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RESEARCH ARTICLE

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Spatio-temporal dynamics of the common skate species complex: Evidence of increasing abundance

Ryan McGeady[1] | Sophie L. Loca[2] | Chris McGonigle[1]

[1]School of Geography and Environmental Sciences, Ulster University, Coleraine, UK

[2]School of Biological Sciences, Queen's University Belfast, Belfast, UK

Correspondence
Ryan McGeady, School of Geography and Environmental Sciences, Ulster University, Coleraine BT52 1SA, UK.
Email: r.mcgeady@ulster.ac.uk

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Abstract

Aim: The critically endangered common skate species complex is a large-bodied and long-lived batoid, which has experienced local extirpations and population declines over the past century mainly due to overfishing. Due to its decline, fisheries management measures were introduced to prevent further decline and fragmentation of populations. For example, in 2009, a landings prohibition was introduced in the European Union, which banned the retention of common skate onboard commercial fishing vessels with captured individuals to be discarded. We aimed to explore the spatial and temporal population dynamics of the common skate species complex, against the backdrop of changes in fisheries management measures.

Location: Northeast Atlantic Ocean.

Methods: We used publicly available fishery-independent trawl survey data from several regions of the Northeast Atlantic shelf to examine trends in incidence and abundance for the common skate species complex. We also constructed a species distribution model to identify changes in the spatio-temporal distribution of the common skate.

Results: A sustained increase in the common skate species complex was evident in several areas of its distribution. An increase was observed in five separate trawl surveys encompassing distinct regions of its distribution. Despite the observed increase, little evidence of recolonizing previously extirpated areas was evident.

Main Conclusions: The findings demonstrate the effectiveness of fisheries management measures in contributing to an increase in the common skate species complex. Such measures may also be effective if applied to numerous other batoid species currently threatened with extinction.

KEYWORDS
blue skate, common skate, conservation, elasmobranch, endangered, flapper skate

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1 | INTRODUCTION

Many elasmobranch species, i.e. sharks, skates and rays, have experienced population declines and one-third are considered threatened with extinction (Dulvy et al., 2021; Ferretti et al., 2010). Several direct and indirect human-mediated pressures impact elasmobranchs such as overfishing, bycatch, habitat degradation and climate change (Jennings et al., 2008; Osgood et al., 2021; Stevens et al., 2000). Many elasmobranchs are considered *k*-strategists meaning they are long-lived, slow-growing, late to reach maturity, have prolonged reproductive periods and produce few offspring (Stevens et al., 2000). Such life-history attributes increase susceptibility to anthropogenic impacts due to long generation times (Wheeler et al., 2020).

The common skate species complex is composed of two large-bodied, long-living and slow-reproducing elasmobranch species that have experienced dramatic declines in abundance over the past century, primarily due to unsustainable commercial fishing (Rogers & Ellis, 2000; Walker, 1998). Both species are considered critically endangered by the International Union for the Conservation of Nature (IUCN) and have been extirpated from many regions of their former distribution (Brander, 1981; Ellis, McCully-Philipps, Sims, Derrick, et al., 2021; Ellis, McCully-Philipps, Sims, Walls, et al., 2021; Sguotti et al., 2016).

In 2010, morphological and genetic evidence showed that the common skate complex (*Dipturus batis*) is in fact two separate species, the larger flapper skate (*D. intermedius*) and the blue skate (now *D. batis*; Griffiths et al., 2010; Iglésias et al., 2010). Its estimated distribution ranges from the Azores and Portugal as far north as Iceland and southern Norway, with "hotspots" off the coasts of Ireland and Scotland (Bache-Jeffreys et al., 2021). Although the species largely overlap in their specific distributions, flapper skates inhabit a larger thermal range associated with inshore areas, in comparison to the more offshore blue skate (Frost et al., 2020). They also differ in terms of their size; the flapper skate reaches lengths of at least 229 cm, compared with the blue skate that grows to at least 143 cm (Iglésias et al., 2010).

As the name suggests, common skate were once abundant across their range. However, with advances in fishing gear efficiency and increasing commercial demand for common skate in the early 20th century, the aforementioned life history characteristics proved detrimental to maintaining healthy populations (Engelhard, 2008; Steven, 1932). In the southern North Sea, the percentage of trawl survey samples with the species complex present declined from ~30% in the early 1900s to less than 5% in the 1960s, and thereafter, absence from the 1970s (Sguotti et al., 2016). In the Irish Sea, records declined from the early 20th century until their disappearance by the late 1970s (Brander, 1981). France, the largest skate fishing nation, reported an over 90% decline in landings from two major ports between 1964 and 2006 (Iglésias et al., 2010). While overexploitation was likely the main cause of depletion, habitat degradation may also have been a contributory factor. For example, large areas of the North Sea were historically covered by oyster reef, which are now functionally extinct (Hayer et al., 2019). Such reefs may have provided important egg-laying and feeding sites. For example, it has been documented that flapper skate lay eggs on hard substrate to retain egg cases and provide shelter (Phillips et al., 2021).

In many regions, the decline went relatively unnoticed due to the lack of species-specific landings information, instead classification under the umbrella term "skates and rays" was used up until 2008 (Silva et al., 2012). Therefore, despite declines in landings, the trend was masked by the stability or even increase in abundance of other species (Dulvy et al., 2000). In addition, landings were often mislabelled. Iglésias et al. (2010) noted that 93% of landings labelled as long-nosed skate (*Dipturus oxyrinchus*) were flapper skate or blue skate. Added to the fact that common skate in reality consist of two species with the larger flapper skate attaining maturity later (19–20 years) and at greater length (185.5–197.5 cm) than blue skates, which mature at 11 years and 115–122.9 cm length (Iglésias et al., 2010). This would render the former species more vulnerable to fishing pressure due to longer generation times and immature individuals unable to avoid capture from an earlier age (Dulvy & Reynolds, 2002).

In 2009, the European Union (EU) prohibited the retention of common skate onboard commercial fishing vessels, with individuals captured in EU waters to be discarded. The action was implemented as a conservation measure to prevent further depletion and fragmentation of populations. Elsewhere, landing prohibitions have proven successful; off the coast of France, the undulate ray (*Raja undulata*) benefited with an increase in abundance when a fishery ban was introduced in 2009 (Elliott et al., 2020). Landings of "skates and rays" in the Celtic Seas ecoregion (around Ireland and the UK) have also been declining since the early 2000s, partly due to a Total Allowable Catch (TAC) being established in 2009, which has ranged between 8032 and 15,748 t since its introduction (ICES, 2021). A TAC for "skates and rays" was also established in 1999 for the greater North Sea and has been reduced over time (ICES, 2021; Silva et al., 2012). Increases in common skate abundances have been reported in recent years, possibly as a result of these conservation measures (ICES, 2021).

In order to assess the status of threatened species, it is critical to evaluate the influence of management measures (Ward-Paige et al., 2012). In the present study, we aim to explore the spatial and temporal population dynamics of critically endangered taxa (common skate species complex) of high priority conservation interest, against the backdrop of changes in fisheries management measures using publicly available fisheries-independent trawl survey data. It is essential to the ongoing monitoring and management of this species complex to assess and evaluate conservation efforts and determine their effectiveness. In this context, we aimed to (1) evaluate annual trends in incidence (i.e. percentage of trawl samples containing common skate), Catch-Per-Unit-Effort (CPUE; i.e. abundance) and maximum length (i.e. prevalence of large individuals) to determine the current status of common skate in the Northeast Atlantic and investigate how populations have responded to conservation measures and (2) examine variation in spatial distribution over time by building a species distribution model that predicts the probability of occurrence.

TABLE 1 Summary of trawl survey data from DATRAS.

Survey	Year	Quarter	Gear	Samples	Common skate occurrences	Common skate no.
Scottish West Coast Bottom Trawl Survey (SWC - IBTS)	1985–2020	1, 4	GOV trawl	4125	915	2645
Irish Groundfish Survey (IE - IGFS)	2003–2020	1, 2	GOV trawl	2880	445	786
Scottish Rockall Survey (ROCKALL)	1999–2020	3	GOV trawl	798	197	640
North Sea International Bottom Trawl Survey (NS - IBTS)	1966–2021	1–4	GOV trawl, Dutch herring trawl, herring bottom trawl, SOV-NET	34,087	243	577
French Bottom Trawl Survey (EVHOE)	1997–2020	4	GOV trawl	3294	225	571
Spanish Porcupine Bottom Trawl Survey (SP - PORC)	2001–2020	3, 4	Porcupine baka trawl	1739	74	170
Northern Ireland Groundfish Survey (NIGFS)	2005–2019	1, 2, 4	Rock hopper otter trawl	1394	1	1

Note: Quarter 1: January–March, Quarter 2: April–June, Quarter 3: July–September, Quarter 4: October–September.

2 | METHODS

Data for the common skate species complex were obtained from DATRAS (DAtabase of TRAwl Surveys; ices.dk/data/data-portals/Pages/DATRAS.aspx), an open access database of fishery-independent trawl surveys hosted by ICES. Data from 7 groundfish surveys with varying spatial and temporal coverage were acquired (Table 1). The surveys provided a temporal range between 17 and 56 years. Spatial coverage varied depending on the survey. However, data were available for much of the Northeast Atlantic shelf area (Figure 1).

Data consisted of the number of skate at 1 cm length classes along with associated information on haul duration, date, location and from 2010 onwards, species-level data. The data were used to examine temporal and spatial trends in incidence and abundance of the common skate species complex between trawl surveys. Incidence rates (%) were estimated by calculating the proportion of samples in which at least one common skate complex individual was identified. CPUE was calculated as the number of individuals caught in a sample per hour of trawling (ind. h^{-1}). To examine the occurrence of large-bodied individuals, maximum length (cm), that is, the largest size class observed, was compared between years. Finally, to predict spatio-temporal probability of occurrence, presence-absence data were used to create a species distribution model for the common skate species complex.

Efforts were made to ensure that spatial coverage for each year was similar when comparing years for individual surveys. For example, The Irish Sea was sampled in 2003 and 2004 but in no further years for the Irish Groundfish survey. Therefore, Irish Sea samples were removed to avoid artificially decreasing incidence and CPUE for those years. For the Scottish west coast survey, only samples collected between 54.89 to 60.1°N latitude and 10.45 to 3.53°W longitude were retained to maintain consistency in spatial coverage. Finally, for the North Sea survey, samples from 1965 to 1973 were excluded as sampling coverage was less extensive in comparison to subsequent years.

2.1 | Environmental data

Several predictor variables were used in distribution modelling to examine their effect on common skate complex occurrence probability and were each rescaled to a resolution of 0.005° (556 m). This resolution was used to achieve a balance between computing power and the highest resolution data available, e.g. bottom depth. Bottom depth (m) was obtained from the European Marine Observation and Data Network bathymetry portal (emodnet-bathymetry.eu) at a spatial resolution of 0.001° (EMODnet, 2020). Temperature (°C) at the seabed and depth-integrated salinity (PSU) and current velocity (ms^{-1}) were obtained from the Atlantic – European Northwest Shelf – Ocean Physics Reanalysis on the Copernicus Marine Service (marine.copernicus.eu) with a spatial resolution of 0.111° × 0.067° and 24 depth layers.

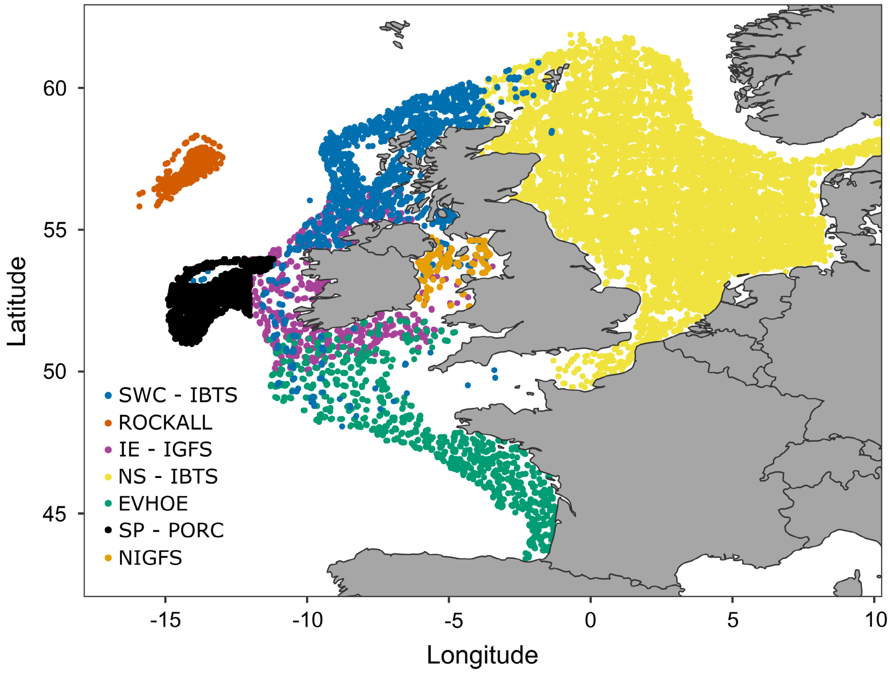

FIGURE 1 Map of the study area displaying sampling stations for each trawl survey. EVHOE, French Bottom Trawl Survey; IE – IGFS, Irish Groundfish Survey; NIGFS, Northern Ireland Groundfish Survey; NS – IBTS, North Sea International Bottom Trawl Survey; ROCKALL, Scottish Rockall Survey; SP – PORC, Spanish Bottom Trawl Survey; SWC – IBTS, Scottish West Coast Bottom Trawl Survey

2.2 | Statistical modelling

A Generalized Additive Model (GAM) with thin-plate regression splines was used to separately model annual variability in maximum length and species distribution modelling. GAMs are a nonparametric regression model that accepts various error distributions and allow for complex nonlinear relationships between predictor and response variables. To examine annual trends in the prevalence of large-bodied individuals, the effect of year on maximum length was modelled using a GAM with a Gaussian error distribution and identity link. Model residuals were inspected to check for non-normality and heteroscedasticity. Only years with a minimum of five sampled individuals were included in the analysis to minimize the effect of small sample size.

Using presence-absence data, the probability of common skate occurrence was modelled using a binomial GAM with a logit link. Predictors variables used in the model were depth (m), bottom temperature (°C), depth-integrated salinity (PSU) and current velocity (ms^{-1}) as continuous variables and time period (2003–2005, 2006–2008, 2009–2011, 2012–2014, 2015–2017 and 2018–2020) and gear type (GOV trawl, Porcupine baka trawl and rock hopper otter trawl) as categorical variables. Spatial variables latitude and longitude were included as an interaction term in the model to account for spatial autocorrelation (Salazar et al., 2021; Schwemmer et al., 2019). Gear type was included as a predictor variable to account for differences in fishing gears used between some trawl surveys (Table 1; see datras.ices.dk/Home/Descriptions.aspx#IBTS for further details on gear specifications). The temporal range of 2003–2020 was used as it provided the greatest spatial and temporal overlap between distinct bottom trawl surveys. Temperature, salinity and current velocity were averaged for 3-year periods to account for changes in physical oceanography from 2003 to 2020. The maximum degrees of freedom (knot, *k*) for individual terms were set to 5 to prevent smoothers overfitting the data and inferring biologically unrealistic relationships. The gam.check function was used to ensure the k-index was close to 1 with nonsignificant *p* values. Collinearity between variables was checked using variance inflation factors (VIFs), and no variables were removed as VIFs remained below 3 (Zuur et al., 2010). The most parsimonious model was selected based on Akaike's Information Criterion (AIC), whereby, a stepwise forward selection of variables was used to find the optimal model based on the lowest AIC value. The use of AIC balances complexity in contrast to goodness of fit to find the optimal model (Akaike, 1974). The relative importance of each predictor variable in the final model was examined by assessing the difference in AIC (Δ AIC) and deviance explained (Δ Deviance) when each predictor variable was removed (Rooker et al., 2012).

Model validation for the GAM predicting the probability of common skate occurrence was conducted by randomly splitting data into a training (80%) and testing (20%) dataset 10 times. The ability of the training dataset to predict the probability of presence was tested using the area under the curve of the receiver operating characteristic and the true skill statistic. Area under the curve ranges from 0 to 1 with values between 0.7 and 0.9 considered good prediction, whereas values over 0.9 indicate excellent prediction (Hosmer et al., 2013). The true skill statistic is a threshold-dependent metric that accounts for sensitivity and specificity and ranges from −1 to 1 where 1 demonstrates perfect agreement (Allouche et al., 2006). The threshold was chosen to maximize the sum of sensitivity and specificity. The mean and standard deviation of area under the curve, sensitivity, specificity and true skill statistic were then calculated by applying 10 cross-validation models using 80% of the data for training and 20% for testing. Statistical analyses and model validation were conducted in R version 4.0.3 (R Core Team, 2020) using the "mgcv," "PresenceAbsence" and "ggplot2" packages (Freeman & Moisen, 2008; Wood, 2011). R code and data are provided in the Supplementary Materials (Appendices S1 and S2).

3 | RESULTS

Incidence (%) and CPUE (ind. h^{-1}) increased over the time series for the Scottish West Coast, Rockall, Irish Groundfish and EVHOE surveys, while the longer North Sea survey time series initially exhibited a decline followed by an increase from the mid-2000s (Figure 2). For the Scottish West Coast, incidence and CPUE increased from an average of 12.9% and 0.44 ind. h^{-1} from 1985–2005 to 42.9% and 2.78 ind. h^{-1} from 2012–2020 (Figure 2a). On Rockall Bank, incidence (7.5%) and CPUE (0.42 ind. h^{-1}) remained low from 1999 to 2009 before an increase in incidence (44.7%) and CPUE (3.56 ind. h^{-1}) between 2016 and 2020 (Figure 2b). The Irish Groundfish survey exhibited a relatively constant increase from the beginning of the time series in 2003 (3.4%, 0.17 ind. h^{-1}) to 2020 (23.6%, 0.87 ind. h^{-1}; Figure 2c).

Most occurrences from the EVHOE survey were observed in the Celtic Sea and incidence rose to a maximum of 19.9% in 2020 in comparison to an average of 4.7% between 1997 and 2014 (Figure 2d). Meanwhile, a large increase in CPUE for the EVHOE survey was evident from 2016. Incidence for the North Sea exhibited an inverted bell-shaped curve, whereby, peaks of incidence at the beginning and end of the time series are separated by 2–3 decades of low values (Figure 2e). In 1982 and 1983, a large number of individuals recorded in relatively few samples led to inflated CPUE values. However, subsequent to those years, CPUE remained very low until a sustained increase from the mid-2000s (Figure 2e). The majority of presence records in the North Sea occurred in northwestern areas (Figure 2f).

Each of the Scottish West Coast, Rockall, Irish Groundfish, EVHOE and North Sea surveys displayed a positive relationship between maximum length and year (Figure 3). For the Scottish West Coast, maximum length underwent a large increase in the early 2000s before stabilizing between 202 and 233 cm in the 2010s ($p < .001$, deviance exp. = 89.4%; Figure 3a). The Rockall survey had an increase of approximately 40 cm over the time series ($p < .001$, deviance exp. = 76.9%; Figure 3). The Irish Groundfish survey showed an initial increase at the beginning of the time series before stabilizing ($p < .001$, deviance exp. = 68.8%; Figure 3c). Maximum length increased to a high of 190 cm in 2020 for the EVHOE survey ($p < .01$, deviance exp. = 54%; Figure 3d). Finally, for the North Sea, many of the years in the first half of the time series were removed from the analysis due to a low number of presences (Figure 3e). However, a positive trend was also evident for the region ($p < .001$, deviance exp. 43.9%). Where available, species data indicated that Scottish West Coast and North Sea surveys primarily observed flapper skate in samples, while ROCKALL and EVHOE survey samples were dominated by blue skates. For the Irish Groundfish survey, samples were more balanced with flapper skate dominating slightly.

A total of 13,232 samples collected from 2003 to 2020 were used in modelling the distribution of the common skate complex. The number of samples increased from a minimum of 1877 for 2003–2005 to a maximum of 2369 for 2015–2017. A total of 1665 samples contained common skate and the incidence rate increased from 6.2% in 2003–2005 to 20.1% in 2018–2020 indicating increased prevalence in trawl samples.

The optimal binomial GAM relating probability of occurrence to predictor variables included latitude and longitude, time period, depth, current velocity, salinity, bottom temperature and gear and explained 32.1% deviance (Table 2). Although gear type was retained in the optimal model its effect was only marginally significant ($p = .06$). Spatial variables exhibited the highest relative importance, followed by time period, depth, current velocity, salinity and temperature (Table 2). The effect of physical variables indicated that maximum probability of presence occurred in areas of 75–300 m depth, 32.5–34 PSU salinity, 9–11°C temperature, and despite a relatively small effect size for current velocity, the probability was higher for low (<0.02 ms^{-1}) and high (>0.15 ms^{-1}) current velocities (Figure 4). Model validation indicated an area under the curve of 0.88 ± 0.01 (mean ± SD), sensitivity of 0.87 ± 0.02, specificity of 0.73 ± 0.01 and true skill statistic of 0.61. The higher sensitivity value in comparison to specificity indicated that the model was more adept at identifying true positives than true negatives. However, validation metrics signified good model performance overall.

The common skate complex exhibited an increasing probability of occurrence over the 6 time periods from 2003 to 2020 (Figure 5). The increase in occurrence probability was highest for areas to the west of Scotland, Rockall Bank and the Celtic Sea (Figure 5). Several inshore areas to the west coast of Scotland also signified suitable areas of habitat (Figure 5). However, despite the increased presence of the species complex across much of its distribution, probability remained extremely low for areas such as the Irish Sea and North Sea, which were part of its former distribution. Although, in recent years northwestern areas of the North Sea have seen an increased likelihood of common skate presence (Figure 6).

4 | DISCUSSION

The present study used publicly available fisheries-independent trawl survey data from several regions of the Northeast Atlantic to examine trends in incidence, abundance and spatial distribution of the critically endangered common skate species complex. Documented increases in incidence, CPUE and maximum length indicate that populations are in a state of recovery; the results signified that individuals are being observed more often, in higher abundances and at larger sizes, suggesting that older individuals are more prevalent. The differences in maximum length between surveys also reflect the dominant species in the region, where the larger flapper skate was more common in the Scottish West Coast and North Sea surveys, while the blue skate was

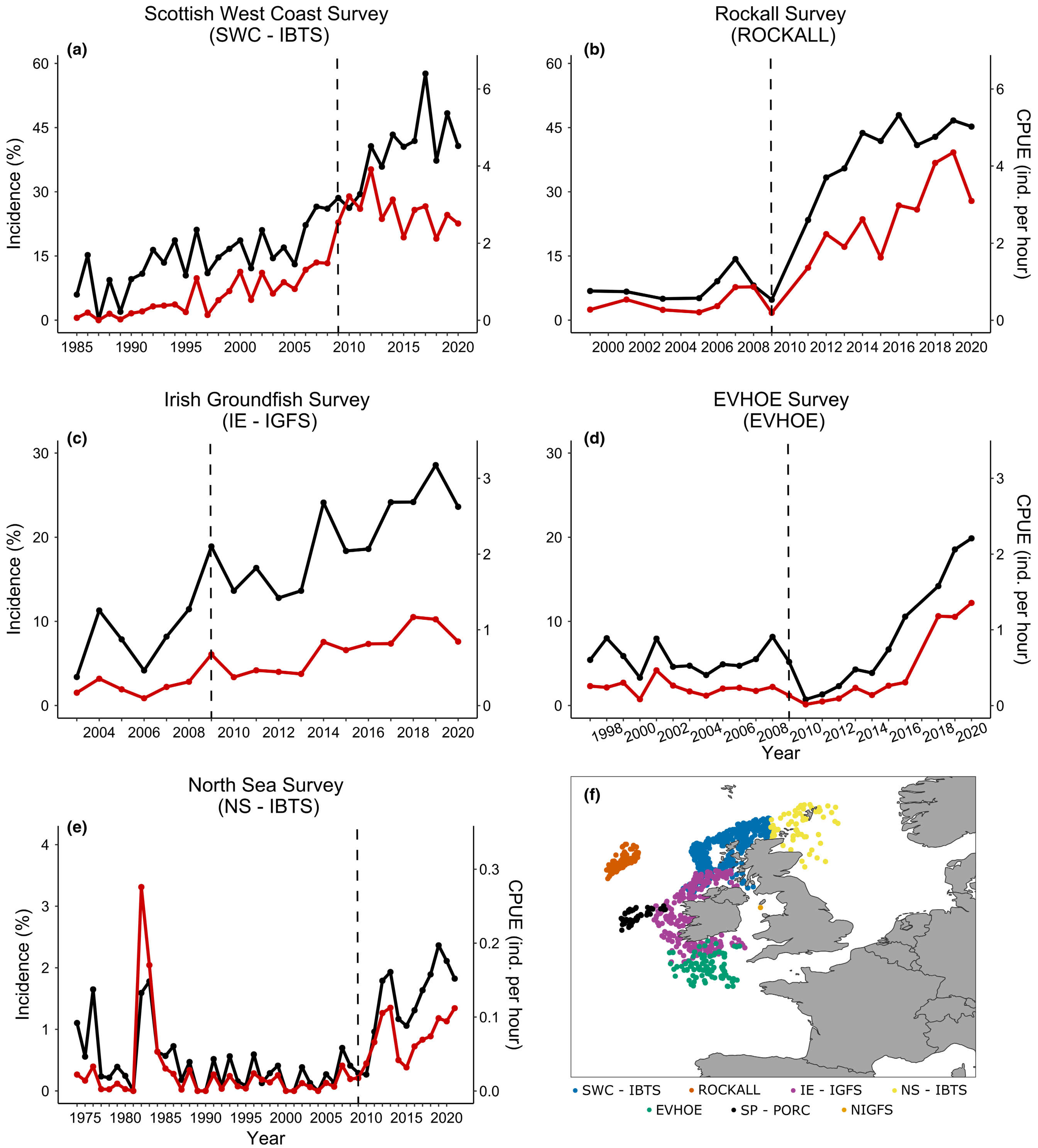

FIGURE 2 Annual common skate complex incidence (%; black) and CPUE (ind. h^{-1}; red) for the (a) Scottish West Coast, (b) Rockall, (c) Irish Groundfish, (d) EVHOE and (e) North Sea surveys. Vertical dashed line indicates the year that a landing prohibition for common skate was introduced in European Union waters. (f) Map of present records for the period 2003–2020. EVHOE, French Bottom Trawl Survey; IE – IGFS, Irish Groundfish Survey; NIGFS, Northern Ireland Groundfish Survey; NS – IBTS, North Sea International Bottom Trawl Survey; ROCKALL, Scottish Rockall Survey; SP – PORC, Spanish Bottom Trawl Survey; SWC – IBTS, Scottish West Coast Bottom Trawl Survey

mainly sampled in the Rockall and EVHOE surveys. Indeed, much of the population growth has occurred since the introduction of fisheries management measures such as those introduced in 2009, a landing prohibition for common skate in EU waters and a TAC for "skates and rays" in the Celtic Seas ecoregion. These findings demonstrate the value of open access long-term biological time series that enable the identification of trends in nontarget species. It also allows an assessment of the effectiveness of conservation measures, which is essential

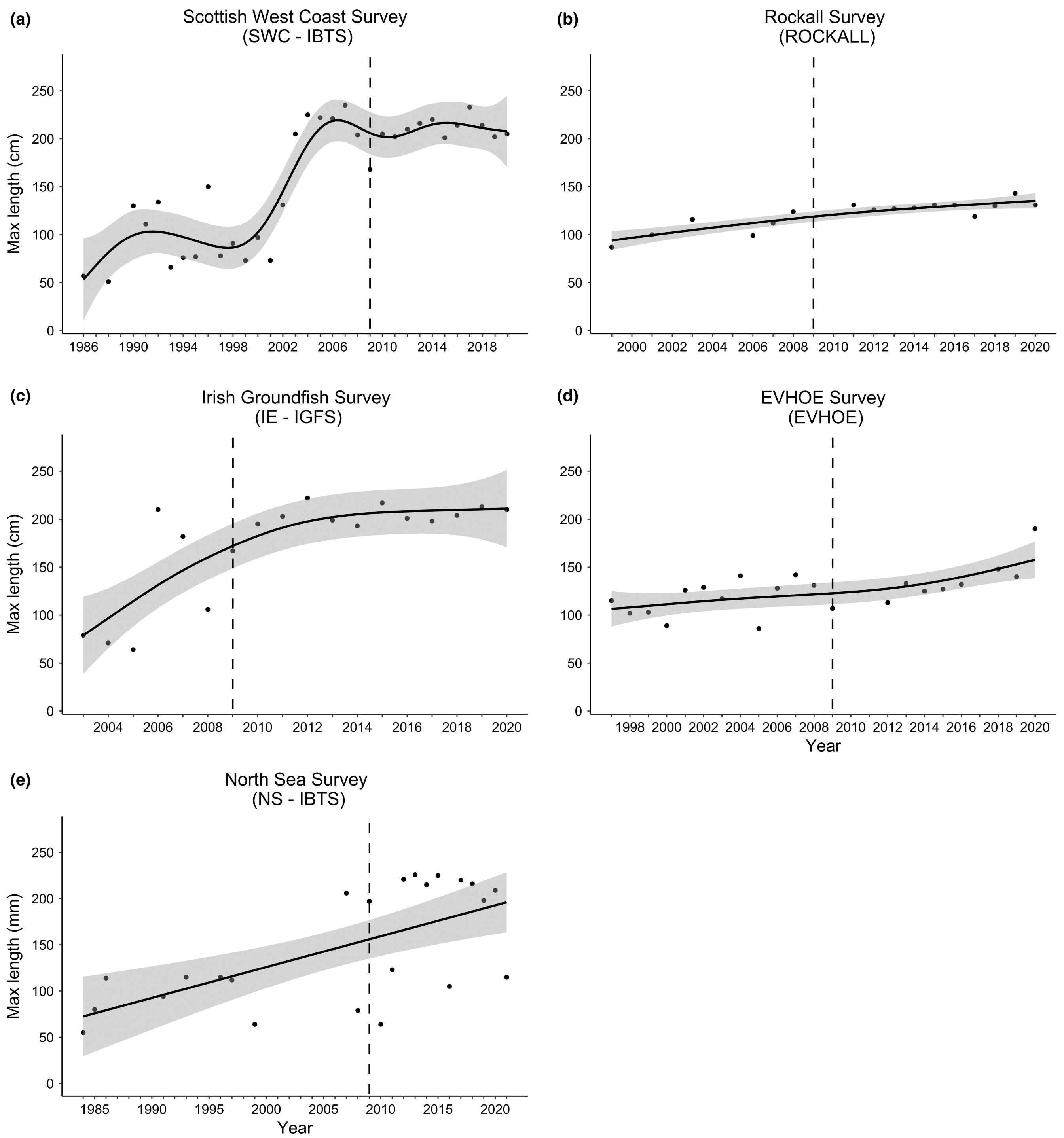

FIGURE 3 Annual common skate complex maximum length (cm) fitted with a GAM smoother for the (a) Scottish West Coast (SWC – IBTS), (b) Rockall, (c) Irish Groundfish (IE – IGFS), (d) EVHOE and (e) North Sea Surveys (NS – IBTS). Vertical dashed line indicates the year that a landing prohibition for common skate was introduced in European Union waters.

to ongoing efforts to halt population decline and enable the recovery of threatened species.

Elasmobranchs are amongst the most vulnerable groups to anthropogenic pressures in the marine realm due to the slow-growing, late-maturing and low fecundity characteristics of many species (Wheeler et al., 2020). A pattern of decline has been observed worldwide, these changes could lead to a reduction in natural mortality of associated prey species, which has further implications for predator–prey interactions and for the wider ecosystem (Ferretti et al., 2010). Ward-Paige et al. (2012) reviewed the drivers of recovery for 40 elasmobranch populations with the majority (53%) attributed to small-bodied species benefiting from a decline in predators and 25% due to a decrease in human-related mortality.

Term	df/edf	Chi- square	*p*-Value	Δ AIC	Δ Deviance
s(Lon, Lat)	23.4	593.9	<.001	779.73	8.3
s(Depth)	3.9	128.3	<.001	162.37	1.7
s(Current velocity)	3.8	11.7	<.02	58.97	0.8
s(Salinity)	3.9	62.7	<.001	52.44	0.6
s(Temperature)	3.8	25.7	<.001	22.13	0.3
Period	5	206.2	<.001	330.87	3.5
Gear	2	5.6	.06	57.77	0.7
Deviance explained: 32.1%					
AIC: 6897.15					
n: 13,232					

TABLE 2 Optimal binomial GAM model for common skate species complex indicating the degrees of freedom (df) for parametric terms and estimated degrees of freedom (edf) for smoothed terms (s), chi-square, *p*-value and variable importance

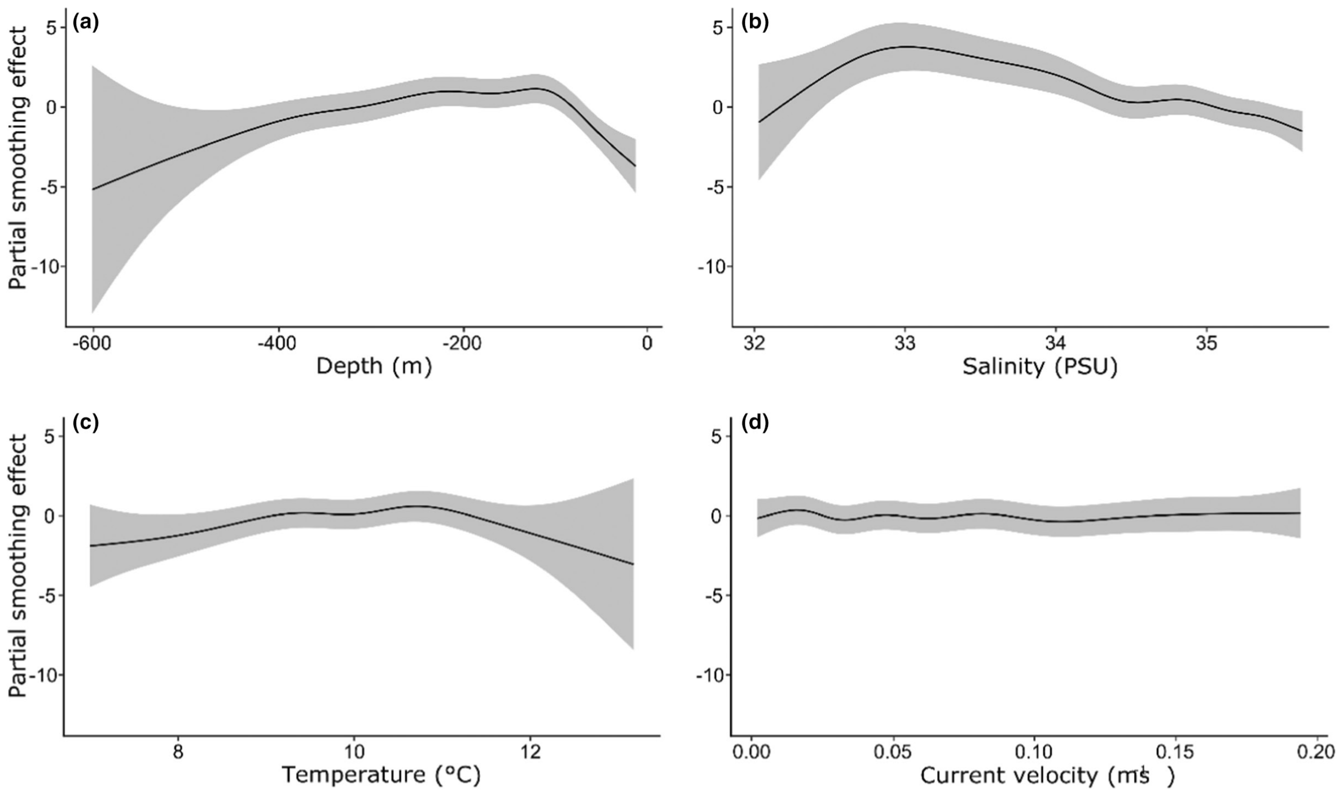

FIGURE 4 Partial effects plots of (a) depth, (b) current velocity, (c) salinity and (d) bottom temperature for the optimal binomial GAM model. Black line and grey shaded areas indicate fitted values and 95% confidence intervals, respectively.

The findings of the present study indicate that populations of the common skate species complex are recovering from declines brought on by commercial overexploitation and habitat degradation. The landing prohibition introduced in 2009 may be a key driving factor behind the sustained increase in several areas. Similarly, a TAC was introduced in 2009 for the Celtic Seas ecoregion and in 1999 for the greater North Sea and subsequent reduction in the TAC over time would have also decreased fishing intensity for "skates and rays" (ICES, 2021). For Rockall Bank and the Celtic Sea, increases in CPUE were evident immediately from 2009 onwards. For the Scottish West Coast and Irish groundfish survey, an increase appeared to be underway even before the prohibition. Landings of "skates and rays" for the Celtic Seas ecoregion and Greater North Sea had been falling since the 1990s (ICES, 2021). The Scottish fishing fleet also decreased from 1333 vessels over 10 m to 763 between 1993 and 2002 (Stead, 2005). In addition, the common skate was listed in the Biodiversity Action Plan in the UK in 1999 and as a Priority Marine Feature in Scotland and Northern Ireland (Garbett et al., 2021). Reduced fishing mortality and conservation actions prior to the introduction of the landing prohibition and TAC may have contributed to the observed earlier recovery in these regions.

It is also important to note that for the North Sea survey, many different vessels took part in the survey and different fishing gears

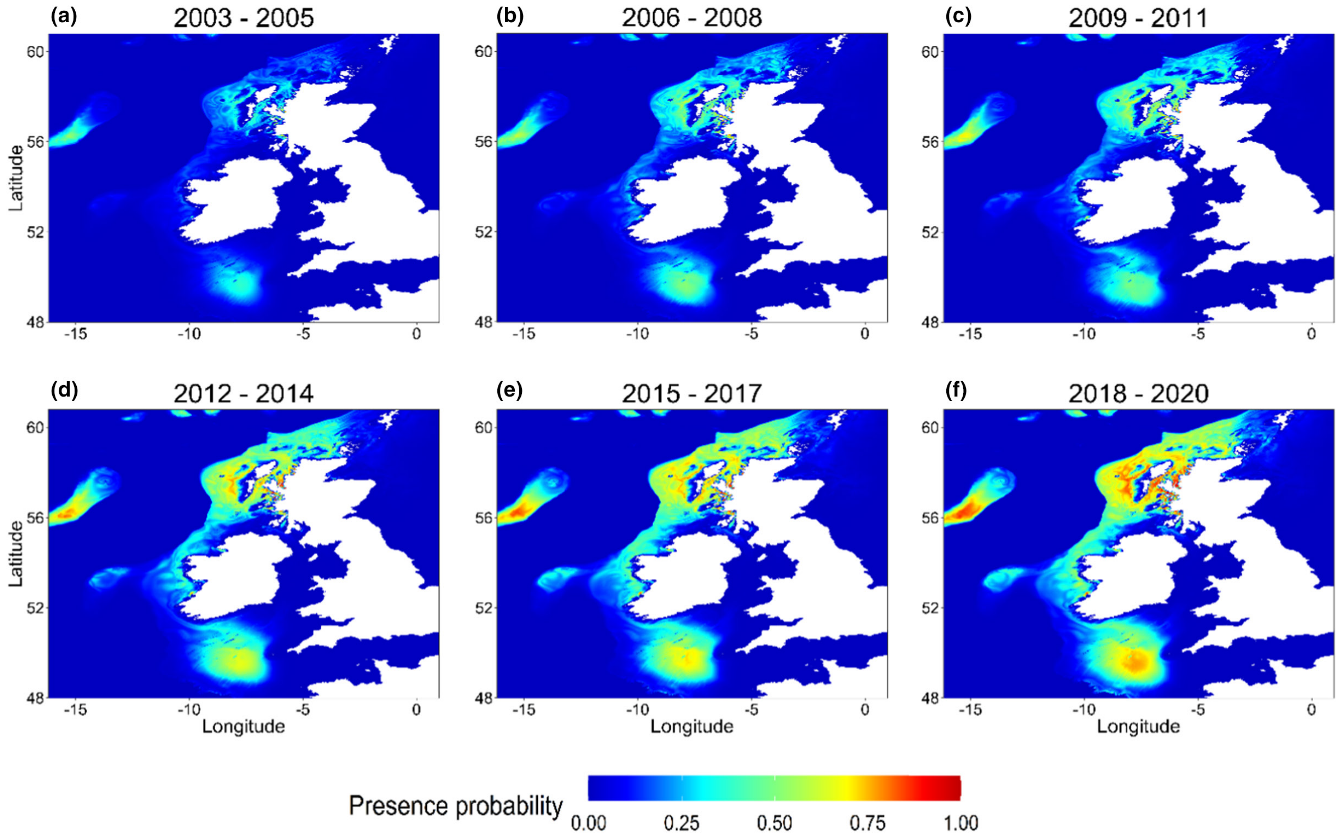

FIGURE 5 Spatial probability of occurrence predictions of the common skate species complex from binomial GAM distribution model for (a) 2003–2005, (b) 2006–2008, (c) 2009–2011, (d) 2012–2014, (e) 2015–2017 and (f) 2018–2020

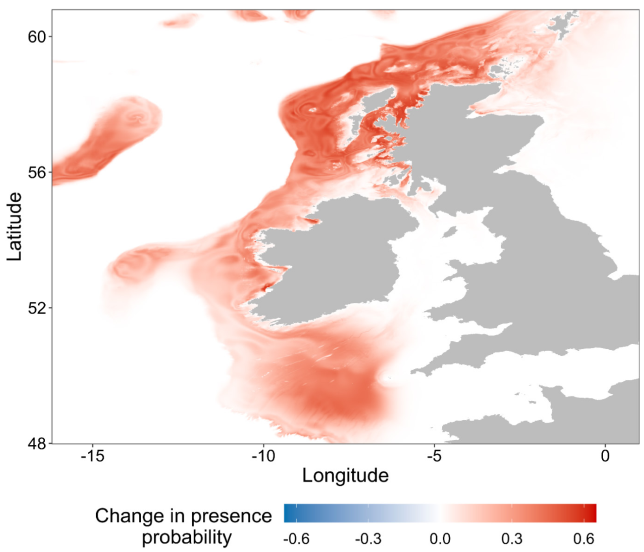

FIGURE 6 Difference in common skate species complex probability of occurrence between first (2003–2005) and last (2018–2020) year periods from binomial GAM distribution model

were used (Table 1) throughout the time series, which may have affected catchability. However, observed trends in common skate incidence were similar to that reported in previous studies covering parts of the North Sea (Bom et al., 2019; Sguotti et al., 2016). For other surveys, vessel and gear type were more consistent throughout the time series (Table 1). Moreover, modifications to survey design and gear configuration occurred over the course of certain bottom trawl survey time series. For example, in 2011 the survey design for the Scottish West Coast and Rockall surveys changed from a fixed station to a random stratified design (ICES, 2017). From 2011, modifications to ground gear on the GOV trawl for these surveys also occurred (ICES, 2017). These changes likely would have influenced the catchability of demersal fish and therefore, observed incidence and CPUE levels for the common skate species complex. However, after 2011, the increasing trend in incidence was maintained for both surveys and an increase in both incidence and CPUE was evident for the Scottish West Coast survey prior to 2011.

There was little evidence of the common skate recolonizing previously extirpated areas. The local extinction of the common skate complex occurred by the 1970s in the Irish Sea and southern North Sea due to overfishing (Brander, 1981; Sguotti et al., 2016). These extirpated areas are amongst the most widely and intensively trawled areas in the Northeast Atlantic indicating that significant pressures remain (Eigaard et al., 2017). In the North Sea, a north–south gradient in beam trawl fishing effort occurs with most activity concentrated in the south (Couce et al., 2020). The fitness and viability of returning individuals may be compromised even with fisheries management measures in place. In the Celtic Sea, areas with low fishing activity due to the unsuitable substrate and large distance to ports act as de facto refugia for several elasmobranch species including the common skate complex (Shephard et al., 2012). Indeed, a genetically distinct population of flapper skate on Azorean seamounts appears to be isolated from populations on the European continental shelf (Bache-Jeffreys et al., 2021). The population may have been insulated from overexploitation due to the lack of a fishery for the species and early Marine Protected Area (MPA) designations (Bache-Jeffreys et al., 2021). Such refugia may be few and far between in extirpated regions, which, as a result, limit recolonization potential.

Tagging studies indicate that the known maximum travelled distance is 372 km (Bird et al., 2020). However, a significant proportion of populations demonstrate site fidelity, suggesting limited migratory behaviour (Neat et al., 2015; Wearmouth & Sims, 2009). In addition, unlike many marine teleosts with planktonic eggs and larvae, which disperse large distances, the egg cases of skates are relatively large and tend to remain on the seabed with limited dispersal (Gordon et al., 2016). Perhaps a further increase in abundance could induce greater adult dispersal from existing refugia as carrying capacities become exceeded and greater competition for resources prompts individuals to go in search of new areas to inhabit. Though, due to the apparent limited migratory behaviour of the species complex, it is difficult to predict whether it is possible for recolonization of extirpated areas in the near future without human intervention measures such as reintroduction or re-establishment of suitable habitat as steppingstones.

The effectiveness of a selected conservation measure will rely heavily on its suitability to the species in question. For example, due to the size, thick skin in females and lack of a swim bladder, large skates may exhibit lower discard mortality due to trawl capture (e.g. physical damage, abrasion, scavengers, impaired respiration and barotrauma) relative to other species, particularly teleost fish (Benoit et al., 2013; Broadhurst et al., 2006; Mandelman et al., 2013). Demersal elasmobranchs with buccal-pump ventilation, e.g. skates, tend to exhibit better discard survival than obligate ram ventilators as they are capable of stationary respiration (Ellis et al., 2017). In addition, females tend to have a higher survival rate than males due to thicker skin and often larger size (Laptikhovsky, 2004). Bendall et al. (2012) reported common skate (1234 blue skate and 8 flapper skate) discard survival rates of 92% using trammelnets and gillnets in comparison to 73% for spurdog and 20% for porbeagle using gillnets. However, discard mortality is also dependent on factors relating to the method of capture (gear, tow/soak duration, catch volume and composition, handling method and exposure time) (Ellis et al., 2017). More research is required to determine the discard mortality of the common skate species complex using different fishing methods. Any differential survivability between species or size classes would also have implications for their recovery and management.

Landing prohibitions have been utilized elsewhere and appear effective in promoting the revival of skate populations. For example, a 2009 fisheries ban for undulate ray led to increases in the target species (Elliott et al., 2020). Moreover, the barndoor skate (*Dipturus laevis*), a large species closely related to the blue skate (Bache-Jeffreys et al., 2021) occurring in the Northwest Atlantic, underwent large declines between the early 1960s and mid-1970s due to high levels of fishing mortality (Gedamke et al., 2008; Kulka et al., 2020). A landing prohibition was introduced in the United States from 2003 to 2018, which contributed to a subsequent recovery by 2012 to abundances greater than those observed in the 1960s (Kulka et al., 2020). Many skate species worldwide are vulnerable to overexploitation with 45 species classified as threatened by extinction (IUCN, 2021). Therefore, the evident success of landing prohibitions in promoting the recovery of skates is highly relevant to their conservation and should be considered where appropriate.

The observed changes to the spatio-temporal distribution of the common skate species complex would also have been highly influenced by recruitment dynamics. Little is known of recruitment rates for the species complex and only recently a flapper skate egg was incubated successfully in captivity for the first time (Benjamins et al., 2021). Further research is required in this area to gain a greater understanding of variations in annual recruitment levels and possible anthropogenic impacts. Moreover, climate change is predicted to impact skate populations in the future (Grieve et al., 2021). Bottom temperature showed low variable importance in the species distribution model. The model domain did not cover its entire distribution or more specifically the edges of its distribution, where temperature effects are likely more important. Moreover, modelling at the species complex level may confound the biological relationship with temperature exhibited by individual species. However, it is important to consider that the distribution and abundance of the common skate species complex may be influenced by climate change and the knock-on effects to oceanography.

It is also likely that predator–prey interactions have been altered from when common skates were previously abundant until now. Gut content analyses of blue skates in the Celtic Sea revealed that small and immature individuals mainly feed on shrimps and prawns while large and mature individuals become top predators in the ecosystem, feeding on teleost fish (Brown-Vuillemin et al., 2020). Declines of up to two-thirds have been reported for predatory fish species in the North Atlantic during the latter half of the 20th century (Christensen et al., 2003). Therefore, common skate may have been somewhat aided by a lack of competition for prey and lower predation on juveniles brought on by a decline in large marine predators.

The findings of the current study indicate that implementing targeted fisheries management measures can help to promote the recovery of diminished skate populations, though the recolonization of previously extirpated areas might require additional measures, if possible for such species. In order to determine the effectiveness of proposed management actions, a clear understanding of what caused the initial decline and knowledge of life-history characteristics is essential. Here, the common skate species complex likely benefited from a reduction in fishing effort and a landing prohibition preventing their retention onboard commercial fishing vessels. The efficiency of the landing prohibition may have also been enhanced by relatively high discard survival rates, suggested by skate species. The results of the present study indicate the importance of ongoing monitoring to enable evaluation of the effectiveness of management actions in achieving their intended conservation objectives.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Common skate data and R code (Appendix S1) are available in the manuscript's Supplementary Material (Appendices S2 and S3).

ORCID

Ryan McGeady https://orcid.org/0000-0001-5129-6778

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BIOSKETCH

Ryan McGeady is a researcher based in the School of Geography and Environmental Sciences in Ulster University. His research focuses on understanding the dispersal and distribution of marine species as well as developing biophysical models intended to improve sustainable fisheries management.

Author contributions: C.M.G., R.M.G. Conceptualization; S.L., R.M.G. Data curation; R.M.G. Formal analysis, Writing - first draft; C.M.G., S.L., R.M.G. Writing, review & editing.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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