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Changing fish distributions challenge the effective management of European fisheries

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Ecography
42: 1–12, 2020
doi: 10.1111/ecog.04864

Subject Editor: Gretta Pecl
Editor-in-Chief:
Jens-Christian Svenning
Accepted 29 November 2019

Changes in fish distribution are being observed across the globe. In Europe's Common Fisheries Policy, the share of the catch of each fish stock is split among management areas using a fixed allocation key known as 'Relative Stability': in each management area, member states get the same proportion of the total catch each year. That proportion is largely based on catches made by those member states in the 1970s. Changes in distribution can, therefore, result in a mismatch between quota shares and regional abundances within management areas, with potential repercussions for the status of fish stocks and the fisheries that depend on them. Assessing distribution changes is crucial to ensure adequate management and sustainable exploitation of our fish resources. We analysed scientific survey data using a three-tiered analytical approach to provide, for the first time, an overview of changes in distribution for 19 northeast Atlantic fish species encompassing 73 commercial stocks over 30 yr. All species have experienced changes in distribution, five of which did so across management areas. A cross-species analysis suggested that shifts in areas of suitable thermal habitat, and density-dependent use of these areas, are at least partly responsible for the observed changes. These findings challenge the current use of relative stability to allocate quotas.

Keywords: density-dependence, fish distribution, fisheries management, relative stability, suitable habitat, warming seas

Introduction

The abundance of commercial fish can vary significantly in time and space, thus requiring regular monitoring and effective management to ensure sustainable exploitation. Lately, changes in distribution have been reported for many commercial fish species across the globe (Booth et al. 2011, Pinsky et al. 2013, Hughes et al. 2014). Many

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of these changes are poleward and are attributed to warming (Parmesan and Yohe 2003, Perry et al. 2005, Poloczanska et al. 2013). In the last 30 yr, sea temperatures have risen throughout the northeast Atlantic shelf where most of the northern European fisheries operate (González-Pola et al. 2018). Widespread warming is likely to have affected the location and extent of the areas of suitable habitat for commercial fish species. In the northern hemisphere these areas will either: 1) expand, for a population located at the northern boundary of a species' thermal range; 2) contract, for a population located at the southern boundary of a species' thermal range; with the co-occurrence of 1) and 2), resulting in a poleward shift of the overall species distribution (Poloczanska et al. 2016).

Within areas of suitable habitat, fish spatial occupancy is usually related to abundance: at low abundance, a species occupies areas corresponding to the most favourable habitat, and if abundance increases, the species expands its distribution to less suitable habitats with lower abundance of conspecifics (MacCall 1990). Thus, in the absence of mitigating factors such as species interactions, fish distribution tends to expand and contract as abundance increases and decreases (Bartolino et al. 2011). Fishing, alongside changes in environmental conditions that affect recruitment and productivity, is one of the main factors impacting the abundance of commercial fish species (Pauly et al. 2002). European fish stocks endured a period of high unsustainable fishing mortality throughout the second half of the 20th century (Hutchings 2000). The 2002 reform of the Common Fisheries Policy (CFP) led to an overall reduction in fishing mortality so that most stocks under European management are now exploited sustainably (Fernandes and Cook 2013) or showing signs of recovery (Fernandes et al. 2017), albeit with some recent high profile exceptions (e.g. North Sea cod). Akin to warming, stock recovery and the subsequent increase in abundance has been linked to distribution changes (Engelhard et al. 2014, Baudron and Fernandes 2015).

Fish stocks are the fundamental units on which fisheries management is based. Stocks are considered to be biological populations: self-contained and interbreeding sub-units of fish species confined within clear geographical boundaries (MacLean and Evans 1981), although these assumptions are often branded unrealistic (Reiss et al. 2009). Changes in distribution are likely to challenge these assumptions even further (Pinsky et al. 2018). In Europe, each stock is defined by the International Council for the Exploration of the Sea (ICES) division(s) it occupies, henceforth called 'stock areas'. Annual allowable catches (TACs) are determined for each stock based on scientific advice resulting from stock assessments and forecasts. The TAC is then allocated per management unit, henceforth called 'TAC areas'. Despite being stock-specific, TAC areas do not always match with stock areas, and many stocks are distributed over several TAC areas. For example, the northern stock of European hake *Merluccius merluccius* stretches across four different TAC areas (Supplementary material Appendix 1 Fig. A1). When this occurs, the TAC determined for the stock is split among the different TAC areas covered by the stock area (four in this example). Following annual negotiations between coastal states, the quotas allocated to each TAC area are then distributed among the countries that target this stock.

Under the CFP, quotas are allocated following the principle of 'relative stability' (RS). RS uses a fixed allocation key based largely on historical catch records for each country in 1973–1978 (Symes 1997). This allocation key remains unchanged to this day such that, each year, the TAC for a stock is distributed among TAC areas and member states using the same proportions. Changes in distribution, if they result in changes in the proportion of a stock located within each TAC area, can result in a mismatch between regional stock abundances and quotas allocated by RS which can, in turn, lead to extensive discarding or a 'choke species' effect in fisheries (Baudron and Fernandes 2015). Such issues are likely to become more prevalent as distribution changes are expected to increase the number of transboundary stocks in the coming decades (Pinsky et al. 2018).

The confluence of rising sea temperatures and stock recovery may be both affecting fish distributions. To date, most fish distribution studies have focused on either a single region or a single species. Here, we performed a systematic assessment of distribution changes for 19 fish species encompassing 73 commercial stocks across the northeast Atlantic shelf. Changes in distribution were assessed by linking both presence–absence data and abundance estimates as recommended by Blanchard et al. (2007). This is the first time such an approach has been implemented in European waters over such a large scale for so many species and stocks. The ecological and managerial implications of the distribution changes identified are discussed.

Material and methods

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, Fig. 1a, Supplementary material Appendix 1 Table A1–A3). In the northern part of the area, data were available from the late 1960s, while in the south most started in the late 1990s (Supplementary material Appendix 1 Table A2, A3). ICES divisions are spatial fisheries management units 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). ICES divisions are disaggregated further into ICES statistical rectangles which are standard spatial units of 1° longitude by 0.5° latitude. Countries with relevant fisheries carry out annual surveys sampling a grid of ICES statistical rectangles to estimate abundance (Fig. 1b). Bottom and beam trawl survey data (Fig. 1c–d) were obtained from the ICES DATRAS database (<www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx>).

Different surveys cannot be simply merged to assess the distribution of species' abundances. However, presence–absence

Table 1. List of species included in this study, with the latitudes of their northern and southern range boundaries and centres of distribution (taken from Whitehead et al. 1989), as well as the corresponding number of stocks occurring in ICES divisions (*: both species of anglerfish are considered jointly in the official stock assessments). Species are ordered from top to bottom by decreasing latitude of centre of distribution. Species were split into two groups based on their latitude of centre of distribution: species above 55°N were considered as northern while species below were considered as southern.

Common name	Scientific name	Northernmost latitude	Southernmost latitude	Latitude centre	Stocks	Group
Norway pout	*Trisopterus esmarkii*	78	47	62.5	1	Northern
Herring	*Clupea harengus*	80	44.5	62.25	6	
Haddock	*Melanogrammus aeglefinus*	79	44	61.5	4	
Cod	*Gadus morhua*	76.3	46.25	61.275	8	
Saithe	*Pollachius virens*	77.87	44	60.935	1	
Pollack	*Pollachius pollachius*	71.1	44.74	57.92	3	
Plaice	*Pleuronectes platessa*	71	44	57.5	10	
Whiting	*Merlangius merlangus*	72.5	41	56.75	7	
White anglerfish*	*Lophius piscatorius*	73	35	54	3*	Southern
Blue whiting	*Micromesistius poutassou*	80	26.4	53.2	1	
Mackerel	*Scomber scombrus*	72	25	48.5	1	
Sprat	*Sprattus sprattus*	65	30	47.5	5	
Spurdog	*Squalus acanthias*	80	13	46.5	1	
Megrim	*Lepidorhombus whiffiagonis*	67	26	46.5	2	
Hake	*Merluccius merluccius*	71	16	43.5	2	
Sole	*Solea solea*	66	16	41	10	
Black anglerfish*	*Lophius budegassa*	60	12	36	3*	
Horse mackerel	*Trachurus trachurus*	68.55	0	34.275	3	
Anchovy	*Engraulis encrasicolus*	61	0	30.5	2	

information is less likely to be affected by differences in sampling protocols and allows changes in species' spatial occurrence to be assessed across surveys. In addition, each survey is internally consistent, and can be used to quantify changes in distribution of abundances within its area, or describe abundance trends which can then be compared between areas. We therefore applied the following three methods.

Changes in spatial occurrence

Only data spanning 1985–2015 were considered as this period includes data for most surveys, at least in northern parts of the study area (Supplementary material Appendix 1 Table A2, A3), thus allowing comparison of changes in spatial occurrence across areas at a similar time. Changes in species' spatial occurrence were investigated using species' presence–absence within a specific ICES rectangle in a given year. The percent occurrence of species in the rectangles of each ICES division was then calculated. If ten rectangles were sampled, and a species was present in all ten rectangles that year, then the occurrence was 100%. Temporal trends in species occurrence in each ICES division were tested for significance using the Mann–Kendall non-parametric test (Mann 1945).

Changes in species centre of gravity in individual surveys

Changes in the centre of gravity (CoG) (Petitgas et al. 2017) were investigated for each species within each survey. First, the numbers-at-length were converted to weight following Coull et al. (1989). Length measurements for each haul and species were used 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 as follows:

$$\log(\text{CPUE}) \sim \text{gmrf}(\text{statistical rectangle}) \quad (1)$$

where CPUE is modelled using gamma errors with a log link, and 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). Time series of the coordinates of the CoG for each species in each survey were calculated with Eq. 1 fitted to each year and survey. The CoG was computed using the coordinates of the centre of each statistical rectangle covered by the survey, weighted by abundance indices. 95% confidence intervals were computed using the simple percentile method (Davidson and Hinkley 1997).

Comparison of biomass trends across TAC areas

Comparison of biomass trends between adjacent ICES divisions and adjacent TAC areas were conducted to assess directional shifts in relative distribution. Indices of biomass (Eq. 1), summed across each ICES division, were compared for each pair of adjacent divisions. The ratio of these indices for neighbouring divisions was then calculated for each year, and

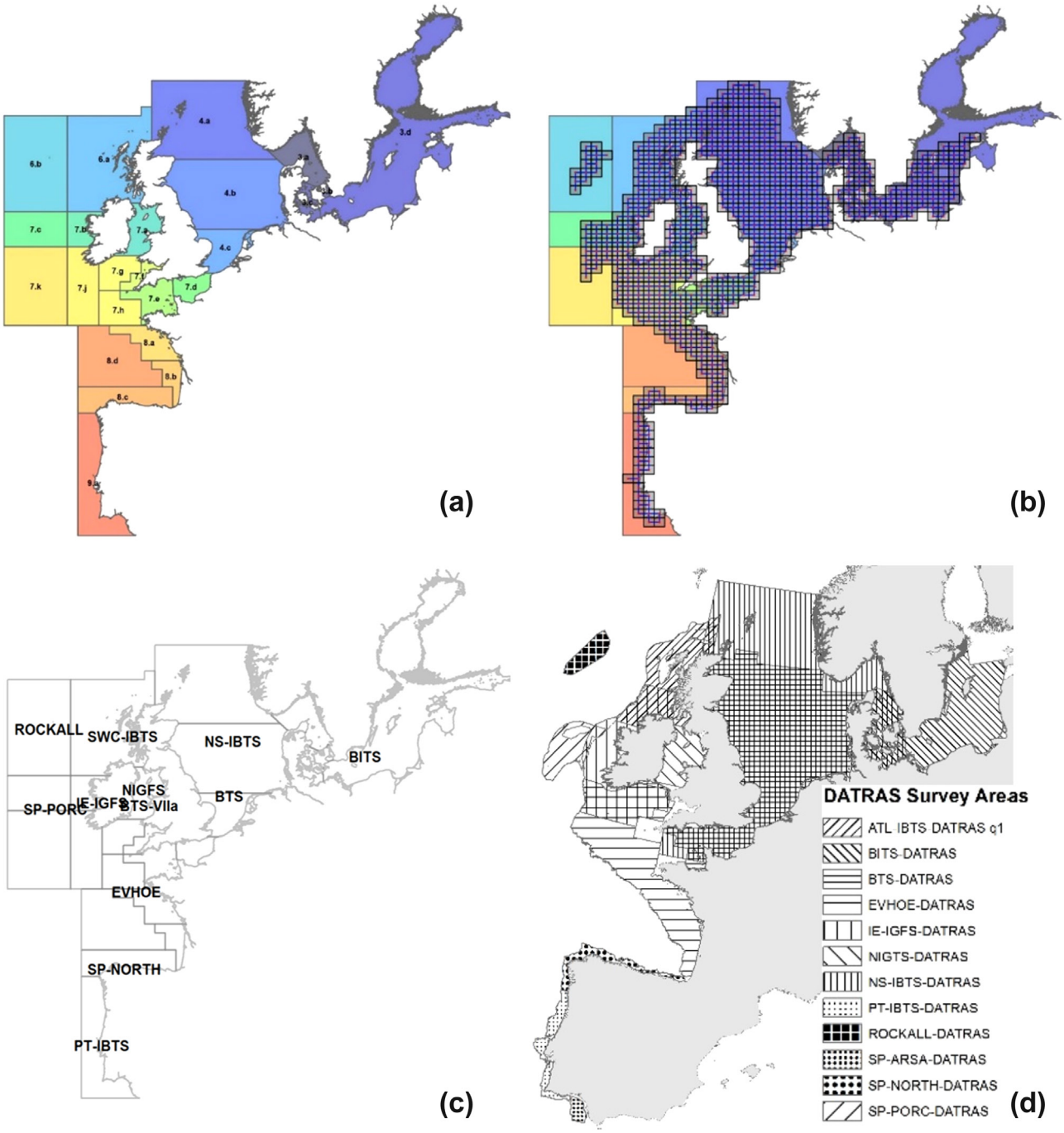

Figure 1. (a) ICES divisions considered in the study. (b) Grid of the statistical rectangles sampled overlaid on the ICES divisions considered. (c) Names and locations of the bottom trawl surveys used in the study. (d) Areas covered by the surveys sampling the statistical rectangles shown in panel (b).

trends in the ratios were used to describe changes in relative distribution. A positive temporal trend in biomass ratio between ICES divisions A and B indicates either 1) biomass increasing in A while decreasing in B, 2) biomass increasing in A faster than in B, 3) 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 relative distribution from area A to area B over time.

The significance of the trends was tested using a stochastic approach: 1) fit Eq. 1, 2) generate 100 000 realisations of the distribution of biomass for each year, 3) estimate the corresponding ratios to obtain 100 000 realisations of the biomass ratios time series, 4) perform a Mann–Kendall test for each simulation (Supplementary material Appendix 2). The results were used to test for the presence of a significant monotonic trend in the log ratios (Supplementary material Appendix 1

Fig. A2). Trends were assessed over the period covered by both surveys for each pair of ICES divisions. The trend was considered significant if the median significance level was less than 0.05.

Cross-species synthesis

In addition to the three-tiered approach, a cross-species synthesis was performed to assess whether the possible impacts of changes in suitable habitat (expected under warming) and density-dependent habitat selection (expected under changing fishing pressure and abundance) on distribution could be detected. 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):

$$\mathrm{Pos}_{\mathrm{sp,div}} = \left(\mathrm{lat}_{\mathrm{div}} - \mathrm{lat}_{\mathrm{centre,sp}}\right) \Big/ 0.5 \times \left(\mathrm{lat}_{\mathrm{north,sp}} - \mathrm{lat}_{\mathrm{south,sp}}\right) \quad (2)$$

where, for a given species, $\mathrm{lat}_{\mathrm{div}}$ is the latitude of the centre of the ICES division div, $\mathrm{lat}_{\mathrm{centre,sp}}$ is the latitude of the centre of the distribution range of species sp, defined by the mean latitude of the northern and southern boundaries (from Whitehead et al. 1989), $\mathrm{lat}_{\mathrm{north,sp}}$ and $\mathrm{lat}_{\mathrm{south,sp}}$ respectively. $\mathrm{Pos}_{\mathrm{sp,div}}$ 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. Observations were classified into bins of value of Pos ranging from −1 to +1 in increments of 0.25. The proportions of increase, no change and decrease in spatial occurrences were then 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 (Supplementary material Appendix 1 Table A1). 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 observed in divisions covered by corresponding stock areas were calculated.

Results

Changes in spatial occurrence

The presence–absence analysis revealed that, while northern species (Norway pout to whiting, see Table 1) were largely absent from the southern ICES divisions (northern Bay of Biscay and south), the opposite was not the case for southern species (white anglerfish to anchovy) which were generally present across all ICES divisions (Fig. 2, Supplementary material Appendix 1 Table A4). The vast majority of significant increases in spatial occurrence were observed in northern ICES divisions (Celtic Sea and north) while significant decreases, although rarer, were observed throughout the study area.

94% (33 out of 35) of the significant changes in spatial occurrence observed for southern species in the seven northernmost ICES divisions (central North Sea and above) were increases. These were particularly pronounced for the two southernmost species, horse mackerel and anchovy, with increases observed in six of the seven northernmost ICES divisions. 73% (16 out of 22) of the significant changes observed for northern species were increases, with two species (cod and saithe) displaying decreases only.

In the 11 mid-range ICES divisions (Irish Sea to southern Celtic Sea), increases observed for southern species still accounted for 73% (13 out of 18) of the significant changes. However, only five of the 11 southern species (white anglerfish, mackerel, black anglerfish, horse mackerel, anchovy) displayed solely increases, and two species (spurdog and sole) displayed only decreases. Likewise, northern species displayed relatively fewer increases and more decreases compared to northern ICES divisions, with increases accounting for 66% (10 out of 15) of the significant observations.

In the five southernmost ICES divisions (northern Bay of Biscay and south), far fewer significant trends were observed, owing to northern species being largely absent. 80% (eight out of 10) of the significant changes observed for the 11 southern species were increases, although most of these (six out of eight) were observed in the northernmost division (northern Bay of Biscay). In the southernmost ICES division (Portuguese waters), the only significant change for southern species was a decrease observed for mackerel, a species which otherwise displayed only increases throughout northern, mid-range and other southern ICES divisions. The only other significant decrease for southern species throughout southern divisions was observed for spurdog, a species which already exhibited only decreases throughout mid-range ICES divisions. The only significant changes for northern species were observed for haddock, which increased in spatial occurrence in the furthest north of these southernmost ICES divisions (northern and Offshore Bay of Biscay).

Changes in species centre of gravity in individual surveys

Latitudinal changes in CoG (i.e. northward or southward) were consistent across quarters of the same survey for all species except white anglerfish, mackerel, sole, horse mackerel and anchovy in the North Sea survey (NS-IBTS), and horse mackerel in the Baltic Sea survey (BITS) for which no conclusions could be drawn regarding northward or southward shifts in CoG (Fig. 3). Aside from these exceptions, and from spurdog in BITS which showed no discernible change in latitude, only half (50%, 17 out of 34) of the significant changes

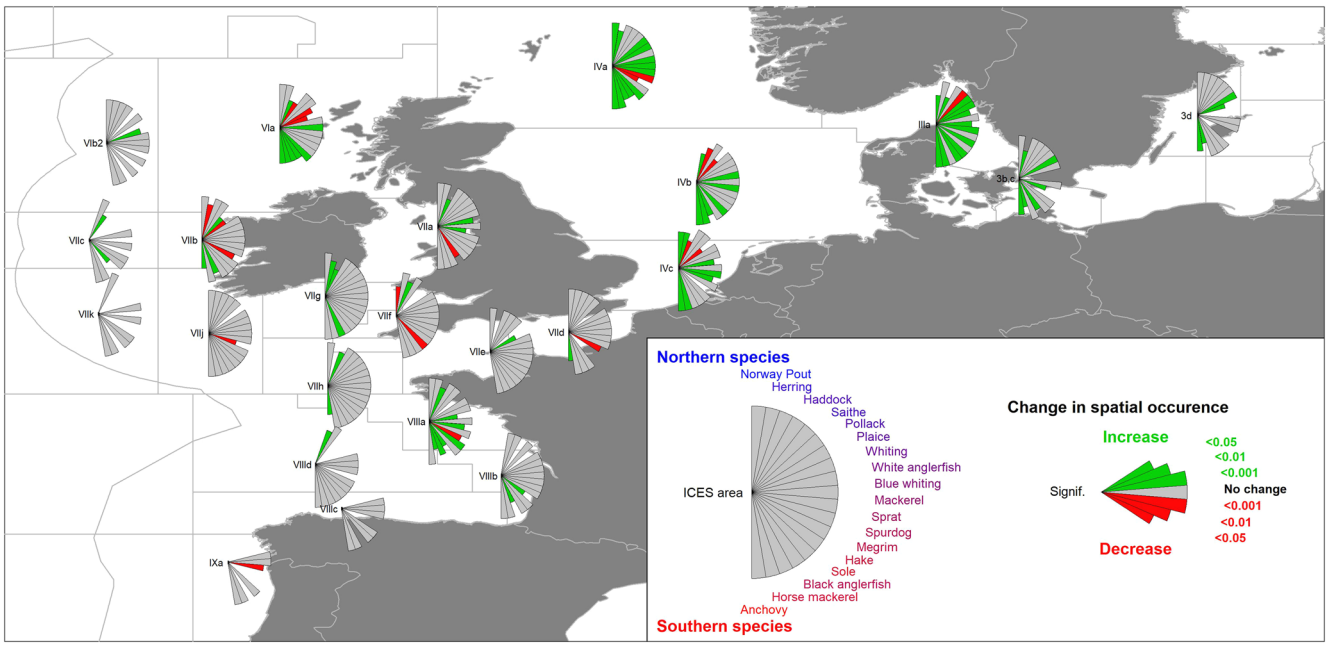

Figure 2. Map of the northeast Atlantic showing the changes in spatial occurrence per species identified by the presence–absence analysis. In each ICES division, the results are showed with a petal plot. Each petal corresponds to a species, and these are ordered from top to bottom by decreasing latitude at their centre of distribution (calculated with data from Whitehead et al. 1989). Missing petals indicate species were not recorded in the ICES division, while grey petals indicate no significant changes were observed for the corresponding species in the ICES division. Significant increases and decreases in spatial occurrence are shown in green and red respectively, with the length of the petals indicating the level of significance.

in CoG observed for southern species were northward shifts. Most of these northward shifts were observed in northern surveys (ROCKALL to BITS), where 85% (11 out of 13) of the significant changes in CoG increased in latitude. In contrast, in mid-range (NIGFS to SP-PORC) and southern (EVHOE to PT-IBTS) surveys only 25% (three out of 12) and 33% (three out of nine), respectively, of the significant changes in CoG were northward shifts.

For northern species, nearly two thirds (64%, 16 out of 25) of the significant changes in CoG observed were northward shifts (discounting whiting in SWC-IBTS which showed no discernible change in latitude). Unlike southern species, just over half (56%, nine out of 16) of the significant changes in CoG observed for northern species in northern surveys were northward shifts, while this proportion increased to 75% (three out of four) in mid-range surveys, and 80% (four out of five) in southern surveys.

Comparison of biomass trends across TAC areas

Seven species displayed significantly different trends in biomass ratios when compared across adjacent ICES divisions, indicating changes in relative distribution: herring, haddock, cod, plaice, hake, sole and horse mackerel (Table 2). Five of these (herring, plaice, hake, sole and horse mackerel) also showed significant changes across adjacent TAC areas. Apart from haddock, all changes occurred in northern and mid-range divisions (English Channel and northward). A majority of these changes (nine out of 16) were northward shifts in the relative distribution. These involved four out of six species (cod, hake, sole and horse mackerel) and occurred within (cod, hake, horse mackerel), and/or towards (hake and sole) the North Sea. All changes in relative distribution across adjacent TAC areas occurred in northern and mid-range divisions, with three out of five species (hake, sole and horse mackerel) showing northward shifts.

Cross-species synthesis

The observed changes in occurrence were clearly related to the position within the species biogeographical ranges. Increases in occurrence were more frequent in the northern part of the species distribution ranges ($Pos_{sp,div}$ values 0.5 and above), while the cases of decrease in occurrence were less frequent (Fig. 4a). Conversely, in the southern part of the species distribution ranges, the proportion of decrease in spatial occurrence was higher than in the northern part. However, this decline in the proportion of 'decrease' observations with $Pos_{sp,div}$ was not as pronounced as the rise in the proportion of 'increase' observations.

The distribution changes observed also appeared at least partly related to changes in stock abundance (Fig. 4b). Increases in occurrence were more frequent for species with increasing stock biomass than for species with no trend or a decreasing trend, and, conversely, decreases in occurrence were more frequent for species with declining stock biomasses.

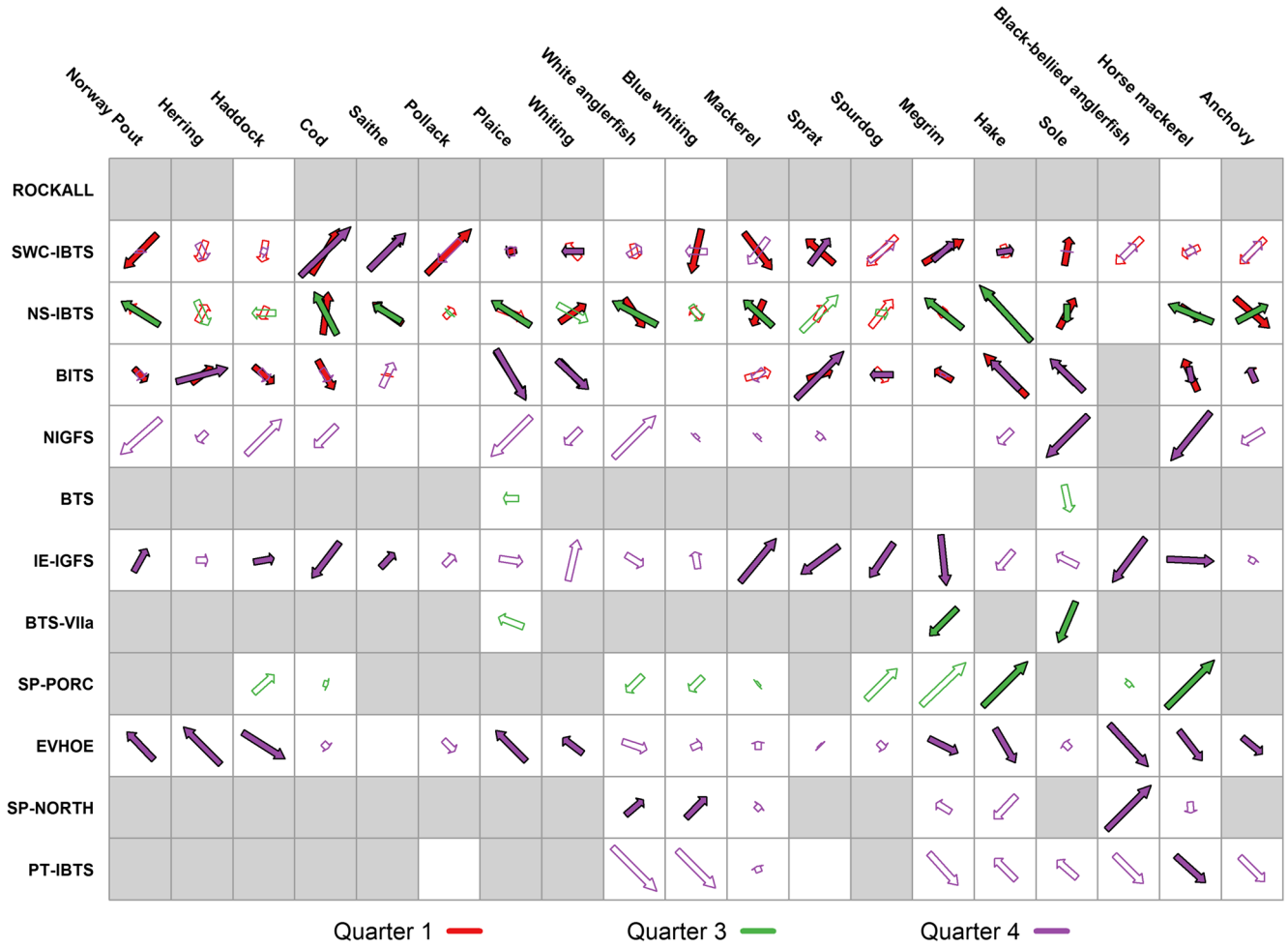

Figure 3. Summary of changes in centre of gravity of distribution observed for each species in each survey. Each species/survey cell has a scale of 1 by 1: the direction of the arrow indicates the direction of change in the centre of gravity, the length of the arrow is defined by the temporal correlations (−1 to +1) of the changes in the longitude and latitude of the centre of gravity in the x and y axes respectively, and arrows are positioned so that the middle of the arrow is centred in the cell. The colour of the arrow indicates the quarter of the survey. Filled arrows correspond to significant changes in centre of gravity over time. Blank cells indicate insufficient data for estimating a trend in centre of gravity coordinates for the corresponding species and survey. Grey cells indicate absence of data for the corresponding species in the corresponding survey. Species are ordered in columns from left to right by decreasing latitude at their centre of distribution (calculated with data from Whitehead et al. 1989). Surveys are ordered in rows from top to bottom by decreasing latitude at their centre (calculated as the median between minimum and maximum latitude surveyed).

Discussion

This study is the first systematic assessment of distribution changes of commercial fish species across the northeast Atlantic. The study area encompasses the southern part of the distribution of subboreal species (such as cod and haddock), the northern part of the distribution of subtropical species (such as anchovy and horse mackerel), and a large part of the distribution range of temperate species (such as mackerel and hake). Within this study area, the three-tiered analytical approach (presence–absence, CoG, abundance trends) applied here for the first time revealed that all 19 species have experienced changes in distribution in some parts of their range over the last 30 yr. However, different patterns were observed between northern and southern species.

While northern species displayed more increases than decreases in spatial occurrence overall, the proportion of increase was smaller at lower latitudes. In fact, apart from haddock and plaice, no increases were observed south of the Celtic Sea despite northern species being recorded as far south as the Bay of Biscay, indicating that the increase in the area occupied by northern species occurred predominantly in the northern part of the study area. In addition, two thirds of the significant shifts in CoG displayed by northern species were northward. While these northward shifts accounted for only half of the significant observations in northern latitudes, they constituted the vast majority (> 75%) of the significant observations in mid and southern latitudes, indicating that the northward shift in the centre of distribution of northern species observed here was much more pronounced in the

Table 2. Summary of species showing significant changes in relative distribution between adjacent ICES divisions as measured by their trend in biomass estimates. For each species the direction of perceived change between two ICES divisions is shown, as well as the estimated trend in biomass in the two corresponding ICES divisions. * indicates that data from multiple surveys and quarters were used. Rows highlighted in grey indicate changes occurring across adjacent TAC areas. Species are ordered in rows from top to bottom by decreasing latitude at their centre of distribution (calculated with data from Whitehead et al. 1989). ICES divisions where the change in relative distribution originates ('From') are also ordered in rows from top to bottom by decreasing latitude at their centre (calculated as the median between minimum and maximum latitude). p-value refers to significance of differences in trends between adjacent areas, based on a Mann–Kendall test.

Species	From	Biomass trend	To	Biomass trend	Direction	p
Herring	3b	decreasing	3d	increasing	eastward	0.013
	3c	decreasing	3d	increasing	eastward	0.013
Haddock	7g	increasing	7h	increasing	southward	0.007
	8a	increasing	7h	increasing	northward	0.007
	8d	increasing	7h	increasing	northward	0.007
	8d	increasing	8a	increasing	northeastward	0.007
	8b	stable	8a	increasing	northwestward	0.007
	8b	stable	8d	increasing	northwestward	0.007
Cod	4b	decreasing	4a	increasing	northward	0.018
Plaice	3a	stable	3b	increasing	southward	0.048
	3a	stable	3c	increasing	southward	0.044
	4c	increasing	7d	increasing	southwestward	0.041
Hake	3a*	increasing-stable	4a*	increasing	northwestward	0.001
	3d	decreasing	3b	decreasing	westward	0.028
	3d	decreasing	3c	decreasing	westward	0.028
	3b	decreasing	3a	stable	northward	0.023
	3c	decreasing	3a	stable	northward	0.023
	6a	stable	4a	increasing	northeastward	0.001
	4b*	increasing	4a*	increasing	northward	0.001
Sole	7d	decreasing	4c	increasing	northward	0.022
Horse mackerel	4b	decreasing	4a	stable	northward	0.001
	4b	decreasing	3a	stable	northeastward	0.031

southern and middle parts of the study area than in the northern part. These findings suggest not only an overall northward shift of the distribution of northern species, previously reported for cod and plaice in the North Sea (Engelhard et al. 2011, 2014), but also a northern shift in their southern range boundaries consistent with previous reports for North Sea haddock (Skinner 2009), which would indicate an overall contraction of the area occupied by species with northern biogeographic affinities within the study area.

Southern species also exhibited more increases than decreases in spatial occurrence overall. However, they did so throughout the study area, including lower latitudes. They also showed relatively more increases than their northern counterparts, especially in northern latitudes. Only half of the significant shifts in CoG displayed by southern species were northward, with most of these observed in northern latitudes. In mid and southern latitudes, southern species displayed mainly southwards shifts in CoG, suggesting that their southern boundaries have generally remained outside the study area. These findings suggest an overall increase in the area occupied by southern species accompanied by a dramatic northward expansion occurring in the northern part of the study area, especially for subtropical species, as previously reported for anchovy and sardine *Sardina pilchardus* in the North Sea (Beare et al. 2004, Petitgas et al. 2012). This would indicate an overall northward expansion of the area occupied by species with southern biogeographic affinities within the study area. However, the few northward shifts and decrease in spatial occurrence exhibited by the more temperate species (white anglerfish, blue whiting, mackerel, spurdog) in the southern fringes of the study area may indicate an overall shift (expansion and contraction) in distribution for these temperate species within the study area, consistent with previous reports of northward shifts of both the southern range boundary and the spawning area of mackerel in the northeast Atlantic (Brunel et al. 2018).

The overall northward direction of the changes in distribution reported here, and the dichotomy between species with northern (contraction) and southern (expansion) biogeographic affinities detailed above, are consistent with the poleward distribution shifts expected from warming sea temperatures (Poloczanska et al. 2016). This interpretation was strongly supported by the cross-species synthesis for the 19 species investigated here, which clearly showed that expansions in occupied area were increasingly more pronounced towards the northern end of species' distribution ranges while, conversely, contractions were more frequently observed towards the southern end of species' distribution ranges. This is consistent with the warming-induced changes in distribution previously reported individually for many species in and around the study area (Engelhard et al. 2011, 2014, Petitgas et al. 2012, Fossheim et al. 2015). This suggests that changes in suitable habitat areas resulting from the rising sea temperatures observed throughout the northeast Atlantic shelf (González-Pola et al. 2018) are at least partly responsible for the large scale distribution changes observed here. Such

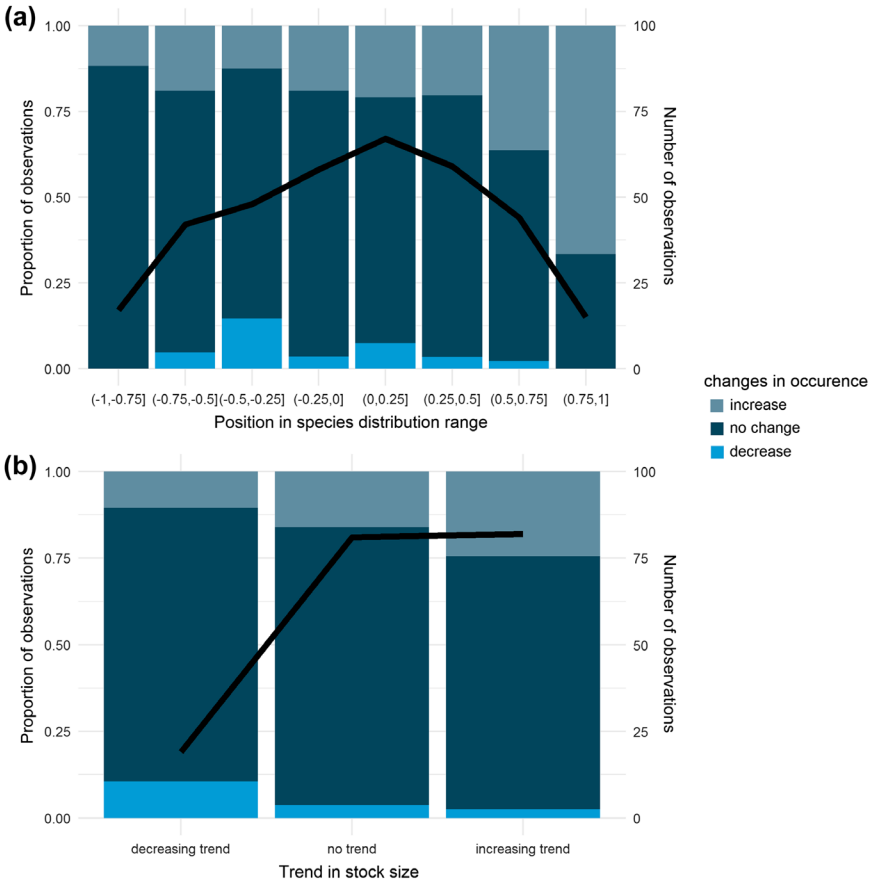

Figure 4. (a) Proportion of observations (i.e. a given species in a given ICES division) with increase, no change and decreases in spatial occurrences (vertical bars) in relation to the position in the species range (−1 corresponding to the southern limit of distribution, 1 to the northern limit and 0 to the centre). (b) Proportion of observations (i.e. a given species in a given ICES division) with increase, no change and decreases in spatial occurrences (vertical bars) in relation to the trend in spawning stock biomass. The black lines in panel (a) and (b) depict the number of observations per bin.

interpretation is consistent with the warming-induced distribution shifts documented for plankton assemblages with different temperatures preferences throughout the north Atlantic (Beaugrand et al. 2009), which encompasses the study area considered here, and is further corroborated by the fact that populations at the warm ends of their thermal niches were more vulnerable than those at the cool ends of their thermal niches which often benefited from historical warming (Free et al. 2019).

The cross-species synthesis also showed that, compared with species showing no trends in abundance, species with increasing abundance trends showed more increases and fewer decreases in spatial occurrence, while species with a decreasing abundance showed more decreases and less increases in spatial occurrence. These findings strongly suggest that density-dependent habitat selection is also occurring, with species increasing and decreasing in abundance expanding and contracting their spatial occupancy respectively, as expected according to the MacCall (1990) basin model. Density-driven changes in distribution have previously been reported for several species within the area considered in this study (Baudron and Fernandes 2015, Brunel et al. 2018, Erauskin-Extramiana et al. 2019). Although the drivers of distribution changes were not formally addressed in this study, our findings indicate that the distribution of the 19 species considered here is at least partly affected by both changes in areas of suitable habitat (possibly as a result of warming sea temperature) and by changes in abundance (due to reduced fishing) via density-dependent habitat selection occurring within these areas. In fact, this interaction between habitat and abundance was specifically identified for two of the most widely spread species in the northeast Atlantic, mackerel and hake, the distribution of which was found to be driven by stock size but constrained by thermal habitat (Baudron and Fernandes 2015, Olafsdottir et al. 2019).

Although a general northward trend in distribution changes was observed across species with all methods employed, some contradictions to this general pattern were also evident. Regional 'anomalies', such as haddock expanding southward in the Bay of Biscay, may be due to unknown favourable environmental conditions (Dickey-Collas et al. 2003). Other contradictions could be linked to the shortcomings of using trawl survey data (Supplementary material Appendix 3). For instance, the lack of consistent sampling

protocol and temporal coverage across surveys (ICES 2012) can hinder the investigation of distribution changes across large areas spanning several surveys (Blanchard et al. 2007). In addition, the poor survey catchability of some pelagic species (ICES 2015) or length classes of some deep water species (Fraser et al. 2007) could lead to some spurious observations, such as distribution being driven mainly by juveniles (Sanchez and Gil 2000). Notwithstanding catchability issues, trawl survey data can be used to assess pelagic species' distribution (Montero-Serra et al. 2015) and do consistently track cohort abundance of deep water species (e.g. anglerfish) (ICES 2019). The shortcomings were mitigated, to some extent, by the three-tiered approach employed here which produced consistent observations supported by the existing literature (Supplementary material Appendix 3).

Distribution changes can have substantial ecological impacts, which may be detrimental to the sustainable exploitation of fish resources. While pelagic species are likely to closely track suitable thermal conditions (Bruge et al. 2016), demersal species are more likely to be limited by physical constraints such as depth (Rutterford et al. 2015) and shift towards deeper waters instead (Dulvy et al. 2008). This may lead to relocation to suboptimal habitats which could result in increased metabolic maintenance costs (Pörtner and Knust 2007) or reduced foraging ability (Teal et al. 2012). Distribution changes can also alter the connectivity between the suitable habitats required by successive life stages which is essential for life cycle closure (Sinclair and Iles 1989). These life cycle 'bottlenecks' have already been reported in the North Sea for plaice and haddock (Petitgas et al. 2013, Asjes et al. 2016). Lastly, distribution changes can affect predator–prey interactions. The recent expansion of hake into the North Sea increased competition with saithe (Cormon et al. 2016). Likewise, the northward expansion of mackerel has led this species to opportunistically prey on herring larvae in the Norwegian Sea, with knock-on implications for the entire food web given the importance of herring as a food source (Skaret et al. 2015). Mismatches between the spatial distributions of predator and prey species can either create or remove prey spatial refugia, which in turn can affect the top–down control by predators (Casini et al. 2012). These examples highlight how distribution changes could jeopardise fish stocks' resilience.

Perhaps the most striking consequences of distribution changes of commercial fish species are the management implications, with both economic and political repercussions. The principle of allocating quotas considering historical catch (i.e. RS) rather than proportions of biomass currently present (i.e. zonal attachment) may be contentious, but respects the United Nations Convention on the Law of the Sea (UNCLOS 1982) which, under Article 51(1), 'shall recognize traditional fishing rights of the immediately adjacent neighbouring States'. However, the distribution of northeast Atlantic commercial fish species has clearly changed: here, seven of the 19 species exhibited changes in relative distribution across adjacent ICES divisions. Most importantly, five species, four of which are reported here for the first time, did so across TAC areas, potentially causing a mismatch between the allocated quotas assigned through RS and the regional abundances.

Hake, in particular, illustrates the problems this mismatch can create (Baudron and Fernandes 2015). In the 1970s, when RS allocations were devised, hake landings in the North Sea were negligible. RS, therefore, allocates only 3% of the TAC to the North Sea, which now has 34% of the entire stock. This imbalance has led to massive discarding: in 2011, Scottish fleets landed 3035 tonnes of hake in the North Sea by arranging almost 2678 tonnes in quota swaps, yet they still discarded 4993 tonnes (Baudron and Fernandes 2015). Such figures emphasize the difficulties in aligning the concept of RS with the recent Landings Obligation (Sobrino and Sobrido 2017), which mandates zero discards of quota species.

Another striking example is the northeast Atlantic mackerel stock, managed by the Northeast Atlantic Fisheries Comission, based on agreements between coastal states in which the TAC is shared according to principles similar to RS. Following the expansion of the summer distribution of this stock to the west and north in the Nordic Seas (Olafsdottir et al. 2019) and an increase in biomass, large quantities of mackerel became available to Greenland, Iceland and the Faroe Islands. As fisheries in these coutries expanded, the coastal states failed to agree quota allocations, which led to some parties unilaterally setting their own quota. Consequently, catches have consistently exceeded scientific advice since 2010 (by up to 100% in 2018) resulting in overexploitation of the stock (ICES 2018).

The above examples highlight the 'wicked problem' (van Hoof 2015) created by fixed allocation schemes like RS, devised under markedly different ecological conditions, when fish distributions were different. Yet, despite its flaws being increasingly documented (Harte et al. 2019), RS is still being used to allocate quotas. While quota swapping mitigates the problem, in some cases not enough swaps can be arranged, and the current swapping systems in the EU are not yet transparent enough to work effectively (Hoefnagel et al. 2015). The imminent departure of the UK from the EU will undoubtedly highlight such issues as the UK seeks to develop its own coastal state fishery management arrangements (Boyes and Elliott 2016). As evidence mounts for changes in the distribution of commercial fish, a revision of RS is crucial if fish stocks are to be managed sustainably.

Data availability statement

Data available from the Zenodo Digital Repository: <http://dx.doi.org/10.5281/zenodo.3600590> (Baudron et al. 2019).

Acknowledgements – The authors wish to thank the participants of the ICES workshop 'Report of the Working Group on Fish Distribution (WKFISHDISH)' (<www.ices.dk/news-and-events/news-archive/news/Pages/Substantial-changes-in-fish-distribution-identified-by-ICES.aspx>).
Funding – This work was supported by the Horizon 2020 European research projects ClimeFish (grant no. 677039) and CERES (grant no. 678193). The authors also would like to acknowledge the

following funding sources: the Danish Recreational Fishers Fund – Marine Fiskepleje; the Research Council of Norway (EcoNorSe, grant no. 243895); the Gipuzkoa Talent Fellowships programme – Gipuzkoa Provincial Council, Spain.

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Supplementary material (available online as Appendix ecog-04864 at <www.ecography.org/appendix/ecog-04864>). Appendix 1–3.

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