Variable trends in the distribution of Atlantic cod (Gadus morhua) in the Celtic seas

Received: 31 August 2023 | Revised: 6 February 2024 | Accepted: 20 February 2024
DOI: 10.1111/jfb.15715

REGULAR ARTICLE

JOURNAL OF FISH BIOLOGY fsbi

Variable trends in the distribution of Atlantic cod (*Gadus morhua*) in the Celtic seas

Jonathan V. Ellis[1] | Pia Schuchert[2] | D. Michael Scantlebury[3] | C. Tara Marshall[1] | Paul G. Fernandes[1,4]

[1]School of Biological Sciences, University of Aberdeen, Aberdeen, UK
[2]Fisheries and Aquatic Ecosystems Branch, Agri-Food and Biosciences Institute, Belfast, UK
[3]School of Biological Sciences, Queen's University Belfast, Belfast, UK
[4]The Lyell Centre, Heriot-Watt University, Edinburgh, UK

Correspondence
Jonathan V. Ellis, 209 Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK.
Email: j.ellis.21@abdn.ac.uk

Funding information
Department of Agriculture, Environment and Rural Affairs (NI)

Abstract

Despite decades of active fisheries management, many stocks of Atlantic cod in its southern range are in a depleted state and mortality estimates remain high. Recovery of these stocks, as defined by management areas, could be confounded by cod distributions shifting outside of these areas. Here, we assess data from internationally coordinated trawl surveys to investigate the distribution of three cod stocks in the Celtic Seas ecoregion, Irish Sea, Celtic Sea, and West of Scotland, from 1985 to 2021. We mapped cod densities, analyzed trends in mean weighted depth and bottom temperature, and calculated the center of gravity and equivalent area of the stocks. The distribution of the West of Scotland stock shifted north and east, spilling into the North Sea, while the Irish Sea and Celtic Sea stocks shifted west. Each stock showed decreasing trends in equivalent area, but there were no clear trends in the average depth occupied by the fish. There was no apparent relationship between temperature and the distribution of cod, as bottom temperature varied little from 1993 to 2021. Although Irish Sea cod showed a shift into warmer water, this was due to changes in survey distribution. The shift in distribution of the West of Scotland cod stock towards the North Sea whilst impairing local recovery provides further justification for the recent definition of its incorporation into a larger stock unit that includes the northwest of the North Sea. The Irish Sea and Celtic Sea cod stocks are neither shifting northwards, nor into deeper waters, but remained within current boundaries. This suggests that recent temperature conditions did not affect their distribution, but this may change as temperatures increase towards the limit for reproduction.

KEYWORDS
Atlantic cod, Celtic seas, distribution shifts, stock decline

1 | INTRODUCTION

Atlantic cod (*Gadus morhua*) is a large gadoid fish that has had great economic and cultural importance for countries of the North Atlantic over the last few centuries (Kurlansky, 1997). As a temperate species, cod is expected to occur in water temperatures between −1.5 and 19°C, although spawning is adversely affected at temperatures above 8°C (Kjesbu et al., 2023; Righton et al., 2010). Following trends in global exploitation rates of fishes (Bell et al., 2017; Watson et al., 2013), annual landings of cod across the North Atlantic peaked in the 1960s, with up to 4 million metric tonnes, before starting to decline (Hayden et al., 2015). By the 1990s dramatic decreases in landings were observed as many important stocks across the region were driven to collapse by high exploitation (Myers et al., 1996), having lasting economic and social consequences for local fishing communities (Haedrich & Hamilton, 2000). The great northern cod stock of Canada is arguably the most famous case study of overfishing a fish stock to depletion (Myers et al., 1997), followed shortly afterwards by the demise of North Sea cod (Horwood et al., 2006). Most cod stocks in Europe remain in a depleted state even after years of great efforts to rebuild them (Sguotti et al., 2019), with the exception of those in Arctic waters, where stock biomass has remained above safe levels since 2000 (ICES, 2021a, 2022e). Northeast Artic cod had its highest recorded spawning stock biomass (SSB) of around 2.3 million tonnes in 2013, although it then declined to 1 million tonnes by 2021 (ICES, 2021a; Kjesbu et al., 2014). This is in contrast to the cod stocks at the southern limit of their range, in the North Sea and the Celtic Seas ecoregion, where rising sea temperatures are suggested to lower recruitment and cause range constrictions (Blanchard et al., 2005; Drinkwater, 2005). These stocks have failed to recover in spite of management measures to reduce exploitation rates (Fernandes & Cook, 2013).

In the Celtic Seas ecoregion there were, until recently, three stocks defined by the International Council for the Exploration of the Sea (ICES): West of Scotland (Division 6.a), Irish Sea (Division 7.a), and Celtic Sea (Divisions 7.e-k). However, from 2023 the West of Scotland is recommended to be added to the Northwestern substock in the North Sea for future assessments (ICES, 2023a). These Celtic Seas stocks have been in decline since the 1980s and have had continued low biomass and recruitment throughout the 21st century (ICES, 2022h). Cod in the West of Scotland region have shown the strongest decline: SSB was estimated at 45,000 t in 1982 and has decreased to around 5000 t since 2002; this is well below the maximum sustainable yield (MSY) reference point of 20,000 t (ICES, 2022a). Although Irish Sea cod SSB has followed the same trend, decreasing from 40,000 t in 1968 to lows of about 5000 t since 2000, it has fluctuated closer to its biomass reference point of 11,500 t (ICES, 2022b). In comparison, Celtic Sea cod SSB has shown more fluctuations, between 5000 t and 15,000 t from 1982 to 2012, and was typically at or above the biomass reference point of 5800 t until 2017, but has fallen below 2000 t since (ICES, 2022c). However, the outlook for West of Scotland cod is improved when viewed within the Northwestern North Sea substock. The ICES assessment for this newly defined stock does not show the same declining trends and aside from a decline in SSB between 2017 and 2020, the stock appears to be in recovery, with SSB above the 30,000 t biomass reference point since 2010 (ICES, 2023b).

The stock assessments on which these population estimates are based are carried out using catch data from the fishery, as well as fishery-independent data from trawl surveys. Annual trawl surveys of fish stocks are routinely conducted by scientific institutes across the Northern Hemisphere, particularly in the Northeast Atlantic (ICES, 2017b), the Mediterranean (Specicato et al., 2019), and in the waters around North America (Stauffer, 2004). Typically, the main objectives of these surveys are to collect standardized and consistent data on the relative abundance, distribution, and composition of fish communities, particularly for commercially important species, to inform the respective stock assessments (ICES, 2017b). The independence of surveys reduces the data biases inherent to fishery-dependent data, lending fish abundances derived from surveys more appropriate to examine temporal changes in species distributions (Mahé & Poulard, 2005; Oeberst, 2008; Stevenson & Lauth, 2019), species richness, and community composition (Greenstreet et al., 2012; Hiddink & Hofstede, 2008).

The shifting distribution of fish stocks presents challenges for fisheries management, particularly as they move across stock boundaries (Link et al., 2011). In the northeast Atlantic, a recent ICES workshop was tasked with describing any distributional changes of northeast Atlantic fish stocks relative to total allowable catch (TAC) areas, and to suggest drivers and implications for stock management (ICES, 2017a). Their work was summarized in Baudron et al. (2020), who examined spatial trends in 19 commercial fishes over 30 years across the northeast Atlantic surveys; for cod and other "northern" species, most significant distribution shifts were northwards but increasingly so at lower latitudes. Moreover, biomass trends between adjacent ICES areas showed evidence of seven species shifts across ICES boundaries and five across TAC boundaries.

Trends in fish distribution can be investigated with various methods (e.g., Baudron et al. 2020; ICES, 2017b). These include trends in biomass and abundance by area, spatial occurrence, and density of fish from survey trawl data. Examining spatial trends may be aided by interpolation of survey data across study areas, facilitated by geostatistics such as Kriging (Petitgas et al., 2017). In addition, a useful spatial statistic to investigate changes in fish distributions is the center of gravity of a stock, which is defined as the weighted center of fish distributions (Woillez et al., 2009). It has been widely used to study the average location of fish populations over time and is typically calculated using fish trawl survey data (Baudron et al., 2020; Nye et al., 2009; Perry et al., 2005; Punzón et al., 2016; Stevenson & Lauth, 2019). This also applies to studies of cod distributions, where it has been widely implemented (Durant et al., 2021; Guan et al., 2017; Rose et al., 2000; Storr-Paulsen et al., 2004; Tamdrari et al., 2010), particularly with cod in the North Sea (Engelhard et al., 2014; Rindorf & Lewy, 2006, 2012). Less attention has been given to the distribution of cod in the Celtic Seas ecoregion.

Here we examine the distribution of cod in the Celtic Seas ecoregion using survey data to determine if their distribution has changed over time. Any distribution shifts into northern waters may explain the low levels of abundance now seen in these stocks, which in turn might be due to changes in their environments, such as warming seas. Specifically, we aimed to determine (1) if distributions of cod have shown a consistent directional change over time, (2) how cod distributions have shifted in relation to management boundaries, (3) whether changes in distribution are related to changes in sea temperature, and (4) whether cod distributions have shifted into deeper water.

2 | MATERIALS AND METHODS

2.1 | Study areas

The areas examined in this analysis were chosen to cover the Irish Sea and its adjacent seas in the West of Scotland and the Celtic Sea (Figure 1). The waters to the West of Ireland (defined here as ICES Divisions 7.b and 7.c) were included to produce the distribution maps but excluded when calculating spatial statistics due to low numbers of cod in survey records (Table 1). ICES division 7.k was excluded from the Celtic Sea spatial statistics due to limited survey coverage (Figure 2).

2.2 | Data sources

2.2.1 | Trawl survey data

Survey data were taken from the ICES DATRAS database (ICES, 2023c). The relevant surveys recorded in DATRAS are the Northern Irish Groundfish Survey (NIGFS), the Irish Groundfish Survey (IE-IGFS), the Scottish West Coast International Bottom Trawl Survey (SWC-IBTS), and the French Southern Atlantic Bottom Trawl Survey (EVHOE). These surveys overlap both temporally and spatially in October–December and use similar fishing gear: Grande Ouverture Verticale (GOV) 36/47 or rock-hopper otter trawls (ICES, 2017a). Survey and year coverage in the West of Scotland, Irish Sea and Celtic Sea is given in Table 1.

The NIGFS series covers quarters 1 and 4 (Q1 and Q4) and data are available in DATRAS from 2005. The survey conducts hauls with a rockhopper otter trawl at 45 fixed stations in the Northern Irish Sea, and a further 12 in St George's Channel towards the Celtic Sea, which are stratified according to depth strata and seabed type (ICES, 2013). Haul durations are typically 20 min in Q1 and 60 min in Q4 but from 2016 the majority of tows are 18–20 min, with some stations retaining 60-min tows for collecting calibration data (ICES, 2023c). The SWC-IBTS mainly covers the West of Scotland region (6.a) in Q1 and Q4, and has additional coverage in the Irish Sea (1996–2006) and Celtic Sea (1990–1996). From 1985 to 2010 the surveys were conducted on fixed trawl stations using GOV 36/47 gear and from 2011 they adopted random stratified stations (ICES, 2013). Hauls were set to 60-min duration until 1998 when they were changed to 30 min (ICES, 2017b). The current IE-IGFS began in 2003 and covers all waters around Ireland from 56.5°N in the West of Scotland to 50°N in the Celtic Sea. In this procedure, hauls are set to 30 min and conducted with GOV 36/47 gear at 170 stations chosen a by a semi-random depth stratified design (ICES, 2017b). The EVHOE covers the Celtic Sea to its southern limit at 48°N and overlaps with the IE-IGFS above 50°N. The survey began in 1997 and until 2016 stations were allocated by a random stratified design; from 2017 fixed stations have been trawled, using the 2016 stations for reference (ICES, 2013, 2017b). The standard GOV 36/47 gear is used with some modifications for the survey (ICES, 2017b).

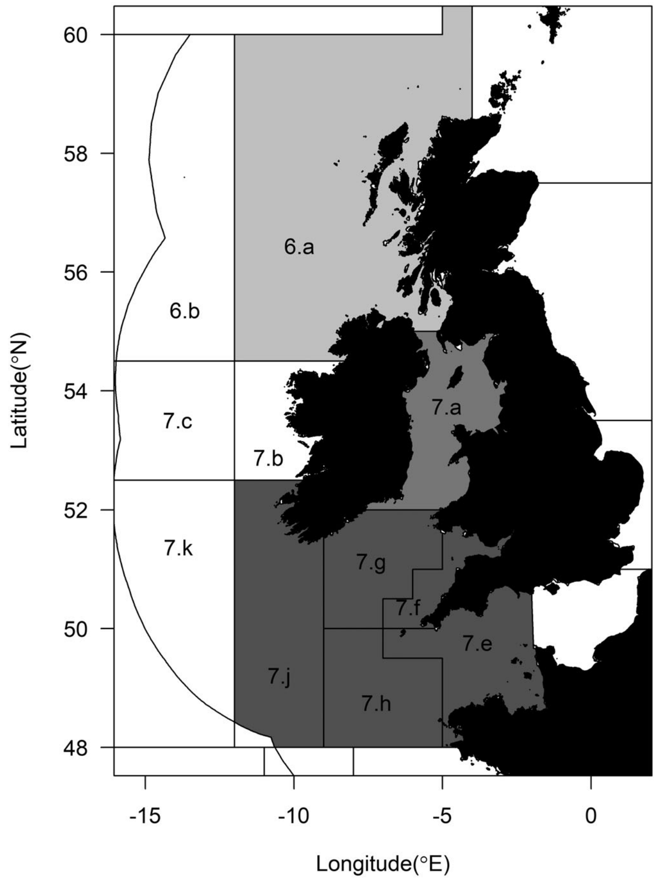

FIGURE 1 Map of northwestern Europe showing the study area of the Celtic Seas ecoregion with ICES divisions labeled. The Irish Sea is defined as ICES division 7.a. The Celtic Sea is defined here as ICES divisions 7.e-j, although 7.e and 7.f have limited survey coverage. West of Scotland is defined by ICES division 6.a.

2.2.2 | Bottom temperature data

Bottom temperature data were downloaded from the Copernicus Atlantic-European North West Shelf- Ocean Physics Reanalysis product as monthly values of seawater temperature (°C) at the sea floor. This is an ocean assimilation model (NEMO) with vertical temperatures assimilated using sea surface temperatures (SST) and subsurface temperatures from satellite and in situ sources (Tonani et al., 2022). The spatial resolution was 0.111° by 0.067° with a temporal scale of January 1, 1993 to present. The data were subset by years and converted into rasters, and mean temperatures within quarters were extracted for trawl stations. These were used to calculate mean temperatures of trawl stations per stock area and the mean weighted bottom temperature.

2.3 | Data processing

The trawl survey data were analyzed to determine the number and biomass of all cod caught in each haul, which were separated into

TABLE 1 Table detailing the survey coverage of the study area.

Sea	Quarter	Survey	Years	Number of hauls	Number of fish
West of Scotland	1	SWC-IBTS Q1	1985-	1848	8239
West of Scotland	4	SWC-IBTS Q4, IE-IGFS	1990-	2288	5923
Irish Sea	1	NIGFS Q1, IE-IGFS, SWC-IBTS Q1	1996-	999	4540
Irish Sea	4	NIGFS Q4, SWC-IBTS Q4	1997-	932	1903
Celtic Sea	4	IE-IGFS, EVHOE, SWC-IBTS Q4	1990-	3142	3324
West of Ireland	3	SP-PORC	2001-	947	75
West of Ireland	4	IE-IGFS	2003-	818	165

Note: Quarter refers to a 3-month period of the year, i.e. January–March is quarter 1.
Abbreviations: EVHOE, French Southern Atlantic Bottom Trawl Survey; IE-IGFS, Irish Groundfish Survey; NIGFS, Northern Irish Groundfish Survey; SP-PORC, Spanish Porcupine Bottom Trawl Survey; Q1, quarter 1; Q4, quarter 4; SWC-IBTS, Scottish West Coast International Bottom Trawl Survey.

adults and juveniles using length at 50% maturity. The swept area (km^2) trawled was estimated for each haul using the distance traveled per haul and the trawl wing spread. The equations for calculating trawled distance and swept area are provided in the DATRAS Procedure Document on Swept area calculation algorithms (ICES, 2022g). The swept areas were then converted into square nautical miles (Equation 1):

$$\text{swept area}\left(\text{nmi}^2\right) = \text{swept area}\left(\text{km}^2\right) \times 0.2915533496 \quad (1)$$

Cod density was then estimated from the number and biomass of fish in each haul divided by the swept area.

2.4 | Density interpolation

Analyses were conducted with the statistical programming language R (v4.3.0; R Core Team, 2023). Kriging is an interpolation method that uses a data-derived covariance or variogram model to create an interpolation function (Chilès & Delfiner, 2012). The kriging algorithm from the RGeostats library was applied to the cod densities calculated from each survey trawl station (kg/nmi^2) using a moving neighborhood (Rivoirard et al., 2000). Grids of the sampling area were created using ICES substatistical rectangles coordinates, subset to the ICES divisions covered by each year and quarter. With each run, an RGeostats prediction grid was created from a polygon of the bounding box of the grid objects maximum and minimum coordinates. The trawl data was subset for each quarter-year step and converted to a database in preparation for kriging. The database geographic projection was set to the mean latitude and a spherical variogram was applied for all runs.

2.5 | Centre of gravity analyses

Spatial statistics formulae were calculated according to Petitgas et al. (2017), which describes each statistic in detail (Table 2).

Centre of gravity (CG) analyses were carried out for the stock regions of Irish Sea, Celtic Sea, and West of Scotland for each relevant year and quarter following the framework given in Petitgas et al. (2017). RGeostats prediction grids and databases of cod density were created in the same format as for the kriging estimation with database geographic projections set to the mean latitude. Areas of influence were calculated for the trawl stations and CGs were calculated separately for adult, juvenile, and all cod densities. Additional spatial parameters calculated were inertia, total biomass, and equivalent area. Global and local indexes of collation (GICs and LICs) were calculated between juvenile and adult CGs to examine their overlap. Unweighted CGs were calculated to represent the mean trawl station position where all densities were set to 1 so that any influence of changes in survey design could be evaluated.

2.6 | Mean weighted depth and bottom temperature

Mean weighted depths and bottom temperature were calculated per year and quarter using the equation:

$$\frac{\sum n^t \times v^t}{N} \quad (2)$$

where t is a given haul (h), n^t is the number of fish in haul t, v^t is the depth (m) or bottom temperature (°C) of haul t and N is the total number of fish caught. These provide the average depth and temperature where fish are residing, weighted by their density to account for the quantity as experienced by the fish.

2.7 | Ethics statement

Ethical review and approval were not required for this study because it did not involve animal experimentation or harm. No animals were involved in the conduct of this study as the analysis was done on previously collected data on wild-caught fish that were sampled on ICES

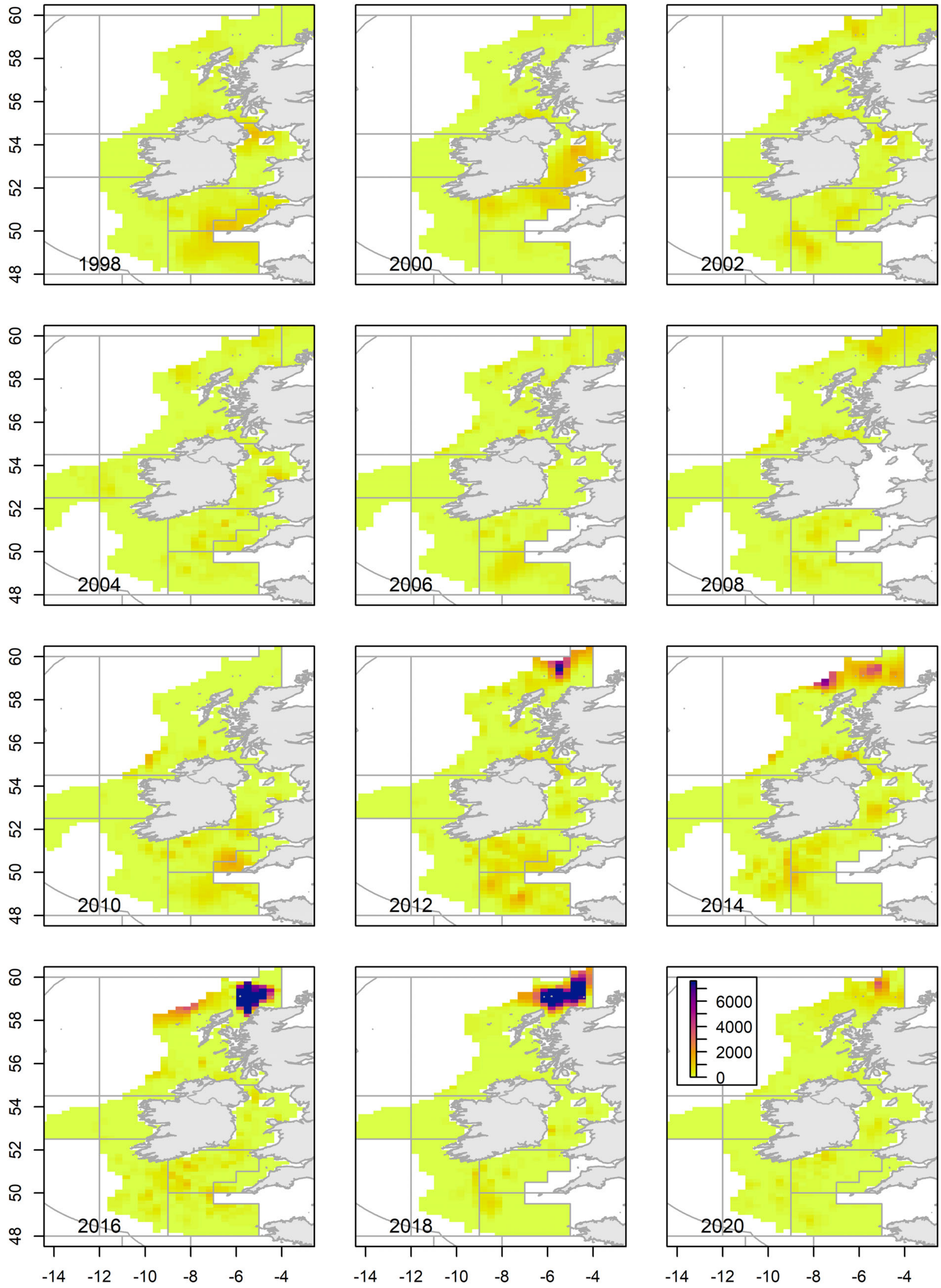

FIGURE 2 Maps of the Celtic Seas showing the interpolated cod density (kg/nmi^2) in 2-year intervals from 1997 to 2021 in quarter 4. The color scale ranges from 0 to over 5930 kg/nmi^2.

TABLE 2 Descriptions of applied spatial statistics taken from Petitgas et al. (2017)

Spatial statistic	Description
Centre of gravity	The mean position of individuals within a population. Estimated from the summation of sample values z_i, weighted by areas of influence s_i at locations x_i
Inertia	The mean square distance of an individual to the CG, i.e. the variance of the CG
Area of influence	The area surrounding a sample location that lies closer to it than other samples
Positive area	The area occupied by all non-zero fish densities, calculated from the summation of the areas of influence around the samples
Equivalent area	The area occupied by the population if all individuals were distributed with equal density, ranging from 0 to the positive area
Global Index of Collocation	A measure of the spatial overlap between two populations, estimated from their inertia and difference in CGs. It ranges from 0 (no overlap) to 1 (complete overlap)
Local Index of Collocation	The co-occurrence of observations from two populations at the same locations. It ranges from 0 to 1 from zero to complete overlap in observations

Abbreviation: CG, center of gravity.

coordinated international fishing trawl surveys, data that are freely available from the online database DATRAS (https://datras.ices.dk).

3 | RESULTS

3.1 | Cod distributions

Within the Irish Sea and Celtic Sea, cod densities decreased over time and were limited to smaller areas (Figure 2). The complete time series of maps 1985:2021 for Q1 and Q4 are given in Figures S1 and S2. High densities of cod were typically found off the southern Irish coast in the Celtic Sea (51°N, 8°W) and off the eastern Irish coast in the Irish Sea (53°N, 6°W). Aggregations of cod densities in the West of Scotland were spatially consistent in the time series but were increasingly concentrated at high densities at its northeastern boundary from 2015. The density of cod at the Irish Sea's management boundaries decreased over time, with lower densities across the Irish Sea's northern and southern borders after 2015. Cod in the Celtic Sea were increasingly separate from the Irish Sea, with higher densities drifting west to its center since 2014.

3.2 | Centers of gravity

In the West of Scotland, CGs of recent years shifted further north and east, particularly in Q1 (Figure 3). The cod CGs in the Irish Sea differed between quarters: in Q1 CGs were clustered on the Isle of Man, with the most recent CGs towards the southwest, while the CGs in Q3 and Q4 had a greater vertical spread extending below the Isle of Man, with more recent Q4 CGs in the south. The Celtic Sea CGs were centrally clustered at the boundaries of 7.g, 7.h, and 7.f, with the most recent CGs to the west. In 7.j there were five CGs further west than the remainder, which was due to uneven survey coverage of the Celtic Sea in those divisions. These points were removed when examining CG trends.

3.3 | GIC and LIC scores of adult and juvenile distributions

The GIC and LIC scores between adult and juvenile cod distributions showed no trend over time, except for Irish Sea Q4 in which LIC decreased significantly over time (linear regression, at a rate of 0.02 (±0.008) per year, $R^2 = 0.21$, $p < 0.05$, $F_{(1,18)} = 6.05$). Mean GIC scores ranged higher than LIC (Table 3), and both statistics were highest in the West of Scotland and Irish Sea Q1 and lowest in the Celtic Sea.

3.4 | CG trends over time

The West of Scotland stock significantly increased in latitude and longitude over time in both quarters (Figure 4), indicating that the distribution of cod there moved north and east, towards the North Sea. The Celtic Sea CGs significantly shifted west with a noticeable shift of 1°W occurring after 2013. CGs in the Irish Sea showed a southwestern shift, with significant decreases in longitude and latitude over time (Figure 4). The results for CG trends with adult and juvenile cod separate are presented in Figures S5–S9, showing equivalent trends to those of all cod combined described here.

The unweighted survey CGs demonstrate to what extent shifts in cod distributions were caused by changes in the distribution of trawl stations (Figure S4). These were relatively constant over time, except for some 1° deviations in the Q4 West of Scotland surveys around 1994 and 2010. The northeastern shifts in West of Scotland cod and western shifts in Irish Sea and Celtic Sea cod occurred while their unweighted lines were relatively constant. In contrast, the southern shift of Irish Sea cod follows the southern shift in the unweighted CG.

Only West of Scotland Q4 showed a relationship between time and the mean weighted depths of the center of gravity, with an increase of 0.86 m (± 0.416) per year (linear regression $R^2 = 0.126$, $F = 4.32$, $df = 1{,}30$, $p < 0.05$). The remaining areas and quarters remained at consistent mean weighted depths throughout the time series. Celtic Sea Q4 and West of Scotland Q1 had mean weighted depths around 100 m, and both Irish Sea quarters were consistently shallower, around 50 m (Figure 5). The West of Scotland shows the widest range in mean weighted depth (~60–190 m), followed by the Irish Sea (~30–100 m), with the Celtic Sea having the narrowest range (~90–120 m).

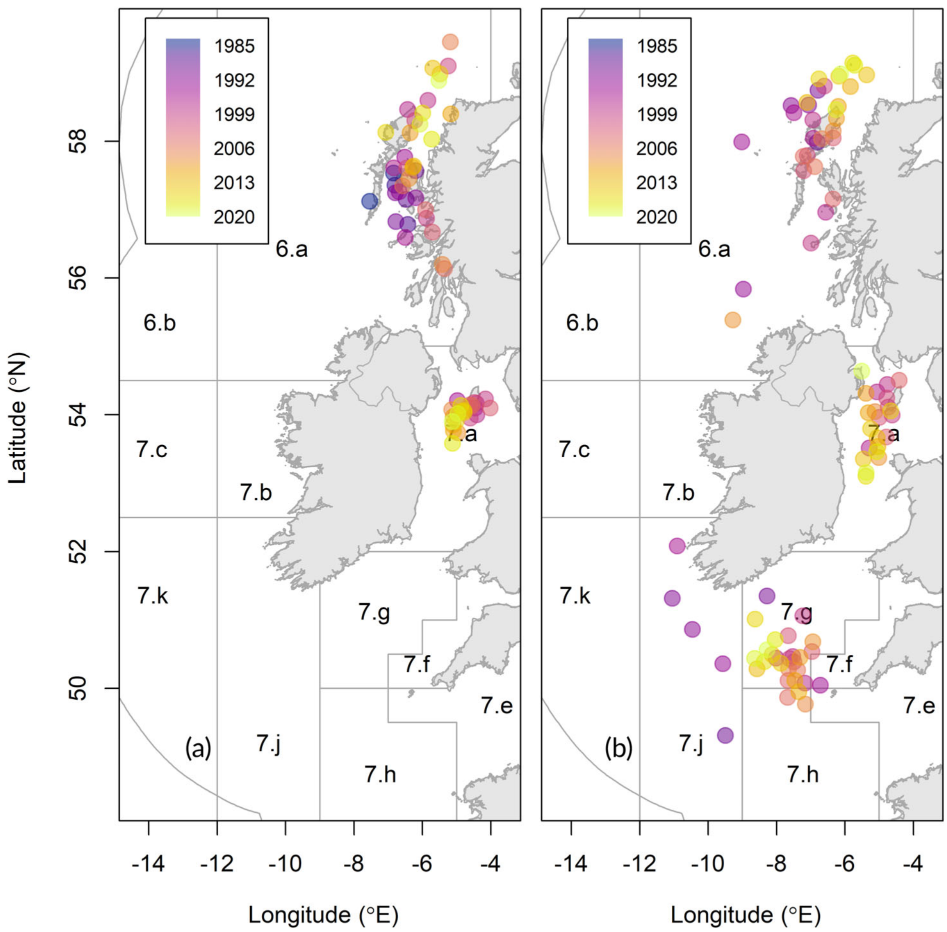

FIGURE 3 Maps of the western British Isles showing the positions of the centers of gravity as points over time for the West of Scotland (6.a), Irish Sea (7.a) and Celtic Sea (7.f-j) for quarter 1 (a) and quarter 4 (b). Points are colored according to year, from purple to yellow.

TABLE 3 Mean and standard error of Global Index of Collocation (GIC) and Local Index of Collocation (LIC) scores between adult and juvenile distributions.

Sea	Quarter	GIC	LIC
West of Scotland	1	0.82 ± 0.029	0.53 ± 0.043
	4	0.82 ± 0.024	0.40 ± 0.045
Irish Sea	1	0.86 ± 0.025	0.40 ± 0.045
	4	0.72 ± 0.049	0.34 ± 0.070
Celtic Sea	4	0.66 ± 0.037	0.25 ± 0.035

Note: Quarter refers to a 3-month period of the year, i.e. January–March is quarter 1.

Both Irish Sea quarters showed significant increases in mean weighted bottom temperature at the centers of gravity over time, increasing at a rate of 0.023°C (±0.0103°C) per year in Q1 ($R^2 = 0.173$, $F = 4.826$, $df = 1{,}23$, $p < 0.05$) and 0.022°C (±0.009°C) per year in Q4 ($R^2 = 0.218$, $F = 5.578$, $df = 1{,}20$, $p < 0.05$). This represents an increase across 1997–2021 of +0.53°C from 11.83 to 12.36°C in Q1 and +0.57°C from 7.29 to 7.86°C in Q4. In the Celtic Sea and West of Scotland there were no evident trends, ranging between 10 and 12°C in Q1 and 7–9°C in Q4 (Figure 5).

In the West of Scotland, the equivalent area of the stock significantly decreased over time in both quarters, decreasing from 17,000 to 7000 nmi^2 from 1985 to 2021 (Figure 6). There was no trend in the Celtic Sea and Irish Sea during Q1, with the long-term mean being around 1000 and 4000 nmi^2 respectively. For Irish Sea during Q4, the equivalent area decreased significantly from 4000 to 2000 nmi^2.

4 | DISCUSSION

The distribution maps and center of gravity analyses suggest that there was no clear evidence of shifts in the distribution of the Irish Sea and Celtic Sea cod stocks away from their management areas. However, the distribution of the West of Scotland cod stock moved to the northeast, with high densities occurring along the border with the North Sea stock in recent years. There appears to have been a westerly shift in Celtic Sea cod between 2013 and 2014, with subsequent years having centers of gravity and density hotpots positioned towards the boundaries of 7.g, 7.h, and 7.h (Figure 2). The Irish Sea cod stock has also shifted slightly west, but the southern shift in distribution is less convincing due to changes in the distribution of the trawl stations over time. The Irish Sea and Celtic Sea CGs typically follow the latitudes of the unweighted CGs, while their shifts west in longitude occur over relatively constant unweighted longitudes, which is evidence of a directional shift in distribution. This shows that a southern shift of Irish Sea cod is less evident but does provide support

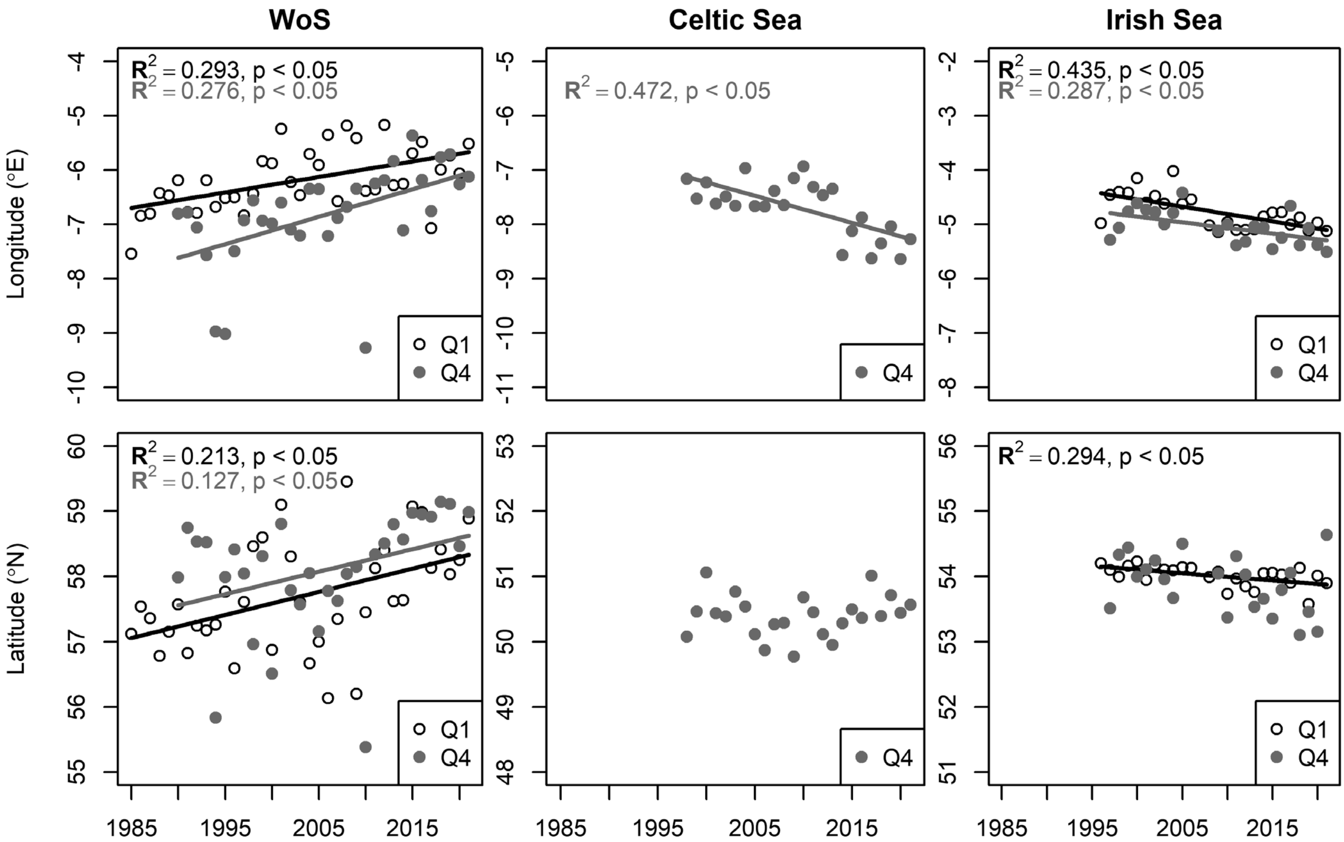

FIGURE 4 Plots showing the longitude (top) and latitude (bottom) of centers of gravity (CGs) over time for the West of Scotland (left), Celtic Sea (center), and Irish Sea (right). Points are open black circles for quarter 1 (Q1) and filled gray circles for quarter 4 (Q4). A solid line indicates a significant relationship of CG latitude/longitude ~ year.

for the western shift of both stocks within their management areas. The deviation from unweighted CGs is particularly evident in the West of Scotland CGs, which increased in latitude from 2005 while the unweighted CGs were relatively constant. This provides more confidence for the evident northeastern shift in the center of gravity of the West of Scotland cod.

The findings for the Irish Sea and West of Scotland follow the same directional trends as suggested by Baudron et al. (2020), who found northeastern shifts for cod from the SWC-IBTS, and a southwestern shift of cod from the NIGFS. However, our findings differ due to our collation of surveys for calculating indices by stock area (Irish Sea, Celtic Sea, and West of Scotland). This is comparable for the Irish Sea and West of Scotland due to the NIGFS and SWC-IBTS being relatively equivalent to our defined stock areas. For the Celtic Sea, a western shift was reported in Baudron et al. (2020) which found southwestern and southeastern shifts from the IE-IGFS and EVHOE. However, the IE-IGFS coverage extends across the west of Ireland to the west of Scotland so the trends are less comparable, although the western shift has been identified here. Our findings also differ in that we present yearly changes in CG that produce the overall trends and show to what extent CG shifts are due to shifts in survey distribution. This has allowed for an assessment of more likely distribution shifts at a finer temporal scale.

In the West of Scotland there tends to be at least two distinct hotspots of cod, one towards its southeastern boundary with the Irish Sea, and another towards its northeastern boundary with the North Sea. This reflects that there is thought to be at least two or three subpopulations of cod in the West of Scotland divided primarily into offshore and inshore groupings, with an additional Clyde subpopulation (ICES, 2021b, 2022i). The northern offshore distribution of cod has typically had higher densities than the southern onshore distribution, with the difference widening over the last 10 years as the stock distribution has shifted (Figure 2). This suggests that the change in distribution is linked to the differing population dynamics of the northern and southern ends of the West of Scotland cod distribution. Individuals may not have moved northeast, but the higher densities of northern cod have shifted the center of gravity northeast.

These high cod densities towards the northeast also suggest that the cod distribution is increasingly linked to the cod stock in the North Sea. This is supported by density maps including the northern region of the North Sea (4.a), which show that since 2008 there has been frequent spill-over of high cod densities around the 4° longitude management boundary with the West of Scotland (Figure S3). This also explains the northeastern CG shifts in the West of Scotland, as the CGs are influenced by these high-density areas around the 4° border. These results suggest that northerly cod in the West of Scotland may

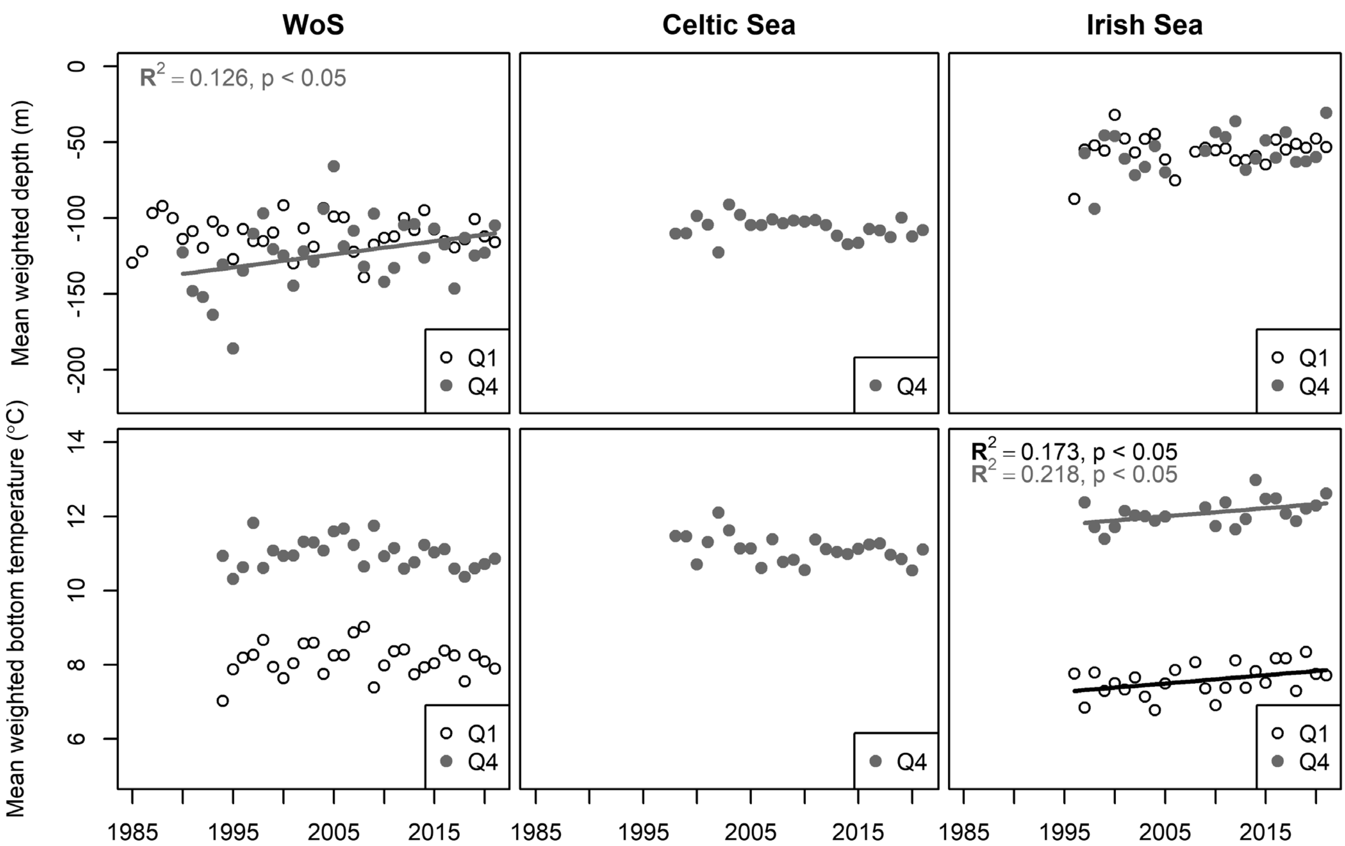

FIGURE 5 Plots showing the mean weighted depth in meters (top) and mean weighted bottom temperature in degrees Celsius (bottom) of centers of gravity over time for the West of Scotland (left), Celtic Sea (center), and Irish Sea (right). Points are open black circles for quarter 1 (Q1) and filled gray circles for quarter 4 (Q4). A solid line indicates a significant relationship of mean weighted depth/bottom temperature ~ year.

be an extension of cod in area 4.a rather than a component of 6.a. This has been considered in recent discussions on stock identity in the region and led to the recommendation to include West of Scotland cod in the North Sea assessments as of 2023 (ICES, 2023a). In addition, the inshore and offshore stocks show high genetic affinity with cod across the North Sea and are distinct to those in the Firth of Clyde, which are more closely linked to cod in the Irish Sea and Celtic Sea (Heath et al., 2014; Wright, 2012). Historic tagging data has shown movements of northern West of Scotland cod across 4° towards Shetland and Moray, and recent spatial distribution has suggested a shift of older North Sea cod to the West of Scotland (ICES, 2020; Wright et al., 2006). This genetic and telemetry evidence demonstrates that the two regions are highly connected, which further explains the northeastern shift of West of Scotland cod observed here. However, the evidence discussed here cannot not determine whether these northern cod in West of Scotland are a recovering subpopulation that has shifted northeast or has shifted westwards from the North Sea.

The distribution of cod around the border between the Irish Sea and Celtic Sea looks to have decreased over time, with the higher densities tending to be more centrally distributed within their stock areas from 2015. This suggests that the distribution of cod between the two areas is less contiguous than in previous years, which could be due to the changes in their spatial range. Although the estimated equivalent area was highly varied over time (Figure 6), the decreasing trends in the Irish Sea and West of Scotland demonstrate that the stocks are increasingly found in smaller areas. In the Celtic Sea, where the trend was not significant, the equivalent area remains noticeable lower within the last 5 years compared to the series average (Figure 6). Alongside the lack of lateral shifts in the center of gravity, these findings suggest that there is reduced mixing between the Irish Sea and Celtic Sea cod at the population level. This appears to contrast with current suggestions to merge the Irish Sea and Celtic Sea cod stocks based on their genetic similarity and tagging studies that show movement across the management boundary (Heath et al., 2014; Lundy et al., 2022; Neat et al., 2014). However, Irish Sea and Celtic Sea cod may yet be a single stock but are two subpopulations that remain connected by individuals moving between them. Further studies into the stock identity of cod in the Irish Sea and Celtic Sea will provide greater information on their connectivity.

Across the Celtic Seas, sea temperature does not always trend with latitude due to the variation in bathymetry, for example the Irish Sea is shallower and thus warmer than the more oceanic Celtic Sea. We have therefore presented the mean weighted depths of each cod stock alongside their CG latitudes. It is expected that with rising sea temperatures, cod and other demersal fish will shift towards northern

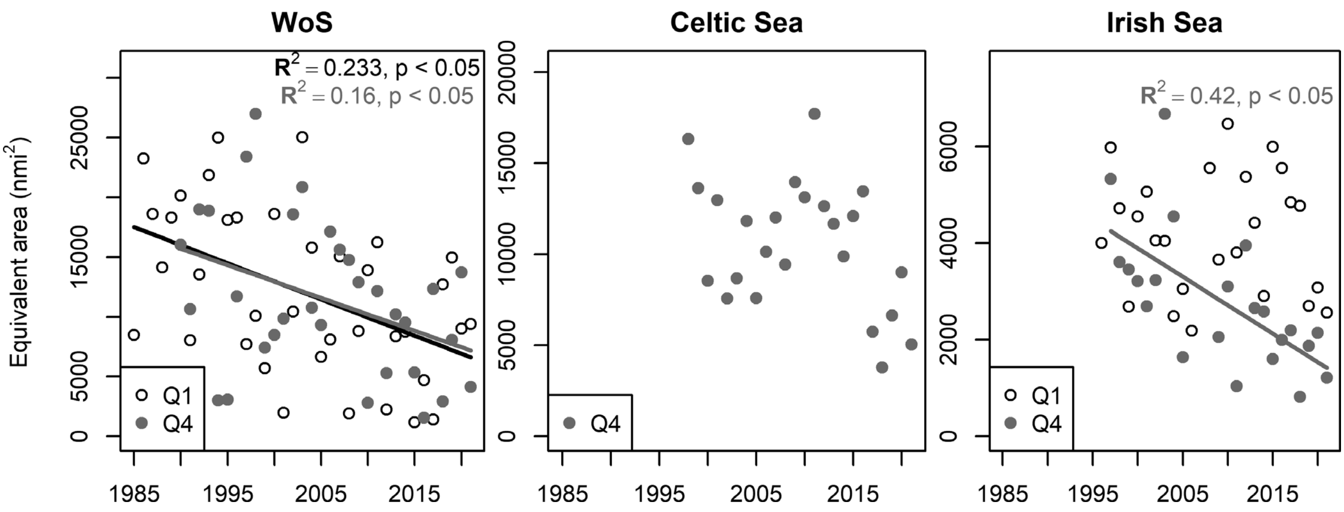

FIGURE 6 Plots showing the equivalent area (nmi^2) over time for the West of Scotland (WoS, left), Celtic Sea (center), and Irish Sea (right). Points are open black circles for quarter 1 (Q1) and filled gray circles for quarter 4 (Q4). A solid line indicates a significant relationship of equivalent area ~ year.

and deeper waters (Brander et al., 2003; Nye et al., 2009; Perry et al., 2005; Rose, 2005), as observed in the North Sea (Dulvy et al., 2008; Engelhard et al., 2014). However, this was not evident here for cod in the Celtic Seas which have not shifted into deeper waters. Although cod in the West of Scotland have shifted northwards, their mean weighted depths have decreased over time (Figure 5). If increased temperatures have influenced this distribution shift it appears that the stock has tracked residency to their preferred temperatures as their mean weighted bottom temperature has stayed consistent over the time series (Figure 5). This may also be the case for Celtic Sea cod with their western shift, which showed no changes in mean weighted depth or bottom temperature over time (Figure 5). The Irish Sea presents a different case as it showed no changes in mean weighted depth but increases in both quarters of mean weighted bottom temperature (Figure 5), which were equivalent to increases over 0.5°C from 1997 to 2021. These increases occurred while there was no trend in the mean (unweighted) temperatures at the trawl stations (Figure S10), which might indicate that cod in the Irish Sea are increasingly found in warmer waters within the stock area than the average rate of warming for the area.

However, the lack of increasing temperature trends is unsurprising given the limited change in bottom temperature seen in the Celtic Seas over the period of this study as mean annual bottom temperature in both quarters has trended lower since 2005 (Figure S11). A similar trend is evident in Ikpewe et al. (2021), which presents sea bottom temperature in the West of Scotland between 1985 and 2016, where bottom temperature increased between 1994 and 2005 but then declined until 2015. SSTs in the Celtic Seas have also trended lower since 2008 (ICES, 2022f), although mean decadal SST increased 0.1–0.25°C per decade across the region from 1982 to 2021 (Cornes et al., 2023). This demonstrates the limited scope of this study to analyze the effects of temperature on the distribution of Celtic Sea cod as sea temperature changed little over the period of the trawl surveys (1997–2021). An updated reanalysis of this dataset in future may allow for a greater exploration of temperature impacts on cod distributions as temperatures rise with climate projections (Cornes et al., 2023).

From the spatial statistics analyzed here, the patterns of cod distributions in the Celtic Seas over time do not provide further explanations for the continued decline of these stocks. The decreasing trends of the equivalent area demonstrate that their ranges are shrinking, which is in line with density-dependent spatial occupation (Atkinson et al., 1997), but this is not associated with notable outward distribution shifts. The West of Scotland cod are the exception, where the stock recovery for the area may be impaired by a distribution shift into the North Sea. Although the North Sea cod stock has not recovered either, higher biomass trends since 2010 in the northwest North Sea suggest some localized rebuilding may be occurring (ICES, 2020, 2022d). The recent high densities of cod in the northern West of Scotland and overlap across the 4° boundary demonstrates that these connected subpopulations of cod are in a better state than their southern components.

Another hindrance to the recovery of cod stocks in the Celtic Seas may be the impact of predation by seals. In the West of Scotland, predation by gray seals (*Halichoerus grypus*) is estimated to be an important component of mortality on cod (Cook et al., 2015). Dietary studies of gray seals in 2002 and 2010 estimated consumption of cod in the West of Scotland to be 8824 and 7632 t, equivalent to 77% and 181% of estimates of total stock biomass (Hammond & Wilson, 2016). Although West of Scotland gray seal population growth has been stable since the mid-1990s, with around 15,000 pups born each year (Russell et al., 2019), their predation rates on cod have been found to increase with declining cod biomass. Therefore, despite not increasing in size, the current gray seal population has likely impaired the recovery of West of Scotland following its collapse under fishing pressure (Cook & Trijoulet, 2016). However, this negative relationship between seal predation and cod biomass suggests that if cod biomass recovers from reduced fishing pressure, the impact of seal predation will be lower. Therefore, unless cod biomass continues to decline, mortalities from seal predation should not put the cod stock at further risk.

As gray seals are also common throughout Irish waters (Russell et al., 2017) and cod are prevalent in their diet across the UK (Brown et al., 2012), predation by gray seals could have similarly been impairing the recovery of Irish and Celtic Sea stocks following their collapses. However, the gray seal population in Irish waters is less than 5% of the UK population and tagged gray seals have been shown to have low spatial overlap with the offshore whitefish fishery in the Celtic Sea (Cronin et al., 2014, 2016), so their impact may be lower. Moreover, predation by gray seals and harbor seals (*Phoca vitulina vitulina*) on the southwest Celtic Sea trawl fisheries was found to have negligible impacts on the SSB of commercial fishes, including cod, compared to fishing pressure (Houle et al., 2016). Therefore, seal predation likely may have a weaker influence on the recovery of cod in the Irish Sea and Celtic Sea than in the West of Scotland.

As zero catch is advised for cod in the Celtic Seas, bycatch in mixed fisheries remains the sole fishing pressure on the stocks (ICES, 2022h). In the West of Scotland, 90% of cod landings come from finfish fisheries, with less than 1% landed by *Nephrops* fisheries, whereas in the Irish Sea the finfish and *Nephrops* fisheries contributions to cod landings are more equivalent at 33% and 37% to cod landings (, 2022a; ICES, 2022b). However, landings do not reflect true catches as the *Nephrops* fleet can discard large amounts of cod and discard estimates are very imprecise, particularly for the *Nephrops* fleet (Fernandes et al., 2011). Without reducing catch limits for mixed fisheries, cod landings are typically minimized through technical measures to improve the selectivity of fishing gear (Catchpole & Revill, 2008; Kennelly & Broadhurst, 2021; O'Neill & Mutch, 2017), although these are ineffective (EFCA, 2019) and uptake of new gear designs by fishers can be poor (Calderwood et al., 2021; Eayrs & Pol, 2019). Catch avoidance is also achieved through spatial and temporal closures of fishing grounds in the Celtic Seas (ICES, 2022h), but also through voluntary avoidance by fishers (Calderwood et al., 2021), although due to the burrowing behavior of *Nephrops norvegicus* in muddy subsrate, *Nephrops* fishing grounds are more spatially restricted so fishing options are more limited (Johnson et al., 2013). However, despite landing and bycatch reductions SSB outlooks remain poor for the Celtic Seas cod stocks, which suggests that current catches are too high to promote stock recovery.

Despite the decline of the Celtic Seas cod stocks since the 1980s, this study shows that there has been little change in their distributions that may explain this. West of Scotland cod are shifting distribution northwards, which supports the revised stock definition with northern North Sea cod. The Irish Sea and Celtic Sea cod stocks are neither shifting northwards nor into deeper waters, suggesting that they are maintaining residency within the defined stock areas. It is possible that warming is not yet limiting their distribution, but this may soon change as spawning season temperatures approach the thermal limit for reproduction (Kjesbu et al., 2023). This highlights the need for further research to understand the causes of the distribution changes described here for Celtic Seas cod. Nonetheless, it remains evident that high fishing pressure, despite restrictions, is the main factor impairing recovery of cod stocks in the Celtic Seas.

AUTHOR CONTRIBUTIONS

J.V.E.: Conceptualization, data curation, generation, and formal analysis, writing the original draft, and manuscript preparation. P.S.: Review and editing. D.M.S.: Review and editing. C.T.M.: Review and editing. P.G.F.: Conceptualization, review, and editing.

ACKNOWLEDGMENTS

This study was conducted using EU Copernicus Marine Service Information, 10.48670/moi-00059.

FUNDING INFORMATION

This research was supported by a Department of Agriculture, Environment and Rural Affairs for Northern Ireland postgraduate studentship.

ORCID

Jonathan V. Ellis https://orcid.org/0009-0006-1652-8661
C. Tara Marshall https://orcid.org/0000-0002-3671-5177
Paul G. Fernandes https://orcid.org/0000-0003-4135-115X

REFERENCES

Atkinson, D. B., Rose, G. A., Murphy, E. F., & Bishop, C. A. (1997). Distribution changes and abundance of northern cod (*Gadus morhua*), 1981 1993. *Canadian Journal of Fisheries and Aquatic Sciences*, *54*(S1), 132–138.

Baudron, A. R., Brunel, T., Blanchet, M.-A., Hidalgo, M., Chust, G., Brown, E. J., Kleisner, K. M., Millar, C., MacKenzie, B. R., Nikolioudakis, N., Fernandes, J. A., & Fernandes, P. G. (2020). Changing fish distributions challenge the effective management of European fisheries. *Ecography*, *43*(4), 494–505. https://doi.org/10.1111/ecog.04864

Bell, J. D., Watson, R. A., & Ye, Y. (2017). Global fishing capacity and fishing effort from 1950 to 2012. *Fish and Fisheries*, *18*(3), 489–505. https://doi.org/10.1111/faf.12187

Blanchard, J. L., Mills, C., Jennings, S., Fox, C. J., Rackham, B. D., Eastwood, P. D., & O'Brien, C. M. (2005). Distribution-abundance relationships for North Sea Atlantic cod (*Gadus morhua*): Observation versus theory. *Canadian Journal of Fisheries and Aquatic Sciences*, *62*(9), 2001–2009. https://doi.org/10.1139/f05-109

Brander, K., Blom, G., Borges, M., Erzini, K., Henderson, G., Mackenzie, B., Mendes, H., Santos, A. M., & Toresen, R. (2003). Changes in fish distribution in the eastern North Atlantic: Are we seeing a coherent response to changing temperature? *ICES Marine Science Symposia*, *219*, 261–270.

Brown, S. L., Bearhop, S., Harrod, C., & McDonald, R. A. (2012). A review of spatial and temporal variation in grey and common seal diet in the United Kingdom and Ireland. *Journal of the Marine Biological Association of the United Kingdom*, *92*(8), 1711–1722. https://doi.org/10.1017/S0025315411002050

Calderwood, J., Pedreschi, D., & Reid, D. G. (2021). Technical and tactical measures to reduce unwanted catches in mixed fisheries: Do the opinions of Irish fishers align with management advice? *Marine Policy*, *123*, 104290. https://doi.org/10.1016/j.marpol.2020.104290

Catchpole, T. L., & Revill, A. S. (2008). Gear technology in Nephrops trawl fisheries. *Reviews in Fish Biology and Fisheries*, *18*(1), 17–31. https://doi.org/10.1007/s11160-007-9061-y

Chilès, J.-P., & Delfiner, P. (2012). *Geostatistics: Modeling spatial uncertainty* (2nd ed.). John Wiley & Sons http://ebookcentral.proquest.com/lib/abdn/detail.action?docID=693179

Cook, R. M., Holmes, S. J., & Fryer, R. J. (2015). Grey seal predation impairs recovery of an over-exploited fish stock. *Journal of Applied Ecology*, *52*(4), 969–979. https://doi.org/10.1111/1365-2664.12439

Cook, R. M., & Trijoulet, V. (2016). The effects of grey seal predation and commercial fishing on the recovery of a depleted cod stock. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(9), 1319–1329. https://doi.org/10.1139/cjfas-2015-0423

Cornes, R. C., Tinker, J., Hermanson, L., Oltmanns, M., Hunter, W. R., Lloyd-Hartley, H., Kent, E. C., Rabe, B., & Renshaw, R. (2023). The impacts of climate change on sea temperature around the UK and Ireland [publication-report]. MCCIP. https://nora.nerc.ac.uk/id/eprint/534103/

Cronin, M., Gerritsen, H., Reid, D., & Jessopp, M. (2016). Spatial overlap of Grey seals and fisheries in Irish waters, some new insights using telemetry technology and VMS. *PLoS One*, *11*(9), e0160564. https://doi.org/10.1371/journal.pone.0160564

Cronin, M., Jessopp, M., Houle, J., & Reid, D. (2014). Fishery-seal interactions in Irish waters: Current perspectives and future research priorities. *Marine Policy*, *44*, 120–130. https://doi.org/10.1016/j.marpol.2013.08.015

Drinkwater, K. F. (2005). The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, *62*(7), 1327–1337. https://doi.org/10.1016/j.icesjms.2005.05.015

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., & Skjoldal, H. R. (2008). Climate change and deepening of the North Sea fish assemblage: A biotic indicator of warming seas. *Journal of Applied Ecology*, *45*(4), 1029–1039. https://doi.org/10.1111/j.1365-2664.2008.01488.x

Durant, J. M., Yaragina, N., & Stige, L. C. (2021). The role of spatial distribution for growth and survival of juvenile cod *Gadus morhua* in the Barents Sea. *ICES Journal of Marine Science*, *78*(8), 2700–2708. https://doi.org/10.1093/icesjms/fsab143

Eayrs, S., & Pol, M. (2019). The myth of voluntary uptake of proven fishing gear: Investigations into the challenges inspiring change in fisheries. *ICES Journal of Marine Science*, *76*(2), 392–401. https://doi.org/10.1093/icesjms/fsy178

EFCA. (2019). *Evaluation of compliance with the landing obligation North Sea demersal species 2016–2017* (p. 3). European Fisheries Control Agency https://www.efca.europa.eu/sites/default/files/atoms/files/Executive%20Summary%20NS%20LO%20Compliance%20Evaluation%20Report%202016-2017%20August%202019.pdf

Engelhard, G. H., Righton, D. A., & Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Global Change Biology*, *20*(8), 2473–2483. https://doi.org/10.1111/gcb.12513

Fernandes, P. G., & Cook, R. M. (2013). Reversal of fish stock decline in the Northeast Atlantic. *Current Biology*, *23*(15), 1432–1437. https://doi.org/10.1016/j.cub.2013.06.016

Fernandes, P. G., Coull, K., Davis, C., Clark, P., Catarino, R., Bailey, N., Fryer, R., & Pout, A. (2011). Observations of discards in the Scottish mixed demersal trawl fishery. *ICES Journal of Marine Science*, *68*(8), 1734–1742. https://doi.org/10.1093/icesjms/fsr131

Greenstreet, S. P. R., Fraser, H. M., Rogers, S. I., Trenkel, V. M., Simpson, S. D., & Pinnegar, J. K. (2012). Redundancy in metrics describing the composition, structure, and functioning of the North Sea demersal fish community. *ICES Journal of Marine Science*, *69*(1), 8–22. https://doi.org/10.1093/icesjms/fsr188

Guan, L., Chen, Y., Staples, K. W., Cao, J., & Li, B. (2017). The influence of complex structure on the spatial dynamics of Atlantic cod (*Gadus morhua*) in the Gulf of Maine. *ICES Journal of Marine Science*, *74*(9), 2379–2388. https://doi.org/10.1093/icesjms/fsx064

Haedrich, R. L., & Hamilton, L. C. (2000). The fall and future of Newfoundland's cod fishery. *Society & Natural Resources*, *13*(4), 359–372. https://doi.org/10.1080/089419200279018

Hammond, P. S., & Wilson, L. J. (2016). Grey seal diet composition and prey consumption. *Scottish Marine and Freshwater Science*, *7*(20), 1–47. https://doi.org/10.7489/1799-1

Hayden, A., Acheson, J., Kersula, M., & Wilson, J. (2015). Spatial and temporal patterns in the cod fisheries of the North Atlantic. *Conservation and Society*, *13*, 414–425. https://doi.org/10.4103/0972-4923.179878

Heath, M. R., Culling, M. A., Crozier, W. W., Fox, C. J., Gurney, W. S. C., Hutchinson, W. F., Nielsen, E. E., O'Sullivan, M., Preedy, K. F., Righton, D. A., Speirs, D. C., Taylor, M. I., Wright, P. J., & Carvalho, G. R. (2014). Combination of genetics and spatial modelling highlights the sensitivity of cod (*Gadus morhua*) population diversity in the North Sea to distributions of fishing. *ICES Journal of Marine Science*, *71*(4), 794–807. https://doi.org/10.1093/icesjms/fst185

Hiddink, J. G., & Hofstede, T. (2008). Climate induced increases in species richness of marine fishes. *Global Change Biology*, *14*(3), 453–460. https://doi.org/10.1111/j.1365-2486.2007.01518.x

Horwood, J., O'Brien, C., & Darby, C. (2006). North Sea cod recovery? *ICES Journal of Marine Science*, *63*(6), 961–968. https://doi.org/10.1016/j.icesjms.2006.05.001

Houle, J. E., de Castro, F., Cronin, M. A., Farnsworth, K. D., Gosch, M., & Reid, D. G. (2016). Effects of seal predation on a modelled marine fish community and consequences for a commercial fishery. *Journal of Applied Ecology*, *53*(1), 54–63. https://doi.org/10.1111/1365-2664.12548

ICES. (2013). Report of the Benchmark Workshop on Western Waters Roundfish (WKROUND) [Report]. ICES Expert Group Rreports (until 2018). https://doi.org/10.17895/ices.pub.5424

ICES. (2017a). Report of the Working Group on Fish Distribution Shifts (WKFISHDISH) [Report]. ICES Expert Group Rreports (until 2018). https://doi.org/10.17895/ices.pub.3798

ICES. (2017b). SISP 15—Manual of the IBTS North Eastern Atlantic Surveys [Report]. Series of ICES Survey Protocols 2012–2020. https://doi.org/10.17895/ices.pub.3519

ICES. (2020). Workshop on stock identification of North Sea Cod (WKNSCodID) [Report]. ICES Scientific Reports. https://doi.org/10.17895/ices.pub.7499

ICES. (2021a). Cod (Gadus morhua) in subareas 1 and 2 (Northeast Arctic) [Report]. ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.advice.7741

ICES. (2021b). Stock annex: Cod (*Gadus morhua*) in division 6.A (west of Scotland) [report]. ICES stock annexes. https://doi.org/10.17895/ices.pub.18622211.v2

ICES. (2022a). Cod (*Gadus morhua*) in Division 6.Aa (West of Scotland) [Report]. ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.advice.19447889.v1

ICES. (2022b). Cod (*Gadus morhua*) in Division 7.Aa (Irish Sea) [rReport]. ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.advice.19447895.v1

ICES. (2022c). Cod (*Gadus morhua*) in divisions 7.e–k (western English Channel and southern Celtic Seas) [Report]. ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.advice.19447898.v2

ICES. (2022d). Cod (*Gadus morhua*) in subarea 4, division 7.d, and subdivision 20 (North Sea, eastern English Channel, Skagerrak) [Report]. ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.advice.21406881.v1

ICES. (2022e). Cod (*Gadus morhua*) in subareas 1 and 2 north of 67° N (Norwegian Sea and Barents Sea), northern Norwegian coastal cod [Report]. ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.advice.20071997.v4

ICES. (2022f). Celtic Seas Ecoregion – Ecosystem overview. In Report of the ICES Advisory Committee, 2022. ICES Advice 2022, Section 7.1. https://doi.org/10.17895/ices.advice.21731615

ICES. (2022g). *Swept area calculation algorithms (p. 7) [DATRAS procedure document]*. ICES Data Centre - DATRAS. https://www.ices.dk/data/Documents/DATRAS/Swept_area_km2_algorithms_pdf.pdf

ICES. (2022h). Working Group for the Celtic Seas Ecoregion (WGCSE) [Report]. ICES Scientific Reports. https://doi.org/10.17895/ices.pub.19863796.v2

ICES. (2022i). Workshop on stock identification of West of Scotland Sea cod [Report]. ICES Scientific Reports. https://doi.org/10.17895/ices.pub.10031

ICES. (2023a). Benchmark workshop on Northern Shelf cod stocks (WKBCOD) [Report]. ICES Scientific Reports. https://doi.org/10.17895/ices.pub.22591423.v3

ICES. (2023b). Cod (*Gadus morhua*) in Subarea 4, divisions 6.a and 7.d, and Subdivision 20 (North Sea, West of Scotland, eastern English Channel, and Skagerrak) [Report]. ICES Advice: Recurrent Advice. https://doi.org/10.17895/ices.advice.21840765.v1

ICES. (2023c). ICES database on trawl surveys (DATRAS). https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx

Ikpewe, I. E., Baudron, A. R., Ponchon, A., & Fernandes, P. G. (2021). Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas. *Journal of Applied Ecology*, *58*(4), 847–856. https://doi.org/10.1111/1365-2664.13807

Johnson, M. P., Lordan, C., & Power, A. M. (2013). Habitat and ecology of Nephrops norvegicus. In *Advances in marine biology* (Vol. 64). Elsevier Ltd. https://doi.org/10.1016/B978-0-12-410466-2.00002-9

Kennelly, S. J., & Broadhurst, M. K. (2021). A review of bycatch reduction in demersal fish trawls. *Reviews in Fish Biology and Fisheries*, *31*(2), 289–318. https://doi.org/10.1007/s11160-021-09644-0

Kjesbu, O. S., Alix, M., Sandø, A. B., Strand, E., Wright, P. J., Johns, D. G., Thorsen, A., Marshall, C. T., Bakkeplass, K. G., Vikebø, F. B., Skuggedal Myksvoll, M., Ottersen, G., Allan, B. J. M., Fossheim, M., Stiansen, J. E., Huse, G., & Sundby, S. (2023). Latitudinally distinct stocks of Atlantic cod face fundamentally different biophysical challenges under ongoing climate change. *Fish and Fisheries*, *24*(2), 297–320. https://doi.org/10.1111/faf.12728

Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjøsæter, H., Howell, D., Ingvaldsen, R. B., Nash, R. D. M., & Skjæraasen, J. E. (2014). Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences*, *111*(9), 3478–3483. https://doi.org/10.1073/pnas.1316342111

Kurlansky, M. (1997). *Cod: A biography of the fish that changed the world*. Vintage books.

Link, J. S., Nye, J. A., & Hare, J. A. (2011). Guidelines for incorporating fish distribution shifts into a fisheries management context. *Fish and Fisheries*, *12*(4), 461–469. https://doi.org/10.1111/j.1467-2979.2010.00398.x

Lundy, M., Poppleton, V., White, J., White, E., Beggs, S., Schuchert, P., Righton, D., Griffiths, C., & Schön, P. J. (2022). *Tagging study to determine mortality sources on cod in the Irish Sea: Final report* (p. 128). European Climate Infrastructure and Environment Executive Agency https://data.europa.eu/doi/10.2926/869813.

Mahé, J. C., & Poulard, J. C. (2005). Spatial distribution and abundance trends of main elasmobranches species in the Bay of Biscay and Celtic Sea from bottom trawl surveys. Theme Session on Comparative Dynamics of Populations in the Baltic Sea and Gulf of St Lawrence Ecosystems. ICES CM 2005/N:04.

Myers, R., Hutchings, J., & Barrowman, N. (1996). Hypotheses for the decline of cod in the North Atlantic. *Marine Ecology Progress Series*, *138*, 293–308. https://doi.org/10.3354/meps138293

Myers, R. A., Hutchings, J. A., & Barrowman, N. J. (1997). Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications*, *7*(1), 91–106. https://doi.org/10.1890/1051-0761(1997)007[0091:WDFSCT]2.0.CO;2

Neat, F. C., Bendall, V., Berx, B., Wright, P. J., Ó Cuaig, M., Townhill, B., Schön, P.-J., Lee, J., & Righton, D. (2014). Movement of Atlantic cod around the British Isles: Implications for finer scale stock management. *Journal of Applied Ecology*, *51*(6), 1564–1574. https://doi.org/10.1111/1365-2664.12343

Nye, J. A., Link, J. S., Hare, J. A., & Overholtz, W. J. (2009). Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series*, *393*, 111–129. https://doi.org/10.3354/meps08220

Oeberst, R. (2008). Distribution pattern of cod and flounder in the Baltic Sea based on international coordinated trawl surveys. Theme Session on Comparative Dynamics of Populations in the Baltic Sea and Gulf of St Lawrence Ecosystems. ICES CM 2008/J:09.

O'Neill, F. G., & Mutch, K. (2017). Selectivity in trawl fishing gears. *Scottish Marine and Freshwater Science*, *8*(1), 1–85. https://doi.org/10.7489/1890-1

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science*, *308*(5730), 1912–1915. https://doi.org/10.1126/science.1111322

Petitgas, P., Woillez, M., Rivoirard, J., Renard, D., & Bez, N. (2017). Handbook of Geostatistics in R for fisheries and marine ecology. *ICES Cooperative Research Report*, *388*, 1–184. https://doi.org/10.17895/ices.pub.3717

Punzón, A., Serrano, A., Sánchez, F., Velasco, F., Preciado, I., González-Irusta, J. M., & López-López, L. (2016). Response of a temperate demersal fish community to global warming. *Journal of Marine Systems*, *161*, 1–10. https://doi.org/10.1016/j.jmarsys.2016.05.001

R Core Team. (2023). R: A language and environment for statistical computing (4.3.0) [cComputer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Righton, D. A., Andersen, K. H., Neat, F., Thorsteinsson, V., Steingrund, P., Svedäng, H., Michalsen, K., Hinrichsen, H. H., Bendall, V., Neuenfeldt, S., Wright, P., Jonsson, P., Huse, G., Van Der Kooij, J., Mosegaard, H., Hüssy, K., & Metcalfe, J. (2010). Thermal niche of Atlantic cod *Gadus morhua*: Limits, tolerance and optima. *Marine Ecology Progress Series*, *420*, 1–13. https://doi.org/10.3354/meps08889

Rindorf, A., & Lewy, P. (2006). Warm, windy winters drive cod north and homing of spawners keeps them there. *Journal of Applied Ecology*, *43*(3), 445–453. https://doi.org/10.1111/j.1365-2664.2006.01161.x

Rindorf, A., & Lewy, P. (2012). Estimating the relationship between abundance and distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(2), 382–397. https://doi.org/10.1139/f2011-153

Rivoirard, J., Simmonds, J., Foote, K. G., Fernandes, P. G., & Bez, N. (2000). *Geostatistics for Estimating Fish Abundance*. Blackwell Science Ltd.

Rose, G. A. (2005). On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science*, *62*(7), 1360–1374. https://doi.org/10.1016/j.icesjms.2005.05.007

Rose, G. A., de Young, B., Kulka, D. W., Goddard, S. V., & Fletcher, G. L. (2000). Distribution shifts and overfishing the northern cod (*Gadus morhua*): A view from the ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(3), 644–663. https://doi.org/10.1139/f00-004

Russell, D. J. F., Jones, E. L., & Morris, C. D. (2017). Updated seal usage maps: The estimated at-sea distribution of grey and harbour seals. *Scottish Marine and Freshwater Science*, *8*(25), 1–25. https://doi.org/10.7489/2027-1

Russell, D. J. F., Morris, C. D., Duck, C. D., Thompson, D., & Hiby, L. (2019). Monitoring long-term changes in UK grey seal pup production. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(S1), 24–39. https://doi.org/10.1002/aqc.3100

Sguotti, C., Otto, S. A., Frelat, R., Langbehn, T. J., Ryberg, M. P., Lindegren, M., Durant, J. M., Chr. Stenseth, N., & Möllmann, C. (2019). Catastrophic dynamics limit Atlantic cod recovery. *Proceedings of the*

Royal Society B: Biological Sciences, *286*(1898), 20182877. https://doi.org/10.1098/rspb.2018.2877

Spedicato, M. T., Massutí, E., Mérigot, B., Tserpes, G., Jadaud, A., & Relini, G. (2019). The MEDITS trawl survey specifications in an ecosystem approach to fishery management. *Scientia Marina*, *83*, 9–20.

Stauffer, G. (2004). *NOAA protocols for Groundfish bottom trawl surveys of the Nation's fishery resources* (NOAA Technical Memorandum NMFS-SPO-65 (p. 205). United States Department of Commerce.

Stevenson, D. E., & Lauth, R. R. (2019). Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species. *Polar Biology*, *42*(2), 407–421. https://doi.org/10.1007/s00300-018-2431-1

Storr-Paulsen, M., Wieland, K., Hovgård, H., & Rätz, H.-J. (2004). Stock structure of Atlantic cod (*Gadus morhua*) in West Greenland waters: Implications of transport and migration. *ICES Journal of Marine Science*, *61*(6), 972–982. https://doi.org/10.1016/j.icesjms.2004.07.021

Tamdrari, H., Castonguay, M., Brêthes, J.-C., & Duplisea, D. (2010). Density-independent and -dependent habitat selection of Atlantic cod (*Gadus morhua*) based on geostatistical aggregation curves in the northern gulf of St Lawrence. *ICES Journal of Marine Science*, *67*(8), 1676–1686. https://doi.org/10.1093/icesjms/fsq108

Tonani, M., Ascione, I., & Saulter, A. (2022). *Ocean physical and biogeochemical reanalysis: NWSHELF_MULTIYEAR_PHY_004_009 NWSHELF_-MULTIYEAR_BGC_004_01 (product user manual issue: 1.3; p. 29)*. EU Copernicus Marine Service https://catalogue.marine.copernicus.eu/documents/PUM/CMEMS-NWS-PUM-004-009-011.pdf

Watson, R. A., Cheung, W. W. L., Anticamara, J. A., Sumaila, R. U., Zeller, D., & Pauly, D. (2013). Global marine yield halved as fishing intensity redoubles. *Fish and Fisheries*, *14*(4), 493–503. https://doi.org/10.1111/j.1467-2979.2012.00483.x

Woillez, M., Rivoirard, J., & Petitgas, P. (2009). Notes on survey-based spatial indicators for monitoring fish populations. *Aquatic Living Resources*, *22*(2), 155–164. https://doi.org/10.1051/alr/2009017

Wright, P. J. (2012). Implications of population structuring to VIa cod assessment [Report]. ICES Working Documents. https://doi.org/10.17895/ices.pub.21805362.v1

Wright, P. J., Neat, F. C., Gibb, F. M., Gibb, I. M., & Thordarson, H. (2006). Evidence for metapopulation structuring in cod from the west of Scotland and North Sea. *Journal of Fish Biology*, *69*, 181–199. https://doi.org/10.1111/j.1095-8649.2006.01262.x

SUPPORTING INFORMATION

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

How to cite this article: Ellis, J. V., Schuchert, P., Scantlebury, D. M., Marshall, C. T., & Fernandes, P. G. (2024). Variable trends in the distribution of Atlantic cod (*Gadus morhua*) in the Celtic seas. *Journal of Fish Biology*, 1–14. https://doi.org/10.1111/jfb.15715