

# Of three sharks and one chimaera: varied habitat preferences across a latitudinal range revealed by coastal and offshore surveys

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## Abstract

Using national and international research survey data and applying a combination of models and mapping tools, this study revealed temperature and depth as the crucial environmental drivers of both the distribution and the abundance of four benthopelagic chondrichthyans inhabiting Norwegian and Icelandic waters: rabbitfish (*Chimaera monstrosa*), velvet-belly lanternshark (*Etmopterus spinax*), blackmouth catshark (*Galeus melastomus*) and spurdog (*Squalus acanthias*). *C. monstrosa* and *E. spinax* seem to prefer similar spatial and ecological habitats, that is deep and cold waters. In contrast, *G. melastomus* and *S. acanthias* both prefer similar ecological habitats, that is warmer and shallower waters; nonetheless, they exhibit a different spatial distribution pattern. The species' varied habitat and spatial preferences may lead to different levels of exposure to fishing activities and associated by-catch risks. Findings of the species' spatial distributions and their driving forces are expected to inform the sustainable management of these species and the ecosystems they inhabit.

## KEYWORDS

density, fisheries, GIS, Northeast Atlantic

## 1 | INTRODUCTION

In recent years, dramatic declines in the biomass of chondrichthyans and in particular sharks have been documented worldwide (MacNeil *et al.*, 2020), also in the North Atlantic Ocean (ICES, 2020; Pawson *et al.*, 2009; Sguotti *et al.*, 2016). Declines were first reported for pelagic species, such as basking shark (*Cetorhinus maximus*), porbeagle (*Lamna nasus*) and shortfin mako shark (*Isurus oxyrinchus*; Clarke *et al.*, 2008; Ferretti *et al.*, 2008; Kohler *et al.*, 2002), but similar concerns are now evident for benthic and benthopelagic chondrichthyan species (ICES, 2020). Over one-third of all chondrichthyans species are currently estimated to be threatened (Dulvy *et al.*, 2021), including

benthopelagic species like the spurdog, or spiny dogfish (*Squalus acanthias* Linnaeus, 1758). As many of these species fulfil important ecosystem functions and services (Hammerschlag *et al.*, 2019), their conservation has increasingly been prioritised all over the world. This is essential, as many of them exhibit low population growth rates making them particularly vulnerable to anthropogenic pressures (Stevens *et al.*, 2000) such as fisheries, coastal development and climate change.

Despite the implementation of various restrictions, benthopelagic chondrichthyans still account for the largest share of unwanted fish by-catch, severely impacting and depleting stocks (ICES, 2020; Jabado *et al.*, 2018; Queiroz *et al.*, 2019). Historically, North Atlantic fisheries

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have caught many chondrichthyans (Hareide *et al.*, 2007). These fisheries started to expand greatly in the 1960s, targeting initially particularly *S. acanthias* and deep-water chondrichthyans in the 1970s (Ellis *et al.*, 2009; ICES, 2020). Restrictive management measures were implemented for the Northeast Atlantic (NEA) at different times to protect some of these vulnerable species, like the EU zero TAC for deep-sea sharks, fishing prohibition for threatened species and gear-specific fishing depth-restrictions (EU, 2016, 2018, 2019). Nonetheless, the by-catch in various commercial fisheries could be a large threat to benthopelagic chondrichthyans with low or no commercial value.

In the light of that, understanding their ecology and distribution, especially as a response to environmental factors, is essential and urgently needed knowledge. Such factors include but are not limited to abiotic ones like temperature, salinity, dissolved oxygen and season (Drymon *et al.*, 2020; Tinari & Hammerschlag, 2021), and biotic ones like foraging (Andrzejczek *et al.*, 2019; Vedor *et al.*, 2021), but also include anthropogenic ones like fishing, aquaculture and global warming (Junge *et al.*, 2019; Queiroz *et al.*, 2019; Sguotti *et al.*, 2016). This knowledge can inform species-focused as well as ecosystem-based approaches to fisheries management and guide long-term monitoring programmes (Espinoza *et al.*, 2016; Moranta *et al.*, 2008; Williams *et al.*, 2018). Baseline information on abundance and distribution allow the detection of spatio-temporal changes in species' populations in response to major stressors such as fishing, habitat degradation or climate change (Espinoza *et al.*, 2020).

To address these critical knowledge gaps, the distribution and abundance of four benthopelagic chondrichthyans found in the northern parts of the NEA, as well as their possible drivers, were investigated in this study. The four studied species were: *Chimaera monstrosa* Linnaeus, 1758 (rabbitfish and ratfish), *Etmopterus spinax* (Linnaeus, 1758) (velvet-belly lanternshark), *Galeus melastomus* Rafinesque, 1810 (blackmouth catshark) and *S. acanthias*. All of them can occur in deep waters to depths of 1500 m (Carrassón *et al.*, 1992; Ellis *et al.*, 2015; Weigmann, 2016), and down to 2490 m for *E. spinax* (Jones *et al.*, 2003), but are most abundant shallower than 500 m (Ellis *et al.*, 2015; Holt *et al.*, 2013; Ragonese *et al.*, 2013; Ruiz-Pico *et al.*, 2020). All are widely distributed, ranging in the East Atlantic southwards to 34°S (*E. spinax*) and northwards reported to 75°N (*C. monstrosa*; Dagit & Hareide, 2015; Guallart *et al.*, 2015). Despite this wide distribution, knowledge of their distribution and abundance on a finer scale is currently poor, especially in the Norwegian Sea and off Iceland. These species differ in their mode of reproduction as *C. monstrosa* and *G. melastomus* are oviparous, that is, they lay eggs (Capapé *et al.*, 2008; Stehmann & Bürkel, 1984), whereas the other two, *E. spinax* and *S. acanthias*, are aplacental viviparous (Capapé *et al.*, 2001; Hisaw & Albert, 1947) with the young being nourished by egg yolk until they are being born live. This creates different requirements for reproduction and early life stages, especially with respect to the required energy and nursery areas, but also the timing and gestation periods. Egg-laying species have variable substrate requirements and need to find waters with high oxygenation to lay their eggs (Barnett *et al.*, 2019; Lennon *et al.*, 2021), whereas aplacental viviparous species invest and need a lot of energy during their longer gestation periods, and may frequently return

to somewhat sheltered areas, often referred to as nursery grounds and often associated with hatching, birthing or pupping [but see Heupel *et al.* (2007) for a critical discussion on the concept of nursery areas].

These four benthopelagic species were selected as they are relatively common in Norwegian waters (Lynghammar *et al.*, 2013; Williams *et al.*, 2008) and vary in life-history strategies and presumably habitat preferences. Sufficient, yet variable, data were also available for each of them, enabling a comparative study. Furthermore, these species have been subject to high levels of by-catch for many years (Finucci *et al.*, 2020; ICES, 2020). In European waters, *C. monstrosa* and *E. spinax* are considered as “Near Threatened” by the IUCN Red List (Dagit & Hareide, 2015; Guallart *et al.*, 2015), whereas *G. melastomus* is considered as “Least Concern” (Abella *et al.*, 2015). *S. acanthias* is considered as “Endangered” in European waters by the IUCN (Ellis *et al.*, 2015) and was newly assessed as “Vulnerable” by the Norwegian Red List (one category improved compared to the previous assessment in 2015; Artsdatabanken, 2021) which is compiled by the Norwegian Biodiversity Information Centre.

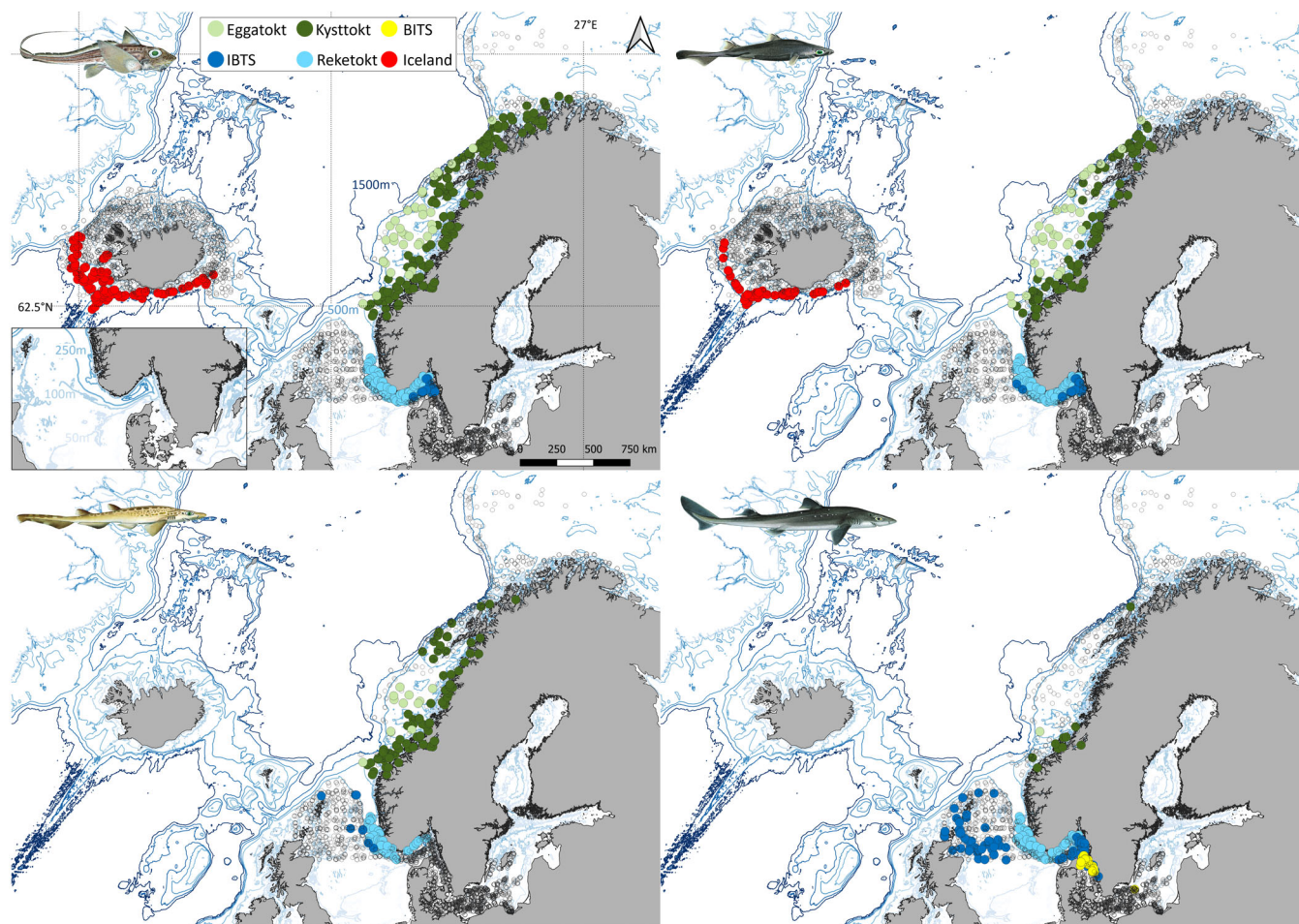
The objectives of this study were therefore (a) to reveal the distribution and abundance of the four species and (b) to identify possible environmental and ecological drivers of their presence and abundance.

## 2 | MATERIALS AND METHODS

### 2.1 | Survey data

Three years (2018–2020) of scientific bottom trawl survey data from several countries and from joint international efforts were used. All survey stations are shown in Figure 1, and the surveys are described in short below; for details see Supporting Information Table S1 in Appendix S1. Together, the surveys cover the International Council for the Exploration of the Sea (ICES) statistical subareas 27.5.a (Icelandic water), 27.4.a (Northern North Sea), 27.3.a (Skagerrak and Kattegat), 27.2.a (Norwegian Sea) and parts of 27.1b (Barents Sea; www.ices.dk, and details in Supporting Information Figure S1 in Appendix S1) at depths between 50 and 1400 m. The total data set was divided into three regions for modelling and description purposes: the Norwegian Sea, the North Sea (northern North Sea, Skagerrak, Kattegat) and Icelandic waters, to allow for meaningful analyses and comparisons among species within regions.

In the Norwegian Sea, data for all four species were collected on the annual coastal survey, “Kysttokt,” and the shelf-break survey, “Eggatokt,” which includes biennially the “EggaSør” (southern) and “EggaNord” (northern) survey, all conducted by the Institute of Marine Research (IMR), Norway. The Norwegian Sea extends along the entire Norwegian coast from 61°N to the Bear Islands. The continental shelf of the Norwegian Sea is small and structurally complex, allowing very deep bottoms around 4000 m depth (Sætre, 1999). Furthermore, average winter temperatures in the Norwegian Current vary from 2 to 5°C, and salinity is less than 34.8 (Mork *et al.*, 2019; Sætre, 2007). The data from the North Sea and the Skagerrak were



**FIGURE 1** Observations of *Chimaera monstrosa*, *Etmopterus spinax*, *Galeus melastomus* and *Squalus acanthias* off Norway and Iceland, 2018–2020. Coloured dots correspond to a trawl with at least one individual caught, whereas empty circles represent zero catch of the respective species. On the bottom-left of the *C. monstrosa* plot the detailed depth contours of the northern North Sea and the southern Baltic Sea are shown, for clarity without the trawl stations. Drawings: *C. monstrosa*, *E. spinax*, *G. melastomus* and *S. acanthias*, CC BY-SA 4.0 Jan Fekjan

mainly collected from IMR's annual shrimp survey ("Reketokt"; Søvik, 2020), and additional data were extracted from the North Sea International Bottom Trawl Survey (NS-IBTS; ICES, 2021a) from the ICES database DATRAS. The "Reketokt" covers areas deeper than 100 m (the Norwegian Trench), whereas the NS-IBTS surveys cover the shallow parts of the North Sea. As this study was intended to investigate the northernmost waters of the NEA, it was decided to retrieve NS-IBTS data only from the northern part of the North Sea. The North Sea is particularly shallow (average depth around 100 m) and relatively warm, except for the Norwegian Trench, which is an elongated depression along the southern coast of Norway. The trench is between 50 and 95 km wide and reaches a maximum depth of 700 m in the central part of Skagerrak, allowing the formation of numerous eddies and upwelling (Furnes *et al.*, 1986; Rodhe, 1989). To better understand the distribution limits of these species towards the southeast, data from the Baltic International Trawl Survey (BITS; ICES subarea 3.a; ICES, 2021a; ICES, 2021b) were also retrieved from DATRAS and included in this study. For Icelandic waters, data from two scientific surveys were available from the Marine and Freshwater

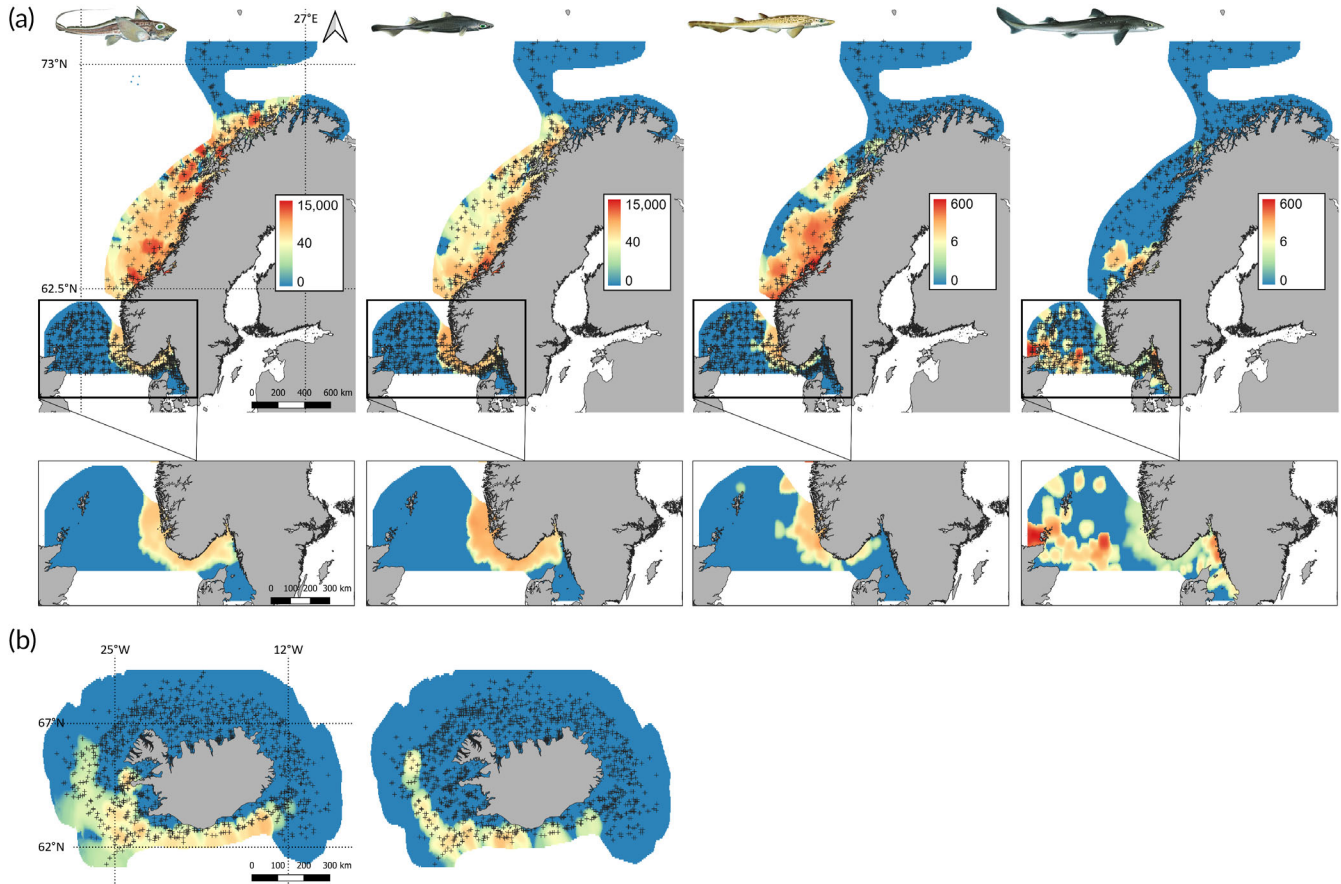
Research Institute (MFRI), Iceland: Icelandic autumn groundfish survey (AGS) and Icelandic Groundfish survey (IGS). Here, the two surveys have been combined under the name "Iceland." Around Iceland, *G. melastomus* is rarely observed and *S. acanthias* is normally not caught in these surveys. Therefore, only data for *C. monstrosa* and *E. spinax* were included in this study, allowing for quantitative analyses. All survey data were mapped using QGIS 3.10.13 (QGIS, 2021) to visualise the distribution and distributional limits of the four target species.

## 2.2 | Environmental and spatial data

To identify the most important factors determining the presence and abundance of the target species, the authors investigated a range of environmental and spatial variables: bottom temperature, bottom salinity, depth, latitude and distance from the coast. To obtain reliable data for the entire study area, monthly average temperature and salinity data were extracted as near-bottom temperature to best reflect the conditions experienced during bottom trawls, from a numerical

ocean model covering all seas between the English Channel, Greenland and the southern Arctic Ocean including the Barents Sea. This three-dimensional ocean general circulation model based on the Regional Ocean Modelling System (ROMS, e.g., Shchepetkin & McWilliams, 2005; Haidvogel *et al.*, 2008 or see <http://myroms.org>) was coupled with an ice module (Budgell, 2005) and implemented with a horizontal grid resolution of 4 km thus ensuring a high resolution over the whole study area (Lien *et al.*, 2013). In this study, as the

species studied are benthopelagic, monthly averages of the bottom salinity and temperature for each year between 2018 and 2020 were used. Finally, as distance from the coast can impact chondrichthyan abundance (MacNeil *et al.*, 2020), and all four species are also found in areas close to the coast, this parameter was calculated using the Near Neighbour Join (NNJoin) function available in QGIS and considered in this study.



**FIGURE 2** Abundance of *Chimaera monstrosa*, *Etmopterus spinax*, *Galeus melastomus* and *Squalus acanthias* for included surveys from 2018 to 2020 off (a) Norway (with the bottom row showing detailed abundance in the North Sea and the southern Baltic Sea, for clarity without trawl stations), and (b) Iceland. The colour scheme is the same for Norwegian and Icelandic waters (from blue to red), and indicates the density (number of individuals per km<sup>2</sup>), with the crosses indicating positions of trawls. The density scales for *C. monstrosa* and *E. spinax* are 25-fold higher than those for *G. melastomus* and *S. acanthias*. Drawings: *C. monstrosa*, *E. spinax*, *G. melastomus* and *S. acanthias*, CC BY-SA 4.0 Jan Fekjan

**TABLE 1** Presence of the four study species per region and survey

Species	Norwegian Sea			North Sea			Iceland
	Eggatokt	Kysttokt	Combined	IBTS	Reketokt	Combined	
<i>Chimaera monstrosa</i>	27% (444)	43% (33,306)	39% (33,306)	2% (89)	72% (3,009)	20% (3,098)	8% (2,032)
<i>Etmopterus spinax</i>	23% (133)	22% (9,421)	22% (9,554)	3% (163)	89% (9,081)	26% (9,244)	3% (1,301)
<i>Galeus melastomus</i>	9% (48)	20% (1,270)	18% (1,318)	1% (25)	16% (228)	7% (253)	-
<i>Squalus acanthias</i>	1% (9)	2% (69)	2% (78)	10% (437)	69% (359)	14% (796)	-

Note: Shown as average percentage (%) and absolute numbers in parentheses. “-” indicates the absence of data for that species-area combination. “Combined” values are per region across surveys.

**TABLE 2** Summary of the effect of best-fit GLM predictors on the presence/absence distributions (Poisson distribution) for each species in each region (variables tested: depth, temperature, distance, salinity and latitude for the Norwegian Sea and Iceland)

Area	Species	Variable	AIC	$\Delta$ AIC	Relative likelihood	Weight	BIC	Residual model	Correlation <sup>a</sup>	Tolerance	
Norwegian Sea	<i>Chimaera monstrosa</i>	NULL	902.53	128.48	1.2616E-28	1.2357E-28	905.91		-	62.1–71.3°N	
		Latitude	810.55	36.50	1.1861E-08	1.1618E-08	319.31		+	2.7–8.6°C	
		+ Temperature	793.25	19.30	6.7728E-05	6.6341E-05	806.40		-	50–670m	
		+ Depth	781.79	7.74	0.02086	0.0204	799.33		+	34.0–35.2	
	<i>Etmopterus spinax</i>	+ Salinity	774.05	0	1	1	795.97	0.0880			
		NULL	635.79	94.23	3.4532E-21	3.4490E-21	640.18		-	62.1–70.4°N	
		Latitude	557.89	16.33	0.0003	0.0003	566.66		+	34.0–35.2	
		+ Salinity	557.13	15.57	0.0004	0.0004	570.29		+	2.6–8.6°C	
		+ Temperature	556.77	15.21	0.0005	0.0005	574.32		-	90–890m	
		+ Depth	541.56	0	1	1	563.51	-0.0864			
North Sea	<i>Galeus melastomus</i>	NULL	501.66	152.87	6.3783E-34	6.1960E-34	640.18		-	62.1–69.7	
		Latitude	366.98	18.19	0.0001	0.0001	566.66		+	3.7–8.6°C	
		+ Temperature	355.85	7.06	0.0293	0.0284	570.30		-	50–560m	
		+ Depth	348.79	0	1	1	574.32	-0.0285			
	<i>Squalus acanthias</i> <sup>b</sup>	NULL	95.41	19.54	5.7140E-05	5.7150E-05	99.80		+	5.6–8.2°C	
		Temperature	75.87	0	1	1	84.64	-0.062			
		NULL	1354.72	466.34	5.4395E-102	5.4395E-102	1359.83		-	5.8–8.2°C	
		Temperature	987.34	98.96	3.2442E-22	3.2442E-22	997.56		-	Coastal	
		+ Distance	916.08	27.70	9.6610E-07	9.6610E-07	931.41		+	130–560m	
		+ Depth	888.38	0	1	1	908.812	0.0221			
<i>Etmopterus spinax</i>	NULL	1522.82	508.55	3.7134E-111	3.4985E-111	1527.95		-	5.8–8.7°C		
	Temperature	1134.28	120.01	8.7128E-27	8.2087E-27	1144.54		-	Coastal		
	+ Distance	1045.12	30.85	1.999E-07	1.8841E-07	1060.51		+	130–560m		
	+ Depth	1019.85	5.58	0.0614	0.05787	1040.36		+	34.8–35.3		
	+ Salinity	1014.27	0	1	1	1039.91	-0.0221				
	NULL	627.36	204.47	2.0626E-23	2.0439E-23	622.55		-	5.8–8.8°C		
	Temperature	532.17	9.38	0.00966	0.0096	542.41		-	Coastal		
	+ Distance	522.89	0	1	1	538.25	-0.0285				
	NULL	1101.37	67.36	2.3603E-15	2.2603E-15	1106.50		+	5.8–8.8°C		
	Distance	1059.52	25.51	2.8879E-06	2.8878E-06	1069.76		+	Coastal		
+ Temperature	1034.01	0	1	1	1049.37	0.1144					

(Continues)

TABLE 2 (Continued)

Area	Species	Variable	AIC	$\Delta$ AIC	Relative likelihood	Weight	BIC	Residual model	Correlation <sup>a</sup>	Tolerance
Iceland	<i>Chimaera monstrosa</i>	NULL	1067.81	1067.81	1.3428E-232	1.3428E-232	1073.36			
		Latitude	737.55	0	1	1	748.64	-0.0321	-	62.4–65.8°N
	<i>Etmopterus spinax</i>	NULL	867.00	867.00	5.4118E-189	5.4118E-189	872.96			
		Latitude	558.81	0	1	1	570.74	-0.0172	-	62.7–65.8°N

<sup>a</sup>Pearson correlation (P-value < 0.05), positive (+) and negative (-).

<sup>b</sup>Analysed carefully as few individuals, NULL = model without external factors.

## 2.3 | Statistical analysis

As a first step, the survey data sets were subjected to a filtering process removing all survey stations not meeting the quality standards of the responsible institute, and the same standards were used for the international data sets. This led to a reduction of the data set by 249 tows in all the areas and years. Two catches, each with one individual of *S. acanthias* from the North Sea, were removed as the reported weight was above 10 kg, which is well above the maximum weight currently recorded for this species in the NEA (Stenberg, 2005). As this study aggregated data from several different benthic trawl types, a standardisation of the data had to be carried out to compensate for the differences between the gears and their operating methods (Rogers & Ellis, 2000). To standardise the data across surveys, the “density” was estimated as a measure of abundance based on the area trawled at each station using the method of Jakobsen *et al.* (1997), using trawled distance and mean trawl opening width, and is expressed as the number of individuals per trawled km<sup>2</sup> (individual per km<sup>2</sup>). The three regions (Norwegian Sea, North Sea and Icelandic waters) were treated separately for analysis purposes, as different environmental and spatial variables could have significant but variable effects on a given species depending on the region in question.

After log- or arcsin transformation of the density without normal distribution, these were interpolated using kriging methods. Kriging is a linear estimation method that generates an estimated surface from a scattered set of points and guarantees the minimum variance (Oliver & Webster, 1990). For each species mapped by interpolation, variograms were adjusted prior to kriging the species density running the “geoR 1” package (Ribeiro Jr *et al.*, 2020) in Rstudio (RStudio, Inc., 2015). All kriging was performed with a resolution of 0.05 decimal degrees (approximately 5.6 km), corresponding to the largest distance between two neighbours, and then smoothed to better illustrate chondrichthyan distribution patterns. To check for consistency in the observed pattern the same analysis was also run using biomass [total catch weight (kg) km<sup>-2</sup>] instead of number of individuals. As the results were consistent, the authors decided to focus only on the “number of individuals per km<sup>2</sup>” for all maps and statistical analyses.

To study the weight (effect) of environmental (temperature and salinity) and spatial variables (latitude, depth, distance from the coast) on the presence of chondrichthyans, generalised linear models (GLMs) combined with a direct elimination procedure, based on AIC (Akaike, 1974) and the BIC (Schwarz, 1978), were used to select the most significant environmental variables. In a second step, to better understand the impact of these variables on the observed density (*i.e.*, in the areas where they are present), linear mixed model (LMM) selection using two information criteria (AIC and BIC) were performed using the “presence only” data. The variables “season” and “year” were defined as random in these models and are not evaluated, thus providing reliable results. These statistical studies were performed using the R packages “MASS” and “lme4” (Bates *et al.*, 2014; Venables & Ripley, 2002). Finally, for each explanatory variable, the weighted mean and standard deviation were calculated using the R package “MetricsWeighted” (Mayer, 2020) to determine a range of values of environmental preferences for each species.

To investigate whether individual size had an effect on their habitat preferences, the average weight of individuals was approximated by dividing the total catch weight by the number of individuals caught for all trawl hauls off Norway.

### 3 | RESULTS

*C. monstrosa* and *E. spinax* were observed in all three regions, whereas no data were obtained for *G. melastomus* and *S. acanthias* in Icelandic waters (Figure 1). In terms of species distribution, the most northerly species observed is *C. monstrosa* with a maximum latitude near 73.0°N. The most common species in the North Sea is *E. spinax*, whereas in the Norwegian Sea and off Iceland it is *C. monstrosa*. Of the studied species, *S. acanthias* showed the easternmost distribution with individuals recorded in the Baltic Sea (Figure 1).

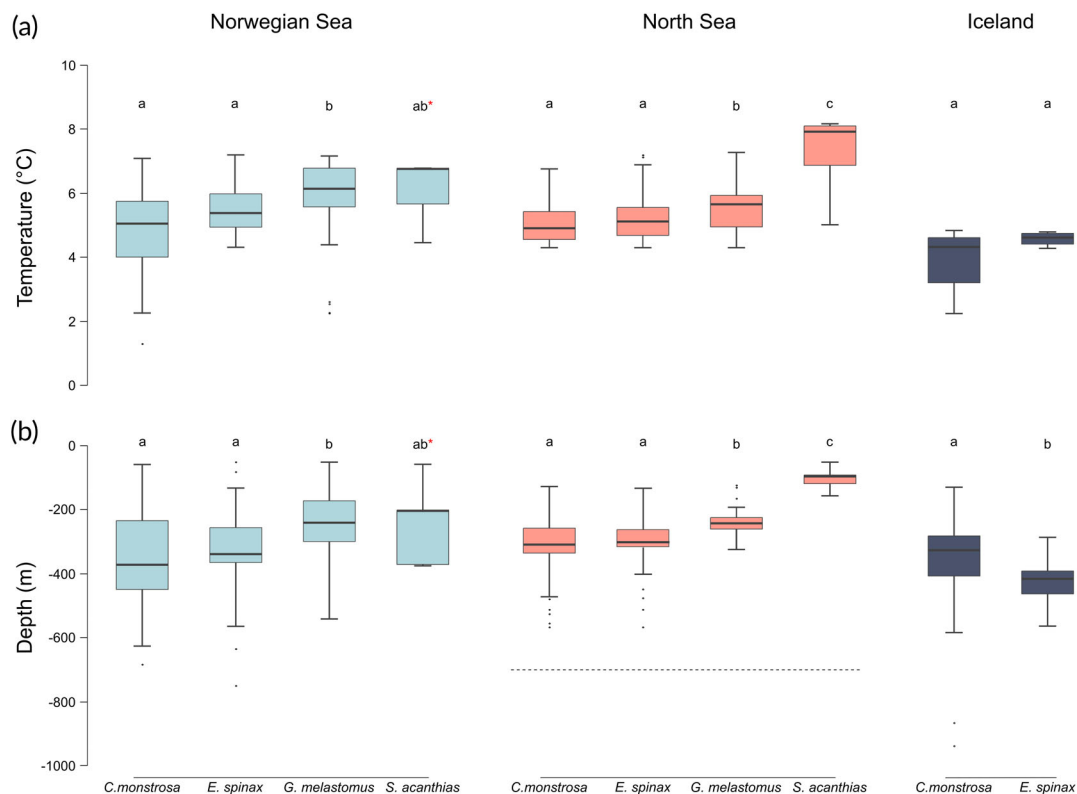
Collinearity between variables was tested by region and none were established. The non-collinearity of temperature and depth in the Norwegian Sea can be explained by the presence, especially in winter, of a large mixed layer and a deep, shallow thermocline (Nilsen & Falck, 2006). In the North Sea, mainly around the Norwegian Trench, their non-collinearity can be explained by the inflow of cold water through numerous upwellings (Rodhe, 1989) and in Icelandic

waters by an increase in water temperature down to 400 m followed by a decrease (Ólafsson, 2003).

*C. monstrosa*, *E. spinax* and *G. melastomus* are found in higher densities in the Norwegian Sea than in the North Sea where they are restricted to the Norwegian Trench. In contrast, *S. acanthias* appears to have a higher density in the North Sea, with a wide distribution extending from Scotland to the Baltic Sea (Figure 2). As the BITS scientific survey provided too little data on the four study species, it was removed from the quantitative analyses.

#### 3.1 | *Chimaera monstrosa* – in Norwegian and Icelandic waters

In the Norwegian Sea, *C. monstrosa* was present along the entire Norwegian coast (presence rate of 39%), with the exception of the northernmost part (Table 1). This species occurs in the lower latitudes of the Norwegian Sea and thus benefits from the relative warmer and shallow waters (Table 2; Figures 2 and 3). It is denser in more saline water between 34.53 and 35.11 (Table 3). In the shallow parts of the North Sea, this species is present in only 20% of the hauls, while showing highest densities in the deeper Norwegian Trench off southern Norway (presence rate of 72%), where its presence depends mainly on temperature, distance from the coast and depth (Tables 1



**FIGURE 3** Weighted (density) boxplot showing variations in (a) temperature and (b) depth for *Chimaera monstrosa*, *Etmopterus spinax*, *Galeus melastomus* and *Squalus acanthias* in the Norwegian Sea, North Sea and Icelandic waters. Boxes represent 75% of the data and the whisker 99%. The letter above boxplots indicates similar means (ANOVA,  $P < 0.05$ ). The dashed line in the North Sea plot indicates water depths beyond the maximum depth of this region; its line is therefore the maximum possible depth for the four study species. Analysed carefully as few individuals

**TABLE 3** Summary of the effect of best-fit LMM model predictors on the density patterns (Gaussian distribution) for each species in each region (variables tested: depth, temperature, distance, salinity and latitude for the Norwegian Sea and Iceland)

Area	Species	Variable	AIC	ΔAIC	Relative likelihood	Weight	BIC	Residual model	Correlation <sup>a</sup>	Preference	
Norwegian Sea	<i>Chimaera monstrosa</i>	NULL	3439.67	12.79	0.0017	0.0017	3450.46				
		Salinity	3426.89	0	1	1	3441.27	-0.2603	+	34.53–35.11	
	<i>Etmopterus spinax</i>	NULL	2119.67	17.29	0.0001	7.556E-05	2127.93				
		Salinity	2104.60	2.22	0.3292	0.1413	2115.61		+	34.48–35.02	
	<i>Galeus melastomus</i>	Distance	2102.38	0	1	1	2113.39	-0.1872	-		
		NULL	1152.55	22.53	1.284E-05	6.389E-06	1159.77				
	North Sea		Temperature	1139.99	9.97	0.0007	0.0034	1149.62		+	6.4–8.5°C
			+ Salinity	1130.02	0	1	1	1142.06	-0.3569	+	34.47–35.09
		<i>Squalus acanthias</i> <sup>b</sup>	NULL	90.99	10.83	0.0044	0.0044	0.0044	91.23		
			Salinity	80.16	0	1	1	80.48	-0.02183	+	34.54–35.02
<i>Chimaera monstrosa</i>		NULL	4566.35	15.30	0.000	9.2751E-05	4576.55				
		Salinity	4551.05	0	1	1	4564.64	-0.3025	+	35.05–35.21	
<i>Etmopterus spinax</i>		NULL	4587.29	36.00	1.525E-08	7.626E-09	4598.54				
		Salinity	4571.83	20.54	3.567-05	1.734E-05	4586.83		+	35.11–35.27	
<i>Galeus melastomus</i>		+ Distance	4551.30	0	1	1	4566.29	-0.1722	+		
		NULL	9002.72	32.05	1.099E-07	1.099E-07	9017.65				
Iceland		Temperature	8970.67	0.43	0.8086	0.8086	8990.58		-	6.3–7.6°C	
		+ Depth	8970.24	0	1	1	8990.15	-0.1262	+	200–321m	
	<i>Squalus acanthias</i>	NULL	3936.01	45.45	1.352E-10	1.352E-10	3945.74				
		Temperature	3890.56	0.81	1	1	3903.53	-0.1687	+	7.8–9.6°C	
	<i>Chimaera monstrosa</i>	NULL	2014.91	12.96	0.0015	0.0076	2023.90				
		Salinity	2001.95	0	1	1	2013.94	-0.4128	+	35.05–35.11	
	<i>Etmopterus spinax</i>	NULL	896.63	7.52	0.00232	0.0079	903.20				
		Distance	889.30	0.19	0.9076	0.3097	898.05		-		
		+ Salinity	889.10	0	1	1	897.97	-0.4069	+	35.07–35.13	

<sup>a</sup>Pearson correlation (P-value < 0.05), positive (++) and negative (-).

<sup>b</sup>Analysed carefully as few individuals, NULL = model without external factors.



and 2). This species occurs at depths between 130 and 560 m with temperatures between 5.8 and 8.2°C and is denser in waters with salinities between 35.05 and 35.21 (Tables 2 and 3; Figure 3). In Icelandic waters, *C. monstrosa* has a localised distribution with an overall presence of only 8% (Table 1; Figure 1). This species occurs in the waters south of Iceland between 62.4 and 65.8°N (Table 2; Figure 1). It is most abundant in waters with salinities between 35.05 and 35.11 (Table 3). In these waters *C. monstrosa* individuals are denser at temperatures and depths relatively similar to those in the Norwegian Sea (Figure 3).

The northernmost *C. monstrosa* are significantly heavier than the southernmost (Pearson correlation: +0.4305; *P*-value <0.001), and individuals deeper in the water column are heavier than those at the surface (+0.1248; *P*-value <0.01).

### 3.2 | *Etmopterus spinax* – in Norwegian and Icelandic waters

In the Norwegian Sea, *E. spinax* was caught in 22% of trawl hauls (Table 1) in the lower latitudes of the Norwegian Sea, in warm, salty and coastal waters (Tables 2 and 3; Figure 2). In the North Sea, it is found in 26% of the overall hauls (all surveys combined). Nonetheless, in the Norwegian Trench, the species is numerous and occurs in 89% of all hauls in the “Reketokt,” compared to only 3% in the IBTS surveys (Table 1; Figure 1). *E. spinax* is only present in coastal, cold and deep waters of the North Sea (Table 2; Figure 3), and it has highest densities in waters with salinities of 35.15–35.27 (Table 3). In Icelandic waters, it is present in only 5% of the hauls (Table 1) between 62.7 and 65.8°N (south Iceland; Table 2; Figure 1), with higher densities in waters with salinities of 35.0–35.13 (Table 3). Similar to *C. monstrosa*, in Icelandic waters *E. spinax* is abundant in relatively similar temperature and depth conditions as in the Norwegian Sea (Figure 3).

The mean weight of individuals is positively correlated with latitude (+0.105; *P*-value <0.05) and depth (+0.3556; *P*-value <0.001). The southern tip of Norway, between ICES sub-areas 4.a and 3.a, appears to divide the North Sea “population” into a population with a lower average weight per individual (east) and a higher average weight per individual (west).

### 3.3 | *Galeus melastomus* – in Norwegian waters

In the Norwegian Sea, *G. melastomus* was present in 18% of the hauls (Table 1) and up to 70°N latitude (Figure 1). Its presence is driven by water temperature, latitude and depth, and therefore occurs in the warm, shallow waters of the Norwegian Sea, which are located south of the Norwegian Sea (Table 2; Figures 2 and 3). The areas of highest abundances are in waters with temperatures between 6.4 and 8.5°C and salinity between 34.47 and 35.09 (Table 3). In the North Sea, this species is caught in only 7% of the hauls, mainly at the southern tip of Norway, but it also occurred in several hauls north of Shetland during the NS-IBTS surveys (Table 1; Figure 1). It is only present in water between 5.8 and 8.8°C, but it is more likely found in waters between 6.3 and 7.6°C (Tables 2 and 3). In these waters, this species is most

abundant in warmer and shallower waters than the other two species studied previously (Figure 3).

The mean weight distribution of *G. melastomus* is only affected by latitude, with larger individuals found at higher latitudes (+0.3120; *P*-value <0.001).

### 3.4 | *Squalus acanthias* – in Norwegian waters

In the Norwegian Sea, only a few *S. acanthias* have been observed recently. It is only present in the lower latitudes of the Norwegian Sea, in the warmer water (5.6–8.2°C; Figure 1; Table 2), and is most abundant in waters with salinities of 34.5435.02 (Table 3). In the North Sea, *S. acanthias* has a wide and dispersed distribution with an overall catch frequency across surveys of 14%, whereby the frequency at the Reketokt is much higher, as for all other species as well (Table 1; Figure 1). Nonetheless, *S. acanthias* was caught in 10% of IBTS stations, which is a much higher presence compared to all other study species, where the presence was between 1% and 3% (Table 1). Three areas of high density seem to emerge in this region, the first at the eastern part of the Skagerrak, the second north of Scotland and the third between Scotland and Norway (Figure 2). Thus, in the North Sea, this species occurs near the coast in a wide range of temperatures but is more dense in warmer (7.8–9.6°C) and shallow waters (Table 3; Figure 3).

The mean weight distribution of *S. acanthias* appears to be significantly determined by depth, with larger individuals found in shallower waters (−0.4228; *P*-value <0.01).

## 4 | DISCUSSION

By using a combination of models and mapping tools this study identified varied habitat preferences of four benthopelagic chondrichthyan species which were mostly consistent across the three regions within the study area in the northern Northeast Atlantic. The presence of all species was driven by temperature, in combination with other factors, in the Norwegian Sea and the North Sea, whereby depth seems mainly relevant for the two deeper occurring species, *C. monstrosa* and *E. spinax*. For Icelandic waters, on the contrary, latitude was the predominant and statistically the only driver of species' presence, which is consistent with previous studies (Campana *et al.*, 2020). Salinity then seems to determine the abundance of the species, with most of them being found in greater densities in the more saline waters of all studied regions. Two species, *C. monstrosa* and *E. spinax*, seem to share a similar ecological habitat, that is deep and cold, whereas *G. melastomus* and *S. acanthias* both prefer warmer and shallower waters, but exhibit a somewhat different spatial distribution.

### 4.1 | Distribution and aggregation

The results indicate a southeastern distribution limit of these species towards the Baltic Sea (ICES subarea 3.a) consistent with expectations

on salinity preferences of these marine species. *C. monstrosa*, *E. spinax* and *G. melastomus* are present eastwards to 12.6°E, although a few individuals of these three species have previously been reported in the Baltic Sea but without a regular presence of mature individuals (Kontula *et al.*, 2012; HELCOM redlist). *S. acanthias*, on the contrary, has a wider distribution into the Baltic Sea, to 20.2°E, however, with comparably few individuals. This species occurs regularly in Kattegat, the Sound and the Danish Belts, but only sporadically in the Baltic proper (HELCOM redlist). The northernmost observations are within the range of previously recorded latitudinal limits.

A high density of all species was found in Norwegian coastal waters and specifically around mid-Norway (in vicinity of the islands Hitra, Smøla and Frøya). This aggregation behaviour has already been highlighted for *S. acanthias* and for several *Etmopterus* species (Finucci *et al.*, 2018) but also for *C. monstrosa* and *G. melastomus* which aggregate, e.g., at coral mounds, cold water sponge beds and high productivity areas (Kutti *et al.*, 2014, 2015). Sexual segregation has been frequently recorded in deep-sea chondrichthyans (Finucci *et al.*, 2018; Jakobsdóttir *et al.*, 2019). The islands in mid-Norway were previously identified as hotspots also for other shark species, like the porbeagle (*Lamna nasus*; González Triginer, 2020) and the basking shark (*Cetorhinus maximus*; Junge *et al.*, in prep). It can thus be speculated that this area of strong aggregation of marine (meso)predators is the consequence of a significant primary productivity creating an important trophic food chain.

## 4.2 | Same deep habitats but different niche: *C. monstrosa* and *E. spinax*

*Chimaera monstrosa* and *E. spinax* have a very similar distribution throughout the study area. Both species were abundant mostly at depths between 300 and 400 m, in line with previous studies indicating preferred depth of 300–500 m for *C. monstrosa* (Holt *et al.*, 2013) and 200–500 m on the outer continental shelves and upper slopes for *E. spinax* (Ruiz-Pico *et al.*, 2020; Sion *et al.*, 2004). Nonetheless, both were found in the study area and period down to over 900 and 800 m, respectively, and even down to 1420 and 1049 m during the entire survey time series (data not shown). They follow the same weight distribution pattern off the Norwegian coast with the largest individuals found in the northernmost areas and in the deepest layers of the water column. This feature was already demonstrated for *E. spinax*, with more mature and older females found in deeper and more northerly waters (Coelho & Erzini, 2010). The results therefore suggest that these two species co-occur within the same habitat; nonetheless, based on different dietary preferences and reproductive modes, they are not directly competing for resources with one another. In the NEA, although both species have ontogenetic changes in diet, they likely do not feed on the same species. *C. monstrosa* feeds on benthic species and *E. spinax* on pelagic ones. In Icelandic waters, *C. monstrosa* feeds mainly on ophiuroids and amphipod (Jakobsdóttir *et al.*, 2020). Another study showed that errant polychaete and small amphipods are the dominant component of the diet of *C. monstrosa*

juveniles, whereas larger ones feed mainly on anemones, decapod crustaceans and spatangoids (Mauchline & Gordon, 1983). For *E. spinax*, juveniles feed on *Meganyctiphanes norvegica* and *Laurolicus luelleri* and larger ones on *Pasiphaea tarda*, squid and other fish species (Klimpel *et al.*, 2003; Mauchline & Gordon, 1983). *C. monstrosa* is oviparous and lays egg capsules mainly in spring and summer at depths often less than 100 m (Stehmann & Bürkel, 1984), whereas *E. spinax* is aplacental viviparous (Capapé *et al.*, 2001) and gives birth to live young. Their requirements related to reproduction are therefore somewhat different, although knowledge about especially the reproductive timing for either of the species in northern waters is absent. Once both reach a developmental stage beyond the presence of a yolk sac, their habitat requirements are similar, which explains the overlap in distribution. The niche differentiation probably occurs when they start to mature and feed on different prey species with different habitat preferences.

The highest densities of *C. monstrosa* and *E. spinax* are found in more saline waters across all regions; nonetheless, both species are most abundant in the Norwegian Sea, suggesting that these waters are favourable for both species. In addition to that, *E. spinax* is found in the highest densities closer to the coast, irrespective of the region, whereby there seems to be no effect of distance for *C. monstrosa*. In the Norwegian Sea, they are both very abundant in the southern parts. *C. monstrosa* is also abundant in the northern part along the Norwegian coast, which might be the result of a higher tolerance for colder waters and therefore an increased thermal range, as shown in Figure 3. In the North Sea, both species prefer the conditions present in the waters of the southern tip of Norway and are absent from the rest of the northern North Sea. The area close to the coast with the deepest, coldest and more saline waters of the North Sea seems to represent a suitable habitat for these species.

Finally, in Icelandic waters, the densities of both species are relatively low compared to Norwegian waters. This difference could be explained by different environmental and physical conditions in these areas. Both species seem to find suitable environmental conditions for development only in southern Iceland which exhibits radically different conditions compared to northern Iceland (temperature, salinity, current) limiting their latitudinal expansion. The area off South and West Iceland is characterised by a relatively warm and saline Atlantic water, but cold-water masses of lower salinity predominate in the north and east creating highly productive transition zone between warm Atlantic and colder Arctic water masses (Astthorsson *et al.*, 2007). The latitudinal difference in environmental conditions in Icelandic waters is a well-documented limiting factor of distributions of numerous fish species in that area (Campana *et al.*, 2020; Mason *et al.*, 2021; Stefánsdóttir *et al.*, 2010; Valdimarsson *et al.*, 2012).

## 4.3 | Different demersal habitat, what about feeding?: *G. melastomus* and *S. acanthias*

*Galeus melastomus* and *S. acanthias* are present in essentially the same ecological conditions, that is in shallower waters than the other two

species, with 50% of the current overall density above 240 and 110 m (although somewhat deeper in the Norwegian Sea), respectively, which is in line with previous work (Carrassón *et al.*, 1992; Ellis *et al.*, 2015). Nonetheless, these two species do not have the same spatial distribution and areas of highest abundance, and rarely share the exact same habitat. Both species are found together in the North Sea, whereby *G. melastomus* shows the highest abundance around the southwestern coast of Norway, and *S. acanthias*, in contrast, has two areas of highest abundance, one eastern, on the Swedish coast, and one western, close to Scotland. The pattern of *G. melastomus* is therefore similar to the ones from *C. monstrosa* and *E. spinax* (albeit in much lower abundance), whereas *S. acanthias* has a wider distribution and bifurcated abundance in the North Sea (with a likewise lower abundance compared to the two deeper species). In the Norwegian Sea, the picture is reversed, with *S. acanthias* exhibiting a very limited distribution with low abundances, and *G. melastomus* showing its highest abundances in the southern to mid-part of this area. As both species occupy a similar trophic level (close to 4), feed mainly on teleosts (Avsar, 2001; Bengil *et al.*, 2019) and show different distribution patterns in Norwegian waters, it could be hypothesized that these two species are in direct competition with each other, which may explain their different finer-scale distribution. Other studies have shown that their diets can be highly variable and differ between regions (Domi *et al.*, 2005), possibly providing an opportunity to avoid competition. Nonetheless, no such analysis exists for these species in Norwegian waters, and future studies could examine the role of prey availability and interspecific competition (Jennings *et al.*, 2001), although disentangling direct effects from indirect consequences and multi-species interactions remains a major challenge (Sguotti *et al.*, 2016).

In the Norwegian Sea, the low overall number of *S. acanthias* individuals limits the interpretation and comparison of results. *G. melastomus* is found in the lower latitudes of the Norwegian Sea and in shallower waters, with larger individuals compared to the North Sea. *S. acanthias* is more widely distributed within the North Sea and occurs in all coastal and warm waters therein. This observation is consistent with the migrations of *S. acanthias* observed between southern Ireland and the North Sea (Daan *et al.*, 2005) and between the northern and southern North Sea (Holden, 1965). In the North Sea, both species are found in a narrow and high salinity range. Noticeably, at the south-eastern fringe of this study area (corresponding to subarea 3.a, between the North Sea and the Baltic) the salinity drops markedly towards the east and only *S. acanthias* has been found.

#### 4.4 | Data limitations

The authors chose not to include the sparse data for *G. melastomus* and *S. acanthias* from Icelandic waters, as, although these two species have previously been recorded there (Abella *et al.*, 2015; Ellis *et al.*, 2015) and seem to occur there regularly, they are not abundant and not well covered through the surveys (Jakobsdóttir, pers. comm.). As this study explicitly only included data from scientific bottom trawl surveys designed for commercial bony fish and shrimp species, the

sampling design and depth ranges (*i.e.*, 50–1400 m) are not optimal for cartilaginous fishes studied here. Nonetheless, when it comes to covering the sizes of the study species, as all surveys are designed to cover a variety of species and life stages and mesh sizes were between 20 and 60 mm, the authors are confident that the gear type and trawling conditions are suitable to catch the four study species, other limitations aside. As all surveys have been standardised, the abundances can be directly compared across regions as well. Although the surveyed depths roughly correspond to the depth ranges of *C. monstrosa*, *G. melastomus* and *S. acanthias* (Calis *et al.*, 2005; Carrassón *et al.*, 1992; Stehlik, 2007), some studies reported that *E. spinax* is found at depths greater than 2000 m (Jones *et al.*, 2003). Depth limitations exist especially in the “Reketokt” data from the Norwegian Trench as the deepest stratum (about 500 m) is poorly covered (only four fixed stations), and areas deeper than 550 m are not surveyed at all.

Seasonal migrations of *S. acanthias* throughout the North Sea (Gauld & MacDonald, 1982) could also impact the results with individuals moving outside the study area during certain periods of the year which would be difficult to reveal using fixed spatio-temporal survey data. For the North Sea, however, both the Reketokt and the NS-IBTS are carried out in January and are therefore directly comparable, although the NS-IBTS is additionally carried out in summer (however, no seasonal effect could be detected). The Norwegian Sea and the Icelandic waters are both covered through surveys in spring and autumn, making those regions and their survey data comparable as well. Given that these surveys are not covering all seasons and especially not within the same area, it is possible that juveniles and/or reproductively active females could be missing from some of these surveys, depending on their spatio-temporal coverage. Here, targeted surveys specifically designed to monitor those species would be needed to ensure that important area-season combinations are covered.

This study focused on some spatial and environmental variables and their effect on species' distribution and density, but the seabed is likely to also be relevant for these four benthopelagic species (Finucci *et al.*, 2020; Kutti *et al.*, 2014, 2015). Nonetheless, as such large-scale data covering the entire study area were not available, the impact of seabed structure will have to be investigated in future work.

#### 4.5 | Interaction with fisheries

The four studied species are all subject to varying, but generally high, degrees of by-catch pressures, together with other pressures such as environmental stressors, especially in coastal areas. This study aimed to provide critical knowledge for understanding not only the distribution of these four cartilaginous fishes but its underlying drivers. Benthopelagic species which prefer coastal areas, like *S. acanthias*, are more likely to encounter coastal fishing vessels. The largest by-catch numbers for this species are from coastal vessels fishing with gillnets, and by-catch numbers have been increasing in recent years (Albert *et al.*, 2019; Junge, pers. comm.). *S. acanthias* has a long history of

exploitation in the North Sea and adjacent areas (Pawson *et al.*, 2009), with peak landings in the 1950–1960s. In the 2000s, stocks were gradually reduced to 20% of the 1940 stock biomass (ICES, 2020). The stock was subsequently protected by restrictive management measures and has not been overexploited since 2005; yet some by-catch occurs. In the Norwegian Sea, *S. acanthias* is still poorly studied, and alternatives to scientific trawl surveys and their resulting time series to study trends, such as species-specific targeted surveys using longlines, have so far been lacking. Although Albert *et al.* (2019) indicate a recovery of the stock in Norwegian waters, indices of abundance are urgently needed for the northern part of its distributional range (ICES, 2020).

As *G. melastomus* has always been a non-commercial species, few studies have been carried out on the impact of fishing on its stock(s), or on its ecology. Furthermore, as this species was de-listed as a deep-sea shark under the EU zero TAC in 2013, it is no longer protected from the associated measures mentioned previously; yet it is among the most discarded species by commercial fishing vessels (ICES, 2020).

The two deeper and cold habitat-preferring species, *C. monstrosa* and *E. spinax*, are found in large numbers in the deep Norwegian Trench off the southern coast of Norway. This region in the Skagerrak is a biologically productive zone due to upwelling (Rodhe, 1989), providing an ideal environment for the regional stock of the northern shrimp (*Pandalus borealis*). Fishing is carried out with both smaller, coastal vessels and large offshore trawlers. Here, both *C. monstrosa* and *E. spinax*, as well as other fish species, end up as by-catch in shrimp trawls. In the Skagerrak and the Norwegian Trench, total annual shrimp landings have fluctuated between 7,000 and 16,000 tons since the 1980s (ICES, 2021d). Due to a lower shrimp stock size, landings have, however, been low since 2018. Effort has decreased during the past 20 years (ICES, 2021c). To what degree this affects the amount of by-catch is not clear, and more detailed investigations are needed.

Future investigations should include the full time series from the scientific surveys which would allow insight into past changes, aiming to understand possible responses to environmental fluctuations and anthropogenic pressures, especially in the light of projected climatic changes. Such historical marine ecology could provide “baselines” for more informed species and ecosystem management.

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## AUTHOR CONTRIBUTIONS

Conceptual idea (CJ, RJ), data generation (CJ, JA, AS, GS, HH), data analysis (RJ, HH), supervision (CJ) and validation (CJ, HH), discussion

of results (all), manuscript preparation (RJ, CJ, with contributions from all authors) and funding (IMR for CJ, HH, JA, GS, AS, RJ, MFRI for KJ).

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