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Original Article

Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2014

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The Northeast Atlantic (NEA) mackerel (*Scomber scombrus*) is a widely distributed pelagic fish species that plays a key role in the marine ecosystem. In recent years, there has been a large fishery targeting mackerel in the NEA. At the same time as the geographic range of the mackerel fishery has expanded and the spatial distribution of the stock been defectively determined, the stock assessment has been considered to be highly uncertain by ICES. Limited tuning data, with only a triennial egg survey, have created challenges for the assessment and management of NEA mackerel, and ICES has repeatedly stated the need for an annual age-disaggregated abundance index of this stock. These were the motivations for establishment of an international pelagic trawl survey in 2007, the International Ecosystem Summer Surveys in the Nordic Seas (IESSNS). The estimated total biomass indices for NEA mackerel based on coordinated and standardized swept-area surface trawling in July–August from IESSNS increased from 1.96 million t [relative standard error (RSE) = 30.35%] in 2007 to 8.77 million t (RSE = 7.95%) in 2014. Simultaneously, the mackerel stock expanded its geographic range during the feeding season from 1.3 million km^2 in 2007 to at least 2.9 million km^2 in 2014, mainly towards western and northern regions of the Nordic seas. Estimates of abundance indices by age group were fairly precise (RSE ~20%) for ages 3–12, while the precision was poorer for ages 1 and 2 and for age groups 13 and older (RSE > 50%). Furthermore, evaluation of the performance of the estimated abundance indices by age for this time-series, based on internal consistency and catch curves, suggest that the abundance indices of ages 3–12 track the temporal variation in abundance reasonably, and thus is applicable for stock assessments.

Keywords: collapsed strata, geographical expansion, IESSNS, increased abundance indices, Northeast Atlantic mackerel, pelagic trawl survey, summer feeding, systematic survey.

Introduction

Northeast Atlantic (NEA) mackerel (*Scomber scombrus*) is a widely distributed, highly migratory pelagic fish (Hamre, 1980; Trenkel *et al.*, 2014). Mackerel play a key ecological role in oceanic and coastal ecosystems and now support one of the most valuable commercial fisheries in the North Atlantic (Trenkel *et al.*, 2014). Since

2007, there has been a large and expanding fishery of mackerel in the NEA (ICES, 2014a). At the same time as the fishery has expanded, the mapping of the actual spatial distribution of the stock has created challenges (ICES, 2013a), and the stock assessment has been considered highly uncertain (ICES, 2014b).

Assessments of mackerel from 1992 onwards relied on a relative index of spawning-stock biomass (SSB) derived from triennial egg surveys along with official catch statistics (ICES, 2013b). Thus, the only fishery-independent information used as a tuning series in the assessment was a triennial SSB index without any information on age distribution in the stock (ICES, 2014a). This, combined with uncertain historical estimates of total catch and catch composition by age, has created problems for the assessment and management of this stock until now (Simmonds et al., 2010; ICES, 2014b). Consequently, ICES has repeatedly stated the need for an annual age-disaggregated abundance index of this stock (ICES, 2014c).

Traditional acoustic methods for abundance estimation used for other pelagic species such as herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) have been attempted for mackerel for decades (Simmonds and MacLennan, 2005; Korneliussen, 2010). Unfortunately, they have not been as successful as anticipated and have not provided abundance or biomass estimates with sufficient quality and consistency needed for quantitative stock assessment (ICES, 2013c, 2014a, b). The reason is that mackerel lack swimbladders and, therefore, provide a very weak acoustic backscattering signal compared with other pelagic species with swimbladders, such as herring and blue whiting (Foote, 1980). Also, since mackerel generally swim near the sea surface during their summer feeding, a significant portion of the stock may occur in the "acoustic blind zone" or be masked for acoustic detection by dense plankton concentrations above the thermocline (ICES, 2014b). Some progress has been made using multifrequency acoustics (Korneliussen, 2010) and multibeam sonar studies on mackerel (Godø et al., 2004; Nøttestad et al., 2015). However, until now, acoustic survey methods applicable for mackerel are premature and remain under development.

Taking into account both the ecological and commercial importance of mackerel, with annual catches close to 1 million t (ICES, 2014a), the spatial distribution and migration pattern of the stock during the feeding period is surprisingly poorly known (ICES, 2013a). Several published papers have addressed aspects of mackerel biology during the feeding period, but these papers have used data from limited geographical areas or from earlier periods (Uriarte and Lucio, 2001, Iversen, 2002; Godø et al., 2004; Churnside et al., 2009; Tenningen et al., 2011; Astthorsson et al., 2012). Earlier studies conducted during summer on mackerel have mainly focused on length-dependent migration pattern (Nøttestad et al., 1999), spawning migration (Punzon and Villamor, 2009; Jansen and Gislason, 2011), growth, diet, and feeding behaviour (O'Connell and Zweifel, 1972; Villamor et al., 2004; Debes et al., 2012; Langøy et al., 2012; Óskarsson et al., 2015), predator–prey interactions (Nøttestad et al., 2014a, b), and spatial overlap and ecology of mackerel, Norwegian spring-spawning herring, and blue whiting (Prokopchuk and Sentyabov, 2006; Huse et al., 2012; Utne et al., 2012). Nevertheless, none of the published papers provide estimates on abundance, biomass, or spatial distribution of mackerel during the feeding period after its appearance in large quantities in the Nordic seas (areas around Norway, Faroe Islands, Iceland, and Greenland) since the mid-2000s.

Mature mackerel spend several months in the Nordic seas and surrounding waters during their summer feeding phase (ICES, 2014a; Trenkel et al., 2014) where they feed mainly on zooplankton in the upper productive ocean layer (Debes et al., 2012; Langøy et al., 2012; Óskarsson et al., 2015). During this period, mackerel are widely scattered in small and sparse schools compared with late autumn and winter when they form large, dense schools (Godø et al., 2004; Iversen, 2004; Slotte et al., 2007). Also, their feeding and searching behaviour to locate available prey during summer limits their directed movement and swimming speed (Godø et al., 2004; Nøttestad et al., 2015). Therefore, mackerel are particularly well suited for pelagic swept-area trawl sampling during the summer feeding period.

Traditionally, standardized swept-area trawl surveys have targeted demersal fish (Aglen, 1996), but such surveys have also been used for quantifying the abundance of pelagic species (Azarovitz, 1981; Pennington, 1986; Harley et al., 2001; Christman et al., 2003). With respect to mackerel, the swept-area approach has recently been used for estimating mackerel recruitment from the International Bottom Trawl Survey (IBTS) in the North Sea and west of the British Isles (Jansen et al., 2015).

The International Ecosystem Summer Surveys in the Nordic Seas (IESSNS) was initiated in summer 2007 because of (i) lack of age-disaggregated abundance indices that could be used to improve the mackerel assessment and (ii) increased commercial catches in the Nordic seas during summer since the mid-2000s [see maps showing the commercial fishery by quarter (ICES, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013c)], as well as more frequent recordings of mackerel during trawl surveys targeting pelagic species other than mackerel, which indicated increasing abundance and an expansion in the geographic range of the stock. This was in conflict with the rather low stock estimates reported by ICES during the same period (ICES, 2013c). The IESSNS was thus intended to be a complementary method to the triennial egg surveys for monitoring the mackerel stock.

The main objective of the present study was to quantify changes in distribution, abundance, and density of the mackerel feeding in the Nordic seas from the standardized pelagic swept-area trawl survey methods and to estimate precision of these estimates. Furthermore, we aimed to develop annual age-disaggregated abundance indices along with associated precision estimates and to evaluate their applicability as a tuning series in the stock assessment. We also aimed to compare the precision of abundance indices using subsamples of ages only from the trawl stations with estimates that use the combined subsamples of age and length.

Material and methods
Survey vessels, timing, and geographic coverage
Research vessels and chartered commercial fishing vessels from Norway, Faroe Islands, and Iceland were used for conducting a mackerel monitoring survey in the Nordic seas and adjacent waters during July–August in 2007–2014 (Table 1). The sampling frame for this study is defined by the areas A, B, C, and D in Figure 1 which we refer to as superstrata (Fuller, 2009). These superstrata roughly separate trawl sampling by the Norwegian and Icelandic vessels, which cover the largest area, allowing for the examination of country (or vessel) effects. The superstrata were substratified into small strata defined by non-overlapping $1° × 2°$ rectangles to ensure more uniform allocation of sampling stations across the range of the stock during summer compared with simple random sampling. The southern range of the distribution of mackerel during summer, which is mainly in European Union

Table 1. Survey year, vessel name, country, and period of chartered and research vessels participating during 2007–2014.

Survey year	Vessel name	Country	Period
2007	MV "Libas"	Norway	15 July–6 August
2007	MV "Eros"	Norway	15 July–6 August
2010	MV "Libas"	Norway	15 July–20 August
2010	MV "Brennholm"	Norway	15 July–6 August
2010	MV "Finnur Fríði"	Faroe Islands	9–23 July
2010	RV "Árni Friðriksson"	Iceland	20 July–12 August
2011	MV "Libas"	Norway	18 July–10 August
2011	MV "Finnur Fríði"	Faroe Islands	8–18 August
2011	RV "Árni Friðriksson"	Iceland	3–31 August
2012	RV "G. O. Sars"	Norway	2–20 July
2012	MV "Brennholm"	Norway	6–27 July
2012	MV "Christian í Grótinum"	Faroe Island	3–18 July
2012	RV "Árni Friðriksson"	Iceland	12 July–10 August
2013	MV "Libas"	Norway	4–29 July
2013	MV "Eros"	Norway	4–29 July
2013	MV " Finnur Fríði"	Faroe Islands	2–17 July
2013	RV "Árni Friðriksson"[a]	Iceland	12 July–9 August
2014	MV "Brennholm"	Norway	2–28 July
2014	MV "Vendla"	Norway	2–28 July
2014	MV "Finnur Fríði"	Faroe Islands	10–21 July
2014	RV "Árni Friðriksson"[a]	Iceland	11 July–12 August

[a]Superstratum D (Figure 1) was covered by Greenland chartering the Icelandic vessel Arni Fridriksson in 2013 and 2014.

(EU) waters around the European shelf and in the North Sea, were not part of the sampling frame.

Cruise tracks of the ships predominantly followed parallel east–west transects. Standardized trawl hauls were taken at fixed sampling stations at predetermined geographical positions within strata (Figure 1). In 2007, the survey was only conducted by two Norwegian vessels. In 2010−2014, one Icelandic research vessel and one Faroese chartered commercial vessel took part in the survey along with the two Norwegian vessels, except in 2011 when Norway only used one vessel. The realized spatial survey coverage of the trawl survey differed from year to year depending on available ship-time and the anticipated geographic expansion of the mackerel stock, but covered major parts of the Norwegian Sea in all years.

In principle, the trawl survey followed a systematic design with one primary sampling unit (PSU) per stratum (Cochran, 1977), where PSUs are standardized swept-area trawl hauls. However, the sampling in any given year was restricted to strata that encompassed the anticipated habitat range for mackerel based on real-time observations from the survey and expert judgement. The number of strata sampled was further restricted towards the boundaries of each superstratum by terminating the cruise track when more than one stratum with zero catches was observed. *In situ* measures of temperature at different depths for each trawl station were used to define the outer boundaries of the mackerel distribution. When *in situ* temperatures were <6−7°C in combination with zero catches of mackerel, this area was defined as the outer boundary for the mackerel distribution. The convex envelope (Berg *et al.,* 1997) of all strata with a completed trawl haul, including those with zero catches, defined the boundary of the survey area in a given year. The convex envelope for the survey area may be visualized as the set of strata enclosed by a rubber band stretched around all strata with trawl observations. The suitable or surveyed habitat for mackerel within a given year was defined by the convex envelope of sampled strata with trawl catches above zero.

Trawl sampling

The specially designed Multpelt 832 pelagic trawl (ICES, 2013d, e) was used on all participating vessels in 2012–2014, while different pelagic trawls suitable for mackerel sampling close to the surface were used before 2012 (Table 2). The trawling protocol and sampling procedures were standardized to the extent possible, using a target towing speed of 5 knots and tow duration of 30 min for all vessels and countries in 2007–2014, except that the Faroese vessel employed a tow duration of 1 h in 2010 and 2011. Towing speed and tow duration were recorded for each haul. Effective towing speed based on GPS varied between 4 and 5 knots depending on vessel performance, currents, windspeed, and wave conditions. The tow track was curved in a banana-shaped pattern to keep the trawl outside the vessel's wake. Size selectivity and catching efficiency of the gear were assumed to be identical for every vessel and trawl used in the survey despite the use of different trawls earlier. Variation in the horizontal trawl opening was adjusted for in the standardized area-swept estimates. In the analysis presented here, it was assumed that all mackerel inside the width of the trawl opening ($\sim$65 m) were caught. The vertical opening also varied before 2012, but this was ignored in the calculations. It was assumed conservatively that all mackerel were caught during trawling in the vertical dimension and that no mackerel were swimming below 30–35 m depth. The trawls were towed in surface waters with help of floats attached to the wings and headline and by the use of kites. Towing was done over a 24-h period. Rigging and trawl operation are described in ICES (2015). After each trawl haul, the total catch of the different species was weighed on board. At least 100 mackerel were randomly sampled from each catch and measured for individual length ($\pm$ 0.1 cm) and body weight ($\pm$ 0.1 g). The subsample of mackerel was randomly selected from the entire catch for further analyses. Otoliths from the first 25 individuals of the randomly selected subsample were retrieved for age reading.

Analytical methods

The annual surveys analysed here followed a stratified systematic design with one PSU per stratum. The design resulted in some analytical challenges in providing unbiased estimates of abundance indices and their associated variances. First of all, the strata ($1° \times 2°$ rectangles) diminished in area from south to north. As a result, the inclusion probabilities of PSUs were not equal within superstrata, and, hence, simple averaging of abundance indices based on observations from the PSUs within superstrata would be biased. Also, the variance of abundance and biomass estimates within strata cannot be estimated from a sample size of one PSU. Lastly, the systematic allocation of stations precludes unbiased analytical variance estimates; if the systematic survey is treated as a simple random design, the estimated variance is likely to be biased upwards (Cochran, 1977).

Collapsing of strata

Stratified systematic surveys with one PSU per stratum are frequently conducted in practice. A common approach to approximate the variances in estimates of means and totals in such designs is to collapse neighbouring strata to yield a pseudo design with more than one PSU per stratum that is treated as if it were the actual design (Wolter, 1985; Dunn and Harrison, 1993, Korn and Graubard, 1999). The variance and the relative standard error (RSE; Jessen, 1978) are then estimated under the assumption of simple random sampling within the collapsed strata (Fuller, 2009). Following the principles of this approach, the original strata were collapsed
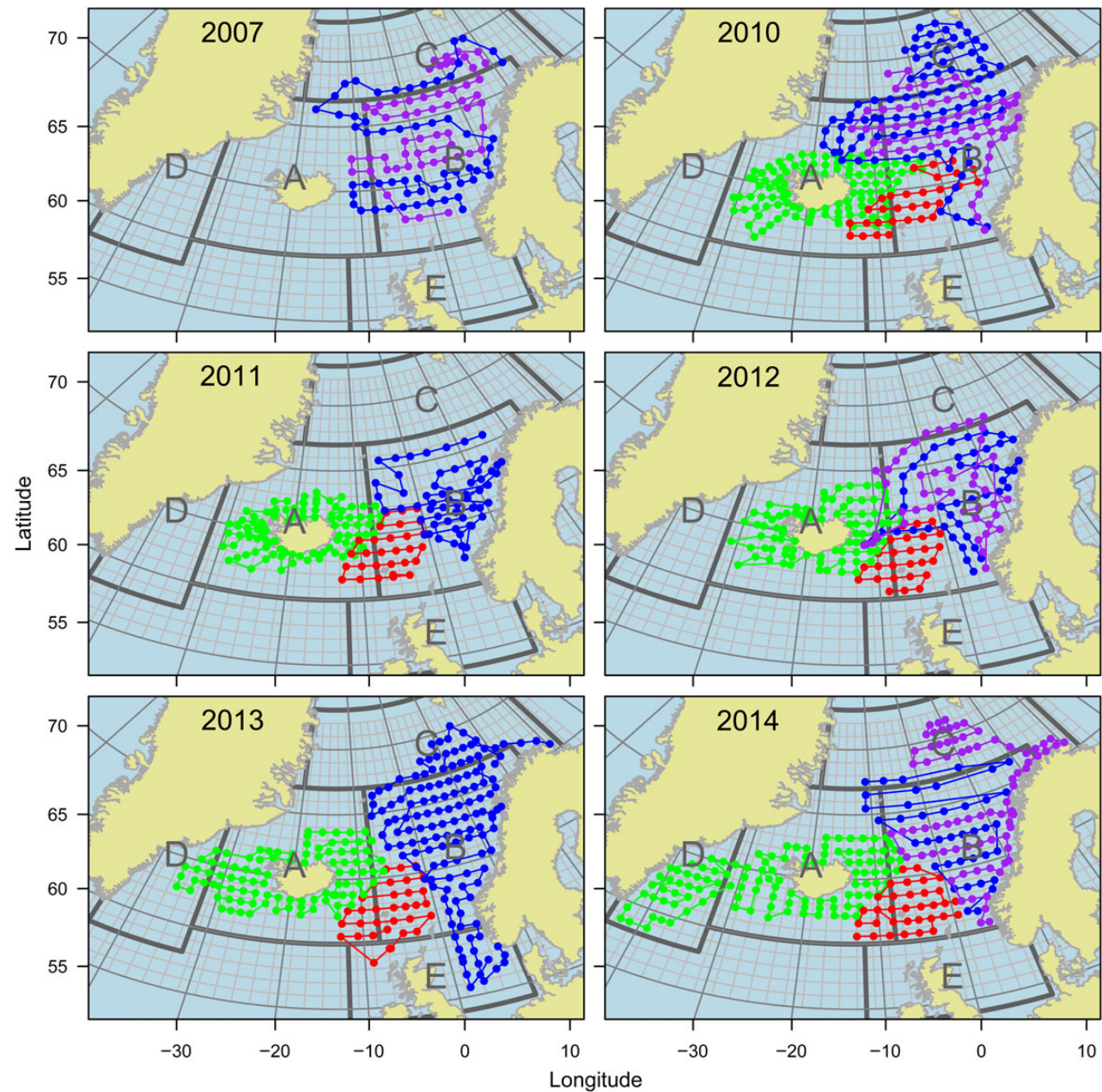
Figure 1. Systematic predefined survey stations including pelagic trawl stations conducted on board two (2007), three (2011), and four (2010, 2012, 2013, and 2014) highly equipped vessels from Norway (blue and purple lines), Faroe Islands (red lines), and Iceland (green lines). The letters A-E represent the superstrata, which borders are drawn with solid lines.

Table 2. The different trawl types used on board the participating vessels from the three countries (FO, Faroe Islands; IS, Iceland; NO, Norway) in the ecosystem surveys in 2007–2014 and their specifications.

Pelagic trawl type	Country	Year	Horizontal opening (m)	Vertical opening (m)
Egersund trawl	NO	2007, 2010, 2011	60	40
Blue whiting trawl	FO	2010	60	30
Wide body 500	IS	2010	23	16.5
Multpelt 832	IS, FO	2011–2014	60–65	30–35
Multpelt 832	NO	2011–2014	65	30

(grouped) into $2° \times 2°$ strata, thus forming pseudostrata (Fuller, 2009) with the spatial extent of $2°$ latitude and $4°$ longitude. This first step minimizes the variation in inclusion probabilities for

PSUs within pseudostrata and significantly reduces the number of pseudostrata with only one PSU, but not completely. All remaining strata with only one PSU were further collapsed into larger

pseudostrata within each superstratum (A–D) according to the following rule. Starting in the southwest, strata are collapsed eastwards until two or more PSUs within each stratum are obtained. By this approach, we define the convex envelope of the survey coverage. Again, the convex envelope of the set of pseudostrata where the mean catch per PSU is greater than zero now defines the habitat.

Estimators

The following estimators are based on the collapsed strata method (Cochran, 1977; Fuller, 2009), with pseudostrata as defined above. At each trawl station i within pseudostratum j, the number of fish caught N_{ji} is divided by the area swept by the trawl A_{ji} to yield a standardized observation of abundance by square kilometre

$$\rho_{ji} = \frac{N_{ji}}{A_{ji}}, \tag{1}$$

for the PSU (trawl haul). The swept-area (A; km^{-2}) for trawl haul i in pseudostratum j is calculated by the formula $A_{ji} = D_{ji} \times H_{ji}$, where D_{ji} is distance (m) and H_{ji} the horizontal opening of the trawl (m). For a random sample of n_j PSUs with equal inclusion probabilities, and under the (strong) assumption of 100% catching efficiency of the trawl for the area swept, an unbiased estimator for the mean density within pseudostratum j is

$$\hat{\rho}_j = \frac{1}{n_j} \sum_{i=1}^{n_j} \rho_{ji}, \tag{2}$$

and an unbiased estimator for the variance of $\hat{\rho}_j$ is

$$\hat{v}(\hat{\rho}_j) = \frac{1}{n_j} \times \frac{\sum_{i=1}^{n_j} (\rho_{ji} - \hat{\rho}_j)^2}{n_h - 1}. \tag{3}$$

An estimate of the total within each pseudostratum is obtained by scaling the density to the total area of the pseudostratum

$$\hat{N}_j = A_j \times \hat{\rho}_j, \tag{4}$$

with variance

$$\hat{v}(\hat{N}_j) = A_j^2 \times \hat{v}(\hat{\rho}_j). \tag{5}$$

It then follows that the total abundance over all pseudostrata is

$$\hat{N} = \sum_{j=1}^{J} \hat{N}_j, \tag{6}$$

with variance

$$\hat{v}(\hat{N}) = \sum_{j=1}^{J} \hat{v}(\hat{N}_j), \tag{7}$$

provided there is independent sampling among pseudostrata.

Estimating biomass and numbers-at-age

Estimates of biomass are derived the same way as for abundance by replacing the total number of fish per PSU with total weights in ρ_{ji} [Equation (1)]. Estimates of numbers-at-age are derived by replacing N_{ji} with the numbers-at-age at each station $\hat{N}_{jia}$, where $\hat{N}_{jia} = N_{ji} \times \hat{p}_{jia}$ and where the proportion at age is estimated using the m_{ji} individuals which are sampled at random for ageing, i.e. $\hat{p}_{jia} = m_{jia}/m_{ji}$. Note that the estimator for variance [Equation (3)] in this case will include the estimator for the proportion at age. When N_{ji} is large relative to m_{ji}, the additional variance from estimating $\hat{p}_{jia}$ will be negligible as the variability caused by subsampling is incorporated in the between-station variability (Williams, 2000), and the estimator for variance above still holds.

Estimates of biomass at age are derived by replacing N_{ji} with $\hat{B}_{jia} = \hat{N}_{jia} \bar{w}_{jia}$ in Equation (1), where $\bar{w}_{jia}$ is the estimated mean weight-at-age for trawl haul i in pseudostratum j. Also in this case, the variance due to estimating $\bar{w}_{jia}$ will be maintained by the variance estimator by the same argument as above.

Imputations for missing age samples

For some trawl stations, the mackerel catches were only subsampled for length, and no otoliths were collected for determining the age of fish taken (22, 8, 30, 15, 6, and 7% of the trawl stations for the years 2007 and 2010–2014, respectively). For these stations, a direct estimate of the age distribution of the catch could not be obtained. For the remaining stations, ages were available for a subsample of the individuals sampled for length (see the Trawl sampling section). We estimated the abundance indices by age group based on two datasets: (i) PSU data with age recordings only for the subsamples, and the additional PSUs with data on total catch in numbers, and no use of additional length data, and (ii) the complete datasets for all PSUs with all length and age data. For both datasets, we used the method of *multiple imputation* to replace missing values for the age distribution in the samples (see, e.g. Lehtonen and Pakhinen, 2004). In general, this approach for filling gaps in data replaces each missing age distribution (or age) independently, possibly based on an auxiliary variable (e.g. a model) and is repeated r times to produce r complete datasets which are analysed. To combine the results across the imputed datasets, the estimate of the total number of an age group is simply the mean of the estimates for each of the "complete" datasets

$$\hat{N}_a^* = \frac{1}{r} \sum_{k=1}^{r} \hat{N}_{ak}^*, \tag{8}$$

where $\hat{N}_{ak}^*$ is the estimate of total number of a-year-olds for the kth complete dataset, and the estimate of the variance may be shown to be (see, e.g. Lehtonen and Pakhinen, 2004, p. 123)

$$\hat{v}(\hat{N}_a^*) = \left[\frac{1}{r} \sum_{k=1}^{r} \hat{v}(\hat{N}_{ak}^*) + \left(1 + \frac{1}{r} \right) \sum_{k=1}^{r} \frac{(\hat{N}_{ak}^* - \hat{N}_a^*)^2}{r - 1} \right]. \tag{9}$$

Here, we recognize that the first component of the variance is based on the PSUs with age data and is calculated using the collapsed strata approach, while the second component represents the additional variance due to imputation. Note that imputation will only affect estimates of abundance indices at age, and not the total abundance index. Also note that if there are no missing age samples, $\hat{v}(\hat{N}_a^*)$ collapses to $\hat{v}(\hat{N})$ since $\hat{N}_{aj}^* \equiv \hat{N}_a$.

For the first dataset, which is a subset of the complete data, we impute the age distribution based on catch size; we found that the mean age is significantly negatively correlated with catch size. The average correlation across years is -0.27 for sample sizes ranging from 85 in 2007 to 230 in 2014, i.e. large catches have younger and

smaller fish than large catches, implying that the age distribution changes with catch size. Therefore, we grouped observed age distributions according to intervals of catch sizes based on their empirical distribution. The interval widths were based on equally extended quantiles of catch size to ensure observations within each interval. We imputed a missing age distribution by resampling observed age distributions at random from age distributions corresponding to the interval of catch sizes. To account for large-scale differences in age composition, this procedure was performed within each superstratum A–D (Figure 1).

For the complete data, we followed the approach in Aanes and Vølstad (2015) which includes the use of age–length keys (ALK, see, e.g. Quinn and Deriso, 1999) to utilize extra length samples with no associated age data. They showed that an ALK approach can obtain unbiased estimates with appropriate levels of uncertainty, provided the ALK is estimated and applied within each PSU. Hence, for the data from the mackerel survey, the ALK, i.e. the matrix with rows holding the estimated proportion at age for each length category l_k, $\widehat{p(a|l_k)}$, is estimated for each PSU. We chose length categories defined by 1-cm length intervals. To include variability due to estimating the age by the ALK, we imputed the missing ages by sampling an age from the categorical distribution defined by $\widehat{p(a|l_k)}$ for each length category to obtain complete datasets (i.e. data with no missing ages).

The sampling strategy of 100 individuals, of which 25 were randomly sampled for age, is different from the data analysed in Aanes and Vølstad (2015), which included age samples for every length category within each PSU. Hence, the strategy of random subsampling for ages did not ensure samples of all length categories such that the analysis was complicated by potential missing values in the ALKs. To resolve this problem, we imputed the missing values in the ALK at each PSU using a nearest neighbour approach with three steps. First, length categories for which ages not collected were imputed using the estimated $\widehat{p_h(a|l_k)}$ obtained by the estimated mean of the ALK within the corresponding pseudostratum h following Aanes and Vølstad (2015). For each length category, the mean in pseudostratum h was estimated as $\widehat{p_h(a|l_k)} = \sum_{j=1}^{n_h} w_{hj}\, p_{hj}(a|l_k)$, where $w_{hj} = \hat{N}_{hj,l_k}/\sum_{j=1}^{n} \hat{N}_{hj,l_k}$, is the weight for PSU j in pseudostratum h. PSUs which contained missing values were omitted to obtain an estimate. This approach does not guarantee estimates of the missing values in the ALK. The second step was that columns in the ALK still missing were replaced by moving up from the estimates within stratum to estimates over the larger superstratum. The stratified estimate of the ALK within each superstratum s was achieved by $\widehat{p_s(a|l_k)} = \sum_{h=1}^{n_s} w_h\, p_h(a|l_k)$ for $h \in s$, and $w_h = \hat{N}_{h,l_k}/\sum_{h=1}^{n} \hat{N}_{h,l_k}$, i.e. the proportion of numbers in length category across the strata in each superstratum. If the ALK was still missing after this step, the third and last step was to replace missing values by the stratified estimate of the ALK for the total. Although missing values in the ALK represented a challenge for estimation, the effect of this procedure was marginal for these data since the proportion of the length categories within each PSU that were missing was very small, i.e. the imputation of the ALK had little effect on the total, but was necessary to be able to utilize all length samples with missing ages.

Evaluating the performance of the survey indices of abundance

In addition to quantifying levels of precision of the estimated abundance indices, it is preferred that their quality be evaluated by other methods. In this paper, we considered two additional approaches commonly employed for evaluating estimates of age-distributed abundance indices used in stock assessments.

Catch curves

The first approach was simply a visual inspection of *catch curves* (e.g. Quinn and Deriso, 1999). We then assessed the quality of the indices by tracing the cohorts at the log scale through time. If the catchability was constant across ages, the error in the index was small, and mortality was constant, the relationship between successive ages would be linear, where the negative slope is the mortality (see Quinn and Deriso, 1999, pp. 319–321 for details). Age-varying catchability would cause biased estimates of mortality, but would result in smooth lines if catchability is a smooth function of age and mortality is constant at age. Sampling error, time-varying catchabilities, as well as varying mortality rates would all reduce the smoothness of the relationship.

Internal consistency

The second approach was based on an evaluation of internal consistency (see Payne *et al.,* 2009; Berg and Kristensen, 2012 for similar approaches). Based on the usual relationship describing the mortality of a cohort $N_{a,y} = N_{a-1,y-1}\exp(-Z_{a-1,y-1})$, where $Z_{a-1,y-1}$ is the mortality-at-age $a-1$ in year $y-1$, it follows that $\log(N_{a,y}) = \log(N_{a-1,y-1}) - Z_{a-1,y-1}$, i.e. linear at the log scale. The common assumption for the abundance indices is related to the actual abundance through $I_{a,y} = q_a N_{a,y}^b$ with exact proportionality if $b = 1$ with constant q_a (the catchability) that possibly depends on age. Combining these two relationships yields $\log(I_{a,y}) = b\log(I_{a-1,y-1}) - \log(q_{a-1}) + \log(q_a) - Z_{a-1,y-1}$, i.e. a linear relationship between successive ages in a cohort if the catchabilities and mortalities are constant over time, and the linear correlation is thus regarded as a quality indicator of the indices. Note that increasing errors in the indices implies lower correlation and particularly that error in the index entering the explanatory variable ($I_{a-1,y-1}$) is recognized as regression with errors in variables (cf. Casella and Berger, 1990, pp. 581–592) and further decreases the correlation as well as introducing bias in the estimates of b towards 0.

Results

The number of original strata in the Nordic seas containing mackerel increased from 2007 to 2014, indicating a geographical expansion of mackerel in these areas from ∼1.3 million km² in 2007 to ∼2.9 million km² in 2014 (Table 3). The mackerel had expanded north to Svalbard and the northern part of the Norwegian coast and west into East Icelandic waters in 2007, and from around 2012 also into Southeast Greenlandic waters (Figure 2). Calculations of total biomass indices from the swept-area analyses show an increase from 1.96 million t (RSE = 30%) in 2007 to 8.77 million t (RSE = 8%) in 2014 (Table 3, Figure 3). However, a drop to 3.54 million t (RSE = 13%) occurred in 2011, which was a year with limited geographical coverage (Table 3). In the same period, the biomass of age groups 6+ increased from 0.30 to 4.6 million t (Figure 3). The mean density from the swept-area analyses showed a significant increase from 1.53 t km⁻² in 2007 to 3.03 t km⁻² in 2014 (Table 3). Therefore, simultaneous with a large expansion of the stock, density in the feeding areas also increased. The biomass increase in the central survey area shows that the occurrence of mackerel in the northern and westernmost areas in the most recent years is due to increased stock size and geographical expansion of mackerel and not due to a general movement or shift in the main summer

Table 3. Estimated abundance and biomass indices by year of mackerel from the swept-area surveys.

Year	Total numbers index[a] (billions)	Total biomass index[a] (million t)	Sampling frame area (million km^2)	Restricted sampling frame area (million km^2)	Area of habitat	Mean density areas A–D (t km^{-2})	Mean density habitat (t km^{-2})
2007[b]	6.99 (42)	1.96 (30)	1.66	1.66	1.28	1.18	1.53
2010	16.47 (20)	5.64 (15)	3.99	2.48	2.35	1.41	2.40
2011[c]	10.41 (15)	3.54 (13)	3.99	1.92	1.92	0.89	1.85
2012	20.57 (11)	5.37 (12)	3.99	2.19	2.07	1.34	2.59
2013	32.21 (8)	8.87 (7)	3.99	2.65	2.88	2.22	3.08
2014	23.35 (8)	8.77 (8)	3.99	3.11	2.90	2.20	3.03

RSE (%) is given in parentheses. The surveyed area is the sum of the strata areas with samples. Coverage includes the areas outside the habitat within A–D (see Figure 1), where habitat is defined as the sum of areas of strata with observations of mackerel.
[a]Under the assumption of 100% catching efficiency within the horizontal opening of the trawl.
[b]Only sampled area B, and partly A.
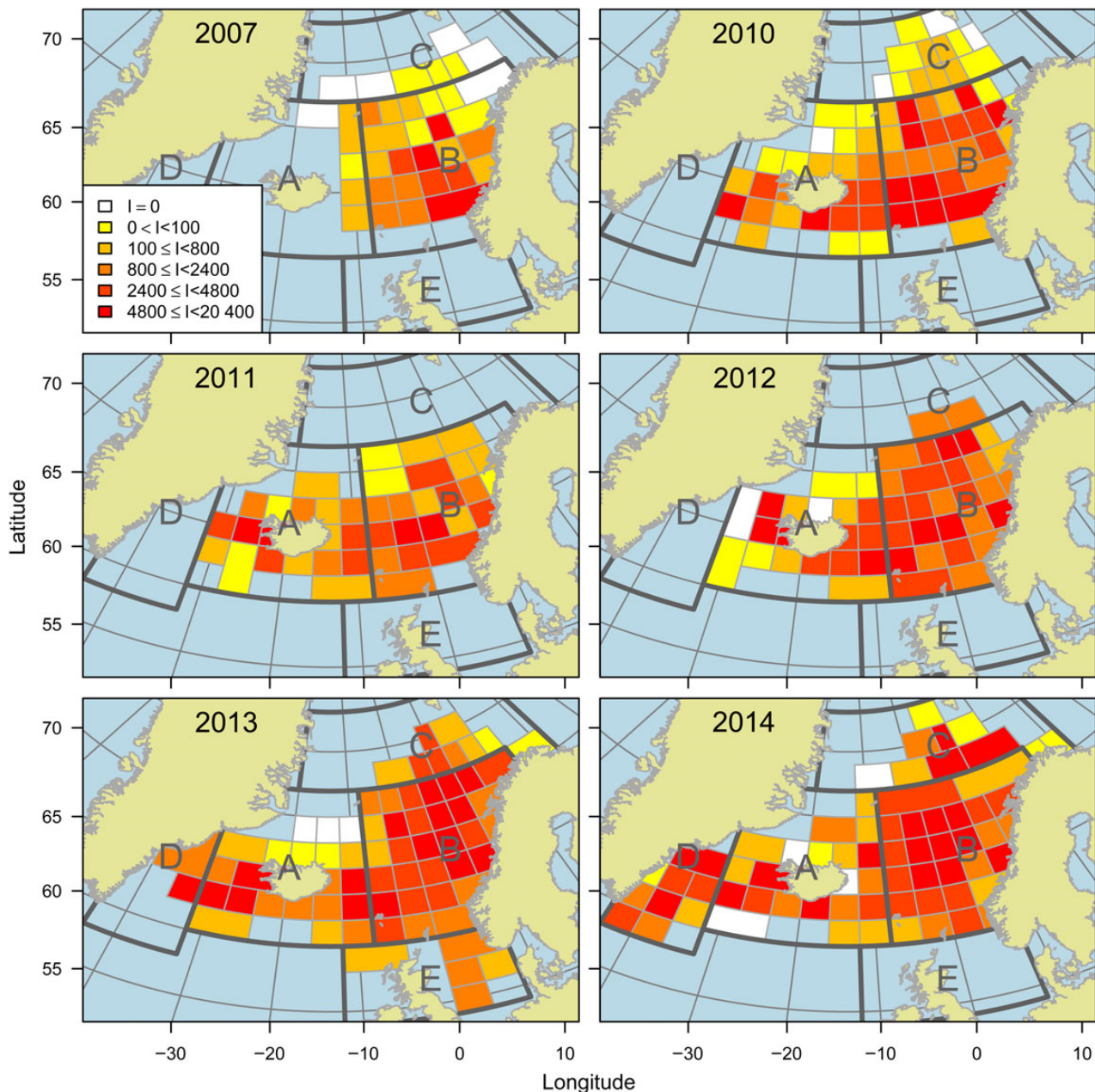[c]Area C is not covered by the survey, but is likely to contain a negligible proportion of the total.

Figure 2. Average catch index (kg km^{-2}) by pseudostrata (see text) for NEA mackerel in July–August 2007 and 2010–2014 with spatial coverages of 1.66, 2.48, 1.92, 2.19, 2.65, and 3.11 million km^2, respectively. The interval widths for the colours are scaled based on the 0, 20, 40, 60, 80, and 100% quantiles of estimated densities in each pseudostratum across years.
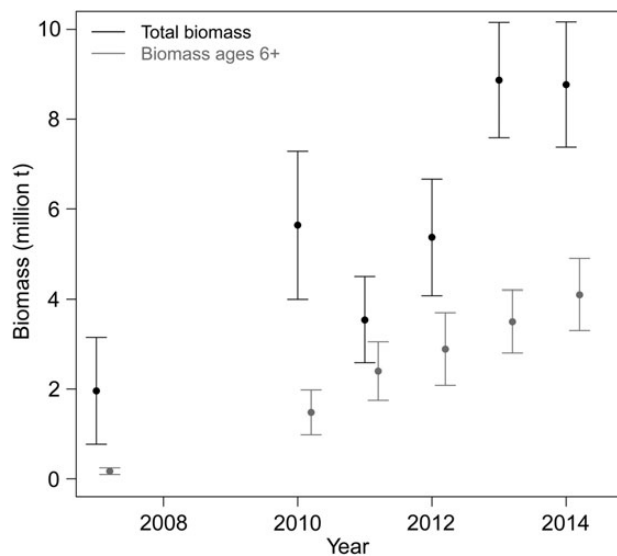
Figure 3. The swept-area estimate of NEA mackerel total biomass (black) and biomass of ages 6+ (grey) for 2007 and 2010–2014 in the ecosystem surveys. Point estimates are shown as dots and approximate 95% confidence intervals as bars.

Table 4. Percentage of total biomass of NEA mackerel by area (Figure 1) for 2007 and 2010–2014 according to the IESSNS swept-area estimates.

Year	A	B	C	D
2007	2	98	0	0
2010	25	74	1	0
2011	43	57	–	0
2012	33	64	2	0
2013	21	69	4	5
2014	22	47	16	15

captured by the indices, as long as the assumptions of constant catchability and mortality hold. Note that abundance of ages 5 and 6 is similar (see also Figure 4) and difficult to separate across cohorts. Consequently, there is poor internal consistency for these ages (Figure 7), whereas internal consistencies for the other ages appear adequate except for the oldest ages which are poorly estimated (Figure 5, i.e. RSE > 50%). There is internal inconsistency for ages 14–15 and 15–16. This is due to imprecise relative abundance estimates for these age groups (RSE > 50%) and years in the time-series without any recordings of these age groups.

distribution area west and north. Therefore, it is not just mackerel from the central feeding area that are switching to new feeding areas.

The different geographical superstrata (Figures 1 and 2), based on post-stratification from 2007 to 2014, are mainly divided according to national jurisdictions (EEZs), such as in superstrata A and D. Superstratum B includes Norwegian, Faroese, and international waters, superstratum C includes Norwegian and international waters in the Norwegian Sea, while superstratum E includes EU and Norwegian waters in the North Sea and west of the British Isles. The proportion of the biomass in superstratum C is very low compared with the total for the years with complete coverage (Table 4), but increased in 2013 and particularly in 2014, where also a significant part was in superstratum D. This increase was seen for ages 4+, but particularly for 7+ (Table 5).

The age-disaggregated abundance indices showed that recruiting year classes first appeared in the trawl survey at age 1 and that mackerel were not fully captured until they reached ages 3–5 (Figures 4 and 5), implying increased catchability with age. High abundance of age 2 fish in 2012, age 2–3 fish in 2013, and age 3–4 fish in 2014 indicated that the 2010 and 2011 year classes were strong. Following this logic, other apparently strong year classes derived from 2005 and 2006, while the 2008 year class might have been above average. Furthermore, the most abundant age groups were 4–7 (Figures 4 and 5). RSE was rather low (~0.2) in the age range 3–12 (Figure 5) for all years except 2007 and high (>0.6) for ages 1 and 13+. Point estimates of mackerel biomass based only on trawl stations with age data were very similar to the estimates obtained when the additional trawl stations with length-only data are included in the analysis, but the inclusion of additional PSUs with length data improved the precision, particularly for the youngest fish (Figure 5).

Figure 6 shows that some cohorts can be visually traced using only age data and that traceability is somewhat improved when additional length-only data are included, which likely is due to the improved precision when using all length and age data (Figure 5). This suggests that the true temporal fluctuations in abundance are

Discussion

The results from this study clearly demonstrate that there have been rapid and large changes in mackerel abundance, distribution, and migration patterns in the Nordic seas in summers 2007–2014. The stock has steadily expanded farther west and north since 2007, with increasing abundance and density in the central part of the Norwegian Sea, in Faroese waters, around Iceland, and at Jan Mayen at the same time. The expansion into the central Norwegian Sea had happened before 2007, as seen from mainly the Russian fishery in the Faroese and international zones starting in the mid-1980s with increasing catches in the 1990s and continuing to the present (ICES, 2014a). Expansion into the East Icelandic zone seemed to start in summer 2007 (Astthorsson et al., 2012). In 2013, mackerel were also caught in East Greenland waters and in July–September 2013 as far northeast as the Barents Sea (ICES, 2014a) and as far north as Icefjord in Spitsbergen at 78°N (Berge et al., 2015). These changes have also been seen in the expanding fisheries in recent years into East Greenland waters and a summer fishery in the Nordic seas (ICES, 2014a).

The uncertainty of estimates based on the swept-area methodology depends, among other things, on the small-scale distribution of fish. Patchy distributions increase uncertainty, while fish that are uniformly distributed are best suited for abundance estimation purposes. Comparisons of acoustic recordings before, during, and after trawling indicated a predominantly uniform distribution of small shoals of mackerel, while the distribution of mackerel during trawling did not indicate any difference from the distribution recorded acoustically before and after trawling (ICES, 2014b). The same trend of low patchiness of mackerel shoals was also seen by using multibeam sonar during the surveys (Nøttestad et al., 2015), as well as rather uniform distribution of zooplankton, the major prey for mackerel during summer (Debes et al., 2012; Langøy et al., 2012; Óskarsson et al., 2015). Furthermore, the horizontal distribution maps (Figure 2) and the overall low RSE for the abundance estimates supports the conclusion that the spatial distribution of mackerel is rather uniform in the Nordic seas during summer.

Table 5. Percentage of total numbers of NEA mackerel in superstratum C (Figure 1) by age group in 2010, 2012, 2013, and 2014 where the spatial coverage in IESSNS was complete.

Year	Age														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
2010	0	0	0	0	1	2	5	3	4	4	3	2	1	13	0
2012	0	0	0	1	1	2	4	5	5	7	6	7	6	6	7
2013	0	0	1	2	4	6	9	11	12	11	10	14	15	14	6
2014	0	0	1	4	11	19	28	37	42	50	49	56	61	61	60
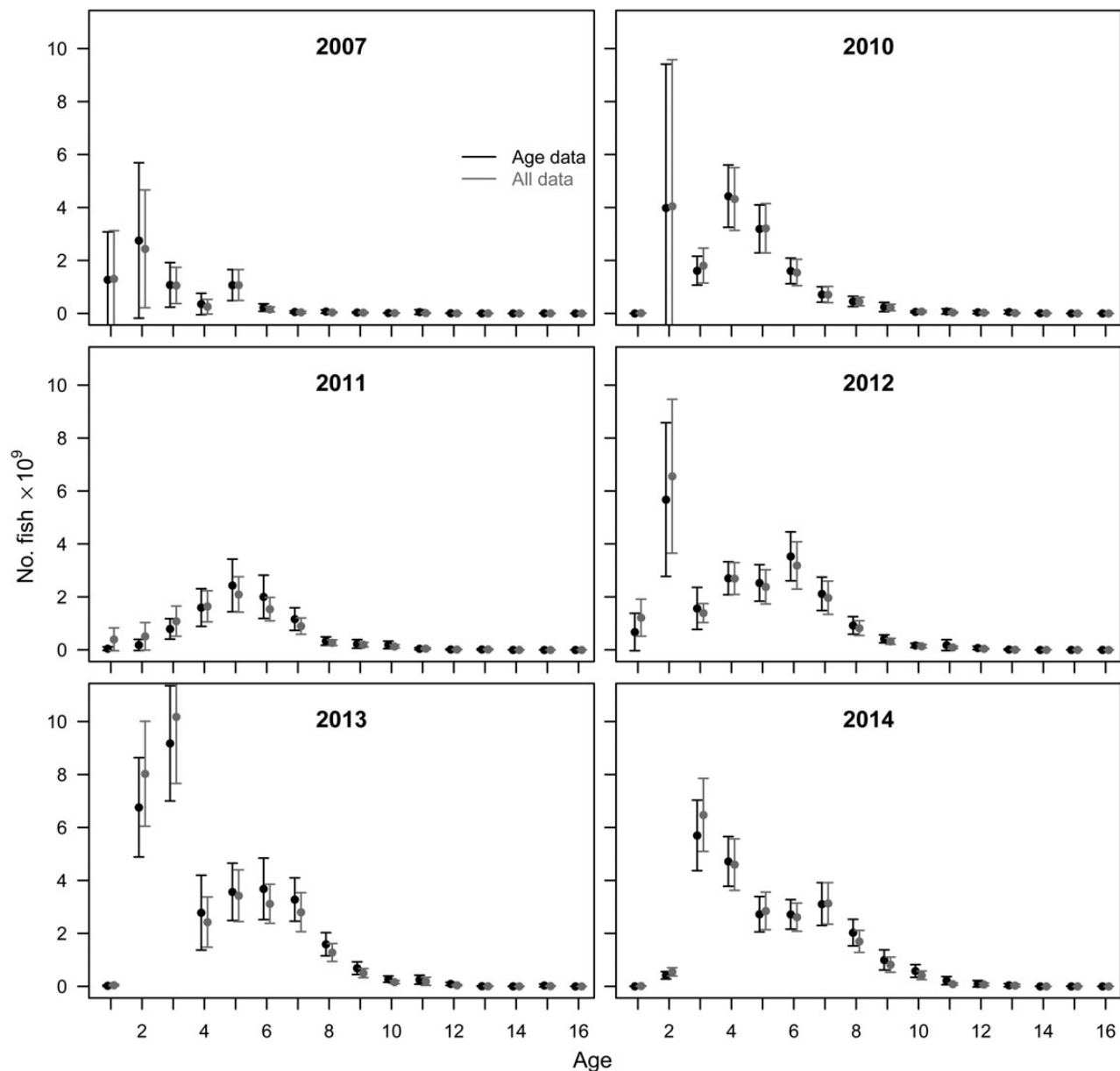
Figure 4. The swept-area estimate of total numbers-at-age of NEA mackerel in the ecosystem surveys from the 2007 and 2010–2014 ecosystem surveys using only age data (black) and using all additional length data (grey). Point estimates are shown as dots and approximate 95% confidence intervals as bars.

Varying survey coverage between years can result in variable biases that add uncertainty to the presented results. Coverage was incomplete in 2011 due to limited funding for the survey. In 2007, coverage was limited in the western and southern areas; however,

as deduced from the Icelandic fishery during that period, significant amounts of mackerel began to be caught east of Iceland in summer 2007 (Astthorsson *et al.,* 2012). We, therefore, consider the western boundary of mackerel to be the East Icelandic waters in 2007, i.e.
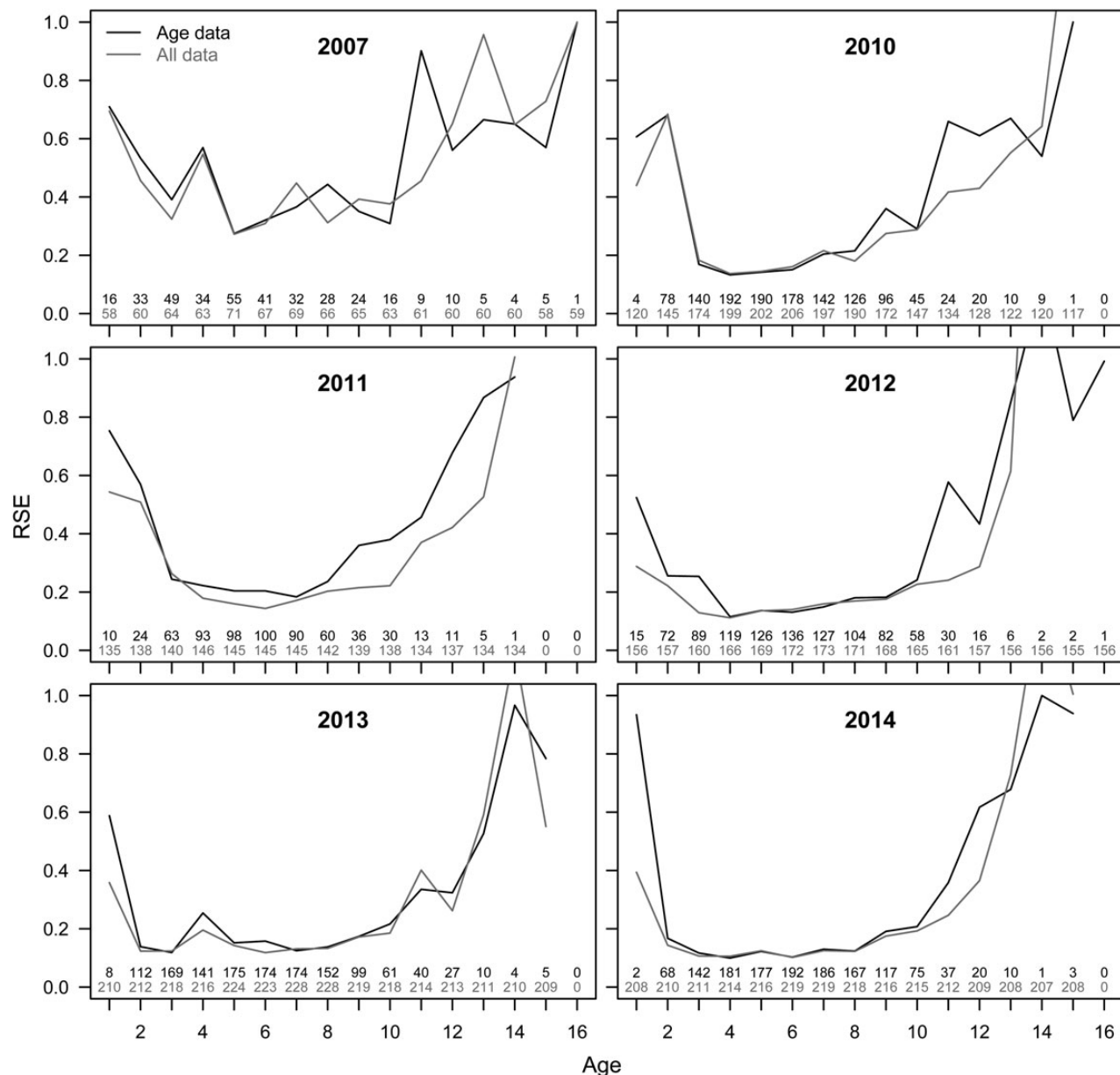
Figure 5. Estimated RSE for numbers-at-age of swept-area estimates of NEA mackerel in the ecosystem surveys for 2007 and 2010–2014 using only age data (black) and using all additional length data (grey). The numbers in black are the number of trawl stations where age is observed in the age data, while the numbers in green are the average number of trawl stations where age is observed when missing ages are imputed applying length data.

roughly in the western boundary that was covered by the 2007 survey. Although coverage in 2011 was limited in the northern part of the Norwegian Sea, this is likely to cause only minor bias due to small proportions of the stock in this area in 2010 and 2012 (Tables 4 and 5). For the other years, the variation in coverage was more related to lack of knowledge about the ongoing expansion of the stock at that time. Thus, the entire horizontal summer distribution area for mackerel was not covered in any of the years. However, coverage was relatively good in 2012–2014, reaching zero abundance (zero lines) of mackerel in most areas, except towards the west in Greenland waters, south in the North Sea, and west of the British Isles. In these years, the survey design was partly adaptive with continuation on transects in northern and

western directions as long as mackerel were caught with the pelagic trawl. In contrast to the coverage, the survey period has been relatively fixed (Table 1).

Mackerel in the "southern" areas, i.e. the portion of the mackerel stock that was not covered by the summer surveys, are naturally not considered in the swept-area abundance indices. If mackerel abundance in the south varies proportionally to the abundance estimated in the "northern" summer feeding areas, i.e. is a fixed proportion of the surveyed stock, then the swept-area biomass estimate is an unbiased estimator of the total stock. Acoustic surveys and bottom-trawl sampling indicate increasing biomass of mackerel in the North Sea during the feeding season in recent years (Fässler *et al.,* 2014). In 2013, a survey covering
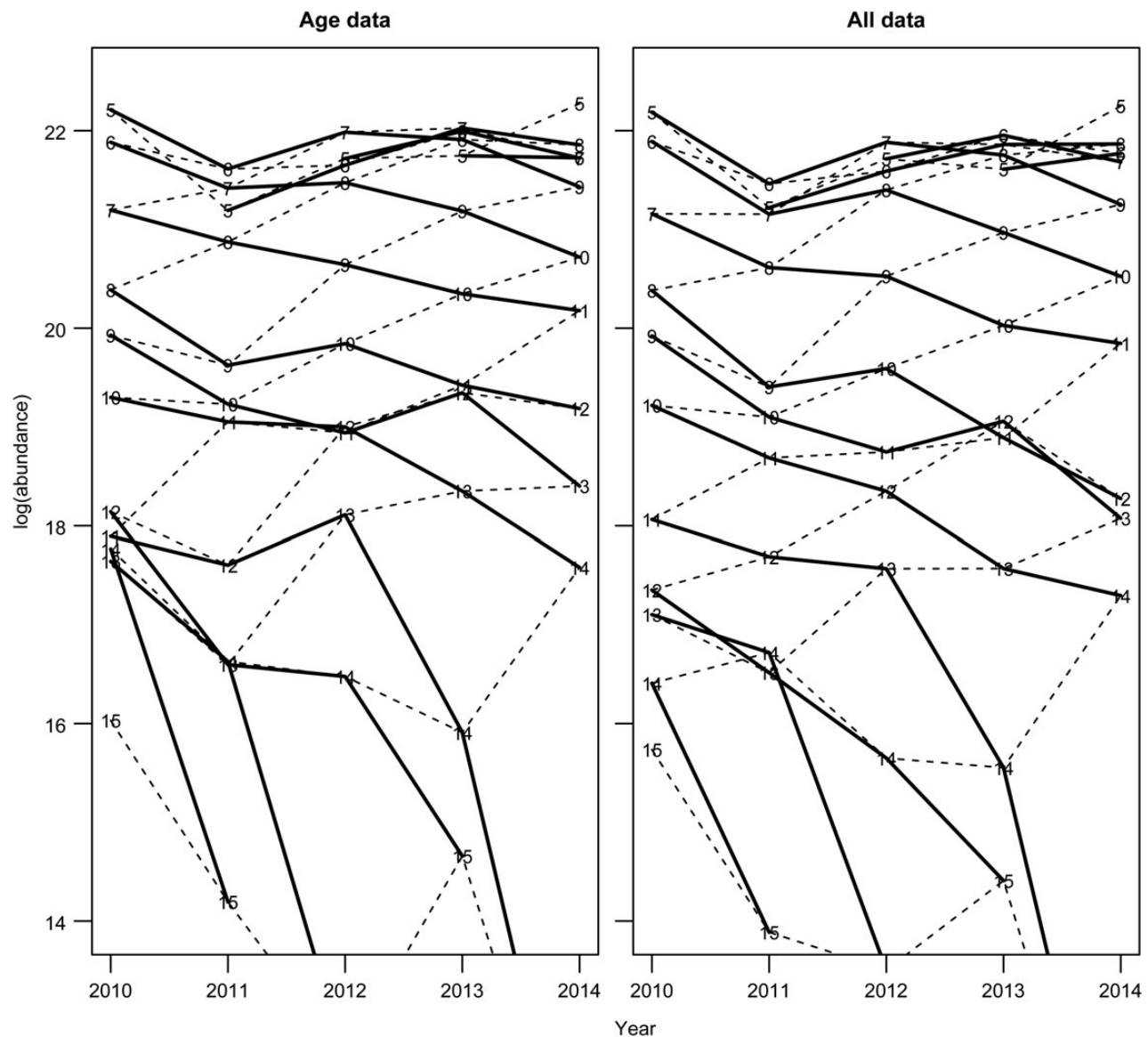
Figure 6. Catch curves for NEA mackerel in the ecosystem surveys at ages 5 – 15 for 2010 – 2014 using only age data (left) and using all additional length data (right). The solid lines trace the log total abundance of each cohort and the broken lines the ages.

parts of the southern areas, i.e. the North Sea and west of Scotland (superstratum E, Figure 1), was attempted. Mackerel were found to be distributed close to the surface in relatively high concentrations in the North Sea, while less mackerel were found in surface waters west of Scotland. Both surveys and the fishery confirm that mackerel also are feeding in the southern (EU) areas during summer (Fässler *et al.,* 2014; ICES, 2014a). Therefore, the presence of mackerel farther north and west is due to increased feeding habitat and not a shift in the spatial distribution (ICES, 2013a, 2014b). A challenge might arise if the age structure of the southern mackerel is different from that in the northern feeding area. Further, there may be some methodological difficulties in sampling these southern waters with pelagic surface trawling due to possible differences in feeding behaviour in the rather shallow North Sea.

Another issue contributing to uncertainty in the results is variability in the size of trawls and towing speed between and within years. Different trawls have different catchability and selectivity,

and the effects on the survey results are not clear. For example, a relatively small trawl was used by the Icelandic vessel in 2010 with lower catch efficiency due to only 16.5 m vertical opening (Table 2). Moreover, the Norwegian vessels used larger pelagic trawls in 2007 − 2011 with larger effective trawl openings including vertical trawl depths down to 40 m, compared with the Multpelt 832 trawl used in 2012 − 2014, which has a vertical trawl opening of 30 − 35 m. Very few mackerel schools were observed deeper than 30 m based on a multibeam sonar study in July 2010 (Nøttestad *et al.,* 2015), and echosounder investigation in July 2013 (Pena *et al.,* 2014). Thus, the majority of the mackerel were equally well accessible by all trawls. Low variability in catchability with different trawls is also indirectly supported by strong internal consistency and smooth catch curves for the survey indices.

Development of the Multpelt 832 trawl in 2011 and adherence to a comprehensive operational protocol for trawling was needed to ensure that the IESSNS provides standardized annual data on
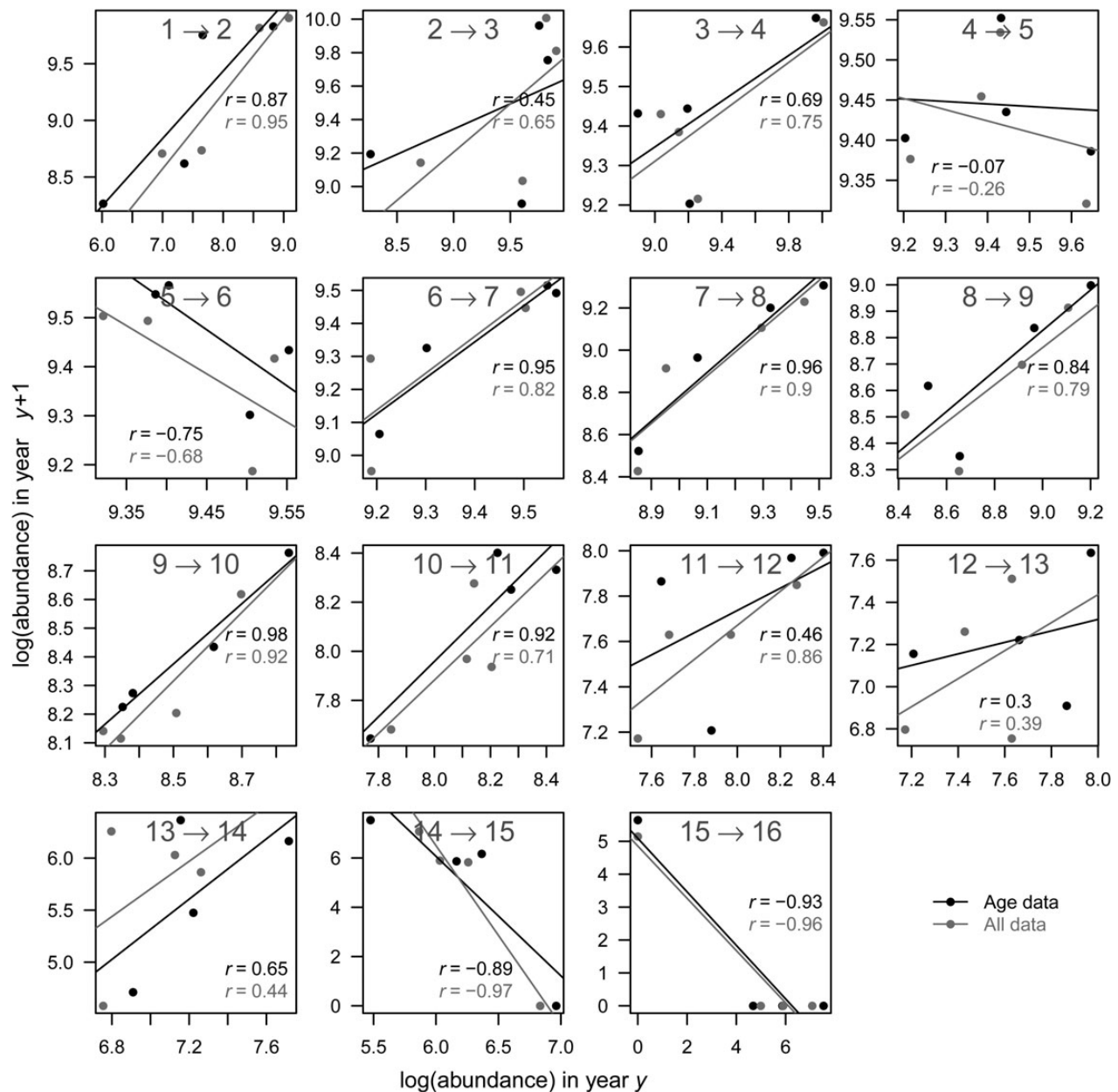
Figure 7. Internal consistency for NEA mackerel in the ecosystem surveys for ages 1–16 in 2010–2014 using only age data (black) and using all additional length data (grey). Internal consistency is measured by the linear relationship between the log numbers-at-age in year *y* vs. the log numbers-at-age+1 in year *y* + 1, where the title indicates the different transitions. The linear correlation is shown as the legend in each figure.

abundance of the NEA mackerel (ICES, 2013e). This trawl is designed to catch mackerel at depths of 0–35 m. This choice of design was based on previous knowledge about the vertical distribution of mackerel during the summer feeding period. Mackerel are predominantly distributed above the thermocline, which is mainly shallower than 20–40 m during summer in the Nordic seas (Nilsen and Falck, 2006). The highest concentrations of zooplankton both during day and night are also found above the thermocline, which likely explains why most mackerel are also distributed near the surface during the summer feeding period. Thus, the design of the Multpelt trawl accounts for the behaviour of mackerel in summer, characterized by small school sizes and near-surface distribution (Godø *et al.*, 2004; Nøttestad *et al.*, 2015).

The main sources of bias in the time-series of swept-area indices of abundance for the total spawning stock can be summarized as follows: (i) incomplete and variable spatial coverage of the summer feeding distribution in all years which would lead to a negative bias; (ii) herding of mackerel into the trawl path by the trawl doors and sweeps, in addition to the curved towing procedures, which possibly could scare fish into the trawl path and thus lead to positive bias; (iii) spatial and temporal variation in the portion of mackerel in the water column beneath the trawl; and (iv) escapement through the meshes or loss during hauling. Further, slow towing speed might cause larger fish to escape the trawl, thus biasing the age composition of the relative abundance estimates. We know at least that some mackerel are distributed below the

trawl opening, causing a negative bias. It is further assumed that all mackerel are caught inside the width of the trawl opening, and all mackerel are caught in the vertical dimension including all depths. The curved "banana" towing was done to avoid trawling inside the vessel's wake where avoidance likely could lead to a reduction in mackerel in the water column. We also assume that the catch in numbers per area swept is the same for 30 min and 1 h tows. Several studies for bottom-trawl surveys show minimal effect of tow duration on catch rates (e.g. Godø *et al.*, 1990; Pennington and Vølstad, 1991; Pennington *et al.*, 2002), but we are not aware of such studies for pelagic trawl surveys. Unfortunately, there are not sufficient data to quantify the magnitude of bias due to the various sources, but the ability to follow cohorts through time, as demonstrated by the catch curves, suggests that the various sources of bias are fairly stable over time and that the estimates do track the stock abundance. It should, however, be noted that the short duration of the time-series weakens the robustness of the conclusion.

In the Northwest Atlantic, swept-area bottom-trawl surveys targeting mackerel have been used in winter and early spring to monitor the distribution of the stock for the last $40+$ years (Overholtz *et al.*, 2011). Those surveys are based on a stratified random design, with spatial strata defined primarily based on bottom depth. A small bottom trawl was rigged with rollers where the height of the opening was only 2 m and the wing spread was 11 m (Azarovitz, 1981). The surveys were undertaken when the mackerel are close to the bottom during winter and early spring, only covering the continental shelf in US waters and thus much more limited both in space and time than the IESSNS. Mackerel behaviour is also significantly different in March during the wintering and spawning season in the Northwest Atlantic, compared with the feeding period in July–August in the NEA. During the feeding period in summer, mackerel are predominantly in the upper water layers feeding on available planktivorous prey species in small and dispersed shoals with low densities (Godø *et al.*, 2004; Nøttestad *et al.*, 2015). In contrast, during the wintering and prespawning period in March, mackerel are practically not feeding, stay deep close to the bottom, have a high degree of patchiness, aggregate in large and dense shoals for protection from predators, and further reduce their swimming behaviour to save energy before spawning (Iversen, 2004).

In general, age samples were only collected from a subsample of 25 fish within each station from the 100 fish that were measured for length in this survey. A number of studies (e.g. Stewart and Hamel, 2014; Aanes and Vølstad, 2015) have shown that it is sufficient to collect ca. 10–20 ages from each station to estimate the age distribution and that larger numbers of age samples will only marginally improve the precision in estimates of age composition, since variance is driven by the number of PSUs sampled (number of trawl stations). Results in this study show that the use of extra length samples within trawl stations and the extra trawl stations with length-only samples increased the precision in the estimates of abundance indices at age for age groups that occur in small proportions or in few trawl hauls. The improved precision achieved for mackerel by also including only length-measured fish was higher than observed for Northeast Arctic cod (*Gadus morhua*; Aanes and Vølstad, 2015). This suggests that the length-at-age of mackerel is fairly stable in the survey area.

The only fishery-independent information used as a tuning series in the stock assessment of mackerel until 2014 was a triennial SSB index from 1992 to 2013 (ICES, 2013c). The mackerel egg survey does not provide information about the age composition of the total stock. Since 2014, data used for tuning the assessment model also included age-disaggregated density indices for ages 6–11 (as number of individuals per surveyed km^2) from this summer survey (ICES, 2014a, b). However, also including the abundance indices for ages 3–5 may be beneficial for the NEA mackerel assessment as there are no other fishery-independent tuning indices for the young mature fish currently available. We postulate that the survey captures the main trend of an increasing mackerel stock, a horizontal expansion, and an overall increasing density from 2007 to 2014. The precision estimates of the age-disaggregated abundance indices in combination with analyses of internal consistency suggest that the indices of ages 3–12 years provide a reliable tuning series for stock assessment, although the entire distribution of mackerel may not be covered in some of the survey years. The time-series is, however, still relatively short, and the interannual variability in survey coverage might have produced variable catchability of the younger fish. We do note that although there is poor internal consistency for ages 5–6, the abundance indices for the same age groups are relatively precise with estimated low RSE, which also indicates that these age groups could be used in the stock assessment soon. The sizes of these cohorts have in recent years been of similar magnitude and, therefore, it is difficult to track the cohorts using the standard measure of internal consistency. With careful behavioural studies of the capture process, adequate survey coverage, and further standardization of the trawling procedures, it should be possible to improve consistency in the age-disaggregated indices for all age groups.

In conclusion, the present paper has demonstrated a large-scale change in the distribution, abundance, and density of NEA mackerel during summer in 2007–2014. Such novel quantitative information is basic for various studies of mackerel biology and its role in the ecosystems. Furthermore, the study has provided a new fishery-independent time-series of age-disaggregated abundance indices with precision estimates considered suitable as a tuning series for ages 3–12 in the stock assessment of NEA mackerel. Such indices have previously been lacking for the mackerel assessment. Hence, the results from the IESSNS appear to provide valuable information on abundance, distribution, and density of NEA mackerel that can improve the assessment and advice used for management of this stock.

References

Aanes, S., and Vølstad, J. H. 2015. Efficient statistical estimators and sampling strategies for estimating the age composition of fish. Canadian Journal of Fisheries and Aquatic Sciences, 72: 938–953.

Aglen, A. 1996. Impact of fish distribution and species composition on the relationship between acoustic and swept area estimates of fish density. ICES Journal of Marine Science, 53: 501–505.

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., and Óskarsson, G. J. 2012. Climate-related variations in the occurrence and distribution of mackerel (*Scomber scombrus*) in Icelandic waters. ICES Journal of Marine Science, 69: 1289–1297.

Azarovitz, T. R. 1981. A brief historical review of the Woods Hole Laboratory trawl survey time series. Canadian Special Publication of Fisheries and Aquatic Sciences, 58: 62–67.

Berg, C. W., and Kristensen, K. 2012. Spatial age–length key modelling using continuation ratio logits. Fisheries Research, 129: 119–126.

Berg, M. D., Kreveld, M. V., Overmars, M., and Schwarzkopf, O. 1997. Computational Geometry—Algorithms and Applications. Springer, New York. 365 pp.

Berge, J., Heggland, K., Lønne, O. J., Cottier, F., Hop, H., Gabrielsen, G. W., Nøttestad, L., *et al.* 2015. First records of Atlantic mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. Arctic, 68: 54–61.

Casella, G., and Berger, R. L. 1990. Statistical Inference. Wadsworth, Belmont, CA. 660 pp.

Christman, M. C., Curti, K., Houde, E. D., Lowensteiner, D., Nye, J. A., Muffley, B., and Vølstad, J. H. 2003. Abundance, distribution and diversity of Chesapeake Bay fishes: results from CHESFIMS (Chesapeake Bay Fishery Independent Multispecies Fisheries Survey). University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory. REF: UMCES CBL 03-023.

Churnside, J. H., Tenningen, E., and Wilson, J. J. 2009. Comparison of data-processing algorithms for the lidar detection of mackerel in the Norwegian Sea. ICES Journal of Marine Science, 66: 1023–1028.

Cochran, W. G. 1977. Sampling Techniques, 3rd edn. John Wiley and Sons, New York. 428 pp.

Debes, H., Homrum, E., Jacobsen, J. A., Hátún, H., and Danielsen, J. 2012. The feeding ecology of pelagic fish in the southwestern Norwegian Sea—Inter species food competition between herring (*Clupea harengus*) and mackerel (*Scomber scombrus*). ICES Document CM 2012/M: 07. 19 pp.

Dunn, R., and Harrison, A. R. 1993. Two-dimensional systematic sampling of land use. Applied Statistics, 42: 585–601.

Fässler, S. M., van der Kooij, M., Lusseau, J. S., Nolan, M. C., and Utne, K. R. 2014. Comparison of acoustic mackerel data from the HERAS and IBTS Q3 surveys with estimates form IESSNS in overlapping areas south of 62°N. *In* Report of the Benchmark Workshop on Pelagic Stocks (WKPELA), 17–21 February 2014, Copenhagen, Denmark. ICES Document CM 2014/ACOM: 43. 341 pp.

Foote, K. G. 1980. Importance of the swimbladder in acoustic scattering by fish: a comparison of gadoid and mackerel target strengths. Journal of the Acoustical Society of America, 67: 2084–2089.

Fuller, W. A. 2009. Sampling Statistics. John Wiley & Sons, New York. 454 pp.

Godø, O. R., Hjellvik, V., Iversen, S. A., Slotte, A., Tenningen, E., and Torkelsen, T. 2004. Behaviour of mackerel schools during summer feeding migration in the Norwegian Sea, as observed from fishing vessel sonars. ICES Journal of Marine Science, 61: 1093–1099.

Godø, O. R., Pennington, M., and Vølstad, J. H. 1990. Effect of tow duration on length composition of trawl catches. Fisheries Research, 9: 165–179.

Hamre, J. 1980. Biology, exploitation, and management of the Northeast Atlantic mackerel. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 212–242.

Harley, S. J., Myers, R., Barrowman, N., Bowen, K., and Admiro, R. 2001. Estimation of research trawl survey catchability for biomass reconstruction of the eastern Scotian Shelf. Canadian Scientific Advisory Section Resource Document. 2001/084. 50 pp.

Huse, G., Holst, J. C., Utne, K. R., Nøttestad, L., Melle, W., Slotte, A., Ottersen, G., *et al.* 2012. Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea—results of the INFERNO project. Marine Biology Research, 8: 415–419.

ICES. 2006. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (WGMHSA), 6–15 September 2005, Vigo, Spain. ICES Document CM 2006/ ACFM: 08. 615 pp.

ICES. 2007. Report of the Working Group on the Assessment of Mackerel, Horse Mackerel, Sardine and Anchovy (WGMHSA), 4–13 September 2007, ICES Headquarters. ICES Document CM 2007/ACFM: 31. 712 pp.

ICES. 2008. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 2–11 September 2008, ICES Headquarters, Copenhagen. ICES Document CM 2008/ACOM: 13. 691 pp.

ICES. 2009. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 2–8 September 2009, Copenhagen, Denmark. ICES Document CM 2009/ACOM: 12. 563 pp.

ICES. 2010. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 28 August–3 September 2010, Vigo, Spain. ICES Document CM 2010/ACOM: 15. 612 pp.

ICES. 2011. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 23–29 August 2011, ICES Headquarters, Copenhagen, Denmark. ICES Document CM 2011/ACOM: 15. 642 pp.

ICES. 2012. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 21–27 August 2012, Lowestoft, United Kingdom. ICES Document CM 2012/ACOM: 15. 931 pp.

ICES. 2013a. Report of the Ad hoc Group on the Distribution and Migration of Northeast Atlantic Mackerel (AGDMM), 30–31 August 2011 and 29–31 May 2012, ICES Headquarters, Copenhagen. ICES Document CM 2013/ACOM: 58. 211 pp.

ICES. 2013b. Report of the Working Group on Mackerel and Horse Mackerel Egg Surveys (WGMEGS), By Correspondence. ICES Document CM 2013/SSGESST: 04. 144 pp.

ICES. 2013c. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 27 August–2 September 2013, ICES Headquarters, Copenhagen, Denmark. ICES Document CM 2013/ACOM: 15. 950 pp.

ICES. 2013d. Report of the Working Group on Improving Use of Survey Data for Assessment and Advice (WGISDAA), 19–21 March 2013, Marine Institute, Dublin, Ireland. ICES Document CM 2013/ SSGESST: 07. 22 pp.

ICES. 2013e. Report of the Workshop on Northeast Atlantic Mackerel Monitoring and Methodologies including Science and Industry Involvement (WKNAMMM), 25–28 February 2013, ICES Headquarters, Copenhagen and Hirtshals, Denmark. ICES Document CM 2013/SSGESST: 18. 33 pp.

ICES. 2014a. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 26 August–1 September 2014, ICES Headquarters, Copenhagen, Denmark. ICES Document CM 2014/ACOM: 15. 971 pp.

ICES. 2014b. Report of the Benchmark Workshop on Pelagic Stocks (WKPELA), 17–21 February 2014, Copenhagen, Denmark. ICES Document CM 2014/ACOM: 43. 341 pp.

ICES. 2014c. Section 9.3.17b. Mackerel in the Northeast Atlantic (combined Southern, Western and North Sea spawning components). Advice for 2015. *In* Report of the ICES Advisory Committee 2014. ICES Advice, 2014. Book 9.

ICES. 2015. Report of the Working Group of International Pelagic Surveys (WGIPS), 19–23 January 2015, ICES Headquarters, Copenhagen, Denmark. ICES Document CM 2015/SSGIEOM: 05. 279 pp.

Iversen, S. A. 2002. Changes in the perception of the migration of Northeast Atlantic mackerel during the last 100 years. ICES Marine Science Symposia, 215: 382–390.

Iversen, S. A. 2004. Mackerel and horse mackerel. *In* The Norwegian Sea Ecosystem, pp. 289–300. Ed. by H. R. Skjoldal. Tapir Academic Press, Trondheim, Norway. 559 pp.

Jansen, T., and Gislason, H. 2011. Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research, 31: 64–72.

Jansen, T., Kristensen, K., van der Kooij, J., Post, S., Campbell, A., Utne, K. R., Carrera, P., *et al.* 2015. Nursery areas and recruitment variation of Northeast Atlantic mackerel (*Scomber scombrus*). ICES Journal of Marine Science, 72: 1779–1789.

Jessen, R. J. 1978. Statistical Survey Techniques. John Wiley & Sons, New York. 520 pp.

Korn, E. L., and Graubard, B. I. 1999. Analyses of Health Surveys. John Wiley & Sons, New York. 408 pp.

Korneliussen, R. J. 2010. The acoustic identification of Atlantic mackerel. ICES Journal of Marine Science, 67: 1749–1758.

Langøy, H., Nøttestad, L., Skaret, G., Broms, C., and Fernö, A. 2012. Overlap in distribution and diets of Atlantic mackerel (*Scomber scombrus*), Norwegian spring-spawning herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*) in the Norwegian Sea during late summer. Marine Biology Research, 8: 442–460.

Lehtonen, R., and Pakhinen, E. 2004. Practical Methods for Design and Analysis of Complex Sample Surveys, 2nd edn. John Wiley & Sons, New York. 360 pp.

Nilsen, J. E. Ø., and Falck, E. 2006. Variations of mixed layer properties in the Norwegian Sea for the period 1948–1999. Progress in Oceanography, 70: 58–90.

Nøttestad, L., Diaz, J. E., Penã, H., Søiland, H., Huse, G., and Fernö, A. 2015. The feeding strategy of mackerel in the Norwegian Sea in relation to currents, temperature and prey. ICES Journal of Marine Science, doi:10.1093/icesjms/fsv239.

Nøttestad, L., Giske, J., Holst, J. C., and Huse, G. 1999. A length-based hypothesis to explain feeding migrations in pelagic fish. Canadian Journal of Fisheries and Aquatic Sciences, 56(Suppl. I): 26–34.

Nøttestad, L., Krafft, B. A., Anthonypillai, V., Bernasconi, M., Langård, L., Mørk, H. L., and Fernö, A. 2014a. Recent changes in distribution and relative abundance of cetaceans in the Norwegian Sea and their relationship with potential prey. Frontier in Ecology and Evolution, 83: 1–11.

Nøttestad, L., Sivle, L. D., Krafft, B. A., Langård, L., Anthonypillai, V., Bernasconi, M., Langøy, H., *et al.* 2014b. Prey selection of offshore killer whales *Orcinus orca* in the Northeast Atlantic in late summer: spatial associations with mackerel. Marine Ecology Progress Series, 499: 275–283.

O'Connell, C. P., and Zweifel, J. R. 1972. A laboratory study of particulate and filter feeding of the Pacific mackerel *(Scomber japonicus)*. Fisheries Bulletin US, 70: 973–981.

Óskarsson, G. J., Gudmundsdottir, A., Sveinbjörnsson, S., and Sigurðsson, Þ. 2015. Feeding ecology of mackerel and dietary overlap with herring in Icelandic waters. Marine Biology Research, doi: 10.1080/17451000.2015.1073327.

Overholtz, W. J., Hare, J. A., and Keith, M. 2011. Impacts of interannual environmental forcing and climate change on the distribution of Atlantic mackerel in the U.S. Northeast continental shelf. Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science, 3: 219–232.

Payne, M. R., Clausen, L. W., and Mosegaard, H. 2009. Finding the signal in the noise: objective data-selection criteria improve the assessment of western Baltic spring-spawning herring. ICES Journal of Marine Science, 66: 1673–1680.

Pena, H., Johnsen, E., and Ona, E. 2014. Acoustic measurements of mackerel close to the sea surface during surface trawling for evaluating the performance of the pelagic trawling. *In* Working Document (WD) submitted to meeting of the Benchmark Workshop on Pelagic Stocks (WKPELA), 17–21 February 2014, Copenhagen, Denmark. 18 pp.

Pennington, M. 1986. Some statistical techniques for estimating abundance indices from trawl surveys. Fishery Bulletin US, 84: 519–525.

Pennington, M., Burmeister, L. M., and Hjellvik, V. 2002. Assessing the precision of frequency distributions estimated from trawl-survey samples. Fishery Bulletin, 100: 74–80.

Pennington, M., and Vølstad, J. H. 1991. Optimum size of sampling unit for estimating the density of marine populations. Biometrics, 47: 717–723.

Prokopchuk, I., and Sentyabov, E. 2006. Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to *Calanus finmarchicus* distribution and temperature conditions. ICES Journal of Marine Science, 63: 117–127.

Punzon, A., and Villamor, B. 2009. Does the timing of the spawning migration change for the southern component of the Northeast Atlantic Mackerel (*Scomber scombrus*, L.1758)? An approximation using fishery analyses. Continental Shelf Research, 29: 1195–1204.

Quinn, T. J., and Deriso, R. B. 1999. Quantitative Fish Dynamics. Qxford University Press, New York. 560 pp.

Simmonds, J., and Maclennan, D. 2005. Fisheries Acoustics: Theory and Practice, 2nd edn. Blackwell Science, Fish and Aquatic Resources Series 10. 456 pp.

Simmonds, J., Portilla, E., Skagen, D., Beare, D., and Reid, D. 2010. Investigating agreement between different data sources using Bayesian state-space models: an application to estimating NE Atlantic mackerel catch and stock abundance. ICES Journal of Marine Science, 67: 1138–1153.

Slotte, A., Skagen, D., and Iversen, S. A. 2007. Size of mackerel in research vessel trawls and commercial purse-seine catches: implications from acoustic estimation. ICES Journal of Marine Science, 64: 989–994.

Stewart, I. J., and Hamel, O. S. 2014. Bootstrapping of sample sizes for length- or age-composition data used in stock assessments. Canadian Journal of Fisheries and Aquatic Sciences, 71: 581–588.

Tenningen, M., Slotte, A., and Skagen, D. 2011. Abundance estimation of Northeast Atlantic mackerel based on tag recapture data – A useful tool for stock assessment? Fisheries Research, 107: 68–74.

Trenkel, V. M., Huse, G., MacKenzie, B., Alvarez, P., Arizzabalaga, H., Castonguay, M., Goñi, N., *et al.* 2014. Comparative ecology of widely-distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts. Progress in Oceanography, 129: 219–243.

Uriarte, A., and Lucio, P. 2001. Migration of adult mackerel along the Atlantic European shelf edge from tagging experiment on the south of the Bay of Biscay in 1994. Fisheries Research, 50: 129–139.

Utne, K. R., Huse, G., Ottersen, G., Holst, J. C., Zabavnikov, V., Jacobsen, J. A., and Nøttestad, L. 2012. Horizontal distribution and overlap of planktivorous fish in the Norwegian Sea during summer 1995–2006, related to water temperature. Marine Biology Research, 8: 420–441.

Villamor, B., Abaunza, P., and Farina, A. C. 2004. Growth variability of mackerel (*Scomber scombrus*) off north and northwest Spain and a comparative review of the growth patterns in the Northeast Atlantic. Fisheries Research, 69: 107–121.

Williams, R. L. 2000. A note on robust variance estimation for cluster-correlated data. Biometrics, 56: 645–646.

Wolter, K. M. 1985. Introduction to Variance Estimation. Springer-Verlag, New York. 450 pp.

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