



Living together, feeding apart: trophic ecology of three demersal sharks in the North-east Atlantic

Viviendo juntos, alimentándose separados: ecología trófica de tres tiburones demersales en el Atlántico nororiental

Lola Riesgo Torres¹, Francisco Baldó¹, José Luis Varela²

¹Instituto Español de Oceanografía (IEO). Cádiz, Spain

²Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, Spain

 Lola Riesgo Torres () E-mail: lola.riesgo@hotmail.es

RESUMEN | En este estudio, se examinaron los hábitos de alimentación, la dieta, y las relaciones tróficas entre tres especies de tiburones demersales (*Galeus melastomus* Rafinesque, 1810, *Etmopterus spinax* (Linnaeus, 1758) y *Scyliorhinus canicula* (Linnaeus, 1758)) del Banco de Porcupine, situado al noreste del Atlántico. Los análisis estomacales revelaron diferencias en la dieta de las tres especies, con una clara preferencia por presas bentónicas en el caso de *S. canicula*, y presas bentopelágicas en el caso de *E. spinax* y *G. melastomus*. Los resultados de este estudio proporcionan nuevos conocimientos sobre el papel ecológico de estas especies en el Banco de Porcupine que serán de crucial importancia para la gestión y conservación de estas especies.

Palabras clave: Tiburones, contenido estomacal, noreste del Atlántico.

ABSTRACT | Feeding habits, diets and trophic relationships among three demersal sharks (*Galeus melastomus* Rafinesque, 1810; *Etmopterus spinax* (Linnaeus, 1758); and *Scyliorhinus canicula* (Linnaeus, 1758)) from the Porcupine Bank, Northeast Atlantic were studied. The stomach content analysis revealed differences between the diet of the three species, with a clear preference for benthonic preys in the case of *S. canicula*, and benthopelagic preys in the case of *E. spinax* and *G. melastomus*. The results of this study provide new knowledge about the ecological role of these species in the Porcupine Bank and will be of vital importance for their management and conservation of these species.

Palabras clave: Sharks, stomach content, Northeast Atlantic.

INTRODUCTION

Understanding the trophic ecology of keystone species is essential to determine their role in marine ecosystems (Ferretti, Worm, Britten, Heithaus, & Lotze, 2010; Dulvy *et al.*, 2014). Deep-sea sharks are considered important predators on marine food webs playing an important role in top-down controls on the dynamics of many ecosystems (Wetherbee, Cortés, & Bizzarro, 2012). During the last decades, elasmobranchs have become the focus of ecological studies (Ferretti, *et al.*, 2010; Dulvy, *et al.*, 2014; Navia, Mejia-Falla, Lopez-Garcia, Giraldo, & Cruz-Escalona, 2017). Nevertheless, only a few studies have focused on the interactions among sympatric elasmobranchs species, which is essential to understand how elasmobranchs coexist in the same habits (Albo-Puigserver *et al.*, 2015; Barria, Navarro, & Coll, 2018; Yemiskan, Navarro, Forero, Megalofonou, & Eryilmaz, 2019).

The small-spotted catshark, also known as the sandy dogfish, lesser-spotted dogfish, *Scyliorhinus canicula* (Linnaeus, 1758), and the blackmouth catshark, *Galeus melastomus* (Rafinesque, 1810, are the most caught shark species by Spain's commercial trawl fleet in the Northeast Atlantic, with reported commercial catches of 816 and 108 ton, respectively (FAO, 2020). The velvet belly lantern shark, *Etmopterus spinax* (Linnaeus, 1758), was one of the most discarded species; however, the reported annual commercial catches decreased from 75 ton in 2005 to 5 ton in 2018 (FAO, 2020). Therefore, this species is considered near threatened by the International Union for Conservation of Nature (IUCN) (Guallart *et al.*, 2021). Although some aspects of the diet of these species have been reported in previous studies, their feeding habits on the Porcupine Bank has not yet been described.

In this study, we investigated the diet, feeding habits and trophic relationships of three species of demersal sharks (*Galeus melastomus*, *Scyliorhinus canicula* and *Etmopterus spinax*) coexisting in the Porcupine Bank (Northeast Atlantic) using stomach contents.

MATERIAL AND METHODS

The Porcupine Bank located is located 200 km off the west coast of Ireland, within the Irish exclusive economic zone. Oceanographic conditions, such as anticyclonic flows and a partly closed circulation pattern, made this area suitable for species settlement.

In September and October 2020, a total of 78 velvet belly lantern sharks, 161 of the blackmouth catsharks and 67 of the lesser spotted dogfish were caught during the fishery-independent Spanish Bottom Trawl Survey on the Porcupine Bank (SP-PORC-Q3), which extends from 12°W to 15°W and

from 51°N to 54°N, at depths ranging from 200 to 800 m. Elasmobranchs were measured (to the nearest cm) and weighted (to the nearest g).

All stomachs were dissected and analysed at sea. Prey items were separated, counted, and identified to the lowest possible taxonomic level. The volume of each prey in each stomach was measured using a trophometer, a calibrated instrument that consists of several different-sized cylinders built into a tray, as used in previous studies (Olaso, Velasco, & Pérez, 1998; Olaso *et al.*, 2005; Valls, Quetglas, Moranta, & Ordines, 2011). Fully and partially digested fishes and cephalopods were identified by their otoliths and beaks, respectively, using identification guides (Clarke *et al.*, 1986). Digested crustaceans were identified from exoskeleton fragments (e.g. rostra, mandibles and telson). Stomachs containing only hard parts such as otoliths, eyes and fish bones were considered empty.

The relative importance of each prey in the diet was assessed by the following indices: (a) frequency of occurrence (%O_i = number of stomachs with the prey *i* / total number of non-empty stomachs); (b) numerical (%N) and volumetric (%V) composition, expressed as the percentage contribution (in number or volume) of each prey to the whole content, ; (c) index of relative importance (IRI = %F(%N+%V), which was standardized following %IRI=(IRI/∑IRI)100 (Cortés, 1997). The vacuity index (*v*; the percentage of empty stomachs) was also calculated. Trophic diversity was assessed with the Shannon-Wiener diversity index (*H*_i): $H_i = - \sum(p_i) (\ln p_i)$; where *p*_i is the numeric proportion of prey *i* in the diet.

To standardize our data and facilitate diet comparisons among species, the following five major prey categories were considered: SHRIMP (shrimp-like crustaceans including shrimps, euphausiids and mysid); OCRUS (other crustaceans including *Brachyura* crabs, ostracods, amphipods, isopods, and unidentified crustaceans), CEPH (cephalopods), FISH (teleost) and OTHERS (including polychaeta, tunicate, cnidaria and other unidentified preys).

Differences in diet based on %V among species were tested using multivariate techniques (PERMANOVA test). PERMANOVA analysis was based on Canberra resemblance matrix after a fourth-root transformation. A multivariate test for homogeneity of variance (PERMDISP) was performed to analyse the multivariate dispersion among size classes and depths strata. All multivariate analyses were performed with R software (R Development Core Team, 2020). The significance level used for all tests was $p < 0.05$.

Feeding strategy was represented graphically by a two-dimensional representation of the prey-specific abundance (%P_i) and the frequency of occurrence (%F) (Amundsen, Gabler, & Staldvik,

1996). This graphical method is a modification to the Costello (1990) method and provides information on prey importance, feeding strategy, and the inter- and intra-individual components of the niche width to be explored together. The prey-specific abundance ($\%P_i$) was calculated as follows: $\%P_i = (\sum S_i / \sum S_t) 100$, where $\sum S_i$ is the sum of the volume of prey i , and $\sum S_t$ is the sum of stomach content of those predators with the prey i in their stomachs. Diet breadth was calculated using the Levins' standardized index (Krebs, 1999) according to the next formula: $B_i = [1/(n-1)][1/\sum p_{ij}^2 - 1]$ where p_{ij} is the proportion of diet of predator i that is made up of prey j and n is the number of prey categories. Values of this index ranges between 0-1, where low values indicate diets dominated by few prey items (specialist behaviour) and higher values indicates generalist behaviour.

RESULTS

A total of 63 prey taxa were identified, namely 14 teleost, 11 cephalopods and 28 crustaceans (Table 1). The vacuity index (v) was clearly higher in velvet belly lantern shark (43.59%) than in the blackmouth catshark (13.66%) and the lesser spotted dogfish (4.48%). The highest dietary diversity was found in velvet belly lantern shark ($H_i = 2.18$), while the lowest diversity index was found in the blackmouth catshark ($H_i = 1.92$) (Table 2).

The diet composition of each species is summarized in this paragraph, taking into account the main prey groups and the lowest taxonomic level identified. In the blackmouth catshark, diet was mainly composed by shrimp-like crustaceans (79.86 %O, 69.75%N, 15.09%V, 64% IRI), with *Meganyctiphane norvegica* being the most frequent prey (37.41% O). However, amphipods also play an important role (42.43%O, 19.04%N and 18.91%IRI). Shrimp-like crustaceans were the most important prey group in the velvet belly lantern shark (38.64 %O, 66.15 %N, 6.55%V and 78.33%IRI), led by the euphausiids *Eusergestes arcticus* (15.26% IRI). In the lesser spotted dogfish diet, shrimp-like crustaceans were again the most representative prey group (73.44 %O, 76,30 %N, 16.13%V and 55.92% IRI), followed by teleost, being the mesopelagic species *Micromisistius potassou* an important prey (41.39%V and 18.40%IRI). In the diets of all three species, cephalopods were poorly represented.

PERMANOVA analysis indicated significant differences among the three species ($p < 0.005$). Further PERMANOVA pairwise comparisons indicated that stomach contents differed between the three species ($p < 0.005$). The PERMDISP analysis showed no significant differences ($p > 0.005$), therefore, differences in diet obtained with PERMANOVA were not due to multivariate dispersion.

Prey importance and feeding strategy of the three species are shown in Figure 2. The blackmouth catshark showed a specialist feeding behaviour. Preys such as cephalopods and teleost have a high prey-specific abundance, but they appeared at low frequencies, suggesting that they were consumed by few individuals. The velvet belly lantern shark showed a moderate specialist feeding behaviour, with teleost being the dominant prey for the whole population, while crustaceans are rarely consumed. The lesser spotted dogfish showed a mixed feeding strategy, at individual level they seem to be specialized in teleost, while shrimp-like crustaceans are mainly consumed by the entire population. Nevertheless, Levin's index showed lower values, which indicates a specialist behaviour in the three species (Table 2).

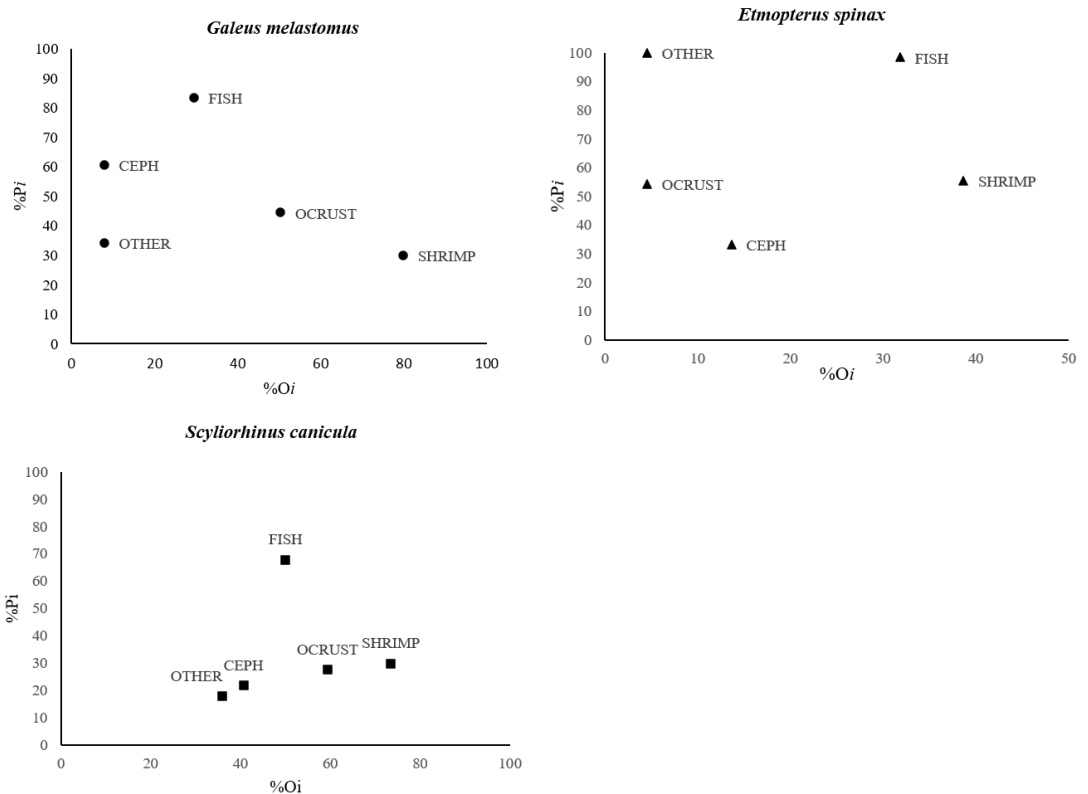


Figure 1. Graphic representation of feeding strategy for *G. melastomus* (a), *E. spinax* (b) and *S. canicula* (c) based on plots of prey-specific abundance in volume (%Pi) against frequency of occurrence of prey species (%Oi) (Amundsen, *et al.*, 1996)

Table 1. Diet composition of *Galeus melastomus*, *Etmopterus Spinax* and *Scyliorhinus canicula* off the Porcupine Bank. Occurrence (%O), numeric (%N), volumetric (%V), and standardized relative importance index (%IRI).

Prey taxa	<i>Galeus melastomus</i>				<i>Etmopterus spinax</i>				<i>Scyliorhinus canicula</i>			
	%O	%N	%V	%IRI	%O	%N	%V	%IRI	%O	%N	%V	%IRI
Fish	29.50	4.43	53.72	16.23	31.82	16.92	0.87	15.79	50.00	4.57	52.13	23.36
<i>Micromesistius poutassou</i>	8.57	1.35	31.27	6.16	2.94	1.39	8.42	2.20	25.00	2.20	41.40	18.41
<i>Lepidorhombus whiffiagonis</i>	0.71	0.10	0.09	0.01								
Myctophidae	2.14	0.67	0.49	0.06	2.94	1.39	0.17	0.35	3.13	0.24	0.22	0.02
<i>Myctophum punctatum</i>	0.71	0.10	0.08	0.01								
<i>Nezumia aequalis</i>	0.71	0.10	2.05	0.03								
<i>Stomias boa</i>	0.71	0.10	0.46	0.01								
<i>Trachurus trachurus</i>	0.71	0.10	0.17	0.01								
<i>Notoscopelus elongatus</i>	0.71	0.10	0.33	0.01								
<i>Artozenus risso</i>					2.94	1.39	4.47	1.31				
<i>Argentina</i> sp.									3.13	0.24	0.50	0.04
<i>Maurollicus muelleri</i>					5.88	5.56	0.50	2.71				
<i>Gadiculus argenteus</i>	1.43	0.38	6.05	0.20	5.88	9.72	67.44	34.59				
Other teleost	25.71	1.83	12.65	8.20	2.94	5.56	6.40	2.68	25.00	1.96	9.33	4.76
Crustaceans	79.86	69.75	15.09	64.11	38.64	66.15	6.55	78.33	73.44	76.30	16.13	55.92
<i>Meganyctiphanes norvegica</i>	37.41	17.98	4.38	18.43	5.88	8.33	1.16	4.25	7.81	6.11	1.09	0.95
<i>Eusergestes articus</i>	24.29	12.69	3.57	8.70	8.82	20.83	1.87	15.27	6.25	7.82	0.93	0.92
Euphausiacea	37.86	37.50	4.03	34.64	11.76	30.56	3.52	30.56	57.81	55.13	6.03	59.71
Mysidacea	2.14	0.19	0.16	0.02								
<i>Sergia robusta</i>	2.14	0.19	0.19	0.02								.
<i>Dichelopandalus bonierii</i>	5.00	0.58	1.84	0.27					10.94	1.71	3.60	0.98
<i>Polycheles typhlops</i>	1.43	0.19	0.01	0.01								
<i>Pasiphaea</i> sp.	0.71	0.10	0.19	0.01								
<i>Pasiphaea sivado</i>	1.43	0.29	0.69	0.03								
<i>Pleisionika</i> sp.									6.25	0.12	0.12	0.03
<i>Processa</i> sp.									3.13	0.49	0.19	0.04

Cont. Table 1

Prey taxa	<i>Galeus melastomus</i>				<i>Etmopterus spinax</i>				<i>Scyliorhinus canicula</i>			
	%O	%N	%V	%IRI	%O	%N	%V	%IRI	%O	%N	%V	%IRI
<i>Processa caniculata</i>									3.13	0.37	0.33	0.04
<i>Pontophilus</i> sp.									3.13	0.24	0.29	0.03
<i>Ponthophilus norvegicus</i>									7.81	2.32	0.76	0.41
<i>Lophogaster typicus</i>									1.56	0.12	0.03	0.00
<i>Solenocera membranecea</i>									12.50	1.10	3.04	0.87
Decapods remains	10.00	1.92	1.44	0.74	5.88	4.17	1.63	2.60	37.50	5.38	4.06	5.97
Other crustaceans	50.36	22.83	15.46	18.25	4.55	4.62	1.63	0.79	59.38	10.00	16.55	12.99
Amphipoda hyperiidae	41.43	19.04	1.67	18.91					7.81	2.08	0.44	0.33
<i>N. norvegicus</i>	6.43	0.77	6.12	0.98								
<i>Gerion trispinosus</i>	3.57	0.38	5.71	0.48								
<i>Pagurus alatus</i>									1.56	0.12	0.04	0.01
<i>Pagurus prideaux</i>									6.25	0.49	5.60	0.64
<i>Pagurus</i> sp.	1.43	0.10	0.08	0.01					9.38	0.98	0.83	0.29
<i>Munida sarsi</i>	1.43	0.10	0.02	0.01					6.25	0.49	4.93	0.57
<i>Munida</i> sp.	2.86	0.29	0.37	0.04					3.13	0.24	0.52	0.04
<i>Gonaplex romboides</i>	0.71	0.10	0.01	0.01								
Brachyura	0.71	0.10	0.02	0.01								
Cephalopods	7.91	1.06	13.97	1.13	13.64	9.23	2.49	4.46	40.63	3.58	9.73	4.46
<i>Histioteuthis reversa</i>	5.71	0.67	12.17	1.62	2.94	4.17	2.15	1.42				
Teuthida					2.94	1.39	0.21	0.36				
Optopodidae									4.69	0.37	0.31	0.05
Sepiolidae									3.13	0.37	0.87	0.07
Omastrephidae	1.43	0.10	0.01	0.01	2.94	1.39	0.09	0.33				
<i>Bathipolipus sponsalis</i>	0.71	0.10	0.10	0.01	2.94	1.39	0.04	0.32	3.13	0.24	0.29	0.03
<i>Todarodes sagitatus</i>	0.71	0.10	1.01	0.02								
<i>Todaropsis eblanae</i>									6.25	0.49	3.55	0.43

Cont. Table 1

Prey taxa	<i>Galeus melastomus</i>				<i>Etmopterus spinax</i>				<i>Scyliorhinus canicula</i>			
	%O	%N	%V	%IRI	%O	%N	%V	%IRI	%O	%N	%V	%IRI
<i>Eledone cirrosa</i>									3.13	0.24	0.17	0.02
<i>Illex condietii</i>	0.71	0.10	0.67	0.01					1.56	0.12	0.81	0.02
Cephalopoda unidentified									20.31	1.71	3.70	1.86
Others	7.91	1.93	1.80	0.28	4.55	3.08	1.93	0.64	35.94	5.56	5.51	3.28
Polychaeta	2.14	0.58	0.07	0.03					14.06	1.22	0.58	0.43
Lumbrineridae									3.13	0.12	0.24	0.02
Afroditidae									1.56	0.24	0.13	0.01
Hipolitidae									1.56	0.12	0.00	0.00
<i>Pontobdella</i> sp.									4.69	0.37	0.37	0.06
<i>Ophiura ophiura</i>	1.43	0.10	0.01	0.01					1.56	0.12	0.01	0.01
<i>Actinauge richardii</i>									1.56	0.12	0.70	0.02
Salpidae	5.71	0.87	1.34	0.28	2.94	1.39	1.72	0.70	17.19	2.93	3.32	1.82
Unidentified remains	2.14	1.44	0.38	0.09	2.94	1.39	0.21	0.36	3.13	0.73	0.14	0.05

Table 2. Data summary of the three species used in this study including number of individuals sampled, total length range, percentage of stomachs containing prey (%Vi), Shanon-Wiener diversity (Hi) and Levin´s niche breadth.

Species	N° sampled	Total length (cm)	Non-empty stomachs (Vi%)	Shanon-Wiener index (Hi)	Levin´s index
<i>G. melastomus</i>	161	21-78	13.66	1.91	0.09
<i>E. spinax</i>	78	17-69	43.59	2.18	0.33
<i>S. canicula</i>	67	23-85	4.48	1.99	0.05

DISCUSSION

In the present study, the feeding habits and trophic ecology of three demersal sharks that inhabit the Porcupine Bank were studied. Based on the results of the stomach content analysis, differences in diet were found among the three species. The vacuity index was clearly higher in *E. spinax*, which had almost half of its stomachs empty. Cephalopods are known to have high nutritional values and few non-

edible remains (Boyle & Rodhouse, 2005), this fact could explain their high vacuity index and the large presence of beaks in several stomachs.

Stomach contents revealed that the diet of *G. melastomus* was mainly composed by euphausiids and teleost remains, in agreement with other previous studies conducted in the Mediterranean Sea (Fanelli, Rey, Torres, & de Sola, 2009; Valls, *et al.*, 2011; Anastasopoulou *et al.*, 2013; Barria, *et al.*, 2018) and Atlantic waters (Santos & Borges, 2001; Olaso, *et al.*, 2005; Neiva, Coelho, & Erzini, 2006; Neves, Figueiredo, Moura, Assis, & Gordo, 2007). Although *S. canicula* also included teleost in its diet, crustaceans were important prey for this species, contributing in large proportions to its diet. *Micromessistius poutassou* is an important species of the demersal catches landed and discarded by the trawler fleet in the Northeast Atlantic (Pérez *et al.*, 1996). Its high occurrence in the stomachs of both selachian sharks suggest that both are consumers of fishery discards (Olaso, *et al.*, 1998). The absence of benthic preys such as polychaetes and reptantid decapods in the diet of *E. spinax* suggest that do not forage in the benthic macrofauna, as reported by other authors (Neiva, *et al.*, 2006; Aranha, Menezes, & Pinho, 2009).

Significant components of the three diets were species with pelagic affinities, including benthopelagic organisms and vertically migrating species usually associated with the Benthic Boundary Layer (BBL) such as *Meganyctiphanes norvegica* and *Eusergestes articus*. The BBL is considered an important pathway in the exchange of matter and energy between the pelagic and benthic ecosystem. The presence of pelagic species at bottom depths makes them available to predators foraging in the BBL (Mauchline & Gordon, 1991; Cartes, 1998), connecting demersal sharks with the pelagic environment.

The existence of interspecific differences in their sensory adaptations to a deep-water environment could explain differences in the dietary composition (Olaso, *et al.*, 2005; Preciado *et al.*, 2009; Barria, *et al.*, 2018). The well-developed olfactory lobe and a high sense of electroreception in *S. canicula* probably offers a greater capacity to locate preys near the sea floor such as crustaceans and polychaetes. In contrast, *G. melastomus* and *E. spinax* have larger eyes, adapted to great depths, that enhance hunting mesopelagic preys found in mid-water depths. Furthermore, most of the benthopelagic assemblage consumed by *E. spinax* and *G. melastomus* were bioluminescent such as *M. norvegica*, *Pasiphaea* sp. or myctophids. Bozzano *et al.* (2001), suggest that the visual pigments of *G. melastomus* have absorption peaks coinciding with the wave lengths emitted by them. *E. spinax* is thought to have the same visual adaptations to capture these bioluminescent preys (Neiva, *et al.*, 2006).

The three sharks are considered generalist feeders (Olaso, *et al.*, 2005; Neiva, *et al.*, 2006; Neves, *et al.*, 2007; Preciado, *et al.*, 2009; Anastasopoulou, *et al.*, 2013; Barria, *et al.*, 2018; Bengil *et al.*, 2019). Yet, the low niche breadth, measured by the standardised Levin's index, suggested a specialist feeding behaviour in the three of them. However, these results should be taken with skepticism, the specialization could reflect the predominance of a few species in the Porcupine food web rather than to feeding on specific resources. Additionally, results in the feeding strategy of *G. melastomus* and *S. canicula* suggested that the populations' broad niches were composed by certain individuals that have narrower niches. An environment with patchy resources could be the main reason of this high level of individuals' specialization in both populations. This fact is agreement with the idea proposed by Bolnick *et al.* (2002), who reported that many apparently generalized populations are in fact composed of individuals specialist using different sub-set of the population resources.

In conclusion, this study presents information on the feeding ecology of three highly exploited demersal sharks (*G. melastomus*, *E. spinax* and *S. canicula*) in the Porcupine Bank, Northeast Atlantic. The results indicate differences in the diet among species. Although the three of them are generalist feeders, the specialist behaviour showed by them could be related to patchy resources. These results can be used by managers to conduct effective conservation strategies and management plans in the Porcupine Bank.

Acknowledgements

We would like to thank the crew of the R/V Vizconde de Eza and the scientific team of the Spanish Institute of Oceanography (IEO) that made the research survey possible. Special thanks are also due to Carlos Farias, Eduardo López, and Miguel Angel Cortés for their invaluable assistance in prey identification. The Spanish Bottom Trawl Survey on the Porcupine Bank (SP PORC-Q3) was funded in part by the EU through the European Maritime and Fisheries Fund (EMFF) within the Spanish National Program of collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy.

REFERENCES

Albo-Puigserver, M., Navarro, J., Coll, M., Aguzzi, J., Cardona, L., & Saez-Liante, R. (2015). Feeding ecology and trophic position of three sympatric demersal chondrichthyans in the Northwestern Mediterranean. *Marine Ecology Progress Series*, 524, 255-268. doi: 10.3354/meps11188

- Amundsen, P. A., Gabler, H. M., & Staldvik, F. J. (1996). A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. *Journal of Fish Biology*, 48(4), 607-614. doi: 10.1111/j.1095-8649.1996.tb01455.x
- Anastasopoulou, A., Mytilineou, C., Lefkaditou, E., Dokos, J., Smith, C. J., Siapatis, A., . . . Papadopoulou, K. N. (2013). Diet and feeding strategy of blackmouth catshark *Galeus melastomus*. *Journal of Fish Biology*, 83(6), 1637-1655. doi: 10.1111/jfb.12269
- Aranha, A., Menezes, G., & Pinho, M. R. (2009). Biological aspects of the velvet belly lantern shark, *Etmopterus spinax* (Linnaeus, 1758) off the Azores, North East Atlantic. *Marine Biology Research*, 5(3), 257-267. doi: 10.1080/17451000802433175
- Barria, C., Navarro, J., & Coll, M. (2018). Feeding habits of four sympatric sharks in two deep-water fishery areas of the western Mediterranean Sea. *Deep-Sea Research Part I-Oceanographic Research Papers*, 142, 34-43. doi: 10.1016/j.dsr.2018.09.010
- Bengil, F., Bengil, E. G. T., Mavruk, S., Heral, O., Karaman, O. D., & Ozaydin, O. (2019). Feeding Ecology of Four Demersal Shark Species (*Etmopterus spinax*, *Galeus melastomus*, *Scyliorhinus canicula* and *Squalus blainville*) from the Eastern Aegean Sea. [Article]. *Turkish Journal of Fisheries and Aquatic Sciences*, 19(6), 475-484. doi: 10.4194/1303-2712-v19_6_03
- Bolnick, D., Yang, L., Fordyce, J., Davis, J., & Ck, R. (2002). Measuring Individual-Level Resource Specialization. *Notes 2936 Ecology*, 83, 2936-2941. doi: 10.2307/3072028
- Boyle, P., & Rodhouse, P. (2005). *Cephalopods: Ecology and Fisheries*. Oxford, UK.
- Bozzano, A., Murgia, R., Vallerga, S., Hirano, J., & Archer, S. (2001). The photoreceptor system in the retinae of two dogfishes, *Scyliorhinus canicula* and *Galeus melastomus*: possible relationship with depth distribution and predatory lifestyle. [Article]. *Journal of Fish Biology*, 59(5), 1258-1278. doi: 10.1006/jfbi.2001.1737
- Cartes, J. E. (1998). Dynamics of the bathyal Benthic Boundary Layer in the northwestern Mediterranean: depth and temporal variations in macrofaunal–megafaunal communities and their possible connections within deep-sea trophic webs. *Progress in Oceanography*, 41, 111-139. doi: 10.1016/S0079-6611(98)00018-4

- Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 726-738. doi: 10.1139/cjfas-54-3-726
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., . . . White, W. T. (2014). Extinction risk and conservation of the world's sharks and rays. *eLife*, 3. doi: 10.7554/eLife.00590
- Fanelli, E., Rey, J., Torres, P., & de Sola, L. G. (2009). Feeding habits of blackmouth catshark *Galeus melastomus* Rafinesque, 1810 and velvet belly lantern shark *Etmopterus spinax* (Linnaeus, 1758) in the western Mediterranean. *Journal of Applied Ichthyology*, 25, 83-93. doi: 10.1111/j.1439-0426.2008.01112.x
- FAO. (2020). FIGIS Data Collection, from <http://www.fao.org/figis>.
- Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, 13(8), 1055-1071. doi: 10.1111/j.1461-0248.2010.01489.x
- Krebs, C. J. (1999). *Ecological methodology*. New York: Harper Collins Publishers.
- Mauchline, J., & Gordon, J. (1991). Oceanic prey of benthopelagic fish in the benthic boundary layer of a marginal oceanic region. *Marine Ecology-progress Series*, 74, 109-115. doi: 10.3354/meps074109
- Navia, A. F., Mejia-Falla, P. A., Lopez-Garcia, J., Giraldo, A., & Cruz-Escalona, V. H. (2017). How many trophic roles can elasmobranchs play in a marine tropical network? [Article]. *Marine and Freshwater Research*, 68(7), 1342-1353. doi: 10.1071/mf16161
- Neiva, J., Coelho, R., & Erzini, K. (2006). Feeding habits of the velvet belly lanternshark *Etmopterus spinax* (Chondrichthyes: Etmopteridae) off the Algarve, southern Portugal. *Journal of the Marine Biological Association of the United Kingdom*, 86(4), 835-841. doi: 10.1017/s0025315406013762
- Neves, A., Figueiredo, I., Moura, T., Assis, C., & Gordo, L. (2007). Diet and feeding strategy of *Galeus melastomus* in the continental slope off southern Portugal. *Vie et Milieu*, 57, 165-170.

- Olaso, I., Velasco, F., & Pérez, N. (1998). Importance of discarded blue whiting (*Micromesistius poutassou*) in the diet of lesser spotted dogfish (*Scyliorhinus canicula*) in the Cantabrian Sea. *Ices Journal of Marine Science*, 55(3), 331-341. doi: 10.1006/jmsc.1997.0263
- Olaso, I., Velasco, F., Sánchez, F., Serrano, A., Rodríguez-Cabello, C., & Cendrero, O. (2005). Trophic relations of lesser-spotted catshark (*Scyliorhinus canicula*) and blackmouth catshark (*Galeus melastomus*) in the Cantabrian Sea. *Journal of Northwest Atlantic Fishery Science*, 35, 481-494. doi: 10.2960/J.v35.m494
- Preciado, I., Cartes, J. E., Serrano, A., Velasco, F., Olaso, I., Sánchez, F., & Frutos, I. (2009). Resource utilization by deep-sea sharks at the Le Danois Bank, Cantabrian Sea, north-east Atlantic Ocean. *Journal of Fish Biology*, 75, 1331-1355. doi: 10.1111/j.1095-8649.2009.02367.x
- Santos, J., & Borges, T. (2001). Trophic relationships in deep-water fish communities off Algarve, Portugal. *Fisheries Research*, 51, 337-341. doi: 10.1016/s0165-7836(01)00257-0
- Valls, M., Quetglas, A., Moranta, J., & Ordines, F. (2011). Feeding ecology of demersal elasmobranchs from the shelf and slope off the Balearic Sea (western Mediterranean). *Scientia Marina*, 75, 633-639. doi: 10.3989/scimar.2011.75n4633
- Wetherbee, B., Cortés, E., & Bizzarro, J. (2012). Food Consumption and Feeding Habits. In J. Carrier, J. A. Musick & M. R. Heithaus (Eds.), *Biology of Sharks and Their Relatives II* (pp. 239-264). Boca Raton: CRC Press.
- Yemiskan, E., Navarro, J., Forero, M., Megalofonou, P., & Eryilmaz, L. (2019). Trophic partitioning between abundant demersal sharks coexisting in the North Aegean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 99(5), 1213-1219. doi: 10.1017/s0025315419000110.

