Structure and composition of the deep-sea fish community between 150 and 2050 m depth on the Canary Islands, eastern-central Atlantic

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ABSTRACT

The structure and composition of the deep-sea fish community living on the slope off the Canary Islands (eastern-central Atlantic) were investigated. Data were collected by means of eight research cruises (165 stations) at depths between 150 and 2050 m. A total of 4475 fish specimens belonging to 43 families and 78 species (21 Elasmobranchii, 1 Holocephali, and 56 Actinopterygii) were collected with longlines. In the number of individuals, the deep-sea demersal fish fauna was dominated by fishes of the family Synaphobranchidae, followed by Sparidae, Somniosidae, Centrophoridae, and Trichiuridae. The main abundant species were *Synaphobranchus affinis, Dentex macrophthalmus, Pagellus acarne, Zameus squamulosus, Aphanopus carbo, Squalus megalops, Centroscymnus coelolepis,* and *Centroscymnus owstonii.* Elasmobranchs, with 1519 individuals, showed a high abundance (33.94%) on the longlines, although their importance increased when the data were analysed by weight, reaching 54.07% (4588 kg), with *Zameus squamulosus* being the fourth most important species.

1. Introduction

Deep-sea ecosystems are considered the largest biome in the biosphere (Romano et al., 2017; Dunlop et al., 2018; Grinyó et al., 2022); however, their structure and biodiversity are not adequately known (Danovaro et al., 2017; Romano et al., 2017; Sinclair et al., 2022). This is particularly true for areas outside the main productive regions (Frederick et al., 2018), such as around the oligotrophic islands of the eastern-central Atlantic, which are outside of the highly productive northwestern African boundary coastal upwelling systems (Frederick et al., 2018).

From the hydrography and oceanography perspective, the eastern-central Atlantic region (FAO area 34) is one of the most intensively investigated marine ecosystems in the world. Numerous studies conducted off the coasts of North Western Africa from the continental shelf to the abyssal plains (e.g., Merrett and Marshall, 1981; Merrett and Domanski, 1985a, 1985b; Pajuelo et al., 2016), but outside of this areas the distribution of demersal deep fish fauna is poorly known. Only one study done off the island of Fuerteventura and Lanzarote (up to 1100 m depth), the islands of the Canary archipelago closest to the African continent, has been reported (Uiblein et al., 1996). The archipelagos located in the eastern-central Atlantic region have different climate regimes and geological evolution. In the Azores and Cape Verde archipelagos, the deep fish fauna has been explored down to 1100–1300 m (Menezes et al., 2006, 2009, 2015). The Canary Islands are in the extreme North of this area perpendicular to the main flow of the Canary Current. These waters are oligotrophic (Davenport et al., 2002) with some influence of coastal upwelling off Northwest Africa as plumes or filaments (Barton et al., 2004). The Canary archipelago is hydrologically characterized by the presence of four water masses located at different depths, each of those with different thermohaline properties (Hernández-Guerra et al., 2001, 2002, 2003; Machín et al., 2006). Although some deep-sea fish species inhabiting island slopes are caught by artisanal deep-water fisheries in this area (Pajuelo et al., 2010), relatively little is understood about how deep-sea fish are spatially distributed, and this information is required for high-quality data in management

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decisions (Milligan et al., 2016).

Islands and seamounts emerging from the ocean floor, such as occurs along the mid-ocean ridge, provide bathyal habitat surrounded by abyssal plains in areas distant from continental slopes, enhance and host benthic biomass, and increase ecosystem heterogeneity on a regional scale (Priede et al., 2013a, 2013b; Alt et al., 2019).

The deep-sea benthic communities along slopes are often structured by geography, habitat and depth (Delavenne and Keszler, 2019); they have also been related to environmental factors such as water mass, temperature, salinity or oxygen content (Stefanescu et al., 1993; Clark et al., 2010; Pajuelo et al., 2015; de la Torriente et al., 2018). Water masses can determine the distribution and community composition of deep-water fishes because they involve critical abiotic factors and also play an important role in larval dispersion over large areas or act as barriers to larval (Menezes et al., 2009, 2015; González et al., 2016; Quattrini et al., 2017).

Deep-sea fish communities are composed of long-lived and slow-growing species with late maturity, low recruitment rates, low resilience to human impacts and a very slow recovering capacity (FAO, 2009a,b; Huvenne et al., 2016; Clark et al., 2019; O'Hea et al., 2020; Grinyó et al., 2022).

Fish communities inhabiting the shelves of the Canary Islands are characterized by a high number of species and are the most well-studied marine fauna around the islands. However, less is known about deep fish species. Studies on demersal deep-sea fish fauna have only been conducted from a faunistic perspective in the Canary Islands (Uiblein et al., 1996). However, the present study examines the community of demersal deep-sea fish along the depth gradient from 150 to 2050 m on the slope of a volcanic oceanic island and analyses the variations in their abundance, biomass, distribution, diversity, and dominance by depth and their possible connections with hydrographic characteristics. Understanding the way in which deep-sea fish species are distributed in deep-sea ecosystems is essential to develop appropriate management plans for their conservation because it provides information on the distribution, composition, and structure of communities (Menezes et al., 2015; Milligan et al., 2016).

2. Materials and methods

2.1. Study area and sampling procedure

The Canary Islands comprise eight volcanic oceanic islands, together with some small islets located in the eastern-central Atlantic. These islands formed by underwater structures that rise abruptly from the ocean floor from depths of more than 4000 m on some cases. Hydrologically, these islands are characterized by the presence of four water masses: the Eastern North Atlantic Central Water (ENACW), the Antarctic Intermediate Water (AIW), the Mediterranean Water (MW), and the North Atlantic Deep Water (NADW), which are located at different depths and have characteristic thermohaline properties (Ríos et al., 1992; Hernández-Guerra et al., 2002, 2003). (Hernández-Guerra et al., 2001; Knoll et al., 2002; Pelegrí et al., 2005).

Data were collected during eight experimental fishing surveys with bottom longlines conducted from February 2015 to November 2017 between 150 and 2050 m of depth. Sampling was performed around the entire perimeter of the central island (Gran Canaria) (Fig. 1). Due to the abrupt submarine topography of the island, which was formed by irregular volcanic rocks and escarpments, it was not possible to sample by trawling. Instead, longlines were used, the efficiency of which has been confirmed by their use in commercial fishing and scientific studies on fishes in the Azores and Cape Verde Islands (Menezes et al., 2006, 2015).

The gear used was a horizontal bottom buoy/stone longline which was composed of 50 m long units, with alternating floats and sinkers, which were connected to each other when the gear was fully deployed (Menezes et al., 2006, 2015). Each unit was equipped with 30, no. 6–9, J-type hooks. The gear soaking time for all stations was approximately 6 h. For each sampling operation, the longline was fully deployed in the same bathymetric strata, and Atlantic chub mackerel (*Scomber colias*) was used as bait.

Stations (n = 155, 165-valid and total-) covered a bathymetric range between 150 and 2050 m deep and included 37 (40) stations at depths between 150 and 500 m, 48 (50) stations between 501 and 1000 m, 39 (40) stations between 1001 and 1500 m and 31 (35) stations between 1500 and 2050 m. At each station, data on the salinity and temperature 3 m above the seafloor were recorded using a CTD sensor. This information was used to assign each station to a water mass.
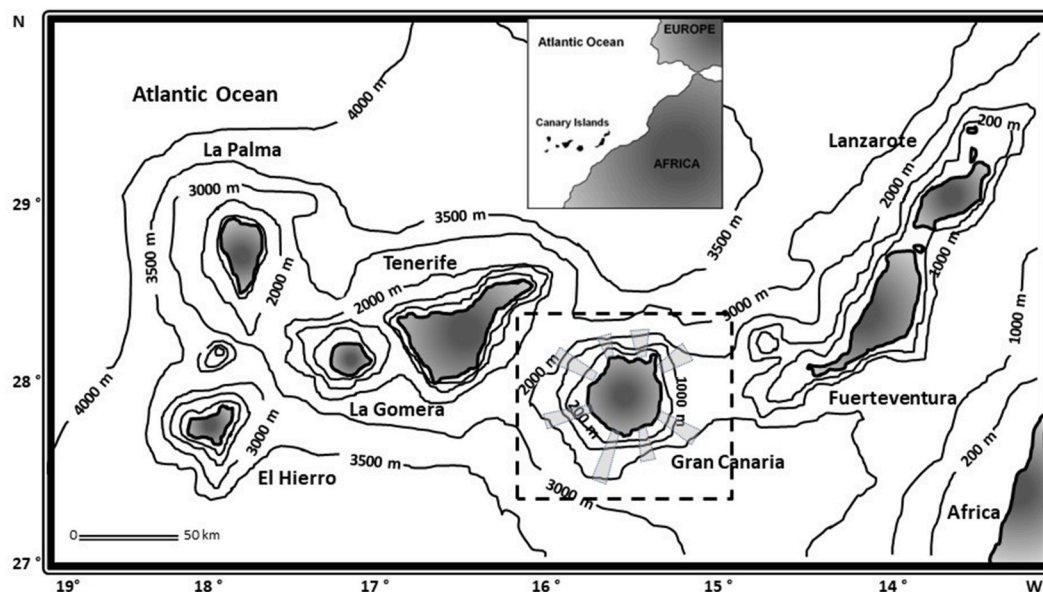
Specimens were identified to species level. Taxonomical

Fig. 1. Geographical location of the study area. Gray areas indicate the stations' locations.

arrangement followed WoRMS (2022). For each collected species, the weight of each individual caught.

2.2. Data analysis

The analyses were focused on benthic and benthopelagic fish species, excluding other groups. For each longline, the species composition, abundance (expressed as the number of individuals/1000 hooks) and biomass (expressed as kg/1000 hooks) were estimated following Menezes et al. (2006, 2015). Species with only one individual present in all samples were removed from the further analysis (Fanelli et al., 2011; Cartes et al., 2014). Data were standardized and logarithmically transformed prior to the analysis (Clarke and Warwick, 2001), after which Bray–Curtis similarity matrices were generated to analyse the data (Clarke and Warwick, 2001; Clarke and Gorley, 2006).

Nonparametric multidimensional scaling ordination (nMDS) was used to examine the sample's relationships on a two-dimensional ordination plane using the standardized abundance data (Clarke and Warwick, 2001; Clarke and Gorley, 2006). The factors considered to explain the ordination of the samples were depth, island, and season. Three assemblages were observed by depth in the nMDS analysis, and they were evaluated using distance-based permutational multivariate analysis of variance (PERMANOVA) (Anderson et al., 2008). PERMANOVA was performed to evaluate three null hypotheses of no differences among the sample assemblages among island area among the seasons, and among three strata depths observed in nMDS (150–300, 300–750, and 750–2050 m). The experimental design was a three-way crossed design with fixed levels for each factor: island area (with four levels, cardinal areas), depth (with three levels), and season (with four levels). The permutation method used was the permutation of residuals under a reduced model with a maximum number of permutations of 9999 due to their good empirical results in the maximum discriminant power (Anderson and Legendre, 1999; Anderson and ter Braak, 2003). For each factor, a *pseudo-F* test (*p-F*) and a pairwise test for significant effects were estimated. The similarity percentage analysis procedure (SIMPER) was used to determine the main species that characterize each assemblage for abundance and biomass data (Clarke and Warwick, 1994, 2001). Statistical analyses were performed by using Primer v.6 with PERMANOVA + software (Clarke and Warwick, 1994; Anderson et al., 2008). All results were considered significant at $p < 0.05$.

The measures of species diversity were estimated for abundance and biomass data with the Shannon–Wiener diversity index (H') using the DIVERSE subroutine within Primer v.6 software. The measures of species diversity were tested for differences among assemblages by an ANOVA test, considering each station as one observation. This analysis was used to evaluate the null hypothesis of equality in means H' among the assemblages, with a significance level of 5% ($\alpha = 0.05$) and a critical value of $F_{0.05, 3, 78} = 2.74$.

The depth trends of the standardized abundance and biomass data and diversity data were explored as functions of depth with generalised additive models (GAMs) (Hastie and Tibshirani, 1990). Models were tested using smoothing splines of depth (as a continuous variable) with factors such as island and season as explanatory variables. This analysis including different interactions (such as depth × island; depth × season) allowed us to test relationships of abundance and diversity with depth potentially differing among levels of the factors. GAM models were used to explore curvilinear relationships with depth. Models for abundance were tested with Gaussian, Poisson and negative binomial errors, and their adequacy was gauged according to both the percentage of the total deviance explained by the model (%DE) and the Akaike information criterion (AIC) (Akaike, 1970) and after inspection of the diagnostic plots. No further model selection was pursued. Models for the index of diversity were tested with Gaussian errors and examined for the abundance and biomass models. These procedures were performed with R version 4.2.1 (R Core Team, 2022) and the specialized package mgcv (Wood, 2006).

3. Results

A total of 4475 individuals (8485 kg) representing 78 fish species were recorded: 21 species of Elasmobranchii (belonging to 10 families, representing 33.94% of the individuals caught in number of individuals and 54.07% in weight), one species of Holocephali (1 family, 0.13% in number of individuals and 0.60% in weight), and 56 species of Actinopterygii (32 families, 65.93% in number of individuals and 45.33% in weight) (Table 1). In terms of individuals, fauna was dominated by the family Synaphobranchidae (14.72%), followed by Sparidae (14.39%), Somniosidae (13.25%), Centrophoridae (10.59%), and Trichiuridae (6.50%). *Synaphobranchus affinis* (11.06%), *Dentex macrophthalmus* (5.83%), *Pagellus acarne* (5.47%), *Zameus squamulosus* (4,84%), *Centrophorus squamosus* (4.47%), *Aphanopus carbo* (3.79%), *Squalus megalops* (3.71%), *Centroscymnus coelolepis* (3.64%), and *Centroscymnus owstonii* (3.10%) were the most abundant species. Elasmobranchs, with 1519 individuals, showed a high abundance on the longlines, although their importance increased when the data were analysed by weight, reaching 4588 kg, with *Z. squamulosus* being the fourth most important species. An nMDS performed for abundance and biomass showed three assemblage patterns at depth (Fig. 2A and B). Longline abundance data showed three well-defined assemblages that basically aggregated as a function of depth. Each assemblage is formed by longlines made at depths of 150–300 m, 300–750 m, and more than 750 m (Fig. 2A and B).

The results of PERMANOVA in abundance and biomass indicate significant differences in the demersal fish assemblage among the depth strata observed in nMDS (abundance *p-F* = 20.77, *p* = 0.001; biomass *p-F* = 20.12, *p* = 0.001) (Table 2). Pairwise comparisons showed that the longlines (assemblages) among the depth strata were significantly different in all cases (*t* > 3.37, *p* < 0.0001). No significant differences were observed between the depth strata, seasons or islands area crossed with other factors (*p-F*<0.90, *p* > 0.5968).

The results of the SIMPER analysis revealed that the most important species contributing to the similarity and dissimilarity between the depth strata were found to be significantly different by PERMANOVA in abundance and biomass (Tables 3 and 4). The results of SIMPER in abundance showed that a few species provided the major contribution for defining the assemblages at depth in abundance, with the values of the dissimilarities ranging from 83.86% (between the strata 150–300 m and 300–750 m) to 99.30% (between the strata 150–300 m and 750–2050 m). Three species, *D. macrophthalmus, S. megalops* and *P. acarne,* provided the major contribution (>60%) for defining the 150–300 m assemblage. In the strata 300–750 m, *Promethichthys prometheus, Helicolenus dactylopterus, Lepidopus caudatus, Beryx decadactylus, Conger conger* and *Pontinus kuhlii* were the most characteristic species of the assemblage in abundance, which contributed >60% of the average similarity. *S. affinis*, *C. squamosus*, *C. owstonii* and *A. carbo* were the main contributors to the average similarity in abundance (>60%) of the depth area (750–2050 m).

In terms of biomass, the SIMPER results (Table 4) showed a similar pattern of high abundance values of dissimilarities between assemblages, ranging from 83.07% (between the strata 150–300 m and 300–750 m) to 98.22% (between the strata 150–300 m and 750–2050 m). Four species, *S. megalops, Dentex macrophthalmus, Conger conger* and *Pagellus acarne,* provided the major contribution (>60%) to defining the shelf and upper slope assemblage. In the depth area of the North Atlantic Central water, *Promethichthys prometheus, C. conger, H. dactylopterus* and *L. caudatus* were the most characteristic species, contributing >60% of the average similarity. *S. affinis*, *C. squamosus*, *C. owstonii* and *A. carbo* were the main contributors to the average similarity (>60%) in the depth area (750–2050 m).

The model for abundance and biomass built with Gaussian errors had good residual graphs (residuals versus predictive values and boxplot of residuals), without hints of heteroscedasticity, highest DE% (70.2%) and lowest AIC, and thus was selected among the Poisson and negative binomial models (Table 5). The Gaussian model suggests that the

Table 1
List of species arranged by families, indicating the number of individuals and weight (kg) collected, and mean abundance and biomass.

Class /Family	Species	Number Ind.	Weight (kg)	Abundance (N.I/1000 hooks)	Biomass (kg/1000 hooks)
Elasmobranchii					
Centrophoridae	*Centrophorus granulosus*	111	438.67	0.72	2.84
	Centrophorus squamosus	200	1055.99	1.17	6.17
	Deania hystricosa	51	113.26	0.66	1.47
	Deania profundorum	112	254.32	0.97	2.20
Dalatiidae	*Dalatias licha*	42	46.98	0.40	0.45
	Squaliolus laticaudus	5	0.30	0.36	0.02
Etmopteridae	*Etmopterus princeps*	64	82.75	0.50	0.65
	Etmopterus pusillus	31	17.81	0.23	0.13
Hexanchidae	*Heptranchias perlo*	46	86.52	0.98	1.84
	Hexanchus griseus	4	221.01	0.33	18.42
Pseudocarchariidae	*Pseudocarcharias kamoharai*	9	29.34	0.64	2.08
Pseudotriakidae	*Pseudotriakis microdon*	3	153.29	0.10	5.11
Pentanchidae	*Galeus melastomus*	35	43.60	0.90	1.13
Somniosidae	*Centroscymnus coelolepis*	163	484.77	1.34	3.99
	Centroscymnus crepidater	70	164.37	0.89	2.10
	Centroscymnus owstonii	139	746.61	0.91	4.86
	Somniosus rostratus	4	21.77	0.50	3.10
	Zameus squamulosus	217	245.13	2.02	2.28
Squalidae	*Squalus megalops*	166	271.46	3.357	5.49
Trikidae	*Galeorhinus galeus*	3	40.85	0.500	6.81
	Mustelus mustelus	44	69.03	5.143	8.07
Holocephali					
Chimaeridae	*Hydrolagus affinis*	6	50.59	0.263	2.22
Actinopteri					
Alepisauridae	*Alepisaurus ferox*	20	71.38	1.46	5.20
Alepocephalidae	*Alepocephalus rostratus*	2	6.33	0.17	0.53
	Narcetes erimelas	2	6.68	0.67	2.22
Aulopidae	*Aulopus filamentosus*	14	26.27	0.500	0.938
Berycidae	*Beryx decadactylus*	101	69.37	2.27	1.55
	Beryx splendens	69	40.51	1.89	1.11
Bramidae	*Brama brama*	23	35.03	0.60	0.91
	Taractichthys longipinnis	18	201.77	1.01	11.27
Bythitidae	*Cataetyx laticeps*	2	0.72	0.40	0.14
Caproidae	*Antigonia capros*	10	0.12	0.49	0.01
	Capros aper	90	9.50	2.35	0.25
Centriscidae	*Macroramphosus scolopax*	10	0.47	0.38	0.02
Chiasmodontidae	*Chiasmodon niger*	15	3.35	0.43	0.10
Colocongridae	*Coloconger cadenati*	7	10.05	1.20	1.72
Congridae	*Conger conger*	119	517.47	1.27	5.54
Epigonidae	*Epigonus telescopus*	32	81.53	0.87	2.21
Gempylidae	*Lepidocybium flavobrunneum*	26	74.07	2.71	7.73
	Promethichthys prometheus	88	286.57	1.72	5.59
	Ruvettus pretiosus	43	116.01	0.93	2.50
Gonostomatidae	*Cyclothone microdon*	1	0.25	0.20	0.05
Nettastomatidae	*Nettenchelys dionisi*	2	0.80	0.33	0.13
Macrouridae	*Bathygadus melanobranchus*	2	0.27	0.66	0.09
	Coelorinchus labiatus	3	0.90	0.33	0.10
	Coryphaenoides mediterraneus	4	3.60	0.30	0.27
	Coryphaenoides rudis	5	31.25	0.44	2.78
	Coryphaenoides thelestomus	2	2.23	0.18	0.20
Merlucciidae	*Merluccius merluccius*	6	3.55	0.09	0.05
Moridae	*Gadella maraldi*	20	8.97	0.44	0.20
	Gadella svetovidovi	5	1.79	0.67	0.24
	Lepidion guentheri	2	0.93	0.22	0.10
	Mora moro	85	149.82	0.82	1.45
Muraenidae	*Muraena helena*	56	98.03	1.23	2.15
Phycidae	*Phycis phycis*	29	38.94	0.71	0.95
Polymixiidae	*Polymixia nobilis*	48	97.72	1.71	3.48
Sciaenidae	*Umbrina canariensis*	23	31.25	0.74	1.01
Scorpaenidae	*Pontinus kuhlii*	72	28.04	1.29	0.50
	Scorpaena scrofa	28	34.56	0.83	1.03
Sebastidae	*Helicolenus dactylopterus*	99	185.20	0.74	1.39
Serranidae	*Anthias anthias*	12	0.31	0.56	0.01
Setarchidae	*Setarches guentheri*	17	2.12	0.71	0.09
Sparidae	*Dentex gibbosus*	37	324.08	5.80	50.80
	Dentex macrophthalmus	261	118.73	5.63	2.56
	Pagellus acarne	245	48.61	6.87	1.36
	Pagellus bogaraveo	51	14.81	1.16	0.34
	Pagrus pagrus	50	174.45	6.29	21.93
Synaphobranchidae	*Simenchelys parasitica*	61	5.84	0.58	0.06
	Synaphobranchus affinis	495	179.29	3.98	1.44
	Synaphobranchus kaupii	103	33.45	0.71	0.23
Tetraodontidae	*Lagocephalus lagocephalus*	38	22.26	0.92	0.54

Table 1 (*continued*)

| Class /Family	Species	Number Ind.	Weight (kg)	Abundance (N.I/1000 hooks)	Biomass (kg/1000 hooks)
	Sphoeroides pachygaster	76	23.66	1.91	0.59
Trachichthyidae	*Hoplostethus mediterraneus*	5	1.21	0.07	0.02
Trichiuridae	*Aphanopus carbo*	170	402.22	1.30	3.08
	Aphanopus intermedius	40	94.39	0.36	0.85
	Benthodesmus simonyi	34	10.30	0.26	0.08
	Lepidopus caudatus	47	89.27	0.70	1.33
Zeidae	*Zeus faber*	25	25.64	1.24	1.27
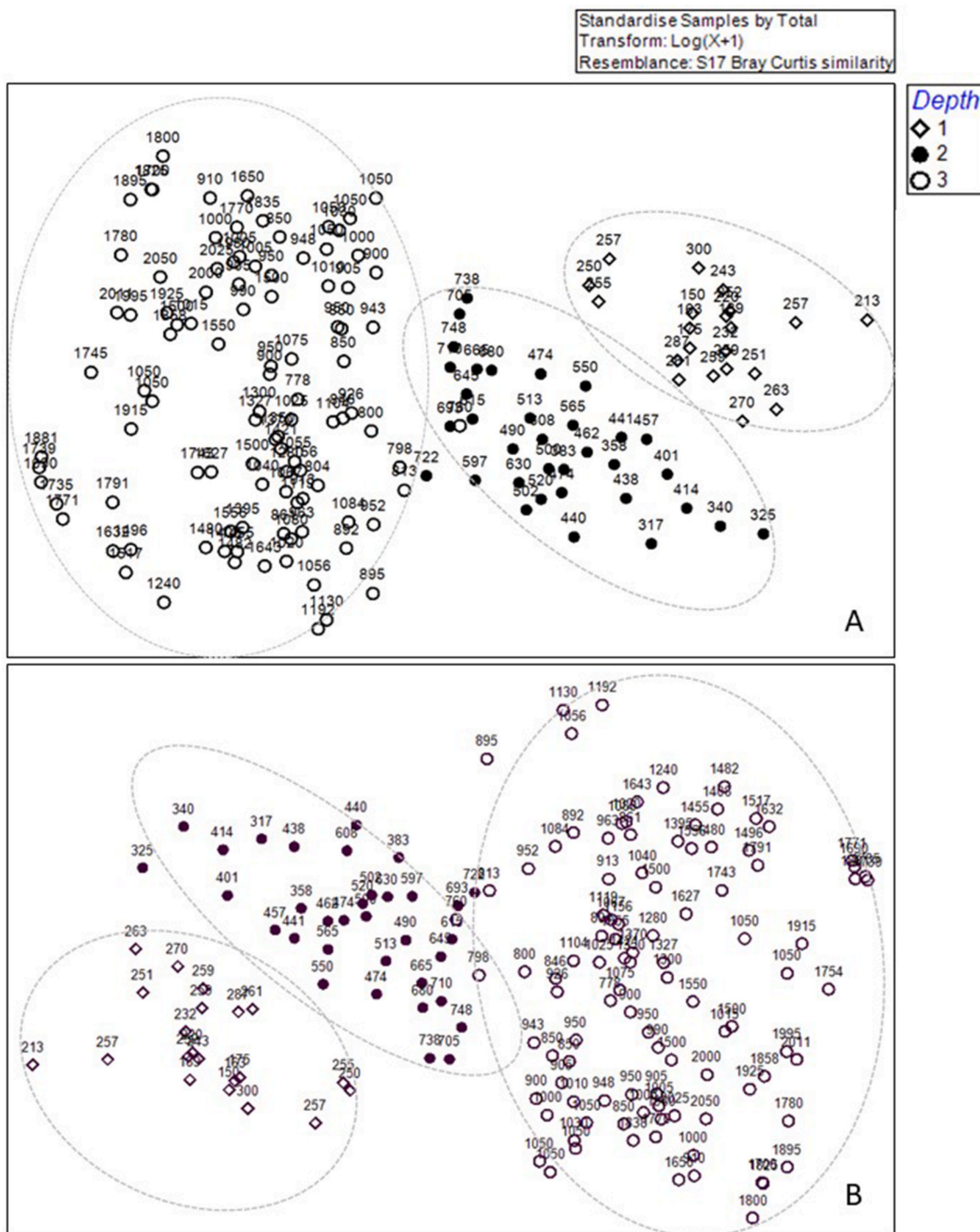
Fig. 2. Non-parametric multidimensional scaling ordination (nMDS) analysis performed on fish abundance (A) and biomass (B).

Table 2
Results of the PERMANOVA analysis for abundance and biomass data. df, degrees of freedom; MS, mean squares; *p-F, pseudo F* value; *p, p*-value; *t, t*-value.

Source	Abundance				Biomass		
	df	MS	*p-F*	*p*	MS	*p-F*	*p*
Depth	2	61154	20.77	0.0001	60105	20.12	0.0001
Island	3	1555	0.53	0.9708	1893	0.63	0.9019
Season	3	2457	0.83	0.6764	2683	0.90	0.5968
Depth × Island	6	1819	0.62	0.9815	2046	0.69	0.9416
Depth × Season	6	2606	0.88	0.6843	2584	0.87	0.7134
Island × Season	9	1877	0.63	0.9914	1764	0.59	0.9955
Depth × Island × Season	14	1937	0.66	0.9967	1901	0.64	0.9992
Residual	113	2943			2973		
Total	156						
Pair-wise test							
Depth groups	t	*p*	t	*p*			
150–300 m/300–750 m	3.4581	0.0001	3.3701	0.0001			
150–300 m/750–2050 m	4.3468	0.0001	4.1387	0.0001			
300–750 m/750–2050 m	4.8437	0.0001	4.8923	0.0001			

Table 3
Results of SIMPER routine for depth strata to analyse the contribution (C, in %; cut off = 80%) in abundance of typifying species to within-group similarity and showing species that most contribute to dissimilarity.

150–300 m Average similarity: 51.80		300–750 m Average similarity: 32.89		750–2050 m Average similarity: 23.22	
Species	C %	Species	C %	Species	C %
Dentex macrophthalmus	21.60	*Promethichthys prometheus*	13.51	*Synaphobranchus affinis*	18.41
Squalus megalops	16.13	*Helicolenus dactylopterus*	11.85	*Centrophorus squamosus*	14.26
Pagellus acarne	13.55	*Lepidopus caudatus*	10.66	*Centroscymnus owstonii*	14.17
Sphoeroides pachygaster	9.22	*Beryx decadactylus*	9.22	*Aphanopus carbo*	12.66
Conger conger	7.35	*Conger conger*	8.65	*Zameus squamulosus*	10.42
Zeus faber	6.36	*Pontinus kuhlii*	7.37	*Synaphobranchus kaupii*	6.97
Heptranchias perlo	4.90	*Ruvettus pretiosus*	6.88	*Centroscymnus coelolepis*	5.27
Pagellus bogaraveo	4.08	*Epigonus telescopus*	3.99		
		Polymixia nobilis	3.57		
		Beryx splendens	3.45		
		Galeus melastomus	2.84		

150–300 m and 300–750 m Average dissimilarity: 83.86		300–750 m and 750–2050 m Average dissimilarity: 94.32		150-300 and 750–2050 m Average dissimilarity: 99.30	
Species	C %	Species	C %	Species	C %
Dentex macrophthalmus	7.22	*Promethichthys prometheus*	4.93	*Dentex macrophthalmus*	8.17
Pagellus acarne	5.78	*Synaphobranchus affinis*	4.54	*Squalus megalops*	6.56
Squalus megalops	5.43	*Helicolenus dactylopterus*	4.22	*Pagellus acarne*	6.42
Promethichthys prometheus	4.25	*Beryx decadactylus*	4.13	*Synaphobranchus affinis*	4.53
Helicolenus dactylopterus	3.93	*Lepidopus caudatus*	4.01	*Sphoeroides pachygaster*	4.28
Beryx decadactylus	3.81	*Centrophorus squamosus*	3.66	*Conger conger*	3.83
Lepidopus caudatus	3.65	*Aphanopus carbo*	3.64	*Centrophorus squamosus*	3.59
Sphoeroides pachygaster	3.53	*Conger conger*	3.59	*Aphanopus carbo*	3.53
Conger conger	3.24	*Centroscymnus owstonii*	3.36	*Centroscymnus owstonii*	3.39
Ruvettus pretiosus	2.97	*Zameus squamulosus*	3.17	*Zameus squamulosus*	3.18
Pontinus kuhlii	2.88	*Ruvettus pretiosus*	3.16	*Heptranchias perlo*	3.07
Heptranchias perlo	2.83	*Pontinus kuhlii*	2.98	*Zeus faber*	2.90
Polymixia nobilis	2.66	*Synaphobranchus kaupii*	2.69	*Synaphobranchus kaupii*	2.57
Pagellus bogaraveo	2.58	*Polymixia nobilis*	2.67	*Centroscymnus coelolepis*	2.21
Beryx splendens	2.47	*Epigonus telescopus*	2.67	*Pontinus kuhlii*	2.20
Zeus faber	2.40	*Beryx splendens*	2.47	*Pagellus bogaraveo*	2.13
Epigonus telescopus	2.39	*Centroscymnus coelolepis*	2.35	*Scorpaena scrofa*	1.89
Muraena helena	2.38	*Centrophorus granulosus*	2.30	*Pagrus pagrus*	1.81
Galeus melastomus	2.18	*Galeus melastomus*	2.22	*Aphanopus intermedius*	1.76
Scorpaena scrofa	1.98	*Pagellus bogaraveo*	2.03	*Mustelus mustelus*	1.74
Phycis phycis	1.87	*Aphanopus intermedius*	1.79	*Gadella moraldi*	1.73
Pagrus pagrus	1.86	*Etmopterus princeps*	1.60	*Umbrina canariensis*	1.62
Umbrina canariensis	1.66	*Deania profundorum*	1.57	*Muraena helena*	1.56
Gadella moraldi	1.64	*Lagocephalus lagocephalus*	1.55	*Dentex gibbosus*	1.55
Mustelus mustelus	1.64	*Mora moro*	1.52	*Phycis phycis*	1.53
Lagocephalus lagocephalus	1.52	*Dalatias licha*	1.48	*Etmopterus princeps*	1.40
		Setarches guentheri	1.45		
		Brama brama	1.38		
		Muraena helena	1.38		
		Phycis phycis	1.32		
		Etmopterus pusillus	1.31		

Table 4
Results of SIMPER routine for depth strata to analyse the contribution (C, in %; cut off = 80%) in biomass of typifying species to within-group similarity and showing species that most contribute to dissimilarity.

150–300 m Average similarity: 46.9		300–750 m Average similarity: 34.93		750–2050 m Average similarity: 23.11	
Species	C %	Species	C %	Species	C %
Squalus megalops	22.52	*Promethichthys prometheus*	18.06	*Synaphobranchus affinis*	18.41
Dentex macrophthalmus	18.21	*Conger conger*	12.73	*Centrophorus squamosus*	14.26
Conger conger	13.7	*Helicolenus dactylopterus*	12.49	*Centroscymnus owstonii*	14.17
Pagellus acarne	8.15	*Lepidopus caudatus*	11.5	*Aphanopus carbo*	12.66
Heptranchias perlo	6.44	*Ruvettus pretiosus*	8.93	*Zameus squamulosus*	10.42
Zeus faber	5.68	*Beryx decadactylus*	6.60	*Synaphobranchus kaupii*	6.97
Sphoeroides pachygaster	4.28	*Epigonus telescopus*	4.46	*Centroscymnus coelolepis*	5.27
Scorpaena scrofa	2.65	*Polymixia nobilis*	4.36		
		Pontinus kuhlii	3.10		

150–300 m and 300–750 m Average dissimilarity: 83.07		300–750 m and 750–2050 m Average dissimilarity: 94.21		150-300 and 750–2050 m Average dissimilarity: 98.22	
Species	C %	Species	C %	Species	C %
Squalus megalops	7.11	*Promethichthys prometheus*	6.69	*Squalus megalops*	8.45
Dentex macrophthalmus	6.15	*Conger conger*	5.52	*Dentex macrophthalmus*	6.80
Promethichthys prometheus	5.76	*Centroscymnus owstonii*	5.04	*Conger conger*	6.61
Conger conger	4.92	*Centrophorus squamosus*	5.01	*Centrophorus squamosus*	4.90
Helicolenus dactylopterus	4.40	*Helicolenus dactylopterus*	4.87	*Centroscymnus owstonii*	4.78
Lepidopus caudatus	4.04	*Lepidopus caudatus*	4.55	*Heptranchias perlo*	4.17
Ruvettus pretiosus	4.01	*Ruvettus pretiosus*	4.35	*Pagellus acarne*	3.84
Heptranchias perlo	3.87	*Aphanopus carbo*	3.90	*Aphanopus carbo*	3.63
Pagellus acarne	3.53	*Polymixia nobilis*	3.38	*Centroscymnus coelolepis*	2.87
Polymixia nobilis	3.38	*Beryx decadactylus*	3.31	*Zeus faber*	2.87
Beryx decadactylus	3.00	*Epigonus telescopus*	3.14	*Synaphobranchus affinis*	2.85
Muraena helena	2.86	*Centroscymnus coelolepis*	3.06	*Dentex gibbosus*	2.80
Epigonus telescopus	2.86	*Synaphobranchus affinis*	3.00	*Pagrus pagrus*	2.73
Pagellus bogaraveo	2.70	*Centrophorus granulosus*	2.97	*Zameus squamulosus*	2.70
Zeus faber	2.62	*Zameus squamulosus*	2.77	*Centrophorus granulosus*	2.40
Dentex gibbosus	2.57	*Galeus melastomus*	2.10	*Muraena helena*	2.24
Pagrus pagrus	2.25	*Deania profundorum*	2.01	*Scorpaena scrofa*	2.08
Phycis phycis	2.19	*Beryx splendens*	1.93	*Umbrina canariensis*	2.05
Scorpaena scrofa	2.14	*Aphanopus intermedius*	1.89	*Mustelus mustelus*	2.05
Umbrina canariensis	2.13	*Mora moro*	1.74	*Aphanopus intermedius*	1.87
Beryx splendens	1.93	*Muraena helena*	1.72	*Phycis phycis*	1.84
Pontinus kuhlii	1.93	*Pontinus kuhlii*	1.55	*Pontinus kuhlii*	1.72
Galeus melastomus	1.91	*Phycis phycis*	1.51	*Centroscymnus crepidater*	1.51
Mustelus mustelus	1.77	*Brama brama*	1.51	*Polymixia nobilis*	1.44
		Etmopterus princeps	1.50	*Promethichthys prometheus*	1.24
		Deania hystricosa	1.48		

Table 5
Results of the (a) Gaussian generalised additive model for the abundance (individuals/1000 hooks) and biomass (kg/1000 hooks) of total deep-sea fish species, bony fishes and cartilaginous fish on depth (m). Values of the parametric coefficient and the corresponding Wald tests (t = estimate/standard error) and p-value and smoothed term as the equivalent degrees of freedom as well as an F test and its associated p-values. DE(%) deviance explained.

Gam (Abundance ~ s(Depth))							
Total fish							
Parametric coefficients	Estimate	t	Pr(>|t|)	Smoothed terms	EDF	F	p-value
Intercept	22.84	29.85	< 0.001	s(depth)	8.84	38.46	<0.001
DE (%) = 70.2							
Bony fish							
Intercept	16.74	22.39	< 0.001	s(depth)	8.72	33.41	<0.001
DE (%) = 68.6							
Cartilaginous fish							
Intercept	7.91	22.47	< 0.001	s(depth)	8.16	10.98	<0.001
DE (%) = 46.2							

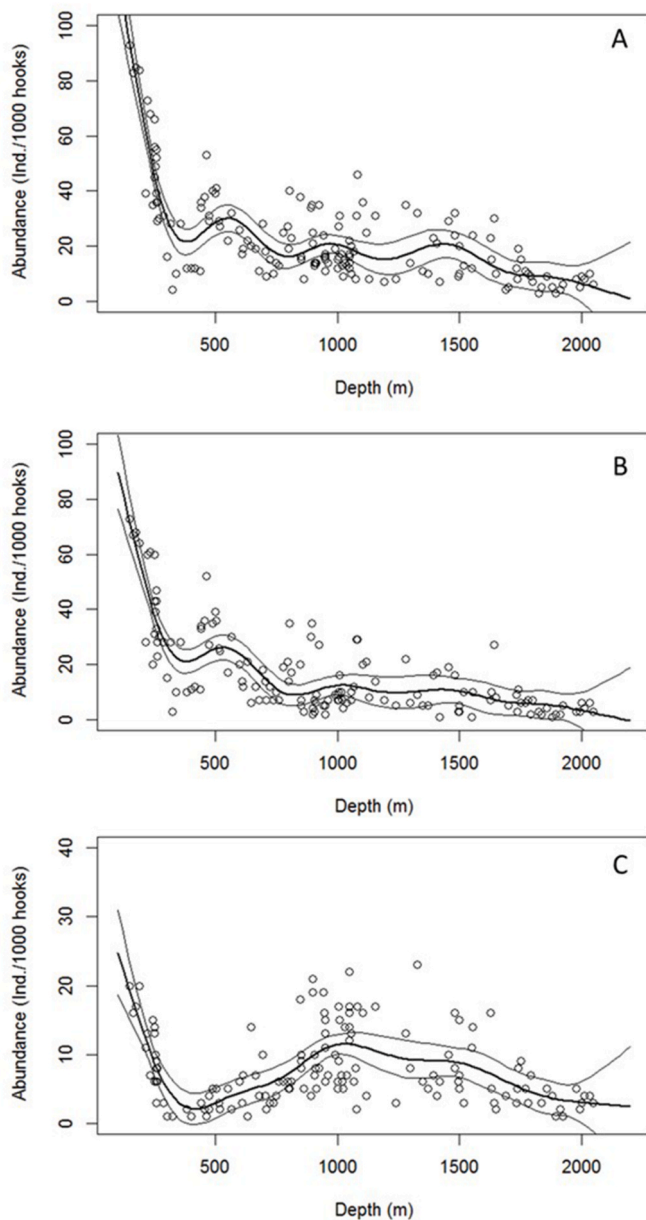| Gam (biomass ~ s(Depth))							
Total fish							
Parametric coefficients	Estimate	t	Pr(>|t|)	Smoothed terms	EDF	F	p-value
Intercept	44.796	27.05	< 0.001	s(depth)	8.89	15.15	<0.001
DE (%) = 48.1							
Bony fish							
Intercept	22.06	19.31	< 0.001	s(depth)	8.93	31.38	<0.001
DE (%) = 67.2							
Cartilaginous fish							
Intercept	26.76	21.13	< 0.001	s(depth)	5.62	15.92	<0.001
DE (%) = 45.6							

Fig. 3. Model for abundance built with Gaussian errors. Abundance for (A) total fish species, for (B) bony and (C) cartilaginous fishes in depths between 150 m and 2050 m.

abundance decreases monotonically with depth for total fish species and for bony fishes (Fig. 3A and B). However, for the cartilaginous fishes, the relationship is concave-down, and thus, increases in abundance with depth are predicted in the depth area between 500 and 1000 m, decreasing thereafter (Fig. 3C). A similar pattern was recorded for biomass (Fig. 4).

ANOVA indicated significant differences in the Shannon–Wiener diversity index among depth strata in number (H', p-F = 7.15, $p <$ 0.0001) and in biomass (H', p-F = 56.32, $p <$ 0.0001). The model for Shannon–Wiener diversity data in abundance and biomass built with Gaussian errors showed good residual graphs (residuals versus predictive values and boxplot of residuals), without hints of heteroscedasticity (Table 6). The GAM models suggested that the diversity estimated with abundance and biomass data decreased with depth, suggesting a relationship with depth, where the diversity decreased with increasing depth (Fig. 5A and B).

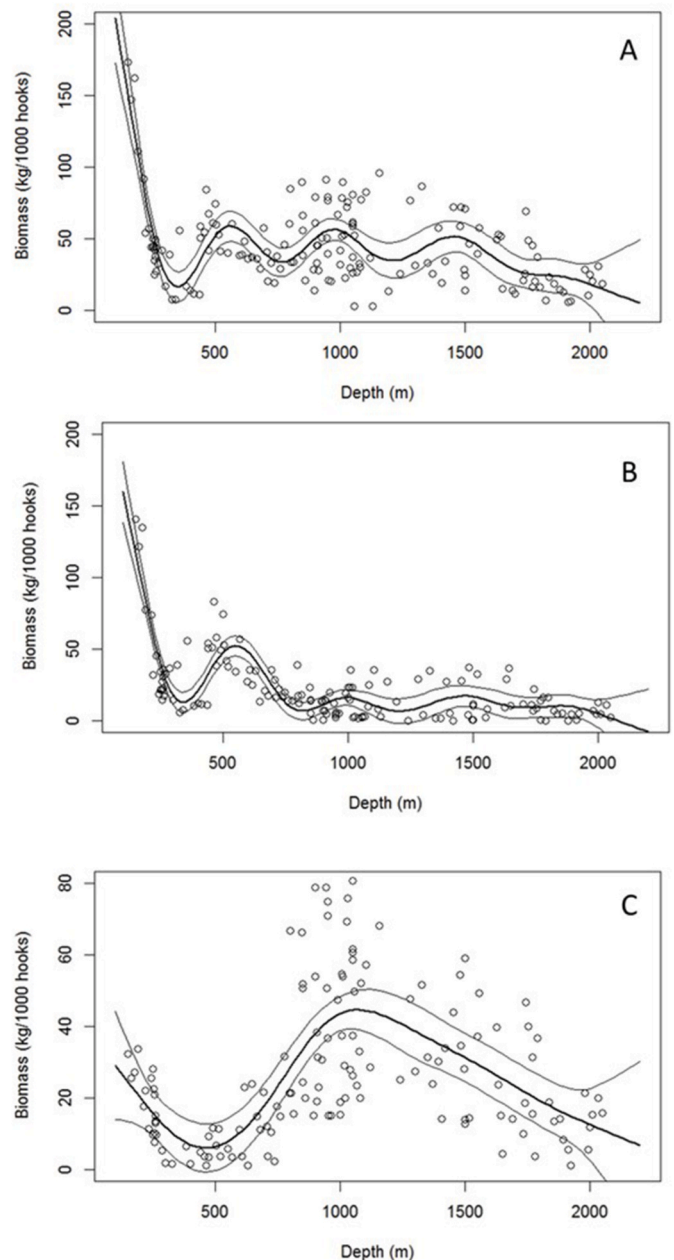The Gaussian model was also used to evaluate the relationship

Fig. 4. Models for biomass built with Gaussian errors. Biomass for (A) total fish species, for (B) bony and (C) cartilaginous fishes in depths between 150 m and 2050 m.

between mean size and depth (Table 7). The results suggest that the estimated mean size increases with depth until 500 m depth. After that depth, the mean size shows little variation when the depth increases (Fig. 6).

The bathymetric distribution range of each fish species is presented in Fig. 7. A short bathymetric range of depth distribution is observed for the more coastal species because the minimum depth was 150 m.

4. Discussion

The depth community and assemblage composition were determined herein by using the sampling technique based on baited hook gear, which may introduce biases due to selectivity of the fishing gear, vulnerability of species to the fishing gear and the catchability of the gear (Das et al., 2022). Most studies on deep-sea communities and

Table 6

Results of the (a) Gaussian generalised additive model for the diversity in abundance and in biomass of total deep-sea fish species on depth (m). Values of the parametric coefficient and the corresponding Wald tests (t = estimate/standard error) and *p*-value and smoothed term as the equivalent degrees of freedom as well as an *F* test and its associated *p*-values. DE(%) deviance explained.

Gam (Diversity ~ *s*(Depth) in abundance							
Total fish							
Parametric coefficients	Estimate	*T*	Pr(>|t|)	Smoothed terms	EDF	*F*	*p*-value
Intercept	1.60	48.63	< 0.0001	*s*(depth)	6.85	21.17	<0.0001
DE (%) = 53.8							
Gam (Diversity ~ *s*(Depth) in biomass							
Total fish							
Intercept	1.41	53.43	< 0.0001	*s*(depth)	7.20	31.45	<0.0001
DE (%) = 64.2							
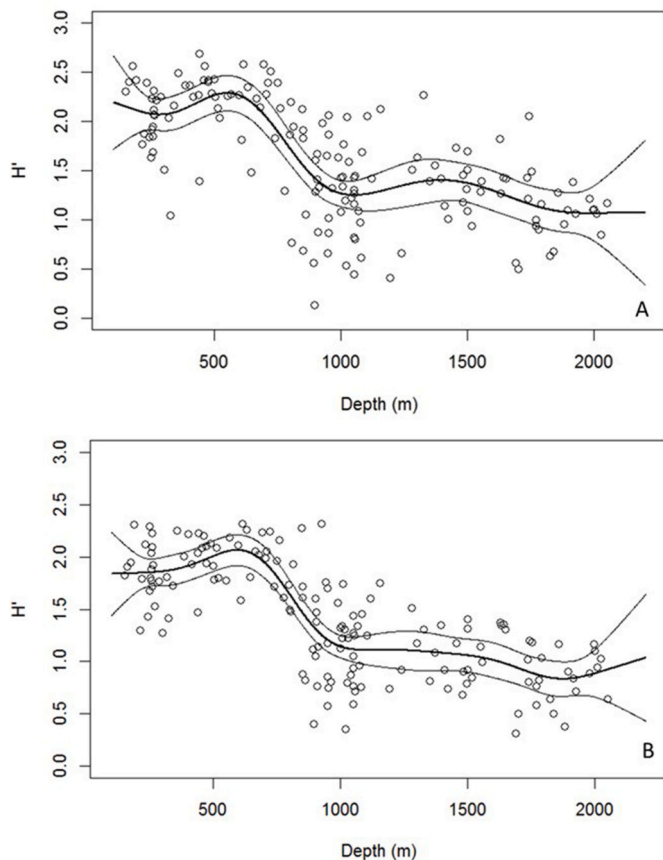
Fig. 5. GAM models for diversity in (A) abundance and (B) biomass with depth between 150 and 2050 m depth.

species assemblages have been carried out using trawl nets as the main sampling method (e.g., Follesa et al., 2011; Pajuelo et al., 2016; O'Hea et al., 2020). However, the Canary Islands, like other archipelagos in the eastern-central Atlantic, do not have trawlable seabeds due to their volcanic origin, so it is necessary to carry out sampling with other gear, such as longlines (Menezes et al., 2006, 2009, 2015; Menezes and Giacomello, 2013; Santos et al., 2021). Research studies have validated the usefulness of longlines as a sampling system for research in areas with nontrawlable bottoms (Uiblein et al., 1996; Menezes et al., 2006, 2009, 2015; Menezes and Giacomello, 2013; Santos et al., 2021), as in the case of oceanic islands where only longline gear can be used on irregular rocky bottoms. Longlines have been used as a sampling system in the majority of the studies developed on the slope of the archipelagos located in the area (Uiblein et al., 1996; Menezes et al., 2006, 2009; Menezes and Giacomello, 2013; Santos et al., 2021). It should be noted that longlines are selective for animal size, according to hook size and they also produce a significant bias towards necrophagous fish and species that are attracted to baits, catching a smaller range of species than trawls (see Bergstad et al., 2008; Fossen et al., 2008). Nevertheless, it is evident that fish species diversity and relative density mainly respond to changes with depth, as observed in other studies in the area (Menezes et al., 2006; Pham et al., 2015).

In the Canary Islands, depth was the main structuring factor of deep-sea fish assemblages, as is the case in other studies (Arantes et al., 2009; Radice et al., 2016; Victorero et al., 2018; Auscavitch et al., 2020; Santos et al., 2021). The pattern of assemblages with depth described in the Canary Islands influenced by the different water masses also has equivalents in the waters of the Azores and Cape Verde (Menezes et al., 2006, 2015; Santos et al., 2021). In the Canary Islands, a drastic reduction in species diversity with depth was observed. This pattern coincides with that previously described for the Canary Islands (Uiblein et al., 1996) and with what was observed in Cape Verde but differs from the Azores for the same depth range (Menezes et al., 2006). This could be related to the intrusion of the Antarctic water mass (colder, with less salinity and low oxygen level). It should be noted that depth is a variable closely correlated with other parameters, such as temperature, amount
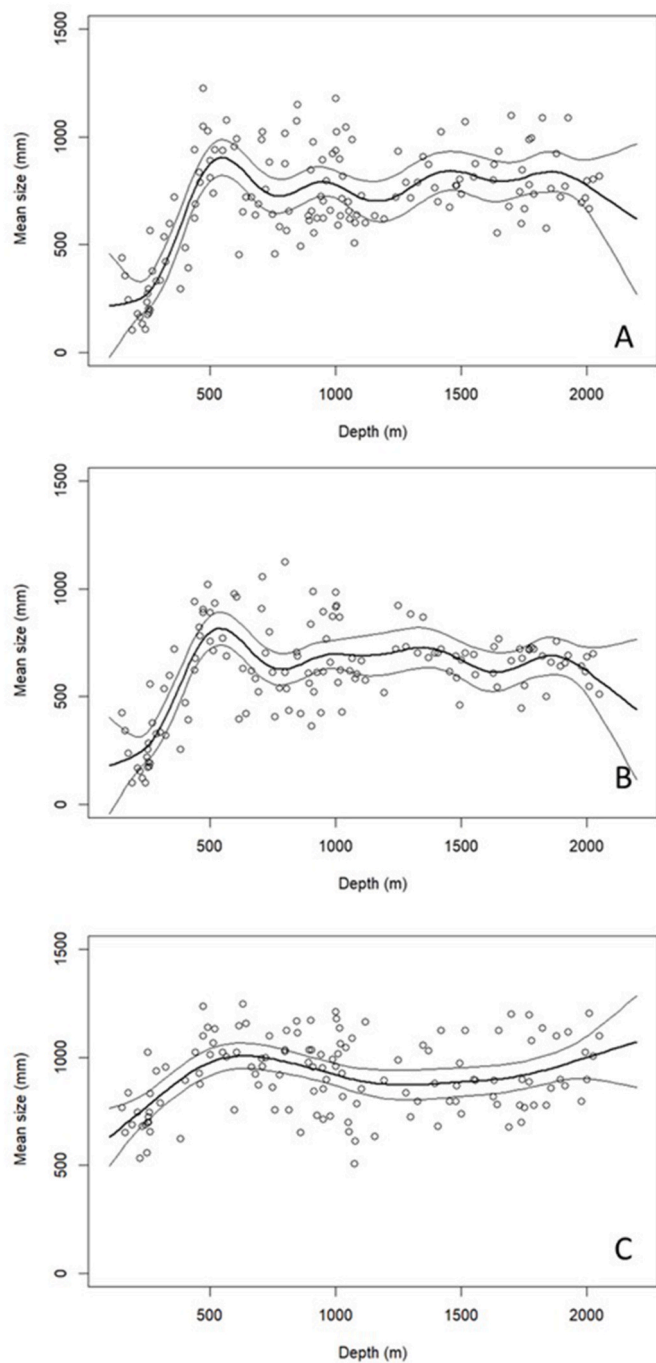
Table 7

Results of the (a) Gaussian generalised additive model for the mean size of total deep-sea fish species, bony fishes and cartilaginous fish on depth (m). Values of the parametric coefficient and the corresponding Wald tests (t = estimate/standard error) and *p*-value and smoothed term as the equivalent degrees of freedom as well as an *F* test and its associated *p*-values. DE(%) deviance explained.

Gam(Mean size ~ *s*(Depth)							
Total fish							
Parametric coefficients	Estimate	*t*	Pr(>|t|)	Smoothed terms	EDF	*F*	*p*-value
Intercept	708.05	51.32	< 0.0001	*s*(depth)	8.61	21.10	<0.0001
DE (%) = 59.2							
Bony fish							
Intercept	616.99	46.59	< 0.0001	*s*(depth)	8.48	16.41	<0.0001
DE (%) = 54.6							
Cartilaginous fish							
Intercept	912.56	68.08	< 0.0001	*s*(depth)	4.77	6.06	<0.0001
DE (%) = 25.3							

Fig. 6. GAM models for mean size for (A) total fish species, for (B) bony fishes and for (C) cartilaginous fishes in depth between 150 m and 2050 m.

of organic matter and food availability or oxygen concentration, which in turn are defined by the presence of water masses (Liu and Tanhua, 2021; Puerta et al., 2020, 2022). In addition, depth from an ecological point of view influences fish distribution, as it conditions biotic relationships such as competition or predation.

A general pattern showing a decreasing number of species related to depth and the dominance of a low number of species has also been described for all the archipelagos of the eastern-central Atlantic (Uiblein et al., 1996; Menezes et al., 2006, 2009, 2015; Menezes and Giacomello, 2013). This general pattern has also been found and can be attributed to the rule of depth-related decrease in food availability throughout the world (Priede et al., 2013b).

The peak in elasmobranch biomass and abundance at approximately 1000 m depth coincides well with that reported by Das et al. (2022), who indicated that *Dalatias licha*, *Etmopterus pusillus* and *Deania profundorum* have a peak of occurrence at 800 m depth, *Deania calceus* and *C. squamosus* at 1200 m depth and *C. owstonii*, *C. coelolepis*, *Centroscymnus crepidater* and *E. princeps* at deeper areas (Das et al., 2022). In addition, the presence of numerous submarine canyons on the island slopes become conduits for the transfer of organic matter from the shelf to deeper regions, which could also help explain the higher abundances and biomasses observed at depth (Vetter and Dayton, 1998; Allen and Durrieu De Madron, 2009; De Leo et al., 2010; Bernardino et al., 2019). The influence of depth on the deep-sea elasmobranch distribution has been previously observed and is well established (Gouraguine et al., 2011; Bottari et al., 2014; Neat et al., 2015; O'Hea et al., 2020; Das et al., 2022). The wide range of depth distributions observed for elasmobranchs is due to the capability to change their depth strata distribution throughout the year or even daily (Klippel et al., 2016; Rodríguez-Cabello et al., 2016). Additionally, some shark species, such as *D. calceus*, *C. crepidater* or *E. princeps*, show a preference for strata at a specific depth related to a high affinity with colder seawater, which could occur at shallower depths in regions located at more northern latitudes or deeper in southern areas (O'Hea et al., 2020). The presence of species with a wide distribution at depth follows the rule described by Merrett and Haedrich (1997) for deep-sea fishes and has been observed for the deep fish fauna of the North Atlantic (Bergstad et al., 2008, 2012). The high percentage of coincidence of elasmobranch species with archipelagos located north or south of the Canary Islands is because elasmobranchs can perform large trophic or reproductive migrations during their life cycle, thus showing a very wide geographical distribution area (Pajuelo et al., 2010; Moura et al., 2014; Rodríguez-Cabello et al., 2016; O'Hea et al., 2020). Furthermore, oceanographic conditions in deep habitats (mainly temperature) are more uniform over wide areas (Gage and Tyler, 1991), allowing deep fish fauna to have a more widespread distribution area than fish inhabiting shallow waters (Clark et al., 2010).

Bathymetric ranges in previous studies carried out in the Azores, Cape Verde, Canary Islands and off the African coast were narrower than those of the present work, and the longline sampling efforts in those studies were mainly concentrated between 0 and 800 m or the sampling method was different (bottom trawl) on the African coast. Despite this, when comparing data from similar bathymetric ranges for the Azores (150–1300 m), Cape Verde (150–1200 m) and the eastern Canary Islands (100–1100 m), the highest similarity in species composition was observed for the eastern Canary Islands (71.6% for all species; 73.0% for elasmobranchs), followed by the Azores (51.4% for all species; 55.0% for elasmobranchs) and Cape Verde (41.3% for all species; 53.8% for elasmobranchs). Differences with the African coast were 27.4% for all species and 50.1% for elasmobranchs. The different species compositions with depth between archipelagic communities located north and south of the Canary Islands may be related to changes in the availability of organic matter (in quantity and/or quality) due to variations in the depth at which water masses are found in these areas (Wigham et al., 2003; Soltwedel et al., 2009). On the other hand, the existence of currents linked to submarine volcanic canyons can influence the biomass or abundance of species when they increase the food available through the flow of organic matter (Levin et al., 2001; Palardy and Witman, 2011).

Differences observed between the species composition in the central islands of the archipelago and the coasts of the eastern islands closest to the African coast and the African coast itself are evidence that the ecological/environmental influence of the African upwelling is strong in this area of the archipelago, with a surface temperature difference of 5 °C between the African coast and the easternmost Canary Islands and 1.5° between these and the central part of the archipelago. Oceanic islands increase environmental heterogeneity on a regional scale, leading to more complex and diverse communities with respect to the ocean floor (Levin et al., 2001). In addition, habitat complexity and heterogeneity can change across a regional area due to abiotic processes such
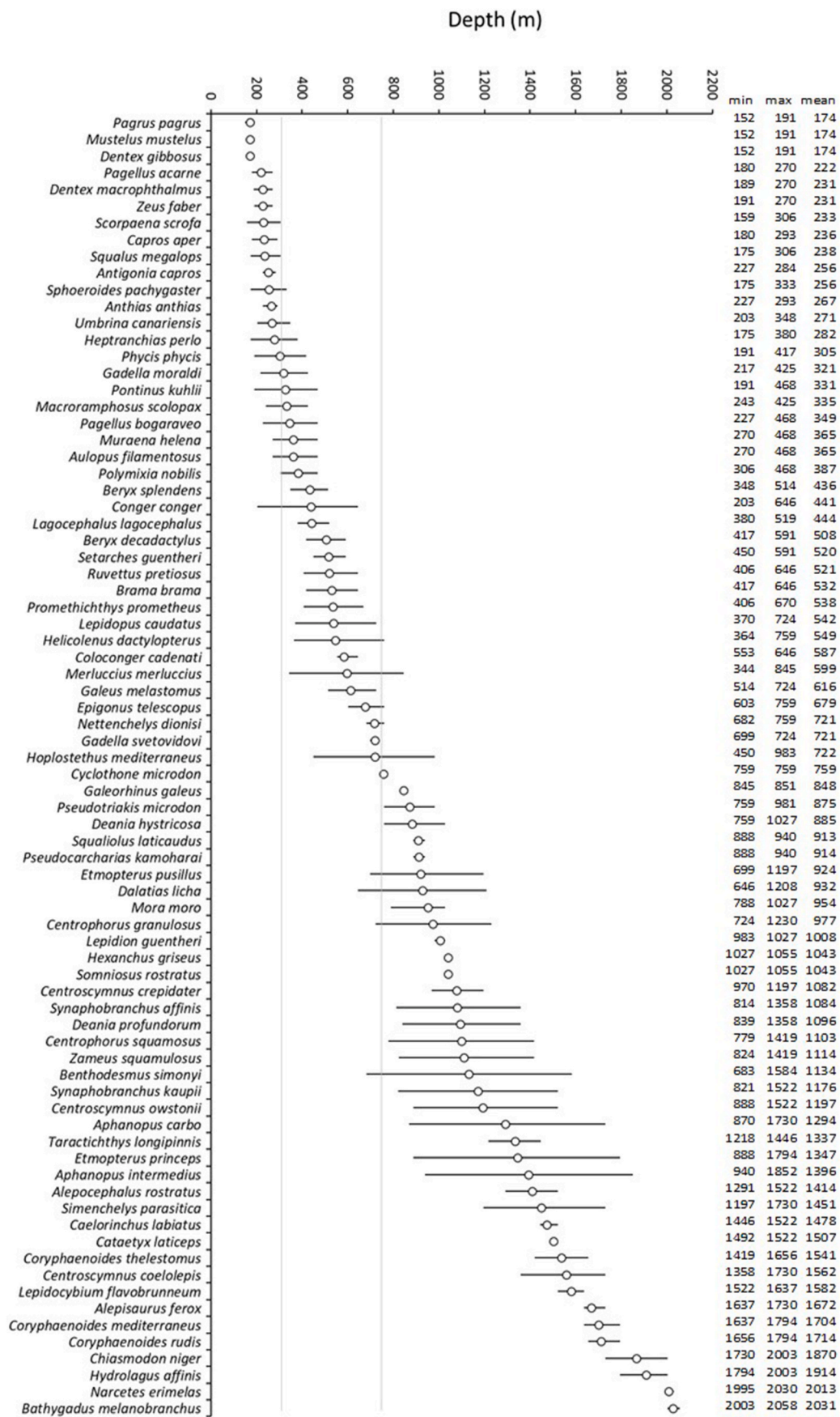
Fig. 7. Bathymetric distribution of the species caught, showing minimum, maximum and mean depth of occurrrence (O).

as hydrography conditions, transport and sediment supply, resulting in changes in the diversity of the communities (Snelgrove and Smith, 2002; Alt et al., 2019). Different biotic processes related to local-scale oceanography and hydrodynamic conditions are also important and can affect habitat heterogeneity (Alt et al., 2019) and community diversity at regional scales as upwelling events.

The Cape Verde archipelago has been recently rejected as a part of the biogeographic region of Macaronesia analysing species composition in coastal waters (Freitas et al., 2019), giving Cape Verde the status of subprovince within the biogeographic West African Transition province. Biogeographic affinities depend on the depth range analysed, and the affinity region may change when depth strata analyses increase to broader biogeographic areas (Bergstad et al., 2008, 2012; Menezes et al., 2015). The differences between the Canary Islands and the Azores (51.4% for all species; 55.0% for elasmobranchs) and Cape Verde (41.3% for all species; 53.8% for elasmobranchs) suggest that the exclusion of Macaronesia should be analysed using the faunal composition of a larger bathymetric range, taking into account that depth can reach values greater than 2000 m in these archipelagos.

In the shallow zone of transition from shelf to slope, the number of species sampled, and their abundances were higher, while in deeper waters, the samples were made up of a low number of species. This has also been observed in all the archipelagos of the eastern-central Atlantic (Menezes et al., 2015) and can be related to the volcanic origin of the archipelagos. The islands are made up of steeply sloping volcanic edifices with small platforms in shallow waters. These platforms allow the development of diverse fish fauna. The fish community structure in the Canary Islands is determined by seawater depth-linked gradients similar to those described for the decapod community in the same region (Pajuelo et al., 2015). The presence of the same species in deeper waters further south of the archipelago would be related to the presence of waters with the same cold temperature at greater depths. This submergence phenomenon has also been described in the North Atlantic (Haedrich and Krefft, 1978; Menezes et al., 2015). Marine water masses favour species dispersal and contribute significantly to connectivity between distant ecosystems, including deep ecosystems (Cowen and Sponaugle, 2009; Gary et al., 2020; Henry and Roberts, 2014; Hilário et al., 2015; Metaxas et al., 2019).

CRediT authorship contribution statement

Raül Triay-Portella: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. José A. González: Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization, Funding acquisition. José M Lorenzo: Writing – review & editing, Visualization, Validation, Methodology, Data curation. José G. Pajuelo: Writing – review & editing, Visualization, Validation, Supervision, Resources, Investigation, Funding acquisition, Conceptualization.

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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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