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ORIGINAL ARTICLE

Influence of environmental parameters on the abundance, biodiversity and distribution of demersal elasmobranchs in the eastern Sea of Marmara, with a focus on deoxygenation

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Abstract: This study investigates the influence of environmental parameters on the abundance, biomass, and spatial distribution of demersal elasmobranchs in the eastern Sea of Marmara over a ten-year period (2014–2024). Catch *per* unit effort (CPUE) data from bottom trawl surveys were combined with *in situ* measurements of dissolved oxygen, temperature, salinity and depth. Multivariate analyses indicate that dissolved oxygen and temperature are key factors associated with spatial variability of demersal elasmobranchs in the investigated area. Temporal patterns show an increase in their abundance until the late 2010s, followed by a marked decline, which may reflect increasing environmental stress as a cause of the decline. These findings suggest that ongoing deoxygenation, together with other environmental parameters, may play an important role in structuring demersal elasmobranch assemblages in the region.
Keywords: Elasmobranchs; abundance; distribution; biodiversity; eastern Sea of Marmara

Sažetak: UTJECAJ OKOLIŠNIH ČIMBENIKA NA BROJNOST, BIORAZNOLIKOST I RASPROSTRANJENOST PRIDNENIH PREČNOUSTA U ISTOČNOM MRAMORNOM MORU, S NAGLASKOM NA GUBITAK KISIKA. Ovaj rad istražuje utjecaj okolišnih čimbenika na brojnost, biomasu i prostornu raspodjelu pridnenih prečnousta u istočnom dijelu Mramornog mora, tijekom desetogodišnjeg razdoblja (2014.–2024.). Podaci o ulovu po jedinici napora (CPUE) iz pridnenih koćarskih istraživanja kombinirani su s *in situ* mjerenjima otopljenog kisika, temperature, saliniteta i dubine. Multivarijatne analize ukazuju da su otopljeni kisik i temperatura ključni čimbenici povezani s prostornom varijabilnošću pridnenih prečnousta u istraživanom području. Vremenski obrasci pokazuju porast njihove brojnosti do kasnih 2010-ih godina, nakon čega slijedi izražen pad, što upućuje na rastući okolišni stres kao mogući uzrok smanjenja. Ovi rezultati sugeriraju da kontinuirani gubitak kisika, zajedno s ostalim okolišnim čimbenicima, može imati važnu ulogu u strukturiranju zajednica pridnenih prečnousta u ovoj regiji.
Ključne riječi: prečnouste; brojnost; rasprostranjenost; bioraznolikost; istočno Mramorno more

INTRODUCTION

Ocean deoxygenation is an increasingly important driver of change in marine ecosystems, with an estimated 2% loss of dissolved oxygen (DO) since 1960, largely attributed to global warming and alterations in circulation, mixing and oxygen respiration (Schmidtko *et al.,* 2017; Oschlies *et al.,* 2018). One of the most threatening environmental problems of marine ecosystems today is the development and expansion of ‘dead zones’, defined as hypoxic (DO<2 mL/L or 2.8 mg/L) or anoxic marine zones associated with anthropogenic activities (Diaz and Rosenberg, 2008). Currently, dead zones have been reported from different marine environments, from coastal systems to deep-sea regions, and are known to affect more than 250,000 km^2 worldwide (Diaz and Rosenberg, 2008). A key ecological consequence of deoxygenation is habitat compression, whereby species are forced into narrower depth ranges with suitable oxygen conditions, potentially increasing their vulnerability to fishing pressure (Gallo and Levin, 2016). From this perspective, elasmobranchs are considered among the groups that are most sensitive to deoxygenation (Waller *et al*., 2024).

Elasmobranchs, including sharks and batoids (skates and rays) and chimaeras, are represented by approximately 1,266 species (Jabado *et al.,* 2024) playing important roles in ecosystem functioning in modern oceans as predators, competitors, mediators and nutrient transporters (Dedman *et al.,* 2024). In the Mediterranean Sea, 88 species of elasmobranch fishes, 48 sharks, 38 batoids and 2 chimaeras, have been currently reported (Barone *et al.,* 2022). According to Bilecenoğlu (2024), a total of 69 elasmobranch species have been recorded so far in Turkish waters, and this number decreases to 25 in

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the Sea of Marmara (SoM) (Kabasakal and Karakulak, 2025).

The SoM is a very small marine basin (11,500 km^2 in surface area and a maximum depth of 1,390 m) connected to the Mediterranean and Black Seas by narrow straits (Beşiktepe *et al*., 1994). With almost a quarter of Türkiye's population (about 22 million people) living in the major cities around the basin, the discharge of domestic/industrial waste from intensive industrialisation and urbanisation, as well as heavy maritime traffic, exert considerable pressure on the SoM (Tan and Demirtaş, 2022). In the eastern Sea of Marmara (ESoM), hypoxic conditions (<80 µmol/L or 2.52 mg/L DO) are increasingly severe and in some areas progressing towards anoxia (Mantıkçı *et al*., 2022). Current DO levels support the transformation of parts of the ESoM into a dead zone extending from the continental shelf (>100 m depth) to deeper bathyal zones (1,390 m at maximum; Beşiktepe *et al*., 1994), where biodiversity is markedly reduced (Karakulak *et al*., 2017; Daban *et al*., 2021).

Although specific studies of elasmobranchs have a history of almost 100 years within the general ichthyofauna of the SoM, the effects of deoxygenation (which stands out as a factor challenging the living conditions in the region (Mantıkçı *et al.,* 2022)) and other environmental parameters on the abundance and distribution of demersal elasmobranch fishes inhabiting the continental shelf (<200 m depth), have not been specifically investigated. In the present study, using fishery-independent and oceanographic data (DO, temperature (T), salinity (S) and depth (D)) collected over a 10-year period, abundance, diversity and spatial distribution of demersal elasmobranchs in ESoM continental shelf waters were investigated, with a particular focus on the role of bottom DO.

MATERIAL AND METHODS

Study area

The main study area, ESoM, was defined as the region located east of the line connecting stations MD6 and MD10 (Fig. 1). This area is heavily impacted by domestic and industrial waste (Mantıkçı *et al.,* 2022) and intense fishing pressure (Akçay *et al.,* 2025). In addition to the fixed sampling stations (MD1-10), a number of supplementary stations (MD3A, MD14, MD18, MD75 and MD90) were selected at different locations across the SoM. These stations were selected opportunistically and are spatially distributed outside the core study area. Due to their non-systematic location and limited temporal replication, no statistical comparisons were performed between these stations and the main sampling stations (MD1-10).

Sampling at the supplementary stations was conducted using bottom trawling at irregular intervals over the 10-year period, with each station sampled up to five times. Although CTD measurements of environmental parameters were also obtained at these stations, the associated CPUE data were not included in the quantitative analyses due to the lack of consistent environmental matching. Instead, these data were used exclusively to document the presence or absence of elasmobranch species. Representative CTD profiles from the MD1-10 stations are presented in Supplementary Figures 1-10 to illustrate hydrographic conditions in the ESoM in recent years.

Sampling design and survey methodology

As part of an extensive and ongoing marine survey "Stock Assessment of Demersal Fishes in the Eastern

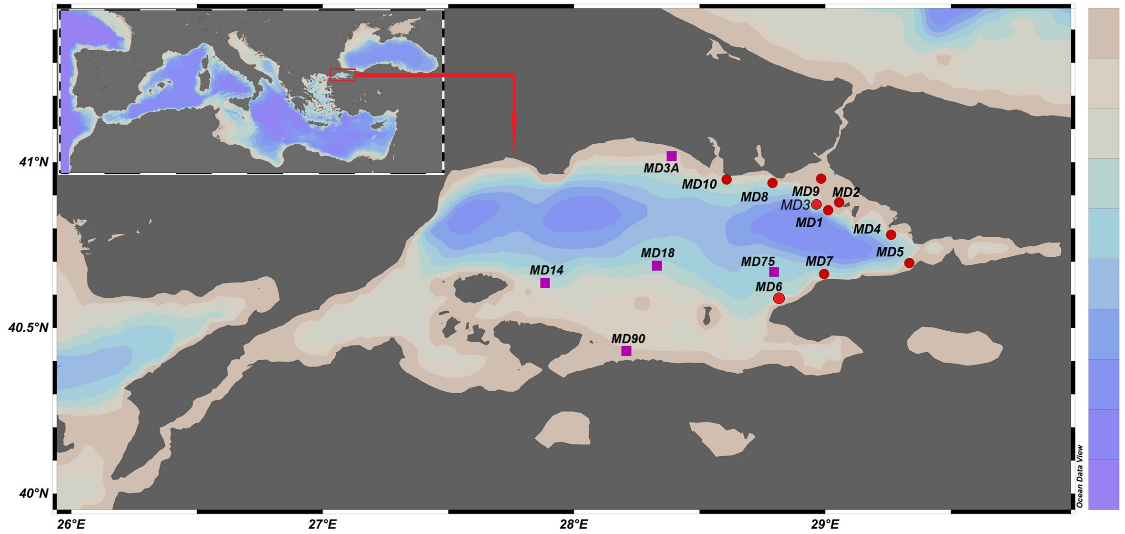


Fig. 1. Main stations (red solid circles) with repeated seasonal sampling and random stations (purple solid squares) with irregular sampling. The red rectangle in the small panel depicts the location of the Sea of Marmara in the Mediterranean basin.

Sea of Marmara, Project No: 51922", seasonal bottom trawling surveys were conducted annually between December 2014 and August 2024 aboard the stern trawl research vessel *R/V Yunus-S* of Istanbul University Faculty of Aquatic Sciences. The first phase of the project (December 2014–July 2017) aimed to provide stock assessments of demersal fish and related environmental parameters in the ESoM. Following the initial phase, seasonal monitoring surveys were conducted until August 2024 to provide updated information on biomass and abundance patterns of demersal fish stocks at fixed stations (MD1-10). Sampling activities were temporarily interrupted during the COVID-19 pandemic, resulting with gaps in the time series.

Over the 10-year period, a total of 205 bottom trawl hauls were conducted at the MD1-10 stations in the ESoM. Elasmobranch fishes were caught in 135 of these hauls (65.9%). However, complete and reliable oceanographic measurements (DO, T, S and D) were available for only 71 hauls (34.6%). Quantitative analyses were restricted to a subset of hauls defined as the environmentally matched dataset, comprising 71 bottom trawl hauls with corresponding and reliable oceanographic measurements (Table 1), in line with the study's objective of examining relationships between environmental and biological variables. The full dataset, which includes the data from 205 bottom trawl hauls, was retained for descriptive analyses of species occurrence and distribution patterns. Restricting the analyses to this subset may limit the representativeness of abundance estimates. Relevant data of the full data set and the subset are provided in Supplementary Tables 1 and 2.

The horizontal opening of the trawl net used in the study was 20 m, with a codend mesh opening of 14 mm

Table 1. Synoptic table summarising fixed (MD1-10; based on environmentally matched dataset) and supplementary (MD3A,14,18 and 90) stations. Total-N, total number of times each station was sampled between 2014-2024 (MD1-10) or in 2019, 2021 and 2024 (MD3A, 14, 18 and 90); W-N, Sp-N, Su-N and A-N, total number of times each station was sampled in winter, in spring, in summer and in autumn, respectively. Avg, average; DO, dissolved oxygen (mg/L); T, temperature (°C); S, ‰ salinity, over sea bottom; D, depth (m); min, minimum; and max, maximum. The grey shaded area represents the supplementary stations.

	MD1	MD2	MD3	MD4	MD5	MD6	MD7	MD8	MD9	MD10	MD3A	MD14	MD18	MD90
Total-N	8	9	4	8	9	8	8	6	7	4	3	2	3	3
W-N	3	4	N/A	2	3	3	3	2	2	2	N/A	N/A	N/A	N/A
Sp-N	N/A	N/A	N/A	1	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Su-N	3	4	2	3	3	3	3	3	3	2	2	2	2	2
A-N	2	1	2	2	2	2	2	1	2	N/A	1	N/A	1	1
Avg D (min-max)	78 (26.3-86.4)	66.7 (60.4-71.7)	101.1 (91.2-132)	85.9 (75.3-94.5)	62.6 (52.9-67.1)	122 (99.3-140)	94.3 (91.4-96)	70.5 (46.1-79	38.5 (24.6-45.3)	51.9 (41.5-57.8)	67.2 (62.7-72)	58.4 (57.7-60)	132.6 (122-138.6)	44.8 (43.4-45.8)
Avg DO (min-max)	1.43 (0.50-3.18)	1.54 (0.85-2.76)	1.42 (0.53-1.99)	1.29 (0.61-2.20)	1.8 (1.25-2.68)	1.46 (1.25-1.72)	1.46 (1.09-1.71)	1.53 (0.70-2.30)	2.87 (1.69-7.07)	1.82 (1.16-2.98)	0.81 (0.52-1.21)	3.86 (2.08-5.64)	1.78 (1.39-1.99)	2.93 (2.41-3.61)
Avg T (min-max)	14.34 (8.91-17.12)	14.57 (8.93-16.31)	15.45 (15.26-15.82)	13.54 (8.96-15.67)	14.10 (8.97-16.29)	15.35 (15.29-15.48)	13.83 (8.96-15.57)	13.68 (8.92-16.05)	13.29 (9.04-16.35)	13.91 (8.96-16.62)	15.72 (15.59-15.82)	16.54 (15.96-17.12)	16.19 (15.31-17.86)	16.51 (16.37-16.68)
Avg S (min-max)	38.68 (38.27-38.81)	38.73 (38.65-38.81)	38.74 (38.70-38.82)	38.76 (38.71-38.82)	38.71 (38.51-38.82)	38.75 (38.72-38.81)	38.76 (38.69-38.82)	38.76 (38.65-38.82)	36.34 (30.05-38.70)	38.59 (37.91-38.80)	38.77 (38.71-38.8)	38.94 (38.83-39.06)	38.81 (38.8-38.82)	38.28 (37.29-38.79)

in stretched length. The haul duration was fixed at 30 minutes on depths less than 200 m and at 60 minutes at depths greater than 200 m at a constant speed of 2.5-3 mph on the ground. The design of the trawl net and the duration of the trawl surveys followed the standard protocol for the International Bottom Trawl Survey in the Mediterranean (MEDITS) (MEDITS Working Group, 2017). Before the start of every bottom trawl hauling at fixed stations of MD1-10 and random stations, *in situ* hydrographic data - sea bottom (1 to 2 meters above the sea bottom) DO, T, S and depth (D) - were collected using the SeaBird CTD device.

Identification of elasmobranchs species followed Ebert *et al.* (2021) and Barone *et al.* (2022), and species nomenclature followed WoRMS (2026). A 3-alpha codes of demersal elasmobranch species followed FAO (2025). Specimens were held in a survival tank supplied with ambient seawater directly from the sea (without temperature control) until basic morphometric measurements (total length (TL) to the nearest 0.5 cm and body mass (TW) to the nearest 0.5 g) were recorded and counted, after which they were rapidly released back into the sea.

Biomass, catch *per* unit effort (CPUE), alpha diversity indices and multivariate analyses were all calculated based on the above defined environmentally matched dataset. Detailed results for the full dataset and the subset are provided in Supplementary Tables 1 and 2, respectively.

Equations of DO conversion, biomass, CPUE and biodiversity indices

In the available literature, different units of DO were used to characterize the hypoxic conditions of the SoM. Those different units were converted to mg/L by the following equation (Levin, 2018): 1.4 mg/L= 1.0 mL/L= 44.4 µmol/L O_2.

Biomass was estimated using the swept-area method (Equation 1), which accounts for trawl catch, swept area and catchability (Sparre and Venema, 1998):

$$\sum_{i=1}^{n} B_i = \frac{A*C_i}{a_i*q} \quad (1)$$

where B is the mean biomass estimate, C_i, mean catch in sample i; A, total area (1 km^2) from which biomass was estimated; a_i, swept area in sample i; q, trawl catchability coefficient. In this study, q was assumed to be equal to 1, implying full catchability. This assumption allows biomass estimated to be interpreted as relative indices rather than absolute population estimates, and is consistent with standard practice in similar survey-based studies.

CPUE was used as an index of relative population density and calculated using Equation (2) (Phiri and Shirakihara, 1999):

$$CPUE = \frac{\Sigma C_i/N_h}{t/N_h} \quad (2)$$

where C_i is the catch (kg) in each trawl, t is the trawling time; N_h is the number of hauls. CPUE was calculated in two forms: biomass-based CPUE (CPUA, kg/km^2), derived from total catch weight, and abundance-based CPUE (CPUN, ind./km^2), derived from the number of individuals caught.

The Shannon diversity index was calculated using Equation (3) (Shannon, 1948; Bhardwaj *et al.,* 2023):

$$H' = -\sum P_i * Log(P_i); P_i = \frac{n_i}{N} \quad (3)$$

where H' is species diversity, P_i is the ratio of the number of individuals of species i to the total number of individuals of all species obtained, n_i represents the number of individuals of species i, N is the total number of individuals of all species obtained in the sample. Values of H' typically range between 0 and 5, with higher values indicating more diverse and balanced communities.

Species richness was estimated using the Margalef index (Equation (4)) (Margalef, 1969; Bhardwaj *et al.,* 2023):

$$d = \frac{S-1}{lnN} \quad (4)$$

where S is the total number of species and N is the total number of individuals. This parameter has no threshold values and higher values indicate higher biodiversity.

Species dominance was calculated using the Simpson index (Equation (5)) (Simpson, 1949):

$$C = \sum_{i=1}^{K} P_i^2 \quad (5)$$

where P_i is the proportional abundance of species i.

Species evenness was assessed using the Pielou index (Equation (6)) (Pielou, 1966; Bhardwaj *et al.,* 2023):

$$J' = H' / lnS \quad (6)$$

where H' is the observed Shannon index and S is the natural logarithm (ln) of the total number of species.

The frequency of species was determined using the index of Soyer (1970) (Equation (7)):

$$F = \left(\frac{N_a}{N_n}\right) \times 100 \quad (7)$$

where N_a is the number of samples in which a species was recorded and N_n is the number of samples. Species were classified as continuous (F≥50%), common (25%≥F<50%) or rare (F<25%).

Analytical and statistical methods

To examine temporal changes in biomass and abundance in relation to bottom water DO, Gaussian response models were fitted to $\log_{10}$-transformed CPUE values for biomass (CPUA, kg/km^2) and abundance (CPUN, ind./

km^2) (Gordó-Vilaseca *et al.,* 2024). These analyses were performed using the "Species Packing (Gaussian normal distribution)" function implemented in the PAST - Palaeonthological Statistics ver. 4.03 programme (Hammer *et al*., 2001), which fits species response curves along environmental gradients. The software automatically calculates Akaike Information Criteria (AIC) values and 95% confidence intervals, and produces smoothed response curves.

Differences in community composition between fixed stations (MD1-10) were assessed using Bray-Curtis similarity matrix based on fish count data (Gallo *et al.,* 2020). SIMPER analysis was used to identify taxa contributing most to similarity patterns, while ANOSIM was applied to test for differences between stations (Gallo *et al.,* 2020). Non-metric multidimensional scaling (NMDS) ordination, based on the Bray-Curtis dissimilarity matrix, was used to visualise patterns in community composition and their relationship with environmental variables (DO, T, S and D) (Rincón-Díaz *et al.,* 2018; Gallo *et al.,* 2020). Differences in biomass in relation to environmental variables across fixed stations were tested using permutational multivariate analysis of variance (PERMANOVA). The relationships between species and environmental parameters in the ESoM were analysed using canonical correspondence analysis (CCA) (Legendre and Legendre, 1998) based on species biomass (kg/km^2) and CTD data.

All data were log-transformed prior to analysis. Parametric or non-parametric tests were used depending on the data distribution as determined by the Shapiro-Wilk normality test (Legendre and Legendre, 1998). Pairwise differences in species abundance among stations were evaluated using the Mann-Whitney test, while differences across depth and years were tested using the Kruskal-Wallis test (Legendre and Legendre, 1998). Statistical significance was assessed using 9,999 permutations, with a significance threshold of $p<0.05$. All analyses were performed using PAST - Palaeonthological Statistics ver. 4.03 programme (Hammer *et al*., 2001).

The datasets and additional supplementary files supporting the findings of this study are available from the corresponding author upon reasonable request.

RESULTS

Overview of total elasmobranch species caught in the period 2014-2024

Between December 2014 and August 2024, a total of 205 bottom trawl hauls were conducted at stations MD1-10 in the ESoM, yielding 3,384 demersal elasmobranch fish representing 11 species (Table 2). Of these, sharks were represented by six species (54.5% of the total number of species) and batoids (skates and rays) by five species (45.4%). In terms of abundance, sharks dominated the elasmobranch assemblage, comprising 81.5% of all individuals (n=2,761), whereas batoids accounted for 18.4% (n=623).

The lowest number of elasmobranch fishes was caught at station MD10 (n=28) and the highest number at station MD6 (n=1,215). The numerical distribution of sampled species across stations is provided in Supplementary Table 3. Despite these differences, no statistically significant variation in abundance between stations was detected (Mann-Whitney pairwise test, $p>0.05$). No elasmobranch species was recorded at the deep station MD75 (≥300 m), where DO was measured as 0 mg/L. In contrast, several deep-sea shark and ray species were recorded at supplementary stations MD3A and MD18. In addition, occurrences of neonates, juveniles and gravid females at stations MD14 and MD90 indicate the presence of potential nursery areas.

Squalus blainville was the most frequently recorded species during the study period, representing 62.3% (n=2,109) of all individuals. The frequency of occurrence of all other species was below 25%. Accordingly, *S. blainville* was classified as a "common" species, while all remaining species were categorized as "rare" based on their frequency of occurrence (Table 2). When only the most recent sampling year (2024) is considered, species richness declined to seven species. Four species (*Galeus melastomus*, *S. acanthias*, *Raja miraletus* and *Dasyatis tortonesei*) were not recorded in the ESoM stations after 2022.

Biodiversity indices

The alpha diversity indices of demersal elasmobranch species (n=11) sampled in the ESoM between 2014 and 2024 are summarized in Table 3. Significant differences were detected for the Shannon diversity index (H'), Simpson index (1-D) and Margalef richness index (D) (Kruskal–Wallis test, $p<0.05$). In contrast, no significant differences were observed among stations for the Pielou evenness index (J') ($p>0.05$).

SIMPER analysis

The results of the SIMPER analysis assessing the contribution of elasmobranch fish taxa to community dissimilarity among stations (MD1-10) over the period 2014-2024 are presented in Table 4. The analysis indicated a high level of dissimilarity in species composition among stations, with a mean dissimilarity of 82.2%. *S. blainville*, *Raja clavata* and *Squalus acanthias* were the primary contributors, each accounting for more than 10% of the observed dissimilarity. Differences in species composition among stations were statistically significant (ANOSIM, $p<0.05$). In addition, a global R value of 1 indicated complete separation among stations (MD1-10) based on demersal elasmobranch fish abundance.

Bottom water DO and T values showed limited variation across stations, with DO values generally at or below the hypoxia threshold and T ranging between 15.41 ºC and 15.96 ºC (Table 1). Substrate composition was also similar among stations, consisting predominantly of sand, mud and mixed sediments with shell

Table 2. An overview of the number of specimens of demersal elasmobranch species sampled at stations MD1-10 from 2014-2024, and at supplementary stations. Frequency of occurrence (%) of demersal elasmobranchs caught at stations MD1-10 during the same period. N, number of captured specimens; F, frequency; OS, occurrence status; R, rare; and C, continuous.

	Fixed Stations									
Species	**MD1**	**MD2**	**MD3**	**MD4**	**MD5**	**MD6**	**MD7**	**MD8**	**MD9**	**MD10**
Galeus melastomus						1				
Scyliorhinus canicula						3				
Mustelus mustelus	7	2	2	1	2			3	145	8
Oxynotus centrina	1		1		3				1	
Squalus acanthias		1		6	434	9	22			
Squalus blainville	413	3	66	300	15	1185	45	12	70	
Raja clavata	36	21	1	34	29	17	152	13	65	
Raja miraletus							1			
Dasyatis pastinaca	2	4			38			9	27	19
Dasyatis tortonesei					21			2	7	
Myliobatis aquila				120				3	1	1
Total	459	31	70	461	542	1215	220	42	316	28

	Supplementary Stations				Frequency of occurence			
Species	**MD3A**	**MD14**	**MD18**	**MD90**	**Species**	**N**	**F%**	**OS**
Hexanchus griseus			1		*Galeus melastomus*	1	0.02	R
Scyliorhinus canicula		73	1	10	*Scyliorhinus canicula*	3	0.08	R
Mustelus mustelus	2		1		*Mustelus mustelus*	170	5.02	R
Oxynotus centrina		2			*Oxynotus centrina*	6	0.17	R
Centrophorus uyato			1		*Squalus acanthias*	472	13.94	R
Echinorhinus brucus			17		*Squalus blainville*	2,109	62.32	C
Torpedo marmorata				1	*Raja clavata*	368	10.87	R
Dipturus oxyrinchus	1				*Raja miraletus*	1	0.02	R
Raja clavata		4	4	15	*Dasyatis pastinaca*	99	2.92	R
Myliobatis aquila				33	*Dasyatis tortonesei*	30	0.88	R
					Myliobatis aquila	125	3.69	R

Table 3. Results of diversity indices for demersal elasmobranch species (n=11) sampled at station MD1-10, calculated on the basis of log-transformed individual numbers (2014-2024). N, number of demersal elasmobranch species *per* station; n, total number of demersal elasmobranch individuals caught at the relevant station. Estimated diversity indices represent a single value based on the aggregation of all data from each station.

	MD1	**MD2**	**MD3**	**MD4**	**MD5**	**MD6**	**MD7**	**MD8**	**MD9**	**MD10**
N	5	5	4	5	7	5	4	6	7	3
n	459	31	70	461	542	1,215	220	42	316	28
Shannon (H’)	0.396	1.042	0.278	0.892	0.796	0.141	0.835	1.573	1.348	0.740
Margalef (D)	0.653	1.165	0.706	0.652	0.953	0.563	0.556	1.338	1.042	0.600
Simpson (1-D)	0.184	0.510	0.110	0.503	0.349	0.049	0.471	0.764	0.690	0.457
Pielou (J’)	0.297	0.567	0.330	0.488	0.317	0.230	0.576	0.804	0.550	0.699

fragments. *S. blainville*, the major contributor to dissimilarity, was sampled at all stations except MD10. *R. clavata*, the second most important contributor, showed a similar distribution pattern. *Mustelus mustelus* was recorded at eight stations (n = 170), whereas *S. acanthias* was recorded at five stations but with higher number of

Table 4. Contribution of elasmobranch species to community similarity.

SIMPER (2014-2024)		
Species	**Average dissimilarity**	**Contribution (%)**
Squalus blainville	39.5	48.04
Raja clavata	12.68	15.42
Squalus acanthias	12.44	15.13
Mustelus mustelus	6.35	7.72
Myliobatis aquila	4.06	4.94
Dasyatis pastinaca	3.69	4.48
Scyliorhinus canicula	2.29	2.79
Dasyatis tortonesei	0.95	1.15
Oxynotus centrina	0.19	0.23
Raja miraletus	0.04	0.05
Galeus melastomus	0.01	0.02

individuals (n = 472). Several species, including *G. melastomus*, *Scyliorhinus canicula* and *R. miraletus* were represented by low sample numbers. *Oxynotus centrina* was recorded at four stations with only six individuals captured in total.

Change of elasmobranch species abundance with time and DO in the ESoM

Gaussian response models were applied to $\log_{10}$-transformed CPUE data across the bottom water DO values. During the 10-year study period, the abundance (ind./km^2) of demersal elasmobranchs increased at all stations except MD8, with peak values generally observed between 2018 and 2019, followed by a marked decline (Figs. 2,3). Biomass (kg/km^2) exhibited station-specific patterns. Increases were observed at stations MD1 (peaking between 2019 and 2021), MD2 (2019), MD4 (2020), MD5 (2019), MD6 (2021), MD9 (2019-2021) and MD10 (2021). In contrast, biomass at station MD7 showed a continuous decline throughout the study period. At station MD3, biomass increased over time, coinciding with the recurrent capture of relatively low numbers of larger subadult and adult individuals. Station MD8 differed from all other stations, exhibiting a continuous decline in both biomass and abundance throughout the study period (Figs. 2,3). Temporal changes in biomass and abundance in relation to bottom water DO levels were not statistically significant at stations MD1–7 ($p>0.05$). However, significant relationships between DO and both biomass and abundance were detected at stations MD8–10 ($p<0.05$).

Change of the most abundant species with time and DO in the ESoM

Temporal and DO-related changes in biomass and abundance were analysed separately for the six most abundant species (*Mustelus mustelus*, *Squalus acanthias*, *Squalus blainville*, *Raja clavata*, *Dasyatis pastinaca* and *Myliobatis aquila*). The remaining five species (*Galeus melastomus*, *Scyliorhinus canicula*, *Oxynotus centrina*, *Raja miraletus* and *Dasyatis tortonesei*) were not included in detailed analyses due to their low sample sizes ($n\leq30$ *per* species) and lack of repeated occurrences across the study period.

Mustelus mustelus

The variation in biomass and abundance of *M. mustelus* in the ESoM over time and DO conditions indicates a divergence between these two metrics, with biomass values generally exceeding abundance in later years. Biomass increased from 2014 onwards, reaching 713.9 kg/km^2 in 2016, 935.9 kg/km^2 in 2023 and 664.5 kg/km^2 in August 2024. In contrast, abundance decreased over time, with values of 1,719.8 ind./km^2 in 2016, 172.7 ind./km^2 in 2023 and 83.1 ind./km^2 in August 2024. A statistically significant difference between biomass and abundance was detected in 2021 (Kruskal-Wallis test, $p<0.05$; Fig. 4).

Squalus acanthias

The biomass and abundance of *S. acanthias* in the ESoM showed a marked decline over the study period. Biomass and abundance, estimated at 924.1 kg/km^2 and 13,498.9 ind./km^2 in 2014, decreased substantially to 14.4 kg/km^2 and 51.4 ind./km^2 in 2022. Both the biomass and abundance exhibited statistically significant decreases over time (Kruskal-Wallis test, $p<0.05$). After 2022, *S. acanthias* was not recorded in subsequent samples from the ESoM (Fig. 4).

Squalus blainville

The abundance of *S. blainville* in the ESoM increased rapidly between 2014 and 2018, reaching a peak in 2018, followed by a marked decline in 2019. In February 2024,

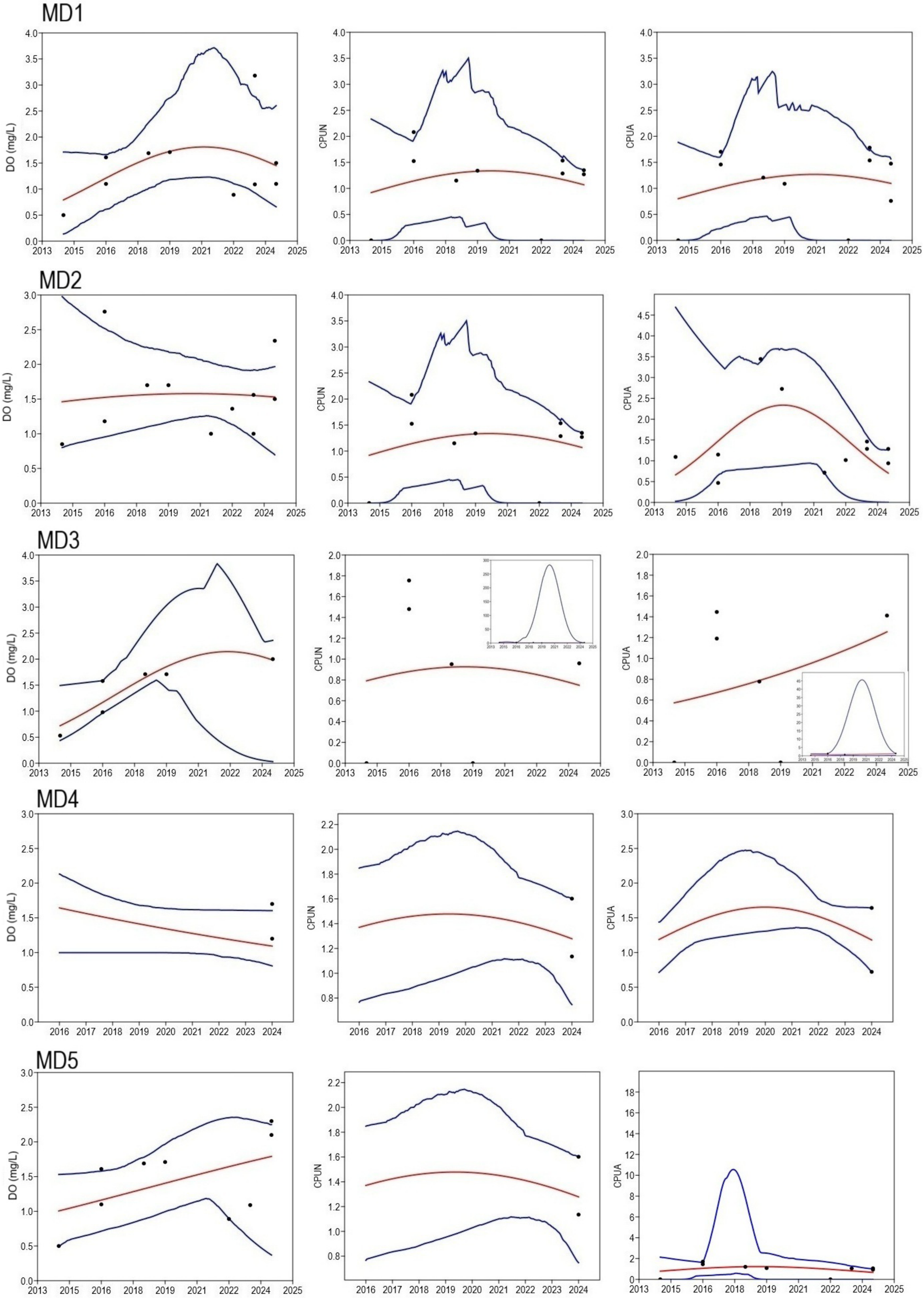


Fig. 2. Gaussian distribution smoothing (red lines) of log transformed CPUN (ind./km^2) and log transformed CPUA (kg/km^2) of demersal elasmobranch species, and variation of DO (mg/L) at the MD1-5 stations during the period 2014-2024. Blue lines indicate 95% confidence interval. For MD3 station, 95% confidence interval lines are shown in small panels to avoid hiding the CPUN and CPUA curves.

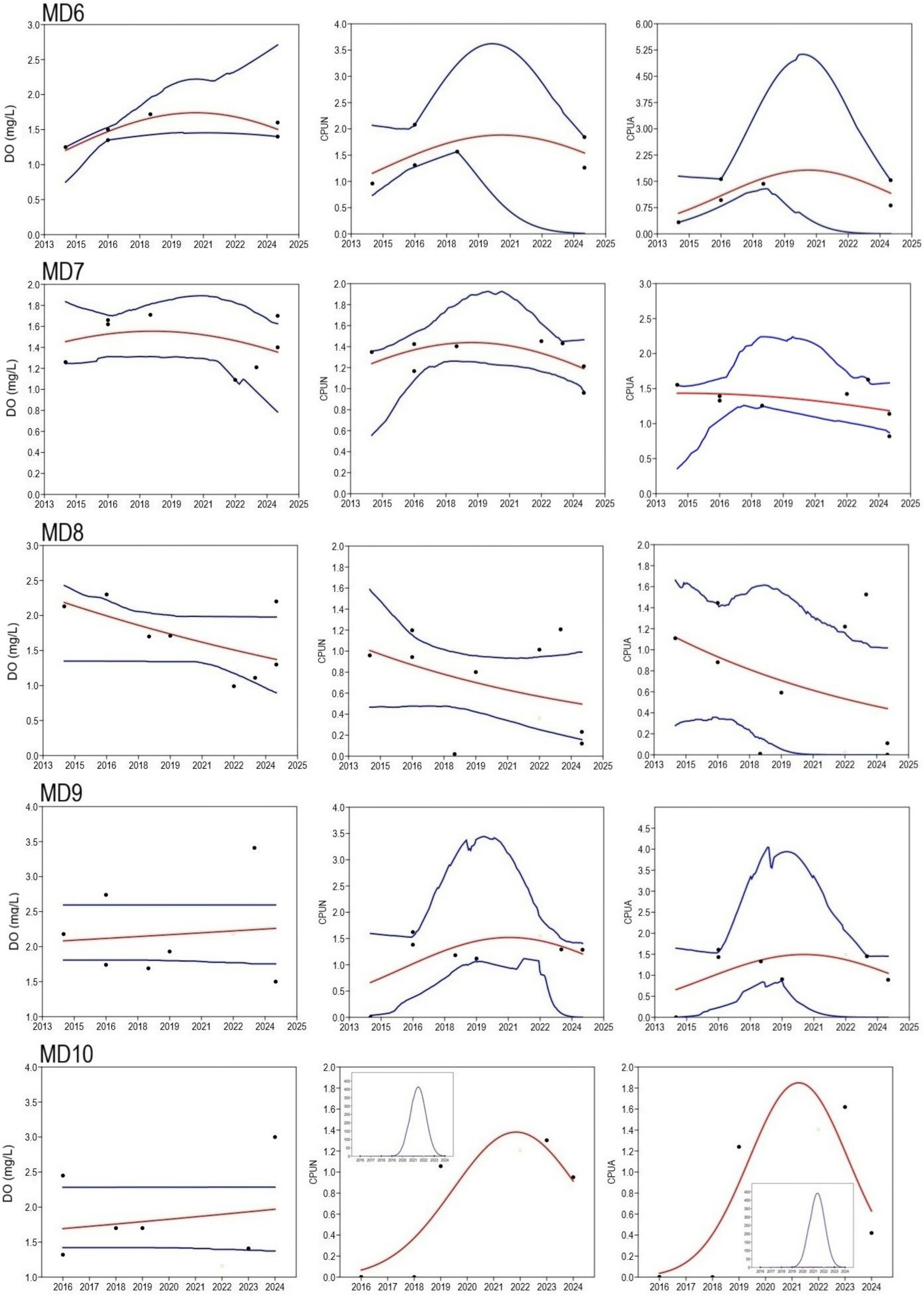
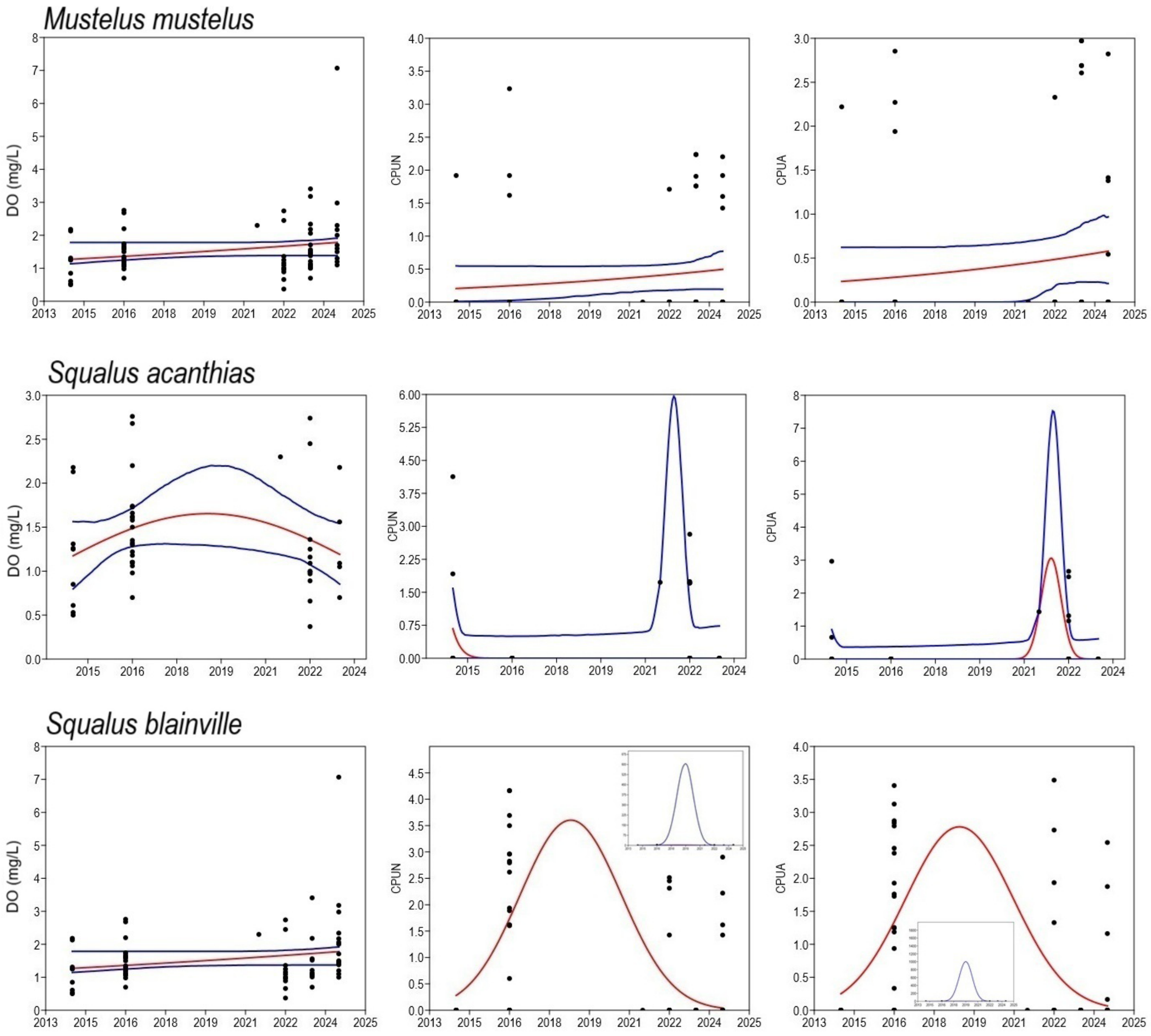


Fig. 3. Gaussian distribution smoothing (red lines) of log transformed CPUN (ind./km^2) and log transformed CPUA (kg/km^2) of demersal elasmobranch species, and variation of DO (mg/L) at MD6-10 stations during the 2014-2024 period. Blue lines indicate 95% confidence interval. For MD10 station, 95% confidence interval lines are shown in small panels to avoid hiding the CPUN and CPUA curves.


Mustelus mustelus

Squalus acanthias

Squalus blainville

Fig. 4. Gaussian distribution smoothing (red lines) of log transformed CPUN (ind./km²) and log transformed CPUA (kg/km²) of *Mustelus mustelus*, *Squalus acanthias* and *Squalus blainville*, and the variation of DO (mg/L) in the ESoM during the 2014-2024 period. Blue lines indicate 95% confidence interval. For *S. blainville,* 95% confidence interval lines are shown in small panels to avoid hiding the CPUN and CPUA curves.

a localized aggregation of approximately 200 individuals was recorded at station MD6. The majority of these individuals (n=178) were juveniles, with individual weights ranging between 21 g and 145 g to a total biomass of 13.2 kg. Biomass and abundance, estimated as 2,552.9 kg/km^2 and 14,557.2 ind./km^2 in 2016, declined to 350 kg/km^2 and 799.9 ind./km^2 by August 2024. Both biomass and abundance showed a statistically significant decrease over time (Kruskal-Wallis test, $p<0.05$; Fig. 4).

Raja clavata

The biomass and abundance of *R. clavata* in the ESoM showed an overall increasing pattern over the study period. Biomass and abundance were recorded as 1,221.1 kg/km^2 and 456.8 ind./km^2 in 2014, 726.8 kg/km^2 and 1,794.7 ind./km^2 in 2023, and 759.9 kg/km^2 and 1,553.9 ind./km^2 in August 2024, respectively. In August 2024, a relatively high number of individuals with lower body weights compared to adults was recorded. *R. clavata* was the most abundant batoid species in the ESoM throughout the study period. Changes in biomass and abundance were not statistically significant (Kruskal-Wallis test, $p>0.05$; Fig. 5).

Dasyatis pastinaca

The biomass and abundance of *D. pastinaca* on the continental shelf of the ESoM showed temporal variability over the study period. Biomass and abundance values were recorded as 1,011.4 kg/km^2 and 249.2 ind./km^2 in 2016, decreased to 462.8 kg/km^2 and 25.7 ind./km^2

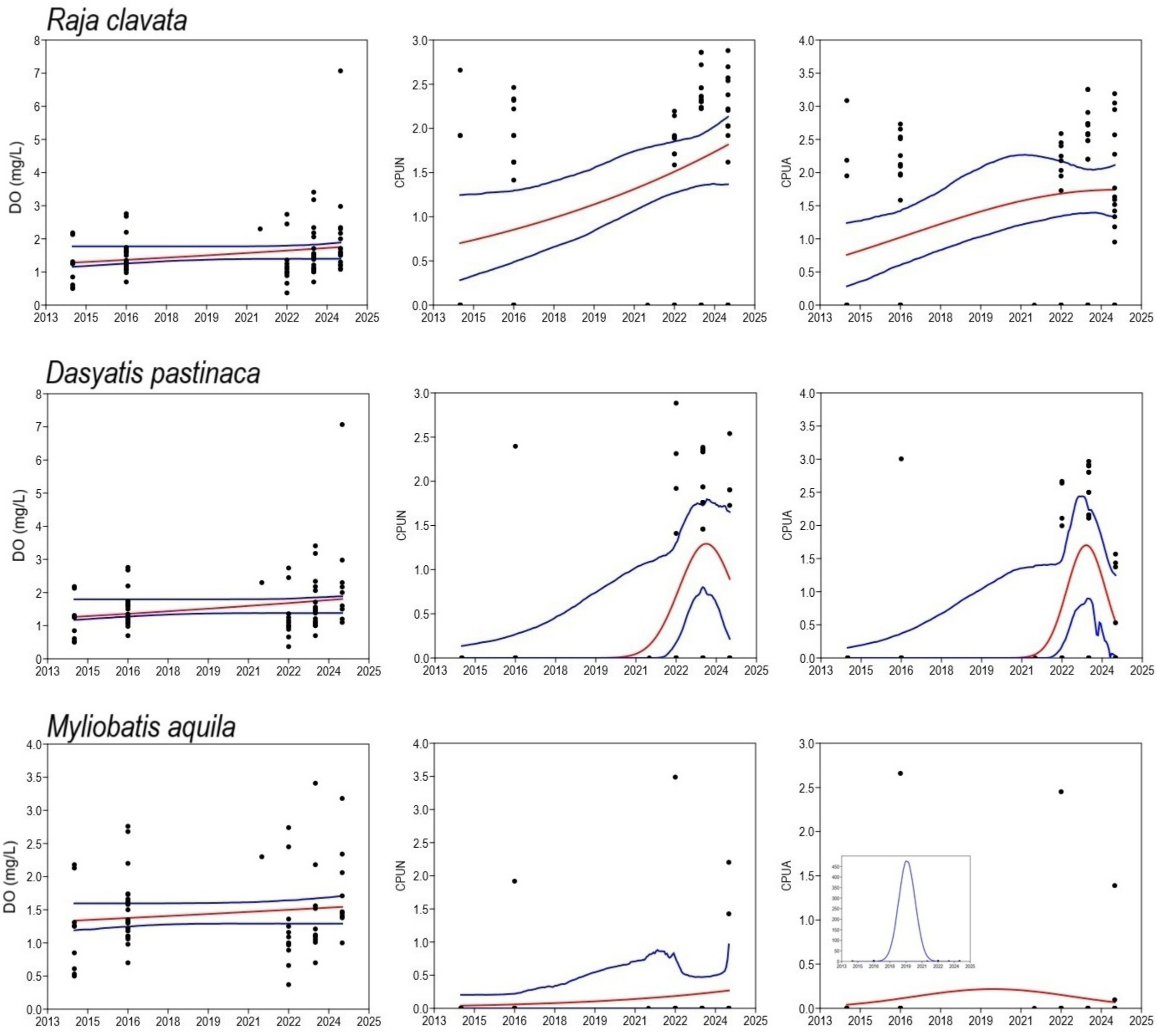


Fig. 5. Gaussian distribution smoothing (red lines) of log transformed CPUN (ind./km^2) and log transformed CPUA (kg/km^2) of *Raja clavata*, *Dasyatis pastinaca* and *Myliobatis aquila*, and the variation of DO (mg/L) in the ESoM during the 2014-2024 period. Blue lines indicate 95% confidence interval. For *M. aquila*, 95% confidence interval lines are shown in a small panel to avoid hiding the curve.

in 2022, and increased again to 929.2 kg/km^2 and 242.4 ind./km^2 in 2023, respectively. In August 2024, both biomass and abundance declined to zero in the ESoM (Fig. 5). It should be noted that the temporal pattern of change is based on a limited number of observations for this species, and the absence of data for certain intermediate years may influence the apparent trends and their representation in the Gaussian model. Overall, both biomass and abundance of *D. pastinaca* significantly decreased (Kruskal-Wallis test, $p<0.05$).

Myliobatis aquila

In 2016, the biomass and abundance of *M. aquila* were recorded as 456.9 kg/km^2 and 83.1 ind./km^2, respectively, while in 2022 these values were 282.8 kg/km^2 and 3,085.5 ind./km^2. By 2024, biomass declined to 24.5 kg/km^2, whereas abundance remained relatively higher at 160 ind./km^2 (Fig. 5). Both biomass and abundance showed statistically significant changes over time (Kruskal-Wallis test, $p<0.05$).

Impact of environmental parameters on species diversity - nMDS analysis

PERMANOVA analysis indicated that DO, T, S and D had statistically significant effects on the biomass of demersal elasmobranch species in the ESoM over the entire study period ($p<0.05$ for all variables). The proportion of total variance explained by each variable was 21.9% for DO, 20.4% for T, 18.0% for S and 16.6% for D. The 3D stress of the nMDS analysis for the full dataset (2014-2024) was 0.24. When the analysis was restricted to the period between 2022 and late summer 2024, the 3D stress decreased slightly to 0.22.

For the 2022-2024 subset, the proportion of variance explained by DO, T, S and D decreased to 11.2%, 10.6%, 9.4% and 8.9%, respectively. However, the effects of these environmental variables on biomass were not statistically significant for this period (PERMANOVA, $p>0.05$ for all variables). The ordination pattern of the nMDS plot (Fig. 6) reflects the relative contribution of these environmental variables to variation in demersal elasmobranch biomass across stations and sampling periods.

Impact of environmental parameters on species - CCA analysis

CCA showed that the first two canonical axes explained 95.9% of the total variance associated with DO, T, S and D at stations MD1-10 during the period 2014-2024. During this period, DO was associated with the distribution of several species, including the viviparous *S. acanthias*, *M. mustelus*, *D. pastinaca* and *M. aquila* as well as the oviparous batoid *R. clavata* (Fig. 7). In contrast, T, S and D were associated with *S. blainville*, *O. centrina* and *R. miraletus*.

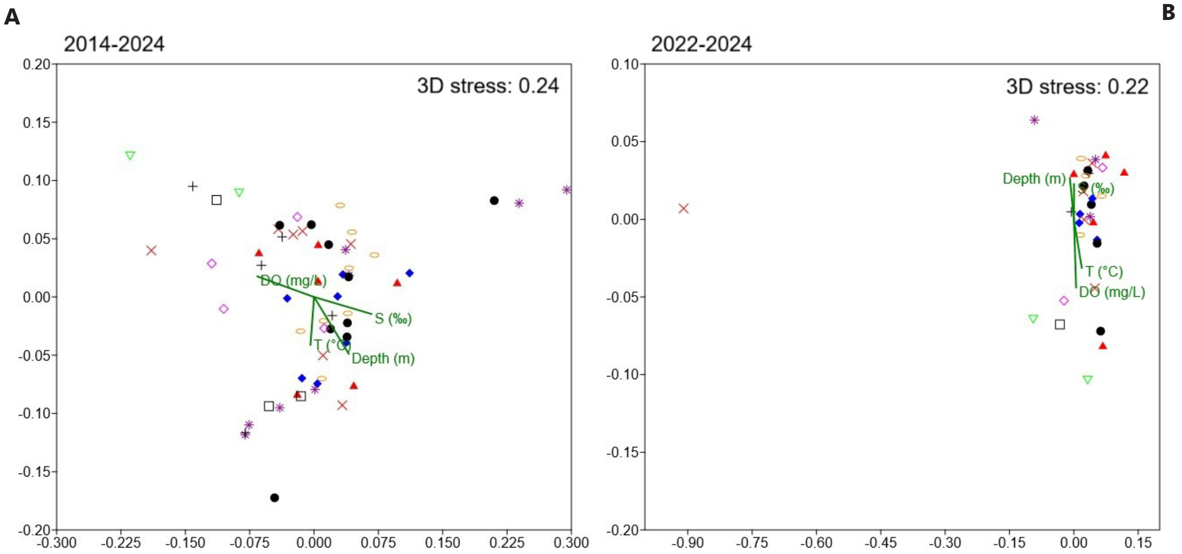


Fig. 6. Plots of nMDS ordination depicting the change of species diversity (based on Bray-Curtis similarity matrix) across MD stations for 2014-2024 period **(A)** and 2022-2024 period **(B)**. Icons on the plots are the representatives of biomass (kg/km^2) of demersal elasmobranch species in response to environmental parameters. Station codes: MD1 (X), MD2 (●), MD3 (☐), MD4 (▲), MD5 (◆), MD6 (✳), MD7 (θ), MD8 (+), MD9 (◇) and MD10 (▽).

When the analysis was restricted to the period 2022-2024, the first two canonical axes explained 96.5% of the total variance. During this period, DO, T and D showed stronger contributions to the ordination structure. DO and T were associated with *O. centrina*, *M. mustelus*, *D. pastinaca* and *R. clavata*, whereas D was associated with *S. acanthias*, *S. blainville* and *M. aquila* (Fig. 7).

DISCUSSION

This study provides a decadal perspective (2014–2024) on the structure, abundance, biomass and diversity of demersal elasmobranch assemblages in the ESoM. Overall, the assemblage was characterised by low species richness, strong spatial structuring, numerical dominance of a limited number of shark species, and a pronounced decline in both abundance and biomass during the most recent years of the study period. Multivariate analyses consistently identified bottom-water DO and T as the most influential environmental variables associated with biomass variability, jointly explaining the largest proportion of variance across the dataset. Temporal patterns revealed a general increase in abundance and biomass until the late 2010s, followed by a rapid and spatially widespread decline, suggesting a system-level shift affecting demersal elasmobranch populations in the ESoM.

Globally, elasmobranchs are among the most vulnerable marine taxa due to their life-history traits, including slow growth, late maturity and low fecundity, which limit their resilience to fishing pressure and environmental degradation (Stevens *et al.*, 2000). In the Mediterranean Sea, declines have reached critical levels (Dulvy *et al.*, 2014), with pelagic shark populations reduced by more than 90% over the last century (Ferretti *et al.*, 2008).

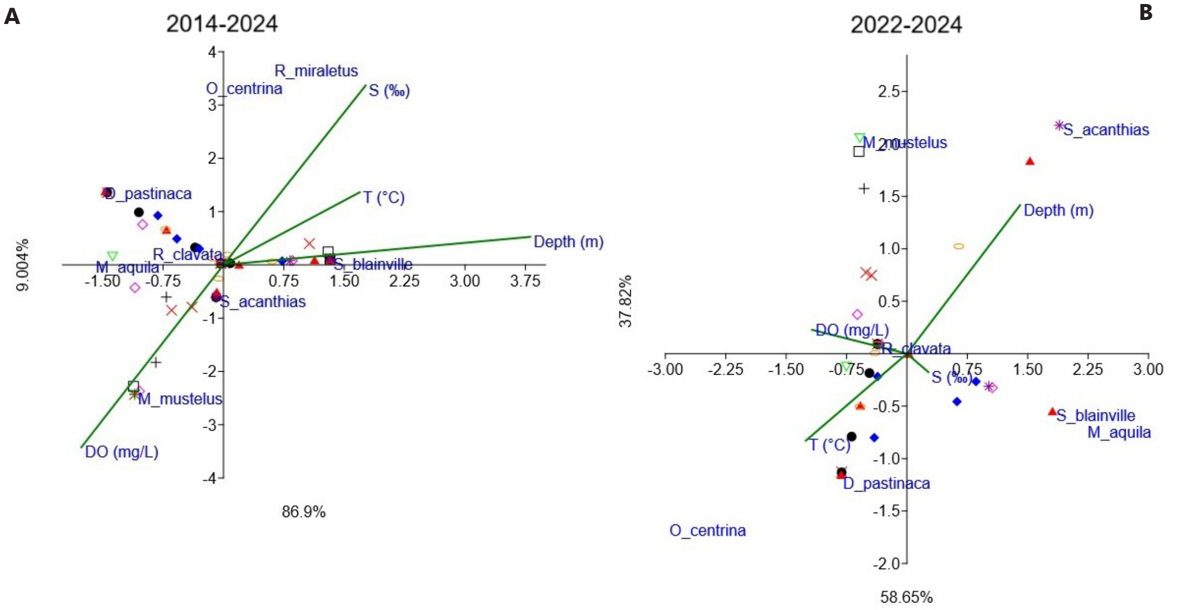


Fig. 7. CCA tri-plots of elasmobranch species in response to environmental parameters (dissolved oxygen, DO; temperature, T; salinity, S; depth, m) for 2014-2024 period **(A)** and 2022-2024 period **(B)**. Station codes: MD1 (X), MD2 (●), MD3 (☐), MD4 (▲), MD5 (◆), MD6 (✱), MD7 (θ), MD8 (+), MD9 (◇) and MD10 (▽).

Similar declining trends have also been reported for demersal elasmobranchs across Mediterranean subregions, with reductions in abundance, frequency of occurrence and species richness (Follesa *et al*., 2019). Consistent patterns have been reported in the SoM, where decreases in demersal elasmobranch abundance and bycatch frequency have been observed (Demirel *et al*., 2020; Gül and Demirel, 2021; Akoğlu *et al*., 2024).

The results of the present study indicate that demersal elasmobranch populations on the ESoM continental shelf have undergone a marked decline, particularly after 2019–2021, as reflected by decreasing biomass (kg/km²) and abundance (ind./km²). While earlier studies in the region primarily focused on landings, bycatch, or general demersal fish assemblages (JICA, 1993; Zengin *et al*., 2004; Bayhan *et al*., 2006; Yazıcı *et al*., 2006; Bök *et al*., 2011; Keskin *et al*., 2011; Daban *et al*., 2021), the present study is, to our knowledge, the first to explicitly evaluate the influence of environmental variables on demersal elasmobranch assemblages in the ESoM using ordination-based multivariate approaches. Additional occurrence data were provided by Karakulak *et al*. (2017), while recent biomass estimates were reported by Karadurmuş and Sarı (2024). Notably, Kabasakal *et al*. (2024a) showed that the bycatch of *Hexanchus griseus*, a top demersal predator in the SoM, has declined in parallel with increasing deoxygenation and eutrophication, highlighting the combined effects of environmental degradation and fishing pressure.

Historical comparisons further illustrate the magnitude of recent changes. The JICA report (1993) documented high biomass values of deep-sea demersal elasmobranchs in the western SoM, indicating that anoxic conditions were absent from deeper layers at that time (Kocataş *et al*., 1993). In contrast, species such as *Galeus melastomus*, formerly abundant in the upper bathyal zone, were recorded only sporadically in the present study, despite their widespread occurrence at depths of 200–800 m throughout the Mediterranean (Follesa *et al*., 2019). Similar patterns for other deep-sea taxa, including *Centrophorus uyato* and *Dipturus oxyrinchus*, suggest a contraction of their effective bathymetric ranges in the ESoM, potentially linked to hypoxia and anoxia in deeper waters (Kabasakal *et al*., 2023, 2024b). Comparisons with other Mediterranean regions support this interpretation. MEDITS data indicate that several species recorded in the present study, such as *G. melastomus*, *S. canicula*, *O. centrina*, *S. acanthias*, *S. blainville* and *R. clavata* are capable of occupying continental slope habitats down to 800 m elsewhere (Follesa *et al*., 2019), whereas in the ESoM many of them were restricted to shallower depths. Similar patterns have been reported from the Gulf of Antalya in eastern Mediterranean, where species occur at greater depths under comparatively less degraded environmental conditions (Deval and Mutlu, 2024). While depth is widely recognised as a primary driver of demersal elasmobranch community structure (Deval and Mutlu, 2024), that study did not include bottom-water DO as a predictor. In contrast, the present study indicates that DO, together with T, is strongly associated with biomass patterns, suggesting that deoxygenation may constrain habitat availability and reduce depth-related refugia available to demersal elasmobranchs in the ESoM.

Comparisons with previous studies in the SoM further support the observed trends. Although methodological differences limit direct comparability, earlier studies reported low frequency of occurrence (F%) values for most demersal elasmobranch species, with only a few considered continuous (Bayhan *et al*., 2006; Yazıcı *et al*., 2006; Bök *et al*., 2011; Karakulak *et al*., 2017; see Supplementary Table 4). The present study confirms this general pattern and indicates a further reduction in F% values for most species over the last decade. Apparent increases in *S. blainville* were largely associated with short-term peaks rather than sustained population growth.

Recent biomass estimates based on single-year survey (Karadurmuş and Sarı, 2024) reported relatively high values at several stations overlapping with the present study area. In contrast, the long-term dataset analysed here indicates a consistent decline in biomass 2019–2021. Differences in sampling design, including haul duration, may contribute to these discrepancies, but more importantly, they highlight the limitations of short-term, non-replicated surveys for detecting population trends in elasmobranch populations. In this context, the use of a restricted “environmentally matched dataset” in the present study, based on hauls with concurrent oceanographic measurements, should also be considered when interpreting the results. Although this approach improves environmental matching, it reduces sample size and may influence the detection of temporal trends.

Patterns in species diversity further support the interpretation of environmental degradation in the ESoM. Diversity indices revealed consistently low Shannon (H′) and Margalef (D) values across most stations, with H′ values frequently below 1, indicating polluted or degraded conditions (Vaquer-Sunyer and Duarte, 2008; Bhardwaj *et al*., 2023). These values are generally lower and more homogenous than those reported in earlier studies (Karakulak *et al*., 2017; Karadurmuş and Sarı, 2024), suggesting a continuous decline in habitat quality. This interpretation is consistent with previous findings linking reduced demersal fish diversity in the region to industrial and domestic pollution (Daban *et al*., 2021), now compounded by progressive deoxygenation.

DO and T appear to act as closely interacting drivers of these patterns. Rising seawater temperatures, which are also particularly pronounced in the SoM (Demircan, 2022), reduce oxygen solubility and increase metabolic demand, thereby lowering tolerance to hypoxic conditions (Waller *et al*., 2024). This interaction has been shown to influence demersal fish assemblages in other systems (Gallo *et al*., 2020). The decline in abundance of demersal elasmobranchs observed across ESoM stations is therefore consistent with the combined effects of hypoxia and increasing bottom-water temperature. Restricted depth distribution observed for most species suggests that tolerance to oxygen-depleted conditions with raising bottom-water temperature may play a key role in shaping spatial patterns of demersal elasmobranchs in the region.

Nevertheless, it should be noted that some temporal patterns and species-specific responses, including those described using Gaussian models, may be influenced by uneven temporal coverage and gaps in the dataset. For certain species, the absence of observations in intermediate years affects the apparent trends and their graphical representation. These limitations should be considered when interpreting species-specific responses to environmental gradients.

The patterns observed in the ESoM are broadly consistent with the “habitat trap” hypothesis proposed for sharks and batoids in deoxygenated systems, whereby environmental degradation may increase vulnerability to fishing and contribute to population declines (Waller *et al*., 2024). Nevertheless, occasional records of deep-sea species such as *H. griseus*, *C. uyato* and *O. centrina* suggest that some elasmobranchs may still intermittently utilise degraded habitats, although the ecological significance of these occurrences remains uncertain (Kabasakal *et al*., 2025). Given that demersal elasmobranch assemblages in the SoM are currently dominated by mesopredator species (Gül and Demirel, 2021, 2022), continued declines may have cascading ecological consequences, including reduced top-down control in benthic food webs (Dedman *et al*., 2024). These findings highlight the importance of mitigating deoxygenation and reducing anthropogenic pressures to support the conservation of elasmobranch populations and the functioning of the SoM ecosystem.

CONCLUSION

This study provides the first decadal assessment of the relationships between environmental variables and demersal elasmobranch assemblages in the ESoM. Biomass and abundance declined markedly after 2019–2021, with consistently low diversity levels. Bottom-water DO and T emerged as key drivers, indicating that deoxygenation combined with warming constrains habitat suitability. The simplified assemblage structure suggests increasing vulnerability to environmental and anthropogenic pressures, highlighting the need for integrated management and long-term monitoring.

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