

Distribution of skates and sharks in the North Sea: 112 years of change

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Abstract

How have North Sea skate and shark assemblages changed since the early 20th century when bottom trawling became widespread, whilst their environment became increasingly impacted by fishing, climate change, habitat degradation and other anthropogenic pressures? This article examines long-term changes in the distribution and occurrence of the elasmobranch assemblage of the southern North Sea, based on extensive historical time series (1902–2013) of fishery-independent survey data. In general, larger species (thornback ray, tope, spurdog) exhibited long-term declines, and the largest (common skate complex) became locally extirpated (as did angelshark). Smaller species increased (spotted and starry ray, lesser-spotted dogfish) as did smooth-hound, likely benefiting from greater resilience to fishing and/or climate change. This indicates a fundamental shift from historical dominance of larger, commercially valuable species to current prevalence of smaller, more productive species often of low commercial value. In recent years, however, some trends have reversed, with the (cold-water associated) starry ray now declining and thornback ray increasing. This shift may be attributed to (i) fishing, including mechanised beam trawling introduced in the 1960s–1970s, and historical target fisheries for elasmobranchs; (ii) climate change, currently favouring warm-water above cold-water species; and (iii) habitat loss, including potential degradation of coastal and outer estuarine nursery habitats. The same anthropogenic pressures, here documented to have impacted North Sea elasmobranchs over the past century, are likewise impacting shelf seas worldwide and may increase in the future; therefore, parallel changes in elasmobranch communities in other regions are to be expected.

Keywords: climate change, community shift, elasmobranchs, fishing, habitat degradation, local extirpation, marine historical ecology

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Introduction

Over the past centuries, important changes have occurred in the community structure of exploited seas (Rogers & Ellis, 2000; Sáenz-Arroyo *et al.*, 2005; McHugh *et al.*, 2010). Dramatic declines and collapses of several large fish species have been recorded worldwide (Dulvy *et al.*, 2004; Fock *et al.*, 2014b) for which anthropogenic pressures, notably fisheries and habitat degradation, together with climate change, are thought to have played fundamental roles (Rogers & Millner, 1996; Dulvy *et al.*, 2008; Perry *et al.*, 2010; ter Hofstede & Rijnsdorp, 2011). Elasmobranchs are regarded as particularly vulnerable to anthropogenic pressures, as their life-history traits result in low rates of population growth (Walker & Hislop, 1998; Stevens *et al.*, 2000; Ellis *et al.*, 2008).

Data limitations include a historical lack of species-specific catch data, taxonomic problems, lack of appropriate census methods, as well as the complex habits of many elasmobranchs, such as their tendency to live in aggregations segregated by sex or size or to inhabit areas, such as pelagic and deep-sea habitats, where scientific data are limited (Baum *et al.*, 2003). Furthermore, elasmobranchs were traditionally not considered to be of sufficient commercial value to warrant scientific investigation. In recent decades, however, there has been increased appreciation of the importance of elasmobranchs to commercial and recreational fisheries, as well as their ecological and biodiversity value. Increasingly, a range of management measures, such as quotas, size restrictions, partial closures of habitat or prohibiting the retention of the most threatened species, are being introduced to manage elasmobranch fisheries (Hunter *et al.*, 2006; Ellis *et al.*, 2008; Pawson *et al.*, 2009).

The North Sea has experienced particularly accentuated environmental changes due to anthropogenic

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pressures (Rijnsdorp *et al.*, 1996, 2009; Möllmann & Diekmann, 2012), amongst which fisheries, habitat degradation and climate change are arguably the most evident (Rogers & Millner, 1996; Dulvy *et al.*, 2008; ter Hofstede & Rijnsdorp, 2011) in comparison with other activities (shipping, aggregate extraction, eutrophication, oil and gas exploration, coastal developments and pollution). The North Sea has been exploited since at least the 14th century. Trawl fisheries were widespread by the late 19th century (Engelhard, 2008; Thurstan *et al.*, 2014), but fishing pressure increased dramatically with the introduction of fully mechanised beam trawling in the 1960s (Engelhard, 2008).

The North Sea is also considered a 'hotspot' of marine climate change, and, whilst there have been earlier periods of comparatively warmer (e.g. 1930s) or cooler waters (1960s–1970s), warming was particularly rapid during the most recent three decades. Averaged over the past century, water temperatures in the North Sea have risen more rapidly than in surrounding seas (Brander, 2010; Möllmann & Diekmann, 2012).

During the 20th century, many coastal and seabed habitats were degraded, especially in the south where historical oyster beds, characterized by high biodiversity, were replaced by more depauperate, frequently disturbed sand and gravel beds (Heip, 1989; Kröncke, 1992; Houziaux *et al.*, 2011; Temming & Hufnagl, 2015). Water quality in larger estuaries and adjacent coastal zones has often deteriorated (Wheeler, 1979), and some coastal habitats were lost, such as the Dutch Zuiderzee, which was shut off from the North Sea in 1932 (Redeke, 1939).

Important changes in the composition of various marine faunal groups have been reported, including plankton (Beaugrand, 2004), benthic invertebrates (Callaway *et al.*, 2007) and fish (Rogers & Ellis, 2000; Wolff, 2000; Engelhard *et al.*, 2011; ter Hofstede & Rijnsdorp, 2011). Declines have been documented for several elasmobranch species, including common skate *Dipturus batis*-complex, spurdog *Squalus acanthias* and angel shark *Squatina squatina* (Walker & Heessen, 1996; Rogers & Ellis, 2000; Ellis *et al.*, 2010; ICES, 2014).

Effective management of elasmobranchs is hampered by limited information on population trends and core distribution areas, and further complicated by the shifting baseline phenomenon (Pauly, 1995; Roberts, 2003; Sáenz-Arroyo *et al.*, 2005; Pinnegar & Engelhard, 2008), which tends to skew perception on the status of ecosystems and individual species. In this context, the study of historical data is essential to set potential reference targets for the management of these populations (Fortibuoni *et al.*, 2010; Barausse *et al.*, 2014).

The Centre for Environment, Fisheries & Aquaculture Science (Cefas) has undertaken trawl surveys in the North Sea since 1902 (Engelhard *et al.*, 2013; Cefas,

2014). These historical data, combined with data collected on contemporary trawl surveys (including those undertaken as part of the International Bottom Trawl Surveys, IBTS), can be used to identify potential baselines for elasmobranch populations in the North Sea, as well as identifying areas of high local abundance.

In this article, habitat modelling techniques were used to examine long-term changes in the distribution and occurrence of eight elasmobranch species in the southern North Sea between 1902 and 2013. Results from these analyses are discussed in relation to three widely held theories:

1. That fishing has generally impacted more on those species that would have been targeted by fisheries and/or are larger, slower-growing, in contrast to smaller-bodied and more productive species, and especially after mechanised beam trawling became widespread in the 1960s–1970s;
2. That climate change has benefited warmer water species and adversely affected cold-water species, particularly during the most recent three decades when the rate of warming was most rapid; and
3. That habitat degradation has impacted on elasmobranchs, especially at formerly important nursery and spawning grounds in outer estuarine habitats.

Materials and methods

Creating a historical survey data set

Data from 'historical' (1902–1976) and 'contemporary' (1977–2013) surveys by Cefas research vessels (RVs) in the North Sea were used (Cefas, 2014; Section S1). The 'contemporary' surveys refer to those surveys where the hauls covered a regular grid over the entire North Sea, and where standardized gears and protocols were used; many of these surveys form part of the IBTS, coordinated by the International Council for the Exploration of the Sea (ICES). The 'historical' surveys refer to all surveys that predate the IBTS, in which survey hauls were not laid out systematically as a grid, despite being distributed over large parts of the central and southern North Sea, and in which gears and protocols were not yet standardized (Cefas, 2014). Surveys took place in each season, although there was more effort during Quarter 3 after the 1970s (Section S2.3). Data were lacking for both World Wars, and the periods immediately preceding and following them. Data were more limited for the periods 1930–1936 (when generally only key commercial species were recorded) and 1972–1976 (currently not yet fully digitised).

The 'historical' surveys sampled the southern and central North Sea, so data analyses were restricted to survey hauls undertaken from 51 to 56°N. This area was divided into three zones (NW, E, SW) based on the ICES Roundfish Areas (Fig. S2.1; Section S2), corresponding to regions with different hydrodynamic patterns (Dye *et al.*, 2013).

Historical time series are often characterized by data fragmentation, lack of a homogeneous sampling design and unbalanced sampling effort in both time and space (Bartolino *et al.*, 2012). Whilst the earliest surveys (in the early 1900s) recorded all species, some subsequent surveys (in the 1920s and 1930s) focused on the main commercial species (e.g. plaice *Pleuronectes platessa* and cod *Gadus morhua*), and other species were not always recorded consistently. To exclude survey hauls that may have targeted commercial species only, only those hauls in which the total number of fish species reported was ≥ 10 were included in analyses. These temporal changes in survey priorities implied that the number of well-sampled stations was variable (Figs S2.1 to S2.3 and Table S2.1).

Surveys were furthermore carried out by 11 different RVs, using different gears or gear deployments and catch sampling protocols evolving over time (see S1 in SI). Early, steam-powered vessels towed the trawl at a speed of approximately 2 knots, whereas in current, diesel-powered vessels this is standardized at 4 knots (Garstang, 1905; Davis, 1923; Lee, 1992; Rogers & Ellis, 2000). However, a towing speed of 2–2.5 knots is considered fast enough to catch most except for the fastest-swimming fish species; skates are fairly slow swimmers and probably retained effectively throughout the time series, but some faster swimming pelagic sharks might have been under-represented during earlier years (Rogers & Ellis, 2000). A variety of trawl gears were used (see Figure S1.1), and, although it is possible to compare the catchability of different trawls, this is a complex task and not performed routinely (Rogers & Ellis, 2000). In this study, analyses were restricted to otter trawl catches and, as the species studied are generally large, features such as mesh size and the presence or absence of a fine-mesh cod-end are unlikely to have affected incidence (Davis, 1923; Rogers & Ellis, 2000; Cardinale *et al.*, 2009). However, other gear parameters, largely undocumented historically, could have had subtle effects. Tow duration decreased over time (Fig. S1.1), from an average 4–5 h in the 1900s to the current standard of 0.5 h. Changes in tow duration might have led to overestimates in occurrence in early decades, but this is probably partly (or fully) offset by the slower towing speed and less efficient gear.

The observations of elasmobranchs were analysed as incidence (presence/absence data) and not as number of individuals caught per hour or per haul. To a certain degree, this negates the potential impacts of trawl design and catchability (Rijnsdorp *et al.*, 1996; Rogers & Ellis, 2000) and also allowed for the inclusion of more hauls, as prior to the 1970s only the presence of elasmobranch species was recorded in some hauls. For each haul, presence data were collated for each elasmobranch species. Given potential identification issues relating to skates (Rajidae), the incidence of all skate species combined was also examined. The incidence was defined as the proportion of stations where a presence was recorded, \pm the standard error (SE) to account for differences in survey effort.

In total, eight skate and six shark species were recorded (Tables S4.1 and S4.2), but several of these occurred only sporadically, precluding robust analysis of distribution and incidence changes. Data were considered representative for four skates (common skate *Dipturus batis*-complex, thornback ray

Raja clavata, spotted ray *Raja montagui* and starry ray *Amblyraja radiata*) and four sharks (tope *Galeorhinus galeus*, spurdog *Squalus acanthias*, smooth-hound *Mustelus* spp. and lesser-spotted dogfish *Scyliorhinus canicula*). Data for common skate will potentially confound data for two closely related, 'cryptic' species (Griffiths *et al.*, 2010; Iglésias *et al.*, 2010) and so are referred to as *Dipturus batis*-complex. Whilst nominal data were available for two species of *Mustelus* (*M. asterias* and *M. mustelus*), data were aggregated, as recent studies suggest only one species may occur around the British Isles (Farrell *et al.*, 2009).

In several cases, identification issues were flagged, related with the fact that historically, elasmobranchs were not always seen as commercially important, and data were not always collected accurately. In some periods (1940s, 1950s), elasmobranchs were not always systematically identified to species level during surveys, but reported as 'unidentified skates and rays' or 'dogfish' or 'unidentified sharks'. In the case of common skate, potential confusion exists between use of the term 'skate', which may be applied to this species complex or to any unidentified rajid. Most records were confirmed to relate to common skate based on inclusion of the scientific name (formerly as *Raja batis*), common name ('black' or 'grey skate') or based on size (wingspan) measurements. Some confusion may also have arisen from the use of alternative common names historically, such as 'roker' for thornback ray *R. clavata* vs. 'thorny skate' for starry ray *A. radiata*. Although unlikely to be a major issue on contemporary surveys, identification issues could only be assessed indirectly, for example using spatial patterns, length distributions or published sources (e.g. Garstang, 1905; Lee, 1912; Ford, 1921; Walker & Heessen, 1996).

Environmental variables

Three environmental variables and ancillary data describing the time period and spatial location of the hauls were used in the statistical models. The three environmental variables were depth, type of substrate and sea surface temperature (SST). In addition, the effect of zone (NW, E, SW) was included to account for differences in hydrodynamic characteristics (see Section S2 in SI for details on environmental variables).

Depth and type of substrate were chosen because they are likely key habitat descriptors and thus important to determine the distribution of demersal elasmobranchs, and because they may not have changed markedly over the time period (Martin *et al.*, 2012). These variables were taken from the European Marine Observation and Data Network (EMODNET, <http://www.emodnet.eu/>) and analysed with ARCGIS 10.1 (ESRI 2011, ArcGIS Desktop; Environmental System Research Institute, Redlands, CA, USA). Depth and type of substrate were compared to hauls at a resolution of 0.1° latitude by 0.3° longitude. Water depth in the study area ranged from 0 to 120 m (Fig. S2.5). Data on substrate type were attributed to six broad-scale habitat classes (Fig. S2.6): mud to sandy mud; muddy sand to sand; mixed sediment; coarse sediment; rock or other hard substrates; and 'unknown substrate' (a category that tended to include a limited number of shallow coastal locations).

Sea surface temperature was used in preference to bottom temperature, as data for the latter were not available consistently. Furthermore, most of the study area is relatively shallow and the water column is mostly mixed (OSPAR Commission, 2010), resulting in a close relationship between SST and sea bottom temperature. SST data were collated from the Met Office Hadley Centre observations data set (HadISST; www.metoffice.gov.uk), through the Met Office Marine Data Bank (MDB), and from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS). The spatial resolution of SST data was a 1° by 1° grid, and the temporal resolution was either a 5- or 10-year period. Annual mean SST is, on average, warmer in the south than in the north (Fig. S2.4), and SST has increased progressively over the past century (Fig. S2.7), especially in the SW and E (from approx. 10°C in the early 20th century to approx. 11.5°C in the early 21st century).

Statistical models of spatiotemporal distributions

Generalized linear models for binomial data (GLM) using logistic regressions were used to model spatiotemporal presence/absence data of elasmobranchs. The covariates were depth, substrate type (as factor), temperature and zone (NW, E, SW), together with a temporal covariate (decade or pentad; see below). Exploratory analyses indicated that tow duration had no significant effect and that season (quarter) offered little explanatory power, so we decided to not include them in the models (SI Section S2.3). The environmental variables showed low collinearity (although depth and temperature showed moderate collinearity; Spearman's correlation test $r_s = 0.2$, $P < 0.05$).

For each species, GLMs were used in two different ways using two temporal scales. Firstly, species distributions over time were modelled by decade (henceforth 'distribution model'). A temporal resolution of a decade was used as a covariate to ensure enough sampling stations were included to produce a reasonably accurate and reliable model to map each species' spatial distribution pattern, and how this changed over time. Six representative and well-sampled decades were included (1900s, 1950s, 1960s, 1980s, 1990s and 2000s; cf. Fig. S2.2). These decades were very different in terms of environmental drivers or human pressures (Engelhard *et al.*, 2014). The 1900s, for example, came shortly after the onset of extensive trawling in the North Sea and arguably provide a 'baseline'; the 1960s were marked by a rapid increase in intensive, modern beam trawling and by relatively cool and saline waters (Dye *et al.*, 2013); the 1980s are known for lower salinity and a regime shift in the North Sea, with the plankton community shifting from predominantly cold- to warm-water species (Beaugrand, 2004); and the 1990s and 2000s were marked by further temperature rises (Dye *et al.*, 2013), with reductions in fishing effort in the last decade (Engelhard *et al.*, 2015).

The second approach was aimed at modelling the temporal trends in incidence averaged over the study area, without emphasis on spatial detail. For this purpose, species incidences were modelled using the shorter temporal resolution of a pentad (5-year period), across the whole time series. A

pentad was found to be a good compromise between having sufficient sampling stations to estimate incidence per zone (on average, 156 stations were sampled per pentad; Table S2.1 and Fig. S2.2), and a fine enough temporal resolution to detect trends and changes in incidence over time. The choice of spatiotemporal resolution was based on analyses inspired by the approach of Bartolino *et al.* (2012).

A forward elimination procedure, based on the Akaike information criterion (AIC), was used. For models with equivalent AIC values, Occam's razor was applied and the simplest model chosen. The fitness of a model and its predictive power was evaluated in three ways. First, prediction error maps were plotted for each model, where prediction errors were computed as the difference between the values of the response variables and the predicted values. The qualitative screening of the error maps confirmed the goodness of fit of the model. Secondly, Spearman's rank correlations (r_s) were used to examine the correlation between the survey data and the predictions; following Lauria *et al.* (2011), tests were considered passed if r_s was greater than 0.1 and $P < 0.05$. Thirdly, the receiver operating characteristic curve (ROC) was employed; this quantifies the trade-off between specificity and sensitivity of the model and was considered passed if AUC (area under the curve) was greater than 0.5 with $P < 0.05$ (Lauria *et al.*, 2011). All analyses were performed using R 3.01 (R Development Core Team, 2013), with the generalized statistical analysis package 'GAMM4' (Wood, 2012).

Results

Over the period 1902–2013, 2697 survey hauls (with ≥ 10 fish species recorded) were sampled in the southern North Sea. Presence/absence data, using the four environmental covariates (substrate type, depth, SST and zone), allowed reliable prediction of decadal distribution (in distribution models) and temporal trends in incidence (in trend models) for eight elasmobranch species as well as combined 'skates' and 'demersal sharks' (see Tables 1 and 2, and S3.1). The final models for each species or model type (distribution, trend), selected based on lowest AIC, usually contained most environmental variables; many but not all of these contributed individually to the fit ($P < 0.05$; in some cases $P < 0.1$ only), but their presence increased the goodness of the model overall, as detected by a consistent drop in AIC ($\Delta\text{AIC} < -2$ in all cases). This implied that SST, depth, substrate and zone (NW, E, SW) were significant predictors of elasmobranch distributions (see Tables 1 and 2 for full detail of the final temporal trend models for skates and sharks, respectively, and Table S3.1 for distribution models). Temporal covariates (decade or pentad) increased the model fit for all species, implying that elasmobranch incidence changed significantly over time. All models exceeded the evaluation criteria (Spearman's $r_s > 0.1$, $P < 0.05$; and $\text{AUC} > 0.5$, $P < 0.05$) and had high predictive power (Table S3.1).

Skate assemblage

In total, eight skate species were recorded in the surveys between 1902 and 2013 (Table S4.1). The predominant species (over the entire time series) were thornback ray *Raja clavata* (recorded in 19.0% of all hauls), starry ray *Amblyraja radiata* (17.0%), spotted ray *Raja montagui* (6.7%) and common skate *Dipturus batis*-complex (3.8%). Data were more limited for four other skate species: cuckoo ray *Leucoraja naevus* (0.7% of hauls), blonde ray *Raja brachyura* (0.5%), sandy ray *Leucoraja circularis* (0.1%) and undulate ray *Raja undulata* (0.04%). During the 1950s–1960s, higher numbers of unidentified skates were reported.

Model results showed that historically, skates were distributed fairly evenly throughout the southern North Sea (Fig. S4.2), occurring over a range of depths and sediments (Fig. S2.6), although with increased incidence in the west. There was no significant SST effect on the combined skate assemblage (rejected from the

final model; Table 1 and S3.1). Over time, the overall skate distribution became progressively reduced to the deeper waters in the north-west and the shallower waters in the south-west characterized by favoured substrate types (coarse and mixed sediments), especially after the 1960s (Fig. S4.2).

Common skate Dipturus batis-complex

Common skate was not reported in contemporary surveys of the southern North Sea; however, fairly extensive historical records were found. Our models highlight that common skate was associated with cooler SST and historically was more often found in deeper waters but could still be found on shallower grounds (Fig. 1a). No significant substrate preference could be detected (rejected from the final model; Table 1, and S3.1). A long-term decline in common skate was apparent from the temporal trend model, from an average incidence of ~30% in the early 20th century to <5% in

Table 1 Details of the final statistical models describing the temporal trends in incidence for each skate species and the combined skate assemblage (temporal resolution: 5 years).

Species or species group	AUC	r_s	Predictor variables	Effect	LRT	P
Total skates	0.81	0.55	Substrate	x, c preferred	44.7	<0.0001
			Depth	Shallow		
			Zone	SW > NW > E	143.2	<0.0001
			Pentad	Decline		
			Pentad*Depth	Deepening from 1950s	169.7	<0.0001
Common skate	0.89	0.25	Temperature	Cool	4.9	0.02
			Zone	(SW,NW)>E	6.8	0.03
			Pentad	Disappeared after 1970	142.4	<0.0001
Thornback ray	0.86	0.5	Substrate	x > (c,r,u) > (s,m)	78.4	<0.0001
			Depth		2.1	0.144
			Temperature	Warm	38.5	<0.0001
			Zone	(NW,SW) > E	63.5	<0.0001
			Pentad	Decline	556.7	<0.0001
Spotted ray	0.89	0.34	Substrate	u > (c,s,r) > x > m	18.9	0.002
			Depth		3.0	0.075
			Temperature	Warm	16.3	<0.0001
			Zone	(SW,NW)>E	150.8	<0.0001
			Pentad	1960s–1970s highest	170.5	<0.0001
Starry ray	0.96	0.6	Substrate	m > (s,r,u) > (c,x)	38.2	<0.0001
			Depth	Deep	80.8	<0.0001
			Temperature	Cool	138.4	<0.0001
			Zone		5.74	0.056
			Pentad	Variable	1079	<0.0001

Model evaluation is shown with Spearman's rank correlations (r_s ; all $P < 0.001$) and ROC (receiver operating characteristic curve) with the relative AUC (area under the curve). Predictor variables retained in the final model are shown in the fourth column; two-way interactions, if retained, are shown by the symbol *. The relative effect of the significant predictors, the results of the likelihood ratio test (LRT) and the associated P -value are shown. Bold font indicates if a retained predictor variable showed a significant fit ($P < 0.05$). The codes for substrate types are as follows: m: mud to sandy mud, s: sand to muddy sand, c: coarse sediment, x: mixed sediment, r: rock or hard substrates, u: unknown sediment.

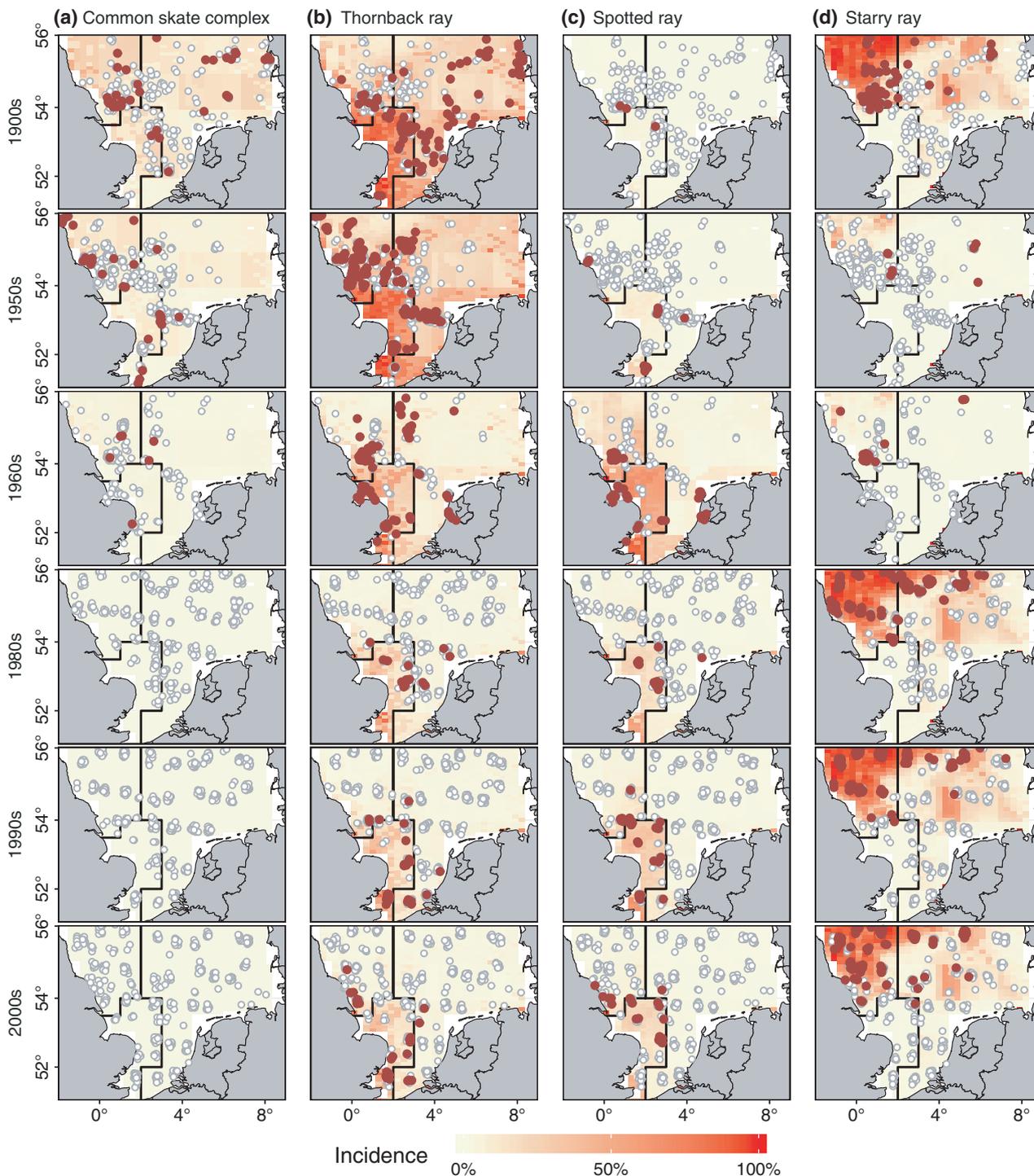


Fig. 1 Changes in modelled spatial distribution of four North Sea skate species: (a) common skate complex, (b) thornback ray, (c) spotted ray, and (d) starry ray. Maps show the predicted distribution patterns in six well-sampled decades: symbols represent survey hauls (filled red if at least 1 individual was observed, otherwise unfilled) and graded background colours indicate predicted incidence.

the 1960s (Fig. 2a). Greater incidence was predicted in the (deeper) north-west at the beginning of the 20th century and during the late 1930s–1940s (Fig. 2a). Surveys suggest that local extirpation of common skate

from the southern North Sea probably occurred during the early 1970s; the last record in the current study is from 4 April 1970 (55.5°N, 2.5°E, onboard RV *Ernest Holt*).

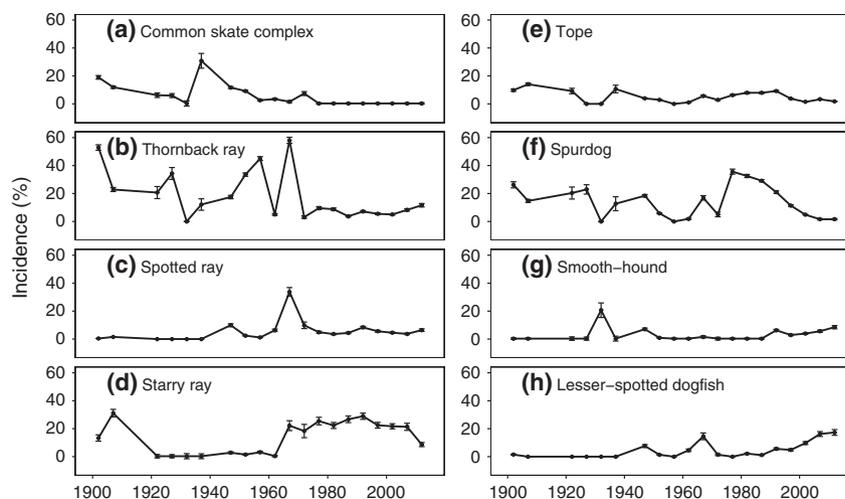


Fig. 2 Trends in incidence of four skate and four shark species in the southern North Sea: (a) common skate complex, (b) thornback ray, (c) spotted ray, (d) starry ray, (e) tope, (f) spurdog, (g) smooth-hound, and (h) lesser-spotted dogfish. Modelled trend plots show the change in incidence (% of hauls where predicted to be caught) by pentad, 1902–2013, for the combined NW, E, and SW study area (bars represent SE).

Thornback ray *Raja clavata*

Models showed a close association of thornback ray with warmer SST (Table 1, and S3.1). Shallower waters (mainly 5–40 m), and hard, coarse, mixed, and ‘unknown’ sediments were moreover preferred (Table 1 and S3.1). Throughout the time series, thornback ray was predicted to be present mostly in the south-west, near the Outer Thames estuary, but also further north-west, close to the Humber estuary (Fig. 1b). The temporal trend model indicated a clear decline around 1970 in each of the three zones (Fig. 2b), with a moderate recovery from the 2000s evident in the south-west (Fig. 1b). The multidecadal distribution maps (predicted by the distribution model) revealed a progressive contraction in distribution (Fig. 1b): historically widespread across the southern North Sea, but becoming increasingly restricted to the west during the 1960s, before contracting mainly to the areas outside the Thames and Humber estuaries in the 1980s.

Spotted ray *Raja montagui*

As with thornback ray, model results showed this species to be strongly associated with warmer SST, preferring some substrate types (‘unknown’, coarse, rocky) typically found in shallower waters (Table 1, and S3.1). As a consequence of the similar preferences, the modelled distribution of spotted ray was comparable to that of thornback ray: high occurrences in the south-west, particularly near outer parts of

estuaries, and low presence over the northern and eastern parts of the basin (Fig. 1c). However, predicted presence increased, rather than decreased, in the 1960s (Fig. 2c), although it should be noted that shallower grounds, preferred by this species in this part of its range, were sampled less during earlier decades. In the 1970s, spotted ray decreased moderately and became more contracted to the south-west, but as then their presence appears stable on shallower grounds off the Humber and Thames estuaries (Fig. 1c).

Starry ray *Amblyraja radiata*

Starry ray was closely associated with cooler temperatures, deeper waters (especially >60 m), and muddy and sandy substrates (Table 1, and S3.1). The general distribution reflected this: predominantly in the north-west, and less so in the north-central parts of the southern North Sea (Fig. 1d). The temporal trend model suggested low presence of starry ray between 1920 and 1950 (but possibly partly due to misidentification, owing to possible confusion with thornback ray), followed by a strong increase after the 1960s in all areas except the more southerly and shallower parts (Figs 1d and 2d). Since 2000, however, starry ray has decreased markedly, contrasting their clear increase during the last quarter of the 20th century; their current incidence is about half that of the 1990s (Fig. 2d). The distribution has also contracted northward (Fig. 1d). The strong relationship of starry ray with colder SST indicates that the marked warming in

Table 2 Details of the final statistical models describing the temporal trends in incidence for each shark species (temporal resolution: 5 years).

Species or species group	AUC	r_s	Predictor variables	Effect	LRT	P
Tope	0.82	0.22	Depth	Shallow	5.2	0.02
			Temperature	Warm	14.9	0.0001
			Zone		5.1	0.08
			Pentad	Decline especially after 1995	74.4	<0.0001
Spurdog	0.83	0.4	Depth	Shallow (in earlier period)		
			Temperature	Cool	47.3	<0.0001
			Zone	SW > E > NW	31.1	<0.0001
			Pentad	Decline		
			Pentad*Depth	Deepening	71	<0.0001
Smooth-hound	0.91	0.24	Substrate	x,c preferred	11.1	0.05
			Temperature	Warm	50.3	<0.0001
			Zone	(NW,SW)>E	6.6	0.04
			Pentad	Increase	103.1	<0.0001
Lesser-spotted dogfish	0.92	0.34	Substrate	x, c preferred	13.3	0.02
			Depth	Shallow	6.2	0.01
			Temperature	Warm	40	<0.0001
			Zone	SW > NW > E	107.4	<0.0001
			Pentad	Increase	105.5	<0.0001

Model evaluation is shown with Spearman's rank correlations (r_s ; all $P < 0.001$) and ROC (receiver operating characteristic curve) with the relative AUC (area under the curve). Predictor variables retained in the final model are shown in the fourth column; two-way interactions, if retained, are shown by the symbol *. The relative effect of the significant predictors, the results of the likelihood ratio test (LRT) and the associated P -value are shown. Bold font indicates if a retained predictor variable showed a significant fit ($P < 0.05$). The codes for substrate types are as follows: m: mud to sandy mud, s: sand to muddy sand, c: coarse sediment, x: mixed sediment, r: rock or hard substrates, u: unknown sediment.

recent decades relates to the species' decline (Table 1, and S3.1).

Demersal shark assemblage

The demersal shark assemblage of the southern North Sea also included species with contrasting trends between 1902 and 2013 (Table S4.2 and Fig. S4.2). Two species were much more common at the start of the time series: spurdog *Squalus acanthias* and tope *Galeorhinus galeus*, recorded in 13.3% and 4.2% of all hauls, respectively. By contrast, smooth-hounds *Mustelus* spp. (3.0%) and lesser-spotted dogfish *Scyliorhinus canicula* (5.7%) have increased. Greater-spotted dogfish *Scyliorhinus stellaris* was observed rarely (0.7%), whilst angel shark *Squatina squatina* (0.04%) was last recorded in the surveys on 8 June 1966 (52.57°N, 4.75°E, onboard RV *Clione*) and is now considered extirpated from the southern North Sea (Table S4.2).

Tope *Galeorhinus galeus*

Tope was closely associated with warmer SST and shallow waters (mostly <50 m), but showed no significant

preference for any particular substrate type (Table 2 and S3.1). Accordingly, tope was generally recorded in shallower, coastal waters in the east and south of the southern North Sea and almost absent from hauls in the deeper north-west (Fig. 3a). The temporal trend model predicted a low occurrence of this species throughout the last century: incidence by pentad was never above 18%, and the current incidence is particularly low (Fig. 2e; recorded in only 2.2% of hauls during 2010–2013). The modelled distribution and incidence of tope were greater in the 1900s, 1980s and 1990s, with reduced incidence at other times, including since the turn of the Millennium (Figs 2e and 3a).

Spurdog *Squalus acanthias*

Spurdog was the most commonly recorded shark species in trawl surveys prior to the 1990s. However, interpretation of the trends in incidence is complicated due to their tendency to aggregate and their seasonal migrations. Our analysis indicated a strong preference for cooler SST (Table 2 and S3.1) and that spurdog were distributed widely, historically in both shallow and deeper waters, but over time increasingly associated with deeper waters (Fig. 3b, Table 2 and S3.1). Given

that spurdog undertake seasonal migrations, differences in incidence were also examined between quarters, but no significant patterns were found (Table S3.1).

The trend model predicted a modest decline during the first half of the 20th century, then an increase during the 1960s–1970s; however, this was followed by a continuous decline to the current low levels of incidence (2.2% during 2010–2013; Fig. 2f). Decadal distribution maps confirmed their widespread distribution in the 1980s including the north-west where it was less frequent in earlier decades, and a scarcity throughout the southern North Sea during the 2000s (Fig. 3b). A link with long-term climate variability was indicated by spurdog's significant association with cooler temperatures ($P < 0.0001$; Table 2), increasing incidence during the colder 1960s–1970s and declining trend coinciding with recent warming SST accelerated since the 1980s (Fig. 2f).

Smooth-hounds *Mustelus spp.*

Due to taxonomic problems, data for smooth-hounds were treated at genus level, and all recent records related to starry smooth-hound *M. asterias* only (ICES, 2014). Smooth-hounds were very closely associated with warmer SST (Table 2 and S3.1) and distributed mainly in the southernmost part of the North Sea (Fig. 3c). The presence was not significantly correlated with depth, but smooth-hounds showed a preference for mixed and coarse sediments, which are usually found near the coasts (Table 2 and S3.1).

The temporal trend analysis revealed very few historical records in the southern North Sea (observed in only 1.3% of hauls sampled during 1902–1989; Fig. 2g). Their incidence only began to increase after the 1980s, mainly in the Southern Bight (Fig. 3c), where smooth-hounds are now caught regularly, and to a lesser extent also in the north-western North Sea. The increase appears closely linked with warming SST owing to the highly significant, positive relationship between their distribution and SST ($P < 0.0001$ in both distribution and temporal trend models; Table 2 and S3.1).

Lesser-spotted dogfish *Scyliorhinus canicula*

Historical records indicated that lesser-spotted dogfish was previously far less frequent in the southern North Sea than it is nowadays. It was very closely associated with warmer SST and preferred shallow waters, and mixed, coarse and 'unknown' substrates (Table 2 and S3.1), reflected in its distribution in the southernmost part of the North Sea (Fig. 3d).

Lesser-spotted dogfish was recorded infrequently during the first half of the 20th century (Fig. 2h).

Modelled incidence increased from the late 1940s to 1960s, was considerably lower again in the 1970s and 1980s, and since then has increased strongly (Fig. 2h). However, this high occurrence is localized to the south-westernmost North Sea, where its predicted incidence in recent years was >60% (Fig. 3d). The strong positive relationship with SST ($P < 0.0001$; Table 2) suggests that warming temperatures have contributed to their marked recent increase.

Discussion

This is the first study to quantify the changes in incidence and distribution of elasmobranchs in the southern North Sea over more than a century. For the skate assemblage, the 1960s–1970s were shown to be a period of major change, as evidenced by the disappearance of common skate from the area, and a decline in thornback ray, but with concurrent increases in the smaller-bodied spotted and starry rays, in agreement with Walker & Hislop (1998). Some of these trends, however, seem to be reversing in recent years.

Within the shark assemblage, six species were recorded, four of which were encountered more frequently; these revealed opposing patterns in recent decades: tope and spurdog declined, but smooth-hound and lesser-spotted dogfish both increased (Figs 2 and 3). Greater-spotted dogfish was only recorded rarely, more so after the 1960s (Table S4.1). Angel shark was reported sporadically over the first half of the 20th century and last recorded in 1966 and is now believed to have been extirpated not only from the North Sea but from other parts of northern Europe (Rogers & Ellis, 2000; Ellis *et al.*, 2005b).

The interpretation of these data, however, requires a degree of caution, due to possible changes in sampling methods over time – issues that are, unfortunately, often associated with long-term, historical data sets that predate full standardisation of surveys and documentation of their gears (Ellis *et al.*, 2005b; Bartolino *et al.*, 2012; Fock *et al.*, 2014a). Despite these issues, the present study can help inform on both the long-term population dynamics of North Sea elasmobranchs and the assemblage at a time of low fishing impacts (Walker & Heessen, 1996; Rogers & Ellis, 2000).

The observed changes are likely driven both by anthropogenic and natural environmental factors, and possibly multispecies interactions, as discussed below. It should be noted, however, that several of these factors are confounded, and whilst correlations may be observed between environmental factors and trends in relative abundance, establishing causal relationships in such data sets is more problematic.

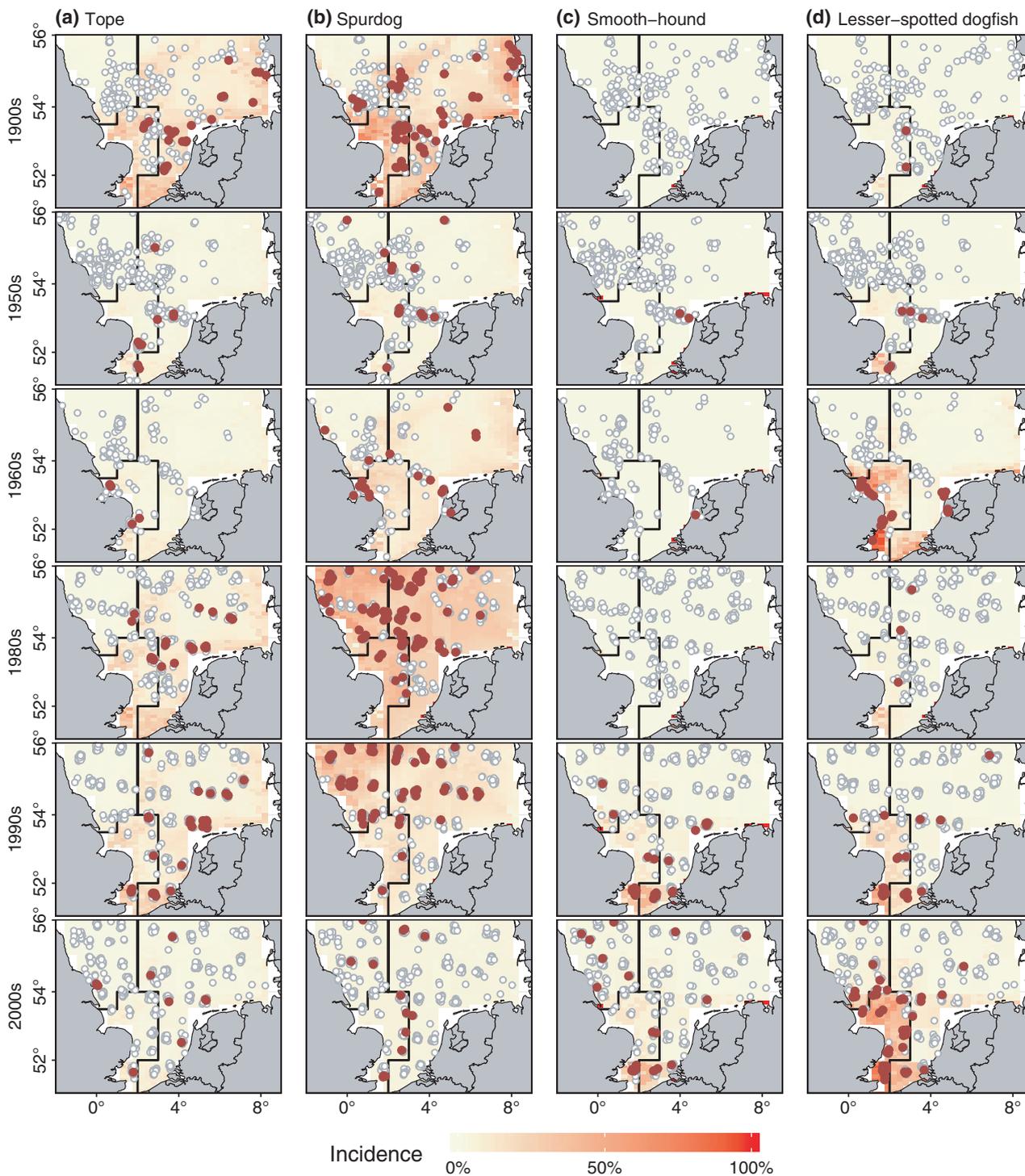


Fig. 3 Changes in modelled spatial distribution of four North Sea shark species: (a) tope, (b) spurdog, (c) smooth-hound, and (d) lesser-spotted dogfish. Maps show the predicted distribution patterns in six well-sampled decades: symbols represent survey hauls (filled red if at least 1 individual was observed, otherwise unfilled) and graded background colours indicate predicted incidence.

Potential fisheries-induced changes

The timing of most fundamental change in the skate assemblage, during the 1960s and 1970s, corresponded

with the widespread introduction of mechanised beam trawling in the North Sea with more efficient and powerful fishing vessels (Engelhard, 2008). This suggests that fishing pressure was a major driver, fully in line

with the 'sensitive skates, resilient rays' hypothesis of Walker & Hislop (1998), whereby larger-bodied skate species (e.g. common skate complex and thornback ray), with a late age and large size at maturity declined, whilst smaller-bodied species (e.g. spotted ray and starry ray) which may be faster growing, subject to relatively greater discarding (and so lower fishing mortality) and/or benefit from some form of 'competitive release' with the decline of larger skates, would increase. There is some indication that these trends have reversed in recent years, possibly as fishing effort has decreased.

This is the first study that times the extirpation of common skate from the southern North Sea: the very last observation during the surveys analysed was in 1970; the larger of the species complex (flapper skate *Dipturus cf. intermedia*) is currently only sporadically caught in the northern North Sea (ICES, 2014). Common skate was exploited during the late 19th and early 20th centuries (Laver, 1898; Murie, 1903) and was widespread in the southern North Sea during the early 20th century (Fig. 1a; Murie, 1903; Garstang, 1905). The regional loss of this species complex from most of the Irish Sea occurred during the 1960s (Brander, 1981) and is comparable to observed in the present study. The loss of this species complex from inshore fishing grounds has been attributed to high sensitivity to fishing due to its large size and vulnerable life-history traits (Walker & Hislop, 1998; Daan *et al.*, 2005).

Two other species, thornback and spotted ray, showed similar spatial patterns (occurring mainly in the south-west), but contrasting temporal trends. Whilst thornback ray was recorded far more frequently prior to the 1960s, spotted ray was recorded rarely in the 20th century but increased in the 1960s, followed by a moderate decline to somewhat lower levels in later decades (Fig. 1b, c). Overall, it seems likely that the significant increases in fishing pressure characterizing the 1960s through to the 1990s, particularly beam trawling (Engelhard *et al.*, 2015), alongside potential impacts on some egg-laying and nursery habitats (Frid *et al.*, 2000; Kinney & Simpfendorfer, 2009), contributed to the sharp decline of thornback ray followed by the more moderate decline of spotted ray (Walker & Heessen, 1996). Thornback ray is generally considered more sensitive to fishing, based on life-history traits and that it is more marketable due to its larger size (Walker & Hislop, 1998; Dulvy *et al.*, 2000; Dulvy & Reynolds, 2002; Ellis *et al.*, 2005b). The initial signs of recovery in both populations recorded since the 1990s may have been facilitated by reductions in fishing effort (Engelhard *et al.*, 2015), as well as *de facto* refugia, created by unfishable areas associated with shipping lanes,

shallow sand banks or offshore windfarms (Hunter *et al.*, 2006; Shephard *et al.*, 2012).

In relation to the demersal sharks, early sources reported that tope was a common shark in the North Sea during the late 19th century and was even of commercial interest (Laver, 1898; Murie, 1903). During the 20th century, however, spurdog became more economically valuable and a target fishery expanded after the Second World War (Holden, 1965). The present study confirms the low occurrence of tope; even in the early 1900s, it was recorded less than spurdog (Fig. 2e, f). Despite widespread beam trawling, records of spurdog clearly increased during the 1960s and 1970s, whilst those of tope increased less markedly. The more benthopelagic lifestyle of these two species suggests that they may have been less impacted by the expanding beam trawl fleet than demersal skates (Ellis *et al.*, 2005b). To some extent, increases in records of these two species could be an artefact due to changes in the sampling method after 1970 (including higher headline height and trawl speed), which appears to have become more effective at sampling pelagic species such as spurdog and tope. Since 1990, however, both tope and spurdog have declined and, in the 2000s, were recorded infrequently in the southern North Sea, in stark contrast with their historically wider distributions (Fig. 2g, h). The recent decline in spurdog in surveys should also be considered in relation to their seasonality, as this migratory species is more abundant in the southern North Sea in the winter and spring, with surveys predominantly undertaken in the summer since 1977.

Potential impacts of climate change

In recent decades, climate change may have also contributed to some recent trends, with the (cold-water associated) starry ray now declining and (warm-water associated) thornback ray (cf. Table 1) increasing. Whilst the increasing SST observed in recent decades occurs at a time when the trends in relative abundance reversed, there are also important temporal changes in fishing effort over the same time period, as well as the introduction of fisheries management measures (a total allowable catch was introduced in 1999).

Within the skate assemblage, starry ray was the only species that increased over the course of the second half of the 20th century (albeit with an apparent decrease since 2000). Although the low incidence reported in the 1950s–1960s could be partly due to misidentification issues, their sharp increase after 1960 is supported by other studies (Walker & Heessen, 1996; Ellis *et al.*, 2005b). According to Walker & Hislop (1998), starry ray is the least sensitive skate to fishing pressure, which may relate to its comparatively small size, early age at

maturity, preference for deeper areas which are generally trawled less, and to the high proportion discarded (Walker & Heessen, 1996; Rijnsdorp *et al.*, 1998; Ellis *et al.*, 2010; Silva *et al.*, 2012). Starry ray might have also benefited from the concurrent decline of other skates, through reduced competition for food and opening up of new ecological space (Walker & Hislop, 1998) as well as through scavenging on trawl-damaged organisms and discards (Templeman, 1982; Groenewold & Fonds, 2000; Stevens *et al.*, 2000; Jennings *et al.*, 2001). The significant decrease since 2000 (Fig. 2d) is notable. Starry ray has a Boreal biogeographical affinity (Engelhard *et al.*, 2011) with a preference for cooler waters (Tables 1 and S3.1). Whilst the cooler conditions of the 1960s–1970s would have then been favourable for starry ray, the recent warming of the southern North Sea might have been a contributing factor to the recent decline of this species at the southern limit of its biogeographical range, with it retracting to deeper and/or cooler areas (Dulvy *et al.*, 2008). Although the decline in spurdog is thought to be largely due to the overexploitation of the stock in the 1960s (De Oliveira *et al.*, 2013), there are also potential impacts of climate change as this species was revealed to have a preference for cooler water (Table 2).

Smooth-hounds and lesser-spotted dogfish both increased over time, from limited occurrences during the early 20th century to clear, well-established presence in the 21st century (Fig. 3). Their distributions in the southernmost North Sea indicate immigration from the English Channel. Both are taxa with Lusitanian affinities (Engelhard *et al.*, 2011), associated with warmer temperatures (Table 2) and likely beneficiaries of climate change, with particularly clear increases since the 1990s (Fig. 2). Their trends mirror those in several other North Sea fish species with Lusitanian affinities, including sardine *Sardina pilchardus*, anchovy *Engraulis encrasicolus* and red mullet *Mullus surmuletus* (Engelhard *et al.*, 2011). Although smooth-hounds were reported in some historical studies (Murie, 1903), they were not included in some early ichthyological lists for the southern North Sea (Laver, 1898), further indicating that they were historically uncommon in the area.

Although lesser-spotted dogfish was historically reported in the area (Murie, 1903), few records were available for the first half of the 20th century, and the occurrence of this species increased sharply during the 1960s (Fig. 2). Whilst lesser-spotted dogfish may have benefited from increasing water temperature, it is also possible that they have benefitted from new ecological space opened by fishery-induced declines in potentially competing skate species, as there is some diet overlap (Ellis *et al.*, 1996; Walker & Hislop, 1998; Stevens *et al.*, 2000). It may also be less impacted by fisheries, as this

species is often discarded, has a high discard survival rate and may scavenge on trawl-damaged organisms (Groenewold & Fonds, 2000; Stevens *et al.*, 2000; Jennings *et al.*, 2001; Revill *et al.*, 2005).

Potential impacts of habitat loss and degradation

In addition to fishing, seafloor degradation has likely had additional impact on skates, particularly on juvenile and egg stages. Many original habitats, including richly colonized biogenic reefs of oyster *Ostrea edulis*, have disappeared from the North Sea over the past century and been replaced by continually disturbed sandy gravel beds which currently predominate (Callaway *et al.*, 2002; Houziaux *et al.*, 2011). Similarly, coastal development and aggregate extraction may have had impacts on a more localized scale.

Trawling, especially beam trawling, also impacts on seabed habitats and can lead to changes in the structure and composition of benthic assemblages (Kröncke, 1992; Frid *et al.*, 2000; Fock *et al.*, 2014b), with potential knock-on effects on skate populations, given their dependence on the seabed. Given the apparent loss of skates from the inshore waters of the south-eastern North Sea, other human activities, such as *Crangon* fisheries but also coastal developments, may have been contributory factors to the loss of some species from the south-eastern North Sea (Heip, 1989; Temming & Hufnagl, 2015). For example, the Zuiderzee was blocked off in 1932, transforming an estuarine embayment into a brackish lagoon (Redeke, 1939). Historically, thornback ray was considered common off the Dutch coast, especially from Wieringen to Terschelling (Redeke, 1941), but this account also stated that it had declined in the Wadden Sea, which would follow the time when the Zuiderzee was blocked off from the sea (creating the IJsselmeer), as well as when the estuarine area around Wieringen was drained to create farmland, connecting the former island to the Dutch mainland.

Cumulative effects of fishing and habitat degradation may be reflected in the long-term distribution shift of the combined assemblage of skate species. Currently, there is a marked west–east gradient in the distribution of the skate assemblage, which has been most evident since the 1960s (Fig. S4.2). Over this period, beam trawl pressure has been higher in the eastern than western North Sea (Engelhard *et al.*, 2015) and has likely impacted not only adult skates but also egg-laying and nursery grounds in coastal zones and outer estuaries (Frid *et al.*, 2000; Ellis *et al.*, 2005a; Kinney & Simpfendorfer, 2009; Fock *et al.*, 2014a). Our results show that, until the 1960s, the overall skate distribution coincided with that of thornback ray, thought to be the historically dominant species. Since

the 1970s, the distribution of the assemblage has become more limited to the deeper north-west, where starry ray is dominant, and the south-west, where spotted and thornback ray predominate. The former constitutes an example of how species dominance tends to shift from more sensitive to more resilient organisms in exploited and stressed communities, a trend that is widespread (North Sea: Walker & Hislop, 1998; Queiros *et al.*, 2006; Irish Sea: Dulvy & Reynolds, 2002; Mediterranean: Fortibuoni *et al.*, 2010; Caribbean: McClenachan, 2009).

Perspectives

This study gives a comprehensive overview of the occurrence and distribution dynamics of the North Sea's elasmobranchs over the past 112 years. It underlines the value of long time series to improve our understanding of the ecology of the species and their trends over time (Pauly, 1995; Pinnegar & Engelhard, 2008; Cardinale *et al.*, 2009) and highlights the potential of marine historical ecology to provide 'baselines' for consideration by managers. Clearly, several elasmobranch species were far more common and widespread at the beginning of the 20th century, even though the North Sea was already widely exploited (Graham, 1956; Thurstan *et al.*, 2014), albeit with less effective fishing gear and that other species have become dominant since then. Climatic and anthropogenic drivers appear to have acted differently upon these species according to their life-history traits, habitat and temperature preferences, and importance and susceptibilities to fisheries.

Evidence that fishing pressure has impacted elasmobranchs (hypothesis 1) comes from the declines over the long term of most large species (common skate complex, thornback ray, tope, spurdog) and long-term increases of smaller species (starry ray, lesser-spotted dogfish), and from the timing of most fundamental change in the skate assemblage coinciding with the 'beam trawling revolution' of the 1960s–1970s (Walker & Hislop, 1998; Dulvy & Reynolds, 2002; Engelhard, 2008); slight recovery of some species (thornback, spotted ray) since 2000 might relate to reductions in trawling effort since then (Engelhard *et al.*, 2015). Evidence that climate change impacted elasmobranchs (hypothesis 2) comes from the recent decreases in cold-water associated species (starry ray, spurdog), which have either declined in or retreated northwards from the southern North Sea. In contrast, warm-water species (most marked in smooth-hounds and lesser-spotted dogfish; cf. Rijnsdorp *et al.*, 2009) have shown recent increases. Evidence for habitat degradation as a potential driver of change (hypothesis 3) comes from the loss

of skate species from estuaries in the eastern North Sea, where habitats have been altered extensively due to coastal works and other pressures (Heip, 1989; Kröncke, 1992; Wolff, 2000; Fock *et al.*, 2014b), and where beam trawl effort has been highest (Engelhard *et al.*, 2015).

In addition to these three major drivers, other factors including prey availability and interspecific competition likely played additional roles (Jennings *et al.*, 2001). Future studies may build upon ours to examine the relative importance of drivers, but this is challenging: although similarly long time series do exist for some environmental variables (e.g. temperature), time series for other variables (notably human pressures including fishing effort) are more sporadic (Pinnegar & Engelhard, 2008). Furthermore, disentangling the direct effects of, for example fishing impacts and water temperature, from the indirect consequences and multi-species interactions remains a key challenge.

This study further emphasizes the vulnerability of larger elasmobranchs (common skate, thornback ray, tope, spurdog) which were subject to historically unsustainable exploitation rates, which combined with other pressures, resulted in declines and changes to the structure of the elasmobranch assemblage and even localized extirpations (Dulvy *et al.*, 2000; Rogers & Ellis, 2000). Losses or declines of larger elasmobranchs have not only happened in the North Sea, but have been documented widely (Irish Sea: Dulvy *et al.*, 2004; Mediterranean: Ferretti *et al.*, 2008, 2010; eastern North America: Lotze, 2010). It has become well established that many elasmobranchs are adversely impacted by fishing; for example, historical studies in the Adriatic Sea and Gulf of Mexico showed similar, fisheries-induced declines of larger and more sensitive species (Fortibuoni *et al.*, 2010; Raicevich & Fortibuoni, 2013; Baum & Myers, 2004). Other studies on reef sharks also showed reductions and did not only link these to fishing pressure but also to habitat loss (Ward-Paige *et al.*, 2010). The present study highlights the roles of (i) fishing, (ii) climate change and (iii) habitat alteration on the North Sea elasmobranch assemblage, with adverse impacts on many species (often those of higher commercial value), although favourable effects upon others. These three, major anthropogenic drivers are not limited to the North Sea but act upon shelf seas across the globe; therefore, parallel changes in elasmobranch communities in other regions are to be expected.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Section S1. Research vessels and gears.

Section S2. Stations sampled, environmental variables, and rationale for chosen zones.

Section S3. Statistical models.

Section S4. Results on the combined skate and shark assemblages.