

Ecography

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**Supplementary material**

## Appendix 1

**Table A1.** List of the stocks within the study area for all species considered, with the corresponding TAC areas these stocks encompass, and whether estimates of trends on stock sizes are available for these stocks (“x” indicates availability). For each species, both ‘Stock divisions’ and ‘TAC areas’ are identified by the ICES divisions they encompass (refer to Figure 2 for the location of ICES divisions).

Common name	Scientific name	Stock divisions	Stock size trend available	TAC areas
Norway Pout	<i>Trisopterus esmarkii</i>	4, 3a	x	2a, 3a, 4 (EC waters)
				4 (Norwegian waters)
Herring	<i>Clupea harengus</i>	Skagerrak, Kattegat, western Baltic (20-24)	x	22-24
		Central Baltic (25, 29, 32)	x	25-27, 28.2, 29, 32 (EC waters)
		4, 3a, 7d	x	2a (EC waters), 4, 7d
				3a
				3a (bycatches)
				4 (north of 53°N)
				Norwegian waters south of 62°N
		6a, 7b-c		5b, 6aN, 6b (EC and international waters)
				6aS, 7bc
				6 (Clyde)
		7a (north of 52°N)	x	7a
7a (south of 52°N), 7g-h, 7j-k	x	7a		
		7e-f		
		7g,h,j,k		
Haddock	<i>Melanogrammus aeglefinus</i>	4, 6a, 20		2a, 4
				Norwegian waters south of 62°N
				5b, 6a
				3a, 22-32
		6b	x	6b, 12, 14
		7a	x	7a
7b-k	x	7b-k, 8, 9, 10, CECAF 34.1.1 (EC waters)		
Cod	<i>Gadus morhua</i>	21		Kattegat (bycatches)
		22-24	x	22-24
		25-32	x	25-32
		4, 7d, 20	x	Skagerrak
2a, 3a, 4				

				Norwegian waters south of 62°N
				7d
		6a	x	6a, 5b east of 12°W
		6b		6b, 5b west of 12°W
		7a	x	7a
		7e-k	x	7bc, 7e-k, 8, 9, 10, CECAF 34.1.1 (EC waters)
Saithe	<i>Pollachius virens</i>	4, 6, 3a	x	2a, 3a, 3bc, 4, 22-32
				Norwegian waters south of 62°N
				5b, 6, 7, 14 (EC and international waters)
Pollack	<i>Pollachius pollachius</i>	4, 3a		
		6, 7		5b, 6, 7, 14 (EC and international waters)
				7
		8, 9a		8abde
				8c
				9, 10, CECAF 34.1.1
Plaice	<i>Pleuronectes platessa</i>	21-23	x	Kattegat
		24-32		22-32
		4, 20	x	2a, 3a, 4
				Skagerrak
		7a	x	7a
		7bc		7bc
		7d	x	7de
		7e	x	
		7fg	x	7fg
		7h-k	x	7hjk
		8, 9a		8, 9, 10, CECAF 34.1.1
Whiting	<i>Merlangius merlangus</i>	3a		3a
		4, 7d	x	2a, 4
				Norwegian waters south of 62°N
		6a	x	5b, 6, 7, 14 (EC and international waters)
		6b		
		7a		7a
		7bc, 7e-k	x	7bcdefghjk
		8, 9a		8
				9, 10, CECAF 34.1.1
White anglerfish	<i>Lophius piscatorius</i>	4, 6, 3a	x	2a, 4 (EC waters)
				4 (Norwegian waters)
				5b, 6, 12, 14
		7b-k, 8ab, 8d	x	7
				8abde
		8c, 9a	x	8c, 9, 10, CECAF 34.1.1

Blue Whiting	<i>Micromesistius poutassou</i>	1-9, 12, 14	x	1, 2, 3, 4, 5, 6, 7, 8abde, 12, 14 (EC and international waters)
				2, 4 (Norwegian waters)
				8c, 9, 10, CECAF 34.1.1
Atlantic mackerel	<i>Scomber scombrus</i>	1-8, 14, 9a	x	2a, 3a, 3bc, 4, 22-32 (EC waters)
				2a, 5b, 6, 7, 8abde, 12, 14 (international waters)
				2a, 4a (Norwegian waters)
				8c, 9, 10, CECAF 34.1.1
European sprat	<i>Sprattus sprattus</i>	22-32	x	22-32
		3a	x	3a
		4	x	2a, 4 (EC waters and international waters)
		6, 7a-c, 7f-k		
		7d, 7e	x	7de
Spurdog	<i>Squalus acanthias</i>	1-10, 12, 14		1, 5, 6, 7, 8, 12, 14 (EC and international waters)
				2a, 4 (EC waters)
				3a (EC waters)
Megrin	<i>Lepidorhombus whiffiagonis</i>	7b-k, 8ab, 8d	x	7
				8abde
		8c, 9a	x	8c, 9, 10, CECAF 34.1.1
European hake	<i>Merluccius merluccius</i>	4, 6, 7, 3a, 8abd	x	2a, 4 (EC waters)
				3a, 22-32
				5b, 6, 7, 12, 14 (EC and international waters)
				8abde
		8c, 9a	x	8c, 9, 10, CECAF 34.1.1
Common sole	<i>Solea solea</i>	20-24		3a, 22-32
		4		2a, 4 (EC waters)
		7a		7a
		7bc		7bc
		7d		7d
		7e		7e
		7fg		7fg
		7h-k		7hjk
		8ab		8ab
		8c, 9a		8cde, 9, 10, CECAF 34.1.1
Black anglerfish	<i>Lophius budegassa</i>	4, 6, 3a	x	2a, 4 (EC waters)
				4 (Norwegian waters)
				5b, 6, 12, 14
		7b-k, 8ab, 8d	x	7
				8abde
8c, 9a	x	8c, 9, 10, CECAF 34.1.1		

Horse Mackerel	<i>Trachurus trachurus</i>	8, 2a, 4a, 5b, 6a, 7a-c,e-k	x	2a, 4a, 5b, 6, 7a-c, 7e-k, 8abde, 12, 14
				8c
		3a, 4bc, 7d		4bc, 7d
		9a	x	9
European anchovy	<i>Engraulis encrasicolus</i>	8	x	8
		9a	x	9, 10, CECAF 34.1.1

**Table A2.** Summary of the bottom trawl survey data.

Species sampled	Division	Survey number	Survey name	Gear	Quarter	Start year	Notes
Anchovy, Black anglerfish, Blue Whiting, Cod, Haddock, Hake, Hake, Herring, Horse Mackerel, Mackerel, Norway Pout, Pollack, Saithe, Spurdog, Sprat, White anglerfish, Whiting	3.a	2341	NS-IBTS	GOV	1, 3	1979, 1991	
	3.b, c	2826	BITS	TVS	1, 4	1996, 1999	
	3.d	2826	BITS	TVS	1, 4	1999	
	4.a	2341	NS-IBTS	GOV	1, 3	1971, 1991	
	4.b	2341	NS-IBTS	GOV	1, 3	1967, 1991	
	4.c	2341	NS-IBTS	GOV	1, 3	1978, 1991	
	6.a	2701	SWC-IBTS	GOV	1, 4	1985, 1990	
	6.b	3473	ROCKALL	GOV	3	1999	Data from some years missing
	7.a	4784	NIGFS	ROR	4	2009	
	7.b	3520	IE-IGFS	GOV	4	2003	
	7.c	3322	SP-PORC	PORB	3	2001	
	7.d	3497	FR-CGFS	GOV	4	1988	
	7.e	3417	BTS	BT4S	3	2006	
	7.f	3488	BTS-VIIa	BT4A	3	1993	Beam trawl survey - not optimal
	7.g	3024	EVHOE	GOV	4	1997	
	7.h	3024	EVHOE	GOV	4	1997	
	7.j	3024	EVHOE	GOV	4	1997	
	7.k	3322	SP-PORC	PORB	3	2001	
	8.a	3024	EVHOE	GOV	4	1997	
	8.b	3024	EVHOE	GOV	4	1997	
	8.c	3321	SP-NORTH	BAK	4	2001	
	8.d	3024	EVHOE	GOV	4	1997	
	9.a	3320	PT-IBTS	BAK	1, 4	1996, 2003	Data from some years missing

**Table A3.** Summary of the beam trawl survey data.

Species sampled	Division	Survey number	Survey name	Gear	Quarter	Start year	Notes
Megrin, Plaice, Sole	3.a	2341	NS-IBTS	GOV	1, 3	1979, 1991	
	3.b, c	2826	BITS	TVS	1, 4	1996, 1999	
	3.d	2826	BITS	TVS	1, 4	1999	
	4.a	3417	BTS	BT8	3	1998	
	4.b	3417	BTS	BT8	3	1987	
	4.c	3417	BTS	BT8	3	1987	
	6.a	2701	SWC-IBTS	GOV	1, 4	1985, 1990	
	6.b	3473	ROCKALL	GOV	3	1999	Data from the years 2000,2004, and 2010 missing
	7.a	3488	BTS-VIIa	BT4A	3	1993	
	7.b	3520	IE-IGFS	GOV	4	2003	
	7.c	3322	SP-PORC	PORB	3	2001	
	7.d	3417	BTS	BT4A	3	1990	
	7.e	3417	BTS	BT4P	3	2006	
	7.f	3488	BTS-VIIa	BT4A	3	1993	
	7.g	3488	BTS-VIIa	BT4A	3	1993	
	7.h	3024	EVHOE	GOV	4	1997	
	7.j	3024	EVHOE	GOV	4	1997	
	7.k	3322	SP-PORC	PORB	3	2001	
	8.a	3024	EVHOE	GOV	4	1997	
	8.b	3024	EVHOE	GOV	4	1997	
	8.c	3321	SP- NORTH	BAK	4	2001	
	8.d	3024	EVHOE	GOV	4	1997	
	9.a	3320	PT-IBTS	BAK	1, 4	1996, 2003	Data from some years missing









**Figure A2.** Trends in adjacent ICES divisions of log biomass and of their log ratio. The first two columns show trends in log biomass within the division specified, the third column 'ratio' shows the log ratio of 'from' column to the 'to' column. Significance was assessed by bootstrapping and 100 realisations shown. Slopes were computed by Mann Kendall tests, P-values are shown in the top left corner of the log ratio plots.

## Appendix 2 – Material and methods (extended)

### *Data*

Data from scientific surveys were available for 19 commercial fish species encompassing 73 stocks occurring in 21 ICES divisions spanning the northeast Atlantic continental shelf (Table 1 and S1, Fig. 1a). In the northern part of the study area (e.g., the North Sea), data time series were available from as early as the late 1960s, while in the southern part (e.g., the Bay of Biscay) most time series started in the late 1990s (Tables S2 and S3). ICES divisions are spatial fisheries management units of various shapes and sizes, and those considered here fall within ICES sub-areas 3 (Baltic), 4 (North Sea), 6 (West of Scotland), 7 (Celtic Seas), 8 (Biscay) and 9 (Portuguese Coast). The sub areas are disaggregated further into ICES statistical rectangles which are standard spatial units of 1° longitude by 0.5° latitude used for the reporting of fisheries landings. Each year, countries with fisheries established within ICES sub-areas carry out bottom trawl and beam trawl surveys designed to sample, with the same protocols, a defined grid of ICES statistical rectangles to gather information about species abundances (Fig. 2b). Survey data for the bottom and beam trawl surveys covering ICES divisions of the northeast Atlantic shelf and Baltic Sea (Fig. 2c and 2d) were obtained from the ICES DATRAS database (<http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx>).

Due to differences in protocol (i.e., design, timing, gear used), data from different surveys are not directly comparable and cannot be merged to provide an overall map of the distribution of abundances for the species considered. However, presence-absence information is less likely to be affected by differences in survey protocols and can depict species' spatial occurrence by combining surveys. In addition, each survey is internally consistent, and therefore can be used to quantify changes in distribution of abundances within the surveyed area or describe abundance trends which can then be compared between different survey areas. Due to this limitation, the three following methods were adopted to describe changes in fish stock distribution.

### *Detecting changes in spatial occurrence*

Changes in species' spatial occurrence were investigated by assessing a species' presence-absence in each statistical rectangle from scientific surveys. Only data spanning 1985-2015 were considered as this period includes data for the bulk of the bottom and beam trawl surveys, at least in northern parts of the study area (Tables S2 and S3), thus allowing comparison of changes in spatial occurrence across areas on a similar time range. When a rectangle overlapped several ICES divisions, it was allocated to the division in which most of the area of the rectangle was contained. The response variable considered was the presence/absence of a given species within a specific rectangle in a given year. The spatial coverage of the data can vary between quarters of the year depending on the survey. To avoid discrepancies between surveys within the same ICES division, only the survey with the longest time series was used (Tables S2 and S3). In addition, Quarter 2 (i.e., second trimester) data were excluded from this analysis since Quarter 2 had not been sampled in recent years in any ICES division. Due to the varying spatial coverage of the trawl surveys in each ICES division over time, the percent occurrence of species in each ICES division was calculated in order to correct for bias in survey coverage. For example, if ten rectangles were sampled, and a species was present in all ten rectangles that year, then the occurrence was 100%. For each species, temporal trends in occurrence in each ICES division were tested for significance using the Mann-Kendall non-parametric tests for monotonic trends (Mann 1945). Results were displayed in a table with ICES divisions ordered by latitude at their centre of distribution (calculated as the median between minimum and maximum latitude) for each species ordered by

decreasing latitude (calculated with data from Whitehead *et al.* (1989)). When significant trends in spatial occurrence were observed, both the direction and level of significance of the trend were indicated in the corresponding cells in the table.

### *Changes in species centre of gravity in individual surveys*

The centre of gravity (CoG) of a species is defined as the biomass-weighted mean latitude and longitude, and is used to track temporal changes in species distributions (Petitgas *et al.* 2017). Here, changes in the CoG of species' distributions within an area covered by individual surveys were investigated based on prediction from a spatial model of species abundances. First, the numbers-at-length caught were converted to weight by modelling individual weight as proportional to individual length raised to some power with log-normal variability (Coull *et al.* 1989). The slope and the power parameters were allowed to vary by year in both a persistent way and with random fluctuations. This resulted in the following log-linear random effects model (Eq. 1) that was fitted to all available observations of length and weight, assuming normal errors:

$$\log(\text{weight}) \sim \log(\text{length}) : (1 + s(\text{year}) + \text{re}(\text{year})) + 1 + s(\text{year}) + \text{re}(\text{year}) \quad (1)$$

where 1 specifies an intercept term,  $\text{re}(\text{year})$  is a random effect for each year, and  $s(\text{year})$  is a smooth trend modelled as a thin plate regression spline. Since the model was being fitted to a large number of cases, the maximum degrees of freedom for the thin plate spline was chosen as exactly half of the number of years in the time series, and in cases where there were more than 18 years, the maximum degrees of freedom was restricted to 9, in order to improve model identifiability. This model allowed for both a different length-weight relationship each year and for trends over time, while also predicting length-weight relationships for unsampled years. Equation (1) was applied to length measurements for each haul and species to estimate the species' total catch weight per haul, which was then divided by the haul duration to obtain a catch weight per unit of effort (CPUE) per haul for each species.

Secondly, spatial smoothers were applied to the CPUEs per haul in order to estimate abundance indices in each ICES statistical rectangle for each species and year. Abundance indices in each statistical rectangle were calculated separately for each survey as follows:

$$\log(\text{CPUE}) \sim \text{gmrf}(\text{statistical rectangle}) \quad (2)$$

where CPUE is modelled using gamma errors with a log link, and  $\text{gmrf}()$  is a Gaussian Markov random field (GMRF) spatial smoother in which neighbouring statistical rectangles are penalised for being similar to each other via a first order random walk on a lattice (Rue and Held 2005). The benefit of using a GMRF smoother is that it can be parameterized to not smooth over land masses, unlike a standard two dimensional smoother (Wood *et al.* 2008).

Finally, for each species, time series of the coordinates of the CoG for each survey were calculated from the spatial model described above (Eq. 2) fitted to each year and survey. The CoG was computed using the average coordinates of the centre of each statistical rectangle covered by the survey, weighted by abundance indices. Additionally, 95% confidence intervals were computed using the simple percentile method (Davidson and Hinkley 1997). Results were displayed as arrows depicting the direction and extent of change in CoG, and arranged in a table with surveys ordered by latitude at their centre (calculated as the median between minimum and maximum latitude) and species ordered by decreasing latitude at their centre of distribution (as done in the presence-absence analysis).

### *Comparison of biomass trends across TAC areas*

Comparison of biomass trends between adjacent ICES divisions and adjacent TAC areas were conducted in order to assess directional shifts in relative distribution. For each year, indices of biomass, calculated using the method described above and summed across each ICES division (Eq. 2), were compared for each pair of adjacent divisions. The ratio of these indices for neighbouring divisions was then calculated for each year, and trends in the ratios were inspected and used to describe changes in distribution. For example, a positive temporal trend in biomass ratio between ICES divisions A and B indicates either (i) biomass increasing in A while decreasing in B, (ii) biomass increasing in A faster than in B, (iii) or biomass decreasing in A slower than in B (and vice-versa for a negative trend). In any case, such a trend indicates a change in distribution (not necessarily involving a physical movement of fish) with an increased concentration of biomass in area A relative to area B over time.

The significance of the temporal trend in biomass ratio between two adjacent ICES divisions was tested using a stochastic approach. First, the model described in equation 2, which is a two-dimensional random walk on a lattice of statistical squares, was fitted to the data. Secondly, the estimates from the model were parametrically bootstrapped to perform 100,000 simulations and obtain 100,000 realisations of the spatial distribution of the biomass for each year. Thirdly, the biomass indices were calculated for each year for both ICES divisions and the corresponding ratios were computed to obtain 100,000 realisations of the biomass ratios time series. Lastly, Mann-Kendall tests were performed for each simulation. The results were used to test for the presence of a significant monotonic trend in the log ratios. Trends were assessed over the time period covered by both surveys for each pair of ICES divisions (Fig. S2). The trend was considered significant if the median significance level was less than 0.05.

Finally, when significant changes in distribution between adjacent ICES divisions were identified, these were compared to the TAC areas defined for the corresponding species (Table S1) to assess whether changes in relative distribution also occurred across TAC areas. The observed significant changes in relative biomass between adjacent ICES divisions and TAC areas were listed in a summary table.

### *Cross-species synthesis*

In order to investigate patterns across the species-specific analyses of changes in distribution described above, a synthesis was done to assess whether the possible impacts of warming-induced changes in suitable habitat, and density-dependent habitat selection on distribution, could be detected across commercial fish species of the northeast Atlantic. For each species, this was done by relating the changes in spatial occurrence observed from the presence-absence analysis in each ICES division to the position of the corresponding ICES division relative to the species' biogeographical range, and to the temporal trend in stock biomass, respectively.

First, for each species, an index of latitudinal position within the species biogeographical range was estimated for each ICES division using the approach developed by Brunel and Boucher (2006) as follows:

$$Pos_{sp,div} = (lat_{div} - lat_{centre,sp}) / 0.5 * (lat_{north,sp} - lat_{south,sp}) \quad (3)$$

where, for a given species,  $lat_{div}$  is the latitude of the centre of the ICES division  $div$ ,  $lat_{centre,sp}$  is the latitude of the centre of the distribution range of species  $sp$ , defined by the mean latitude of the northern and southern boundaries,  $lat_{north,sp}$  and  $lat_{south,sp}$  respectively. The latitudes of species' ranges were obtained from Whitehead et al. (1989).  $Pos_{sp,div}$  values vary between -1 and 1 for divisions located at the southern and northern boundaries of the species range, respectively, while divisions located in the middle of the range will have a 0 value. All the observations for a given species in a given ICES division were then classified into bins of value of  $Pos$  ranging from -1 to +1 by increments of 0.25. Then, the proportions of increase, no change, and decrease in spatial occurrences were calculated for each bin.

Secondly, stock assessment outputs were extracted from the ICES database (<http://standardgraphs.ices.dk/stockList.aspx>) for all 19 species covered by the survey data. Estimates of temporal trends in stock sizes, either from stock assessments or survey indices, were available for 39 of the 73 stocks covered by the survey data (Table S1). Mann-Kendall tests were carried out to test for the existence of a monotonous trend in spawning stock biomass (SSB). The stocks were then classified as decreasing, stable, or increasing SSB trends and for each category, the proportion of observations of increase, no change, and decreases in spatial occurrences were calculated.

All models were fitted in R using the Generalised Additive Model (GAM) function from the 'mgcv' package. Code and data employed can be accessed at: <https://github.com/ices-eg/WKFISHDISH>.

### **Appendix 3 – Using trawl survey data to assess distribution changes: shortcomings and considerations**

A primary concern when using data from different trawl surveys to assess distribution changes is the lack of consistency between sampling protocols and survey designs (Blanchard et al., 2007). Although efforts are being made to standardise trawl survey sampling across EU waters (ICES 2019a), many surveys are conducted in different quarters, using slightly different gears, etc. (ICES 2012). Therefore, abundance estimates cannot be directly compared between surveys. This can hinder investigations of distribution changes when considering a large area sampled by several surveys such as the northeast Atlantic shelf. To circumvent this shortcoming, we followed the recommendations of Blanchard et al. (2007) and linked both presence-absence data and abundance estimates in a three-tier analytical approach to investigate: (i) changes in spatial occurrence, (ii) changes in centre of gravity, and (iii) biomass trends across adjacent ICES divisions. Method (i) is based on presence-absence observations and indicates whether or not a species is observed in a given area (in our case, a statistical rectangle) regardless of its abundance. As such presence-absence is less likely to be affected by differences in survey protocols, and the spatial occurrence (the number of statistical rectangles occupied in each survey area) can be compared between surveys to assess overall changes in distribution area (e.g., expansion or contraction) within our study area. This method (i.e., measuring occurrence rather than abundance) has been applied successfully to assess distribution changes of several pelagic species across the northeast Atlantic (Montero-Serra et al. 2015). In contrast, methods (ii) and (iii) rely on the fact that, within each survey area, sampling is homogenous and consistent through time. In both cases abundance estimates were used to assess: changes in density-weighted mean location (i.e., centre of gravity) with approach (ii), and relative changes in biomass between adjacent ICES divisions with approach (iii). All three methods produced coherent results consistent with the existing literature.

Another shortcoming of using trawl survey data across the northeast Atlantic shelf is the lack of consistent temporal coverage across surveys as shown in Tables S2 and S3. Many surveys contain less or no data prior to 2000, especially in southern areas. This decreases the ability to detect long-term trends in distribution changes in these southern areas, as suggested in previous studies (Punzón et al. 2016), and incidentally may increase the chance of identifying spurious short-term trends. This may explain why, in southern areas, fewer significant observations were made with all three methods employed in the three-tier approach. Such shortcoming could lead to conclusions being driven predominantly by patterns observed in the data-rich northern areas, while patterns occurring in southern areas may go unnoticed or underrepresented. To limit the risk of biased conclusions, only data spanning 1985-2015 was used in the presence-absence analysis conducted across the northeast Atlantic shelf as this time period includes data for most surveys (at least in the more data-rich northern parts of the study area, see Tables S2 and S3), even though data were available from as early as the late 1960s for one survey (NS-IBTS in the North Sea). This allowed comparisons of changes in spatial occurrence across areas on a similar time range (Fig. 2 and Table S4). In addition, the presence-absence analysis was repeated over the 2000-2015 period where data was available for all surveys in both northern and southern areas, in order to assess whether shorter time series would affect our perception of changes in spatial occurrence (see Table S5). Both time periods yielded similar trends overall (see Tables S4 and S5), although the 2000-2015 period resulted in fewer and weaker significant trends in spatial occurrence owing to the shorter data time series.

A common concern when using trawl survey data is the poor survey catchability for some species or length classes. The bottom and beam trawl surveys used in this analysis are by design more suited to catching demersal and benthic species found close to or on the sea floor, compared to pelagic species,



which inhabit the water column. In our case, these pelagic species are herring, blue whiting, mackerel, sprat, horse mackerel and anchovy (six of the 19 species investigated, see Table 1). Data from bottom and beam trawl surveys may not, as a result, provide reliable abundance estimates for these pelagic species, resulting in data from egg surveys being preferred to trawl survey data as a fishery-independent abundance estimates (ICES 2019a). While bottom and beam trawl surveys may not provide reliable abundance estimates for pelagic species, they can still produce information on pelagic species occurrence, if the sampling is consistent through time, as evidenced by Monterro-Serra et al. (2015). In fact, data from bottom trawl surveys are being increasingly used to investigate changes in pelagic species distribution (Beare et al. 2004, Petitgas et al. 2012, Alheit et al. 2012, Jansen et al. 2012). Furthermore, in the case of mackerel it has been shown that bottom trawl surveys can provide reliable abundance estimates in line with those from acoustic surveys (Jansen et al. 2015).

Another potential issue related to survey catchability is the ontogenetic decline in survey catchability of deep water species. For most fish species, ontogenetic deepening results in fish relocating to deeper waters as they grow larger (Baudron et al. 2019). Notwithstanding this, for most species considered in our study the surveys employed have been recognised as providing good indicators of year class strength for adults, and as a results are used in numerous stock assessments as tuning indices (ICES 2019b). However, for species occupying the deep waters off the shelf edge, in our case hake and anglerfish, this can result in large adults moving beyond the survey depth range, thereby being ineffectively sampled by trawl surveys (Fraser et al. 2007, Mahevas et al. 2011). This can then lead to the observed abundances being driven mainly by young individuals which can have different distribution patterns than adults (Sánchez and Gil 2000, Punzón et al. 2016). Nevertheless, although the survey catchability of large adults may be reduced for deep water species, trawl surveys do catch adults (Fraser et al. 2007, ICES 2019c), even though it is a lower proportion than juveniles. In addition, in the case of anglerfish, data from the EVHOE and IGFS surveys which are used in this study has been shown to very consistently track cohorts of young ages (ICES 2019c). Given that each survey operates with a consistent sampling protocol every year, survey data should still allow the assessment of directional distributional changes through time. However, in the absence of reliable data for large adults, caution should still be applied when interpreting the results, as it cannot be discounted that large adults may experience different distribution changes than juveniles, particularly if they encounter different environmental conditions at greater depths.

Lastly, a common limitation of trawl survey data when assessing distribution changes is that surveys rarely encompass species' entire distribution ranges, especially for benthic or demersal species (Thorson et al. 2013). This can prevent identifying the true nature of species' distribution changes, such as misinterpreting a shift as either a contraction or an expansion of a species' distribution range if the area surveyed only covers the boundary of the species' range. Here we circumvented this shortcoming to some extent through the use of our three-tier approach. First, the presence-absence analysis allowed assessing changes in spatial occurrence across the whole northeast Atlantic shelf. While this study area only encompassed the southern part of the distribution of subboreal species (such as cod and haddock) and the northern part of the distribution of subtropical species (such as anchovy and horse mackerel), it did cover a large part of the distribution range of temperate species (such as mackerel and hake). Secondly, the centre of gravity analysis provided indications of changes in the density-weighted mean location of species within each survey area. The advantage of this metric is that, even if the data only covers part of a species range, an observed shift in the centre of gravity of a species, if it is gradual through time, is likely to represent an actual shift (Woillez et al. 2009). Of course, this does not preclude the fact that conclusions can only be drawn upon what is observed within the study area, and one should be careful when speculating about what may or may not occur outside this area.

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