85
<i>Diaphus holti</i>					2.43	6.25	0.45	0.39				
<i>Electrona risso</i>	0.03	2.38	<0.01	<0.01					0.27	4.76	0.03	0.03
<i>Hygophum benoitii</i>					0.40	6.25	0.13	0.07	0.14	2.38	<0.01	0.01
<i>Lamparyctus pusillus</i>	0.03	2.38	<0.01	<0.01	0.40	6.25	0.02	0.06	0.14	2.38	0.01	0.01
<i>Lobianchia</i> sp.					0.81	6.25	0.16	0.13	0.68	7.14	0.18	0.15
<i>Myctophum punctatum</i>	0.17	11.90	0.14	0.07	1.62	12.50	0.49	0.58	0.54	2.38	0.30	0.05
<i>Notoscopelus elongatus</i>	1.59	28.57	0.81	1.29	0.40	6.25	0.19	0.08	0.41	4.76	0.26	0.08
<i>Symbolophorus veranyi</i>	0.07	4.76	0.15	0.02	1.21	12.50	0.79	0.55	0.14	2.38	0.01	0.01
Myctophidae unid.	0.07	4.76	–	–					0.41	4.76	–	–
<b>Notacanthiformes</b>												
Notacanthidae												
<i>Notacanthus bonaparte</i>	0.03	2.38	0.01	<0.01								
<b>Ophiidiforme</b>												
Ophidiidae												
<i>Ophidion barbatum</i>									0.14	2.38	1.86	0.12
Ophidiformes unid.									0.14	2.38	–	–
<b>Gobiiformes</b>												
Gobiidae												

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Table 1 (continued)

	2012				2020							
	n = 41 ( $\bar{x}$ = 92 cm)				LJFL >75 cm ( $\bar{x}$ = 90 cm), n = 16				LJFL <75 cm ( $\bar{x}$ = 66 cm), n = 42			
	N%	F%	W%	IRI%	N%	F%	W%	IRI%	N%	F%	W%	IRI%
<i>Lesueurigobius</i> sp.	0.03	2.38	0.02	<0.01								
Gobiidae unid.					0.40	6.25	–	–				
<b>Eupercaria incertae sedis</b>												
Sparidae												
<i>Boops boops</i>									0.27	4.76	1.91	0.25
<i>Pagellus bogaraveo</i>									0.14	2.38	0.31	0.03
<i>Sparus aurata</i>	0.03	2.38	3.65	0.16								
<i>Spicara</i> sp.									0.41	4.76	3.90	0.50
Sparidae unid.					1.21	6.25	–	–	0.41	7.14	–	–
<b>Scombriformes</b>												
Centrolophidae unid.	0.07	4.76	–	–	0.40	6.25	–	–				
Triachiuridae												
<i>Lepidopus caudatus</i>	0.03	2.38	0.42	0.02					0.27	2.38	0.20	0.03
Scombridae												
<i>Scomber colias</i>					0.40	6.25	4.65	0.69	0.41	7.14	6.81	1.25
<b>Perciformes</b>												
Triglidae unid.	0.03	2.38	–	–					0.14	2.38	–	–
<b>Stomiiformes</b>												
Gonostomidae												
<i>Gonostoma</i> sp.	0.03	2.38	0.07	<0.01					0.41	7.14	0.17	0.10
Phosichthyidae												
<i>Vinciguerra</i> sp.	0.10	2.38	0.03	<0.01								
Sternoptychidae												
<i>Maurolicus muelleri</i>	0.03	2.38	<0.01	<0.01					0.95	11.90	0.10	0.30
Stomidae												
<i>Chauliodus sloani</i>	0.07	4.76	0.03	0.01								
<i>Stomias boa</i>	0.03	2.38	0.68	0.03	0.40	6.25	0.74	0.16				
Stomidae unid.					0.40	6.25	–	–				
<b>Unidentified fish</b>	60.09	64.29	–	–	4.45	25.00	–	–	5.84	47.62	–	–
<b>CEPHALOPODA</b>	4.34	76.19	16.73	4.06	19.84	62.50	46.09	20.85	57.20	85.71	50.99	61.96
<b>Myopsida</b>												
Loliginidae unid.									0.14	2.38	–	–
<b>Octopoda</b>												
Argonautidae												
<i>Argonauta argo</i>	0.20	9.52	0.17	0.07					4.08	35.71	2.70	5.87
Tremoctopodidae												
<i>Tremoctopus</i> sp.									0.14	2.38	0.34	0.03
<b>Oegopsida</b>												
Ancistrocheiridae												
<i>Ancistrocheirus lesueurii</i>					2.83	6.25	2.12	0.68	7.88	26.19	1.52	5.97
Cranchiidae												
<i>Galiteuthis armata</i>					1.21	6.25	4.09	0.73				
<i>Taonius pavo</i>					0.40	6.25	0.12	0.07	0.14	2.38	0.16	0.02
<i>Teuthowenia megalops</i>									0.14	2.38	0.08	0.01
<i>Cranchia scabra</i>									1.49	4.76	2.31	0.44
Enoploteuthidae												
<i>Abralia veranyi</i>									4.21	7.14	5.24	1.64
Enoploteuthidae unid.									2.17	4.76	–	–
Histioteuthidae												
<i>Histioteuthis reversa</i>					0.40	6.25	0.49	0.12	1.90	19.05	1.61	1.64
Ommastrephidae												
<i>Illex coindetii</i>	0.17	7.14	3.02	0.43	1.21	12.50	2.73	1.08	0.82	11.90	9.54	2.99
<i>Todarodes sagittatus</i>	0.51	16.67	8.99	2.97	7.69	18.75	34.78	17.44	17.80	45.24	21.26	42.86
<i>Todaropsis eblanae</i>	0.14	4.76	3.28	0.30					0.14	2.38	5.22	0.31
Ommastrephidae unid.					0.40	6.25	–	–				
Onychoteuthidae												
<i>Ancistroteuthis lichtensteini</i>	0.03	2.38	0.33	0.02	1.62	6.25	0.74	0.32	0.82	2.38	0.52	0.08
Pyroteuthidae												
<i>Pyroteuthis margaritifera</i>					0.81	6.25	0.20	0.14				
<b>Sepiolida</b>												
Sepiolidae												
<i>Heteroteuthis dispar</i>	0.31	11.90	0.94	0.28	1.21	6.25	0.82	0.28	0.54	4.76	0.48	0.12
<i>Rondeletiola minor</i>	0.03	2.38	–	–								
Sepiolidae unid.	0.14	7.14	–	–	0.40	6.25	–	–	0.68	7.14	–	–
<b>Unidentified cephalopod</b>	2.81	42.86	–	–	1.62	12.50	–	–	14.13	40.48	–	–
<b>CRUSTACEA</b>	1.19	38.10	–	–	2.02	12.50	–	–	1.22	14.29	–	–
<b>Euphausiacea</b>												
Euphausiidae												
<i>Meganyciophanes norvegica</i>									0.14	2.38	–	–

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Table 1 (continued)

	2012				2020							
	n = 41 ( $\bar{x}$ = 92 cm)				LJFL >75 cm ( $\bar{x}$ = 90 cm), n = 16				LJFL <75 cm ( $\bar{x}$ = 66 cm), n = 42			
	N%	F%	W%	IRI%	N%	F%	W%	IRI%	N%	F%	W%	IRI%
<b>Decapoda</b>												
Pandalidae												
<i>Plesionika</i> sp.	0.03	2.38	–	–								
Pasiphaeidae												
<i>Pasiphaea sivado</i>	0.03	2.38	–	–	0.40	6.25	–	–	0.95	9.52	–	–
<i>Pasiphaea multidentata</i>	0.14	2.38	–	–								
Penaeidae												
<i>Parapenaeus longirostris</i>					0.40	6.25	–	–				
Sergestidae												
<i>Robustrosergia robusta</i>					1.21	6.25	–	–				
Sergestidae unid.									0.14	2.38	–	–
<b>Unidentified crustacea</b>	0.98	30.95	–	–								
<b>CNIDARIA</b>												
Siphonophorae	0.41	14.29	<0.01	0.11								

previously calibrated with international standards provided by the International Atomic Energy Agency (IAEA, Vienna).

### 2.3. Statistical analyses

Ontogenetic shifts in the diet of the swordfish have been previously reported (e.g., Romeo et al., 2009; Salman, 2004). Since 2012 individuals were larger than 75 cm, individuals from 2020 were split into two groups: small 2020 individuals (LJFL <75 cm) and large 2020 individuals (LJFL >75 cm), to compare only similar body sizes between 2012 and 2020.

We calculated five trophic metrics to characterize the diet of swordfish: i) the frequency in number (%N; percentage of individuals of prey *i* versus the overall number of prey), ii) the frequency of occurrence (%F; percentage of stomachs containing prey *i*), iii) the percentage of reconstructed weight (%W; percentage of the weight of prey *i* versus the overall weight of prey), iv) the Index of Relative Importance (IRI = (%N + %W) \* %F; Hart et al., 2002), and v) the Vacuity Index (%V; percentage of empty stomachs). We used a Costello diagram (Costello, 1990) modified by Amundsen et al. (1996) to evaluate the feeding behavior of swordfish. The frequency of occurrence (%F) was plotted against the prey-specific importance of each prey taxon (%P<sub>*i*</sub>), where the contribution by weight of prey *i* to the stomach content (W<sub>*i*</sub>) was divided by the total stomach content weight (W<sub>*st*</sub>) in those individuals that had consumed prey *i*. Overall, the distribution of prey types in the Amundsen diagram provides insights into the feeding strategy and niche width of the predator population. We assessed prey diversity in the diet composition with the Shannon diversity index (H') calculated from prey abundance composition within the stomachs.

Differences in diet composition between the stomach contents of the three groups (2012, and large and small 2020 individuals) were tested using permutational multivariate analysis of variance (PERMANOVA) based on the Bray-Curtis distance matrix. PERMANOVA tests use an observed value of a statistical test (pseudo-F ratio) compared to a recalculated statistic test generated from a random reordering (Permutation) of the data to obtain the p-values (Anderson, 2001). Data was square-rooted to reduce the impact of outliers prior to statistical testing. When the evidence of differences was strong (i.e., p value < 0.05), pairwise tests were performed. We used the R package vegan v2.6–2 to perform PERMANOVA tests (Oksanen et al., 2022).

Differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values between the three groups were tested using 2-way PERMANOVA tests on the Euclidian distance matrix. To compare the degree of isotopic niche width and overlap between the three groups, corrected standard ellipses area (SEA<sub>C</sub>, area containing 40% of the data) and Bayesian standard ellipses area (SEA<sub>B</sub>) were calculated using the SIBER R package v2.1.6 (Jackson et al., 2011).

To estimate the proportional prey contribution to swordfish diet based on stable isotope values (i.e.,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ), Bayesian Stable Isotope Mixing Models (BSIMM) were computed using the MixSIAR R package v3.1.12 (Stock et al., 2018). The models were run with 3 Markov chain Monte Carlo (MCMC) analyses of 300,000 draws, and a burn-in of 200,000 draws. The convergence of the models was checked using both Gelman-Rubin and Geweke diagnostics (Stock et al., 2018; Stock and Semmens, 2016). BSIMM input data included  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of individual swordfish and potential prey species. Prey groups were selected according to stomach content analysis (i.e., prey species with >10%W) and previous studies in the western Mediterranean, including gelatinous species as important prey for swordfish (Cardona et al., 2012). Stable isotopic prey values were obtained from the literature (see Table A2 from the Appendix) and grouped using a meta-analysis approach (metafor R package v3.4–0; Viechtbauer, 2010).

The diet-tissue discrimination factors (DTDF;  $3.08 \pm 0.29\text{‰}$  for  $\delta^{15}\text{N}$  and  $1 \pm 0.14\text{‰}$  for  $\delta^{13}\text{C}$ ) were estimated following Caut et al. (2009). The appropriate parameterization of the BSIMM was validated through the simulation of mixing polygons, where all consumer data corrected for TDFs should fall within the bounds of the mixing space (Phillips et al., 2014; Smith et al., 2013). In addition, we used diet proportions estimated from the stomach contents from this study to construct informative prior distributions, which allowed us to incorporate both sources of data into a single framework. Models for each group (2012, large 2020, and small 2020) were run twice, first with uninformative Dirichlet priors (predator consumes all *n* prey in equal proportions, 1/*n*,  $\alpha = 1,1,1,1$ ), and second with informative priors, where the prey sources' relevance in the model was scaled by their weight in the stomach samples, which relates to its importance as an energy source (%W for each prey group scaled so that  $\sum \alpha = 5$ , the number of sources).

Table 2

Mean values and standard deviation (SD) of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopes for juvenile swordfish from 2012 (large individuals) and 2020 (small and large individuals). LJFL: lower jaw fork length (cm); n: number of samples.

Group	LJFL range (cm)	n	$\delta^{15}\text{N}$ (‰)		$\delta^{13}\text{C}$ (‰)	
			mean	SD	mean	SD
Large 2012	77–104	25	10.14	0.78	–18.55	0.46
Large 2020	76.6–100	17	11.3	0.61	–18.1	0.34
Small 2020	52–74	41	9.23	0.57	–17.77	0.46



### 3. Results

#### 3.1. Stomach content analysis

A total of 1442 individual prey, belonging to 64 species, 39 families, and 17 orders were identified in swordfish stomachs (Table 1), with all stomachs containing at least one prey (0%V). Overall, teleosts were the most frequent (94%F) and diverse group of prey, with 45 species from the epipelagic (e.g., European anchovy, *Engraulis encrasicolus*), mesopelagic [e.g., elongate lanternfish (*Notoscopelus elongatus*)], bathypelagic [e.g., silvery lightfish (*Maurolucus muelleri*)], and demersal (e.g., European hake) habitats. Swordfish also fed frequently on cephalopods (80%F) from 16 different species, including mainly squid from the family Ommastrephidae [e.g., European flying squid (*Todarodes sagittatus*)], but also octopuses and bobtails [e.g., greater argonaut (*Argonauta argo*), and odd bobtail (*Heteroteuthis dispar*)]. Crustaceans were less frequent in swordfish's stomach contents (24%F). Only five shrimp species were found. Gelatinous organisms were the less frequent group, represented by cnidarians from the order Siphonophorae (6%F), which were only found in swordfish from 2012.

For 2012 individuals, the most important prey in %N, %W, and %IRI were the fish of the order Gadiformes, with blue whiting (*Micromesistius poutassou*) representing 26.6% of the total prey weight (Table 1). In contrast, the diet of large 2020 individuals mainly included cephalopods (*T. sagittatus*, 34.8%W) and mesopelagic fish of the family Paralepididae, with barracudina (*Lestidiops jayakari*) and spotted barracudina (*Arctozenus risso*) representing together the 31% of the total prey weight (Table 1). Remains of Gadiformes consumption were only found in one stomach (*M. merluccius*, 0.5%W). For small 2020 swordfish, the most important prey in %N, %F, %W, and %IRI were the cephalopods from the family Ommastrephidae, with the European flying squid (21%W) as the main prey species (Table 1), followed by mesopelagic (barracudina and spotted barracudina, 15%W) and pelagic fish (round sardinella, 9.4%W).

The most frequent prey had low prey-specific abundance (e.g., barracudina and European flying squid), while some less frequent species,

such as the Mediterranean horse mackerel (*Trachurus mediterraneus*) or the lesser flying squid (*Todaropsis eblanae*), had high prey-specific abundances (Fig. 2). Species with high frequency and high prey-specific abundance were not found.

PERMANOVA tests revealed differences in stomach contents between the three groups ( $p < 0.001$ , see Table A.3 from the Appendix). Pairwise analysis showed strong evidence for diet composition differences between individuals from 2012 and 2020 ( $p$ -value  $< 0.001$ ), but not between small and large individuals from 2020 ( $p$ -value = 0.09). Regarding the diversity of prey species, small 2020 swordfish had the highest dietary diversity (Shannon-Index = 2.43). Large 2020 and 2012 individuals had less diverse diets, with Shannon-Index values of 1.83 and 1.34, respectively.

#### 3.2. Stable isotopes analysis

Differences were found for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopes values between three swordfish groups (pseudo- $F = 51.18$ ,  $p < 0.001$ ; Table 2). Regarding the isotopic niche, large 2020 individuals presented the smallest standard ellipses area (mean  $\text{SEA}_b = 0.69$ ), followed by small 2020 individuals (mean  $\text{SEA}_b = 0.83$ ) and individuals from 2012 ( $\text{SEA}_b = 0.94$ ) (Fig. 3, Table A4). There was no overlap between the isotopic niche of small and large individuals from 2020, and large individuals from 2020 only overlapped with individuals from 2012 by less than 10% (Fig. 3, Table A4).

All except one swordfish isotopic values were inside the 95% mixing region delimited by the mixing polygon of the five prey groups' isotopic values adjusted to DTDFs, thus pointing to a suitable isotopic scenario for the MixSIAR models fitted with those prey groups (Fig. 4).

When comparing MixSIAR dietary reconstructions for large swordfish from 2012 to 2020, mesopelagic fish were found to be the most assimilated prey for both groups (Fig. 5, Table A5). Cephalopods and pelagic fish assimilation were found to be higher in 2020 than in 2012, using both informative and uninformative priors, which was in accordance with the stomach content results. When using uninformative priors, Gadiformes assimilation was higher in 2020 than in 2012,

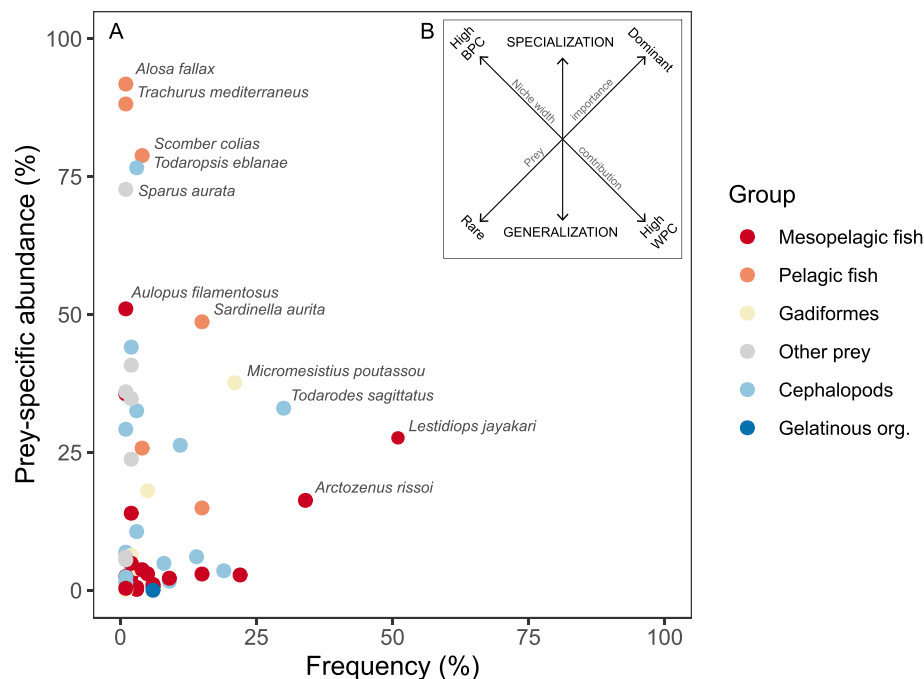
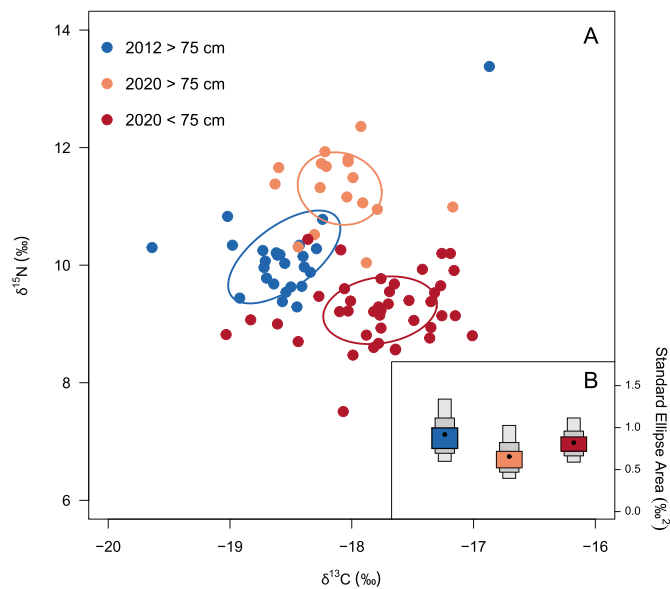
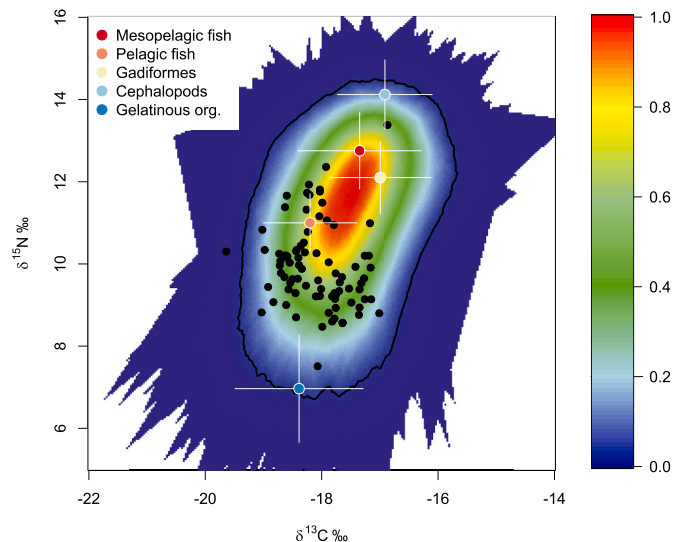


Fig. 2. Prey-specific abundance plotted against the frequency of occurrence of prey species for juvenile swordfish from the northwestern Mediterranean Sea. The explanatory axes used are those of Costello (1990) as modified from Amundsen et al. (1996). The two diagonal axes indicate the importance of prey (dominant vs. rare) and the contribution to the niche width (between-phenotype contribution (BPC) vs. within-phenotype contribution (WPC)); the vertical axis is used to define the feeding strategy (specialist vs. generalist).



**Fig. 3.** (A)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for juvenile swordfish by year and size with the corrected Standard Ellipse Area ( $\text{SEA}_C$ ). (B) Bayesian standard ellipse area ( $\text{SEA}_B$ ) for each group. Density plots represent the 95%, 75%, and 50% credibility intervals of  $\text{SEA}_B$ .



**Fig. 4.** Mixing polygon including the juvenile swordfish isotopic values (black dots) and the potential prey sources (mean  $\pm$  SD isotopic value: coloured dots and error bars). The colour background displays the probability that a consumer's isotopic signature is explained by the proposed mixing model. The probability contour is coloured at a 95% level.

however, the inverse pattern was shown by the model with informative priors and the stomach contents. Gelatinous organisms' assimilation was also found to be higher in 2012 individuals using both informative and uninformative priors, which was aligned with the findings of the stomach contents.

Regarding the individuals from 2020 alone, both informed and un-informed models' results showed that large 2020 individuals had higher consumption of mesopelagic fish and similar consumption of pelagic fish and cephalopods than small ones (Fig. 5, Table A5), as seen in the stomach contents. The proportion of Gadiformes in the uninformed models was higher in large individuals, but higher for small individuals when informative priors were used. The assimilation of gelatinous organisms appeared to be higher for small 2020 individuals, representing

nearly 50% of the diet.

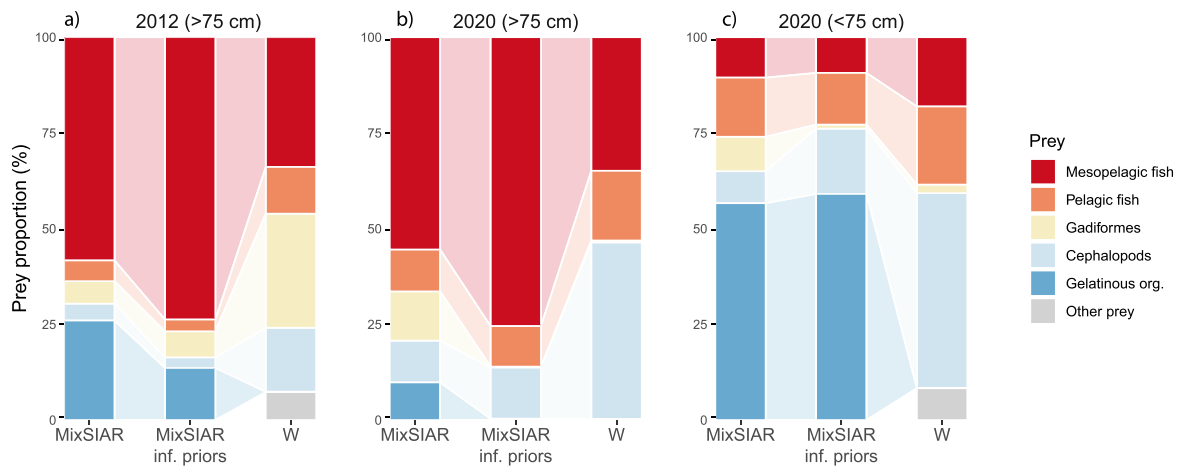
#### 4. Discussion

Here, we combine two complementary sources of trophic information to estimate the diet of swordfish in the northwestern Mediterranean Sea. The results indicate that swordfish predominantly feed on teleosts and cephalopods, but point at gelatinous plankton as an overlooked prey, particularly relevant in the diet of small-sized swordfish. Whether swordfish diets rely on cephalopods or fish is commonly discussed in diet studies based on stomach contents (e.g., Salman, 2004). However, prior research in the western Mediterranean Sea based on stable isotopes has pointed at gelatinous organisms as important swordfish prey (Cardona et al., 2012). Thus, the difference in estimates previously obtained highlights biases when trying to reconstruct the true diet consumed using only stomach contents, which is biased towards species that have hard structures (e.g., otoliths from fish); or BSIMM techniques, which examine assimilation and do not always reflect the ingested diet proportions (e.g., Chiaradia et al., 2014). Indeed, the proportion of cephalopods was higher in stomach contents than in the diet obtained through stable isotopes for the three groups considered in the present study, supporting that cephalopod beaks accumulate in the stomach and may be overrepresented in stomach content studies (Amundsen and Sánchez-Hernández, 2019). To overcome those biases, both methods are combined here by using the prey proportions found in stomach contents to inform the mixing models, which is particularly helpful when prey sources have similar isotopic values (Guerrero and Rogers, 2020). This helped to distinguish between Gadiformes and mesopelagic fish, obtaining more accurate diet estimates. These estimates uncovered a dietary transition in swordfish from 2012 to 2020, which appears to align with documented alterations in the marine ecosystem's structure and subsequent variations in prey availability.

##### 4.1. Feeding strategy

Our study provides insights into the feeding strategy and niche width of swordfish in the northwestern Mediterranean Sea, confirming that this large pelagic fish fed on a wide range of prey. Overall, most prey had low prey-specific abundance and moderate to low occurrence in the diet, which is consistent with a generalist feeding strategy consuming a great variety of prey types. Yet, some species had low frequency but high prey-specific abundance, which could indicate specialized feeding strategies in the population targeting schools of medium pelagic fish (e.g., Mediterranean horse mackerel), or that feeding in coastal habitats is limited to some individuals [e.g., Gilthead seabream (*Sparus aurata*)]. Furthermore, we found that the most frequent prey showed intermediate prey-specific abundances, suggesting that juvenile swordfish have a broad niche width and can exploit a range of prey species with varying levels of abundance.

The diversity of prey consumed both in specific and habitat terms also suggests that swordfish have a flexible foraging strategy. This wide range of prey from different habitats, including demersal, epipelagic, mesopelagic, and bathypelagic, evidences the swordfish's vertical migratory behavior and supports the benthopelagic coupling role of this species. Orders Gadiformes, Aulopiformes, Clupeiformes, and Myctophiformes were the most frequent fish prey for swordfish, while squids from the order Oegopsida, particularly from the family Ommastrephidae, were the most frequent cephalopod prey, which agrees with previous studies on this species (Carmona-Antoñanzas et al., 2016; Logan et al., 2021; Young et al., 2010). Although low in %W, fish from the family Myctophidae were consumed frequently in both years and size groups. Together with the high consumption of mesopelagic cephalopods, this suggests frequent foraging of swordfish in mesopelagic waters, supporting their potential role as mesopelagic samplers. In fact, the swordfish is well-known as an efficient "cephalopod collector" (Romeo et al., 2011) due to the high diversity of cephalopod prey found



**Fig. 5.** Relative proportions of prey groups in the diet of (a) 2012 juvenile swordfish, (b) large 2020 juvenile swordfish (LJFL >75 cm), and (c) small 2020 juvenile swordfish (LJFL <75 cm). Diet proportions were estimated from the MixSIAR models with uninformative (MixSIAR) and informative priors (MixSIAR inf. prior), and from stomach contents (%W; percentage of reconstructed weight).

in their diet, including some species of difficult collection due to oceanic lifestyles (e.g., *Cranchia scabra*, *Taonius pavo*; Fernández-Álvarez et al., 2022).

On the other hand, based on %N from the stomach contents, and therefore omitting the gelatinous organisms' consumption, differences in prey composition between the small and large 2020 individuals were not clear, which supports swordfish as good ecosystem sentinels since they are supposed to eat what is abundant regarding their size. Yet, there was no overlap between the isotopic niche of small and large 2020 individuals, suggesting that although prey ingestion may be similar, assimilation may change with swordfish growth.

Fish and cephalopods dominated the stomach contents of small 2020 swordfish, but these had lower  $\delta^{15}\text{N}$  values when compared with other fish and cephalopod consumers (Cardona et al., 2012), and gelatinous organisms appeared to be a major prey source for them, representing nearly half of the assimilated diet. Although they were only found in the stomachs of 2012 individuals, consumption of gelatinous organisms, primarily tunicates, has been reported in other regions (Preti et al., 2023), and other large pelagic fish species (Thiebot and McInnes, 2020). This high consumption may appear noteworthy, but the abundance of gelatinous zooplankton in the Mediterranean could be enough to provide sufficient sustenance for a large pelagic fish through casual consumption (Cardona et al., 2012). Other possible explanations for this consumption include opportunism, practicing hunting techniques, aggregation of prey, and potential acquisition of bio-active components that could have benefits for homeostatic challenges (Thiebot and McInnes, 2020; and references therein). Further research using other methods such as video cameras or DNA metabarcoding techniques could provide insights into the identification of these organisms that are known to degrade fast (Fernández-Álvarez et al., 2018), and is needed to fully understand the reasons for this behavior.

#### 4.2. Tracking changes in the marine community

The diet of generalist and opportunistic large predators, such as swordfish, closely tracks prey availability in their immediate environment (Palko et al., 1981). Therefore, the trophodynamics of swordfish can inform effectively on temporal changes in prey abundances. However, most of the previous swordfish diet studies were restricted temporally to a few years at most (e.g., Ceyhan and Akyol, 2017). Here, temporal variation in the diet of swordfish was observed. Gadiformes appeared as an important source of energy in 2012, while they seem to be absent in the diet of 2020 individuals. This dietary shift seems to reflect what is being observed in the community: over the last decade,

highly fished gadiform species, such as blue whiting and hake, have experienced declining abundances and have remained at historically low levels in the most recent years in the northwestern Mediterranean (GFCM, 2022a; Mir-Arguimbau et al., 2022; Sion et al., 2019). Moreover, swordfish fed more on pelagic fish in 2020. Small pelagic fish such as European sardine (*Sardina pilchardus*) and anchovy are also suffering from high exploitation and their biomasses are showing declines in the northwestern Mediterranean (GFCM, 2022b; Pennino et al., 2020). At the same time, the thermophilic round sardinella, which is the main pelagic species found in the stomach contents, is expanding its range due to ocean warming (Coll et al., 2019; Sabatés et al., 2006). This is aligned with the increasing water temperatures observed in our study area (see Figure A2), where its catch has increased in the last years (ICATMAR, 2023). On the other hand, changes in mesopelagic fish ingestion and assimilation between years were not observed. Despite that mesopelagic fish occupy a key position in the marine food web, biomass data in the Mediterranean Sea are scarce and they lack systematic monitoring campaigns (Clavel-Henry et al., 2020), therefore we could not evaluate if the swordfish diet is reflecting the mesopelagic community trends.

Our study area is one of the most exploited fishing grounds of the Mediterranean Sea (Coll et al., 2012; Colloca et al., 2017; Fernandes et al., 2017), and is seriously impacted by the effects of other climate and human-driven changes, such as water warming, coastal degradation, and pollution (Navarro et al., 2015; Salat et al., 2019). In this context of disturbance, cephalopods and gelatinous organisms, such as jellyfish and salps, are expected to benefit from the combination of changes in environmental conditions and reduced predators and competitors due to overfishing (Doubleday and Connell, 2018). Their rapid growth and strong life-history plasticity allow them to quickly adapt to changing environmental conditions and may trigger their success under the observed warming conditions (Brotz and Pauly, 2012; Hoving et al., 2013). Although jellyfish blooms have been recorded with increasing frequency and magnitude in many coastal areas, including the western Mediterranean Sea (Báez et al., 2022), gelatinous plankton densities were found to present strong long-term stability in this area (Feuilletoy et al., 2022). Here, we found high proportions of gelatinous plankton in the diet of small 2020 individuals, suggesting their consumption may be related to swordfish size. The abundance or availability of these organisms may have fluctuated over time, but other factors such as changes in other prey availability may have influenced their consumption. Further research is needed to investigate the long-term trends in the abundance and distribution of gelatinous plankton in the study area and their potential impacts on ecosystem dynamics.

On the other hand, Doubleday et al. (2016) suggest that the global



depletion of fish stocks, together with the potential release of cephalopods from predation and competition pressure, could be driving the growth in cephalopod populations. Specifically, the northwestern is one of the Mediterranean areas where the cephalopod community is best described, formed by a rather homogeneous mix of different species (Quetglas et al., 2019). Here, we found a small increase of cephalopods in large 2020 individuals, which seem to have switched to a more teuthophagus diet with regard to those from 2012. This increment may be tracking the putative increase in cephalopods' abundance in the ecosystem, even though the lack of long-term data on mesopelagic cephalopods, the main cephalopods consumed by swordfish, makes it difficult to test the hypothesis. Landings of commercial cephalopods in the study area have fluctuated over the last decade (ICATMAR, 2023), nevertheless, additional fishery-independent data, including non-commercial cephalopods, would be necessary to draw conclusions at the community level, particularly for pelagic species.

#### 4.3. Further steps in ecosystem monitoring

Understanding the dietary preferences of swordfish is essential for developing effective management strategies and conservation efforts for this threatened species and the marine ecosystems they inhabit. We described the diet of swordfish in the northwestern Mediterranean Sea by combining two complementary sources of diet analysis, emphasizing the importance of combining different methods to obtain more accurate diet estimates, while partially addressing the limitations associated with each technique individually. We were able to estimate the consumption of gelatinous organisms and assess changes in the diet of these organisms as a plausible response to variations in prey abundance. These findings should be corroborated through studies incorporating longer time series on diet and prey abundance. Overall, this is a common challenge when analyzing the diet of predatory species in marine ecosystems, where time series of diet information is mostly missing (e.g., Ouled-Cheikh et al., 2022).

In conclusion, our results highlight the role of swordfish as a good candidate to be an ecosystem sentinel in our study area. The lack of data on mesopelagic fish, mesopelagic cephalopods and gelatinous organisms presents a significant challenge for effective ecosystem-based management and conservation efforts, as these species play crucial roles in regulating ecosystem processes. These non-commercial species are frequently consumed by swordfish. Therefore, since swordfish are highly exploited all year long in the northwestern Mediterranean, continuous monitoring could be proposed, providing a long-term sampling of their prey, particularly relevant for the overlooked mesopelagic community. This would allow us to strengthen our understanding of how these organisms respond, in terms of their diet, to changes in the structure and functioning of the ecosystem. Consequently, we could establish the use of this species as valuable sentinels of the ecosystem in which they inhabit.

#### CRedit authorship contribution statement

E. Fernández-Corredor: Conceptualization, Methodology, Formal analysis, Investigation (Stable isotopes analysis), Data Curation, Writing - Original Draft, Visualization. L. Francotte: Investigation (Stomach content analysis). I. Martino: Investigation (Stable isotopes and stomach content analyses). F.Á. Fernández-Álvarez: Investigation, Writing - Review & Editing, Supervision. S. García-Barcelona: Resources. D. Macías: Resources. M. Coll: Funding acquisition, Writing - Review & Editing. F. Ramírez: Conceptualization, Methodology, Formal analysis, Writing - Review & Editing, Supervision. J. Navarro: Conceptualization, Methodology, Writing - Review & Editing, Supervision, Funding acquisition, Project administration. J. Giménez: Conceptualization, Methodology, Formal analysis, Writing - Review & Editing, Supervision, Project administration.

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#### 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.

#### Data availability

Data will be made available on request.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.106190>.

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