ICES Journal of Marine Science

ICES Journal of Marine Science (2016), 73(4), 1115-1126. doi:10.1093/icesjms/fsv243

Original Article

Opportunistically recorded acoustic data support Northeast Atlantic mackerel expansion theory

Jeroen van der Kooij^{1,2*}, Sascha M.M. Fässler³, David Stephens¹, Lisa Readdy¹, Beth E. Scott², and Beatriz A. Roel¹

¹Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK
 ²School of Biological Science, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK
 ³Wageningen Institute for Marine Resources and Ecosystem Studies (IMARES), PO Box 68, IJmuiden 1970 AB, The Netherlands

*Corresponding author: tel: +44 1502 524416; fax: +44 1502 513865; e-mail: jeroen.vanderkooij@cefas.co.uk

van der Kooij, J., Fässler, S. M.M., Stephens, D., Readdy, L., Scott, B. E., and Roel, B. A. Opportunistically recorded acoustic data support Northeast Atlantic mackerel expansion theory. – ICES Journal of Marine Science, 73: 1115–1126.

Received 21 July 2015; revised 15 November 2015; accepted 17 November 2015; advance access publication 19 December 2015.

Fisheries independent monitoring of widely distributed pelagic fish species which conduct large seasonal migrations is logistically complex and expensive. One of the commercially most important examples of such a species in the Northeast Atlantic Ocean is mackerel for which up to recently only an international triennial egg survey contributed to the stock assessment. In this study, we explore whether fisheries acoustic data, recorded opportunistically during the English component of the North Sea International Bottom Trawl Survey, can contribute to an improved understanding of mackerel distribution and provide supplementary data to existing dedicated monitoring surveys. Using a previously published multifrequency acoustic mackerel detection algorithm, we extracted the distribution and abundance of schooling mackerel for the whole of the North Sea during August and September between 2007 and 2013. The spatio-temporal coverage of this unique dataset is of particular interest because it includes part of the unsurveyed summer mackerel feeding grounds in the northern North Sea. Recent increases in landings in Icelandic waters during this season suggested that changes have occurred in the mackerel feeding distribution. Thus far it is poorly understood whether these changes are due to a shift, i.e. mackerel moving away from their traditional feeding grounds in the northern North Sea and southern Norwegian Sea, or whether the species' distribution has expanded. We therefore explored whether acoustically derived biomass of schooling mackerel declined in the northern North Sea during the study period, which would suggest a shift in mackerel distribution rather than an expansion. The results of this study show that in the North Sea, schooling mackerel abundance has increased and that its distribution in this area has not changed over this period. Both of these findings provide, to our knowledge, the first evidence in support of the hypothesis that mackerel have expanded their distribution rather than moved away.

Keywords: feeding season, fisheries acoustics, NEA mackerel, North Sea, Scomber scombrus, ships of opportunity, widely distributed species.

Introduction

Mackerel (*Scomber scombrus*) is one of the most valuable commercial pelagic fish species in Northeast Atlantic (NEA) waters, but it also plays an important role in the ecosystem acting both as predator of zooplankton and small pelagic fish (e.g. Pepin *et al.*, 1987; Knudsen *et al.*, 2009; Langøy *et al.*, 2012) and, in turn, providing food for apex predators such as marine mammals (De Pierrepont *et al.*, 2005; Spitz *et al.*, 2013), birds (Garthe *et al.*, 2007) and pelagic sharks (Stevens, 1973; Ellis and Shackley, 1995). Effective management is therefore of crucial importance. However, mackerel is one of the most widespread pelagic species in the NEA Ocean, conducting large seasonal migrations which makes monitoring logistically complex and expensive. NEA mackerel are considered to consist of three spawning components. The largest one spawns in western waters ("western" mackerel) along the edge of the continental shelf from the northern Scottish coast south to the Bay of Biscay. The highest egg densities are found to the west and south of Ireland (ICES, 2011a). Mackerel spawning north of the Iberian Peninsula are considered a separate stock ("southern" mackerel), although the scientific evidence of this is not conclusive: while genetic studies support this separation (Nesbo *et al.* 2000), tagging studies suggested mixing occurred during the feeding season (Uriarte *et al.*, 2001).

International Council for the Exploration of the Sea

eil International nou

A third much smaller population spawns in the North Sea. Recent work comparing larval time series between the 1950s and 1970 s suggested that the spawning dynamics are more complicated and that the North Sea spawning stock should not be considered an isolated natal homing stock but instead is linked with the western spawning population (Jansen and Gislason, 2013).

Until recently, the only fisheries independent survey used for management of the NEA mackerel stocks was the triennial egg survey (ICES, 2014a), which estimates total egg production through an extensive international collaborative survey effort every 3 years. The survey has provided a valuable time series of mackerel spawning information covering several decades. However, the recent surveys covering the spawning area in western waters found that the distribution of mackerel eggs extended further west than had previously been observed (ICES, 2011a) and that spawning has started earlier (ICES, 2011a) posing challenges to the survey design. In the North Sea, an analysis of a mackerel larvae time series obtained from the continuous plankton recorder suggested that the mackerel spawning area had shifted from the traditional area in the central North Sea to western and southern parts (Jansen et al. 2012a). Hence, achieving full spatial coverage may be challenging for both the North Sea- and the western shelf triennial egg surveys given changes in spawning mackerel distribution. Furthermore, recent work indicates that mackerel may be indeterminate spawners and that it may therefore not be possible to estimate fecundity, a key parameter to convert egg abundance into spawning-stock biomass (SSB; ICES, 2011a). The details on the possible implications for management are not known, but it highlights the need for additional data sources.

The changes in spawning locations are just one example of the seeming adaptability of NEA mackerel behaviour to changing conditions (Trenkel et al., 2014). During the last decades, several changes have been observed in the temporal and spatial patterns of NEA mackerel (Jansen et al., 2012b; ICES, 2013a). One of the most significant of these changes took place in the North Sea in the 1970s when the local spawning stock collapsed (Lockwood, 1988; Jansen et al., 2012a; Jansen, 2014). Despite large numbers of western mackerel migrating into the Northern North Sea during autumn and winter (Reid et al., 2003, 2006), and a fishing ban during the early part of the year, there has been no sign of recovery of the North Sea stock. Reasons for this have been attributed to possible decreases in foraging opportunities due to increased windinduced turbulence and decreasing zooplankton concentrations (Jansen, 2014). Another factor could have been the fishery in the northern North Sea during autumn and winter which targeted mackerel which could have otherwise contributed to spawning in the North Sea (Jansen and Gislason, 2013).

Despite the poor state of the North Sea spawning component, the North Sea has remained important for NEA mackerel. In July and August, after spawning, the western population enters summer and autumn feeding grounds in the southern Norwegian Sea and the northern North Sea. Here the post-spawning mackerel from the west mix with those from the North Sea (Uriarte *et al.*, 2001). The extent of this mixing cannot be quantified at present due to a lack of methods for assigning individual mackerel to spawning components (Jansen and Gislason, 2013).

In the last few years, changes in the summer distribution of NEA mackerel were reported. Commercial landings suggested prevalence of mackerel in Icelandic waters (Astthorsson *et al.*, 2012; ICES, 2013a). While mature mackerel had traditionally been found here numbers were generally small. The start of a warm period from the mid-1990s coincided with an increase in mackerel landings.

More recently, also 0- and 1-groups mackerel have been observed in the area (Astthorsson et al., 2012). The increase in mackerel around Iceland during the summer feeding season meant that mackerel distribution has extended beyond the area regulated in the original management plan (ICES, 2013a). This has led to scientific and political disagreements about quota shares between the respective countries (e.g. http://www.bbc.co.uk/news/uk-scotlandnorth-east-orkney-shetland-26554619). One of the questions at the heart of this disagreement is whether this change is the result of a shift in distribution away from the North Sea or the result of a (north-) westward expansion of the western fraction of the NEA mackerel population. The relative distribution and biomass of mackerel in the waters of the various fishing nations targeting mackerel is likely to affect any future negotiations between parties. Furthermore, theoretical modelling (Hannesson, 2013) has highlighted the importance of the nature of the migration as a factor in determining the bargaining position of each of the parties, distinguishing between density-dependent migration where the mackerel migrates only if it exceeds a threshold density, or stochastic migration where migration is "random", directed by oceanographic conditions that vary randomly. Apart from the political significance, the important ecological role of mackerel in the North Sea ecosystem suggests that any changes in its distribution will have consequences for other species as well. Information on the distribution and biomass of mackerel in the most important feeding areas of the North and Nordic Seas is therefore required. A new international survey in Nordic waters started in 2007 and aimed, among others, at estimating the biomass of the main pelagic fish stocks using a swept-area approach from a number of predefined surface tows (IESSNS; ICES, 2014a). Preliminary results suggested the presence of large numbers of mackerel in the more northwestern waters of its distribution, including the Norwegian Sea. However, that survey series in its current form is relatively short (one survey in 2007 and annually from 2010 onwards) and spatial coverage has been variable, so the results from new methodologies need to be compared with and combined with those from other methods for the stock assessment to be reliable. Crucially, the survey does not routinely cover the northern North Sea, traditionally an important area for mackerel feeding. Although existing pelagic surveys in the area have started to widen the scope beyond the original target species (e.g. North Sea pelagic survey HERAS; ICES, 2015), there are no dedicated fisheries independent surveys targeting mackerel during summer in the North Sea. In addition, even if sufficient funds were available to conduct a survey that would cover the entire distribution of mackerel, there is currently no single accepted method that adequately assesses mackerel in the various areas of its distribution due to the regionally different feeding behaviours and differences in vertical distribution within the water column (Anon., 2009). It is nonetheless important to have a better understanding of mackerel distribution at this time of year as from 2010 to 2013 half of the total annual commercial mackerel landings were taken during the summer feeding period (Quarter 3, ICES, 2013b). Perhaps without an improved understanding necessary to underpin management, continued changes in mackerel distribution may lead potential new mackerel fishing nations to set their own quota to the detriment of the NEA mackerel population.

In this study, we present a new time series of mackerel data from the North Sea during the summer feeding season. The data were obtained by applying an existing mackerel detection algorithm to multifrequency acoustic data, opportunistically recorded aboard the annual August North Sea International Bottom Trawl Survey between 2007 and 2013. It offers a unique opportunity to investigate trends in biomass and spatial patterns in the distribution of schooling mackerel in this traditionally important feeding area, during a period when significant changes have been observed in other parts of its range. Specifically, we aimed to establish whether the recent increase in numbers of mackerel recorded in waters around Iceland and in the Norwegian Sea were the result of an expansion of the stock or a northwest-ward shift in distribution away from the traditional feeding area. If these changes were the result of a shift we expected to observe a decline in annual mackerel abundance in the northern North Sea, possibly combined with a northward change in distribution of mackerel in the northern North Sea. The results are discussed in light of the current knowledge about mackerel behaviour during summer.

Material and methods Survey and acoustic data acquisition

Acoustic data were collected during the Quarter 3 (August–September) International Bottom Trawl Survey (IBTS; ICES, 2013c). The Q3 IBTS is an internationally coordinated survey which aims at providing fisheries independent data to underpin management of demersal fish species, although pelagic species such as mackerel are also frequently caught. A range of vessels contribute to this survey and various components are standardized including the use of the bottom trawl, the Grand Ouverture Verticale, which has a vertical opening of 4-5 m. The current study is based on data collected from 2007 to 2013 during the English component of the IBTS, aboard the *RV Cefas Endeavour*.

The survey duration is a month, typically starting in the first week of August every year. It covers \sim 72 standard bottom trawl stations which are evenly distributed across the entire North Sea (Figure 1). Multifrequency (38, 120, and 200 kHz) acoustic data were recorded and provided coverage of the water column across the North Sea during the steam between stations. Although the order at which the stations are sampled varies from year to year, the survey generally starts in the south and gradually moves north by zigzagging across the North Sea in east-westerly orientated "transects". The three split-beam transducers on the RV Cefas Endeavour were mounted on a drop-keel, deployed at \sim 2 m below the hull (7.7 m below the surface) and their proximity meets recommendations for multifrequency data collection with near-optimum beam overlap (Korneliussen et al. 2008). Ping rate was set to 1 s^{-1} , pulse duration to 0.512 ms, and power setting for 38, 120, and 200 kHz to 2000, 250, and 105 W, respectively. The only exception was during 2007 and 2008, when the pulse duration for the 120 kHz was set to 0.256 ms to correspond to the settings of the available 120 kHz calibration (Table 1).

Acoustic data acquisition was a peripheral aim during the survey and consequently lacked some of the operating standards recommended for dedicated acoustic surveys (e.g. Simmonds and MacLennan, 2005; Korneliussen *et al.*, 2008). There was for example no opportunity to conduct echosounder calibrations during the survey (Foote *et al.*, 1987); acoustic data acquisition was generally monitored by the scientist in charge after relevant settings (existing calibration files and above details) had been loaded by an acoustician at the start of the survey. The unsupervised nature of data acquisition compromised data quality on some occasions: in both 2009 and 2013 technical issues with the network a few days into the survey resulted in a loss of data collection for 2 weeks. Noise of an unknown source interfered with the 200 kHz in 2008 which resulted in unsuitability of quantitative use of these data. During the first 2

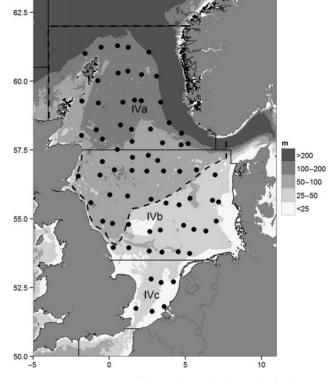


Figure 1. Overview map of the North Sea displaying the bathymetry and positions of the fixed trawl stations (black dots) of the English component of the Q3 (August – September) International Bottom Trawl Survey. Boundaries delineating the three relevant ICES Divisions (roman numerical) are emboldened; the boundary of the 50 m depth stratum is represented by the dashed line.

years (2007 and 2008) acoustic data were only recorded during daylight hours, whereas from 2009 onwards acoustic data were recorded continuously for 24 h.

Acoustic processing: extracting schooling mackerel

Frequency-specific calibration settings obtained during calibration exercises nearest to the specific survey were loaded (Table 1). Acoustic data were cleaned and processed in Echoview software (Myriax Software Pty Ltd, Hobart, Tasmania, Australia) which included: removal of data shallower than 13 m, attributed to the 7.7 m transducer depth plus a maximum of \sim 5 m of instable echoes within the nearfield of the 38 kHz transducer, and <1 m above the seabed ("deadzone"); exclusion of pings collected during stationary or slow vessel movement (e.g. trawling operations) and bad weather. A Background Noise Removal variable (De Robertis and Higginbottom, 2007), available in Echoview Software, was applied to the raw 200 kHz S_v echogram. The algorithm compensates for the effects of noise on echo-integration data by estimating the mean component attributable to noise, and removing this from the measurements. Importantly, the estimate of noise was also used to estimate the signal-to-noise ratio (SNR). A threshold based on the SNR was then applied which improved target detection in low SNR scenarios: at high frequencies; when acoustic targets are weak backscatterers, or weakly aggregated; when occurring deeper in the water column, or a combination of these factors (De Robertis and Higginbottom, 2007)

Mackerel backscatter was extracted from the fisheries acoustic data, using an existing multifrequency mackerel detection algorithm (Korneliussen, 2010), which was converted into Echoview

Table 1. Calibration settings for the three frequencies aboard the RV Cefas Endeavour.

	2006		2009			2012		2013		
Transducer type	ES38-B	ES120-7	ES38-B	ES120-7	ES200 – 7C	ES38-B	ES120-7	ES38-B	ES120-7C	ES200-7C
Absorption coefficient (dB km $^{-1}$)	9.3	40.4	9.9	33.1	46.7	8.9	42.9	8.2	44.0	67.3
Sound speed (m s^{-1})	1498.9	1498.9	1481.9	1481.9	1481.9	1506.5	1506.5	1516.3	1511.0	1511.0
Pulse duration (ms)	0.512	0.256	0.512	0.512	0.512	0.512	0.512	0.512	0.512	0.512
Power (W)	2000	500	2000	250	120	2000	250	2000	250	105
Transducer gain (dB)	24.57	25.44	24.73	25.44	26.76	24.61	26.3	22.85	26.76	26.79
Sa correction (dB)	-0.62	-0.79	-0.71	-0.50	-0.35	-0.56	-0.58	-0.87	-0.35	-0.35
Two wave beam angle (dB)	- 20.6	-20.8	-20.6	-20.8	-20.7	-20.6	-20.8	-20.6	-21.0	-20.7
Major axis 3 dB beam angle (degrees)	7.14	7.13	6.96	7.00	6.73	7.12	7.04	7.09	6.96	6.80
Minor axis 3 dB beam angle (degrees)	7.16	7.12	7.03	7.06	6.73	7.18	7.13	7.02	6.51	6.49

Please note that the 120 kHz in 2006 was calibrated at a pulse duration of 0.256 ms⁻¹. Therefore during 2007 and 2008, the pulse duration for the 120 kHz was kept at 0.256 ms⁻¹, whereas from 2009 onwards the pulse duration for all frequencies was set to 0.512 ms⁻¹. In 2012, no successful calibration was conducted on the 200 kHz echosounder. The 120 kHz transducer was replaced in 2013.

software. The dominant acoustic feature used in this algorithm to characterize mackerel was the typical frequency response of mackerel at the three operating frequencies. Unlike most other pelagic fish species, mackerel backscatter is stronger at 200 kHz than at 38 kHz, a feature that is mainly due to the species lacking a swimbladder (Gorska et al., 2005). In summary, the algorithm is based on a stepwise modular sequence of analyses. The two key steps include: (i) Categorization speedup, which represents a set of simple tests that are minimum requirements for a multifrequency datapoint to be considered as mackerel and included a number of simple threshold rules; (ii) allocation of a mackerel categorization value, or "similarity number" (S), which consisted of a test at a pixel level against known acoustic categories and the most probable acoustic category was connected to that pixel. This resulting number, ranging from 0 to 1 (with 1 representing "mackerel" and 0 "non-mackerel"), is referred to as similarity because in a mathematical sense it is not a probability (Korneliussen, 2010). The variable S was the product of three separate components: (i) The relative frequency response similarity (S_r) . The implemented values of the ideal relative frequency response, r(f), were based on measurements at sea and in pens (Korneliussen, 2010), but to account for interannual variation upper and lower bounds of the error-band at each frequency were included. In addition, as the ability of r(f) to identify mackerel differs between frequencies, the similarity numbers for each frequency were weighted. The values at 200 and 38 kHz were considered most important and were given four and two times the weight of the values at the less stable 120 kHz (Gorska et al., 2007), respectively. (ii) The backscatter strength similarity (S_{sv}) , which avoided very weak or strong scatterers. (iii) The geographical position similarity (S_{pos}) which was set to 1, reflecting the fact that the area is well known to be part of Mackerel's distribution range).

Although the above algorithm was applied at a pixel level, we focused on the schooling component of mackerel. There is anecdotal evidence that during summer at least part of the feeding mackerel population in the North Sea is more loosely dispersed. The relatively weak echoes makes these dispersed mackerel more difficult to distinguish from zooplankton scattering layers within which they are feeding, and we therefore could not confidently extract this mackerel component of unknown quantity. First, all strong marks, representing fish, were distinguished from weaker scatters in a virtual echogram which displayed the thresholded (-212 dB) sum of the three frequencies (Fernandes, 2009). Regions were drawn around all the resulting fish schools, using the SHAPES school detection algorithm (Barange, 1994) available within Echoview software. At this

stage, all fish schools were included, including those with acoustic properties characteristic of fish with swimbladders. However, only selected fish schools for which the average pixels within that school had a similarity value of 0.4 or higher were eventually retained in the final echogram and defined as mackerel. This number was chosen based on results from a pelagic survey where ground-truth hauls of mackerel were available (Peltic survey, Jansen *et al.*, 2015; ICES, 2015).

The school selection and extraction of mackerel data from the acoustic data was automated using a scripting module. As this method resulted in inclusion of small numbers of erroneously selected regions, a final visual scrutiny was conducted before analysis. These erroneously selected "schools" were often caused by interference and bad weather which were easily identified in the data. However, during the visual scrutiny process, particular focus was on the possible inclusion of sandeel echotraces, given the fact that the acoustic signature of sandeel schools (van der Kooij et al., 2008) has some overlap with those accepted within the error distribution of the mackerel algorithm. As part of this scrutiny individual frequency response graphs were plotted and were considered in combination with known behavioural (position in the water column, proximity to sandbanks, and clustering of schools) and morphological characteristics of schools. This process was too timeconsuming to apply to the entire dataseries, and as sandeels have a distinct distribution in the North Sea (Jensen et al., 2011), the focus was on two key areas in the North Sea where sandeels are most abundant: the Dogger Bank (in the central North Sea) and off the Northeast coast of Scotland.

To convert the acoustically derived densities to biomass, standard methods were used (e.g. Simmonds and MacLennan, 2005). We extracted the nautical area scattering coefficient (s_A) allocated to mackerel based on the algorithm at 200 kHz rather than the more conventional 38 kHz. The first reason for this was the possible inclusion of clupeid pixels within selected mackerel schools, which would lead to overestimation of mackerel within the school: although the mackerel detection algorithm would score individual pixels with the properties (S) of clupeids low, for a selected school to be identified as mackerel the average similarity index for all pixels within the boundaries of the school was required to be above the chosen threshold. The risk of occasional inclusion of a non-mackerel pixel would therefore in theory have been possible, so long as the average similarity remained within the defined boundaries. Although this would result in inflated mackerel backscatter when exporting either 38 or 200 kHz frequencies, the effects at 200 kHz are much smaller because mackerel target strength (TS) relative to fish with swimbladders could be as much as 8 dB higher at 200 kHz (Korneliussen, 2010). The second reason for using the mackerel backscatter at 200 kHz was the likely higher stability of the mackerel backscatter at 200 kHz than at 38 kHz, due to potential effects of temperature and fat content on scattering properties of the flesh, which is dominant at 38 kHz (Gorska et al., 2007, Korneliussen, 2010). These physical properties could have been the cause for occasional observations where mackerel schools, present in the 200 kHz echogram, were not visible at 38 kHz. The only mackerel TS values published to date are those at the conventional 38 kHz frequency. We therefore used a simple method (Saunders et al., 2012) to derive a mackerel TS at 200 kHz by using the frequency response equation (Korneliussen and Ona, 2003): r(f) = $s_{\rm v}(f)/s_{\rm v}(38)$. Here f = 200 kHz and r(200) = 3.4 (Korneliussen, pers. comm.). This represents 5.31 dB on the logarithmic scale, which was combined with the existing TS length relationship for mackerel at 38 kHz according to:

- (i) $TS_{38 \text{ kHz}} = 20 \log 10(L) 86.40 \text{ dB}$ (Misund and Beltestad, 1996) becomes
- (ii) $TS_{200 \text{ kHz}} = 20 \log 10(L) 86.40 \text{ dB} + 5.31 \text{ dB}$ which is:
- (iii) $TS_{200 \text{ kHz}} = 20 \log 10(L) 81.09 \text{ dB}.$

We acknowledge that the above method simplifies some of the complex acoustic properties of mackerel (Nesse et al., 2009), and considered this an interim solution until ongoing theoretical and field experiments yield a validated TS value at 200 kHz. To convert the acoustic density of mackerel to numbers, a mean length was required. Due to the absence of dedicated pelagic trawls during the survey, no in situ length frequency data were available. Therefore, we used length data from the bottom trawl catches of the English Q3 IBTS during which the acoustic data were collected. However, as bottom trawl-derived length data were thought not to be fully representative of fish size in midwater schools, we also extracted length data for each of the ICES Divisions, from North Sea mackerel landings (ICES, 2008, 2009, 2010, 2011b, 2012, 2013b, 2014b) at the same time of year (Q3: July-September). The landing-derived mackerel lengths were expected to be overestimates because of a minimum mackerel landing size of 30 cm in the North Sea. Biomass of the schooling component of mackerel was derived by ICES Division for each year using the associated bottom trawl-derived length data and a fixed lengthweight relationship based on fish collected during the IBTS survey (Silva et al., 2013).

As mentioned previously, coverage in 2009 and 2013 was incomplete for the southern North Sea, resulting in an absence of data for parts of ICES Divisions IVb and IVc. To ensure the time series was based on consistent annual survey coverage of the schooling mackerel distribution, a stratum was created based on the areas where depths were >50 m (Figure 1). This stratum overlapped with the area where most schooling mackerel was present. For this stratum, an alternative annual biomass estimate of the schooling component of mackerel was calculated using mackerel length from the survey trawls within the stratum.

Mackerel biomass and distribution

Spatial patterns in the annual biomass of schooling mackerel in the North Sea were investigated using the acoustic densities of schooling mackerel. Schooling mackerel backscatter per ICES rectangle $(1^{\circ} \text{ longitude by } 0.5^{\circ} \text{ latitude})$ were plotted for each of the annual

English IBTS surveys for visual exploration. To assess whether any shift occurred in the distribution of schooling mackerel from 2007 to 2013, the weighted distribution or centre of gravity was calculated (Engelhard *et al.*, 2011) using the backscatter values of the annual 1 nautical mile sampling units. Although in 2008 interference prevented the quantitative use of the data, the efficacy of the mackerel detection algorithm was not adversely affected and hence the distribution of acoustically derived mackerel was included. As the backscatter within the schools was likely to be higher due to inclusion of interference the centre of gravity for 2008 has to be used with caution.

Trends in schooling mackerel biomass estimates derived in this study were compared with two time series available for NEA mackerel: annual values of the SSB for the western component of NEA mackerel stock and 3-year values of the SSB for the North Sea component, both of which are derived from relevant triennial egg surveys (ICES, 2011a). The *annual* values for the western component of NEA SSB were derived in the assessment (ICES, 2013b) by fitting an integrated catch-at-age model following settings defined by benchmark assessments and which uses the SSB from the western triennial egg survey as the tuning index (ICES, 2014a). A similar model is not routinely used for the North Sea SSB and SSB was therefore only available for every third year.

Results

Schooling mackerel schools were less likely to be found at night compared with during the day (Pearson's χ^2 test: $\chi^2 = 121.7796$, d.f. = 1, $p < 2.2 \times 10^{-16}$), although there was no significant difference between the day and night (log-converted) acoustic densities (t =1.1759, p = 0.2437). Due to this diurnal effect and interannual differences in temporal coverage (daytime only in 2007 and 2008 vs. 24 h from 2009 onwards), and with an aim to provide a consistent time series, schooling mackerel distribution and biomass estimates were based on a subset of the data containing the daytime data only.

Mackerel distribution

The distribution of the acoustically derived schooling component of mackerel in the North Sea was consistent between 2007 and 2013 (Figure 2). Mackerel schools appeared to be prevalent in the north of the North Sea (ICES Divisions IV a and parts of b), with a noticeable absence in the southern North Sea (southern part of IVb and IVc). The highest acoustic densities were consistently found in the northern North Sea, particularly off northeastern Scotland/ Shetland and the Norwegian trench. Further south densities of schooling mackerel were found in the central and western parts of the North Sea. The centre of gravity by year confirmed very limited interannual change in mackerel distribution (Figure 3). The annual centres of gravity based on all data (not shown) and those based on the data within the stratum (Figure 3) were at nearly identical positions, confirming that the reduced coverage in the southern North Sea in 2009 and 2013 did not adversely affect the results.

Mackerel biomass

Patterns in the acoustically derived biomass of schooling mackerel remained fairly constant between 2007 and 2010 after which it increased until 2013 (Figure 4a). The trend was similar when biomass was calculated based on ICES Divisions and on the stratum. Between 99.6% (2010) and 100% of all annual acoustically observed mackerel schools were found within the stratum.

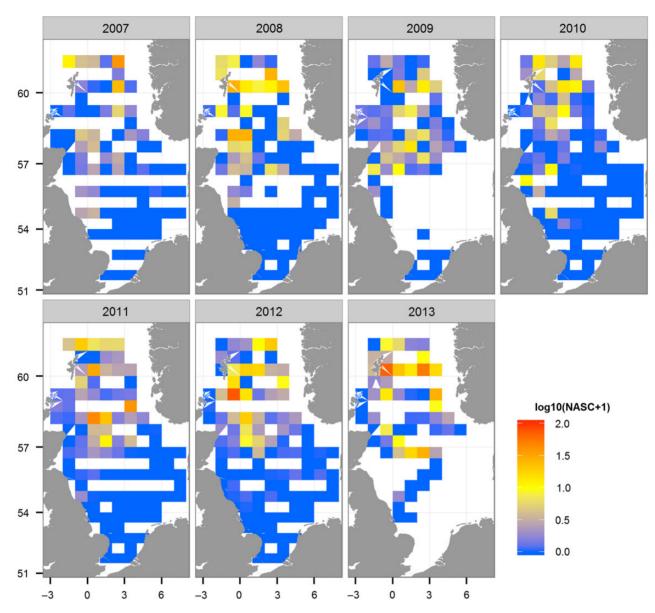


Figure 2. Annual maps of daytime acoustic densities of schooling mackerel at 200 kHz per ICES statistical rectangle (legend: log mean s_A in m² nautical mile⁻²) as derived from the Q3 International Bottom Trawl Surveys (2007 – 2013). Data were log transformed to enhance visibility of spatial patterns.

As expected, mean mackerel lengths by ICES Division were consistently higher in the commercial landings compared with those from the bottom trawls, apart from IVb in 2013 (Table 2; Figure 4b). The highest mean length was in 2007 (35.13 cm, IVa) and the largest length difference between the two datasets was in IVb in 2012 ($\Delta L = 7.0$ cm). Within both datasets, the largest mackerel were found in the northern North Sea (IVa, Table 2). The bottom trawl-derived mean lengths for the three divisions showed similar trends over the study period; increasing from 2007 to 2010, followed by a drop in mean length and increasing again in 2013. The landings derived lengths for IVb and IVc showed similar pattern as those from the bottom trawls, although they did not increase in 2013. In contrast, mean mackerel lengths from the commercial data for division IVa gradually decreased over the time series (by a total of 1.5 cm). The total acoustically derived

biomass values for the North Sea based on commercial length data (Table 2) were, on average, \sim 140 kt higher than those presented here (based on bottom trawl catches; Figure 4a). However, the offset varied between years with the largest difference in 2012 (354 kt). Consequently, despite similar overall patterns in the biomass time series based on landings derived length data, a reduction in the increase between 2012 and 2013 was observed, compared with the biomass trends based on the survey trawl-derived lengths (Table 2).

Mackerel biomass trends derived from other sources are shown for comparison in Figure 4c and d for the period 1999 to 2013. The SSB estimates based on the western egg survey remained below 2500 kt until 2007. From 2007, it increased sharply until its peak in 2011 (\sim 5000 kt) after which numbers fluctuated at high levels of \sim 4500 kt (Figure 4c). The biomass of the North Sea SSB

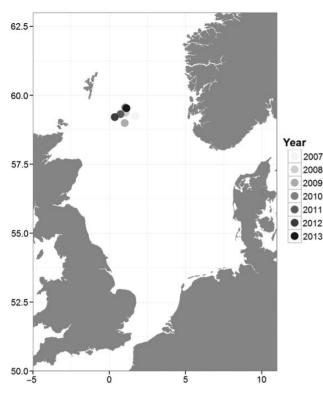


Figure 3. Annual-weighted mean distribution (centre of gravity) of acoustically derived mackerel schools in the North Sea within the stratum.

showed an increase up to 2005, followed by a strong decrease to 2008 and a small increase in 2011 (Figure 4d).

Discussion

In this study, we set out to investigate mackerel dynamics during the summer feeding period in the North Sea using a unique 7-year acoustic dataseries, recorded opportunistically during the Quarter 3 (O3) IBTS. To provide a consistent time series, two modifications were made to the data to address the interannual variability in temporal (daylight vs. 24 h sampling) and spatial (survey coverage) sampling. The former was addressed by focusing only on the acoustic data collected during the daytime and the latter by creating a stratum, consistently covered during all surveys, where the vast majority (>99.6%) of schooling mackerel were present. The time series (2007-2013) of acoustically derived biomass of schooling mackerel showed relatively little change from 2007 to 2010 after which a strong increase was observed. The absence of a decline in mackerel abundance in the northern North Sea provides strong evidence that the reported increase of mackerel in waters outside of the study area (north and northwestwards) is due to an expansion in the distribution of this species rather than a northwards shift. In addition, the results showed no substantial change in the distribution of mackerel schools in the North Sea during summer.

Mechanisms driving mackerel expansion

The reasons for the expansion of mackerel feeding areas to the north and northwest of the current study area are not fully understood, although combined effects of environmental conditions and an increase in the mackerel stock size are likely to play a role (ICES, 2013a). The SSB of NEA mackerel stock in the last 6 years has been at its highest for the last three decades. This has inevitably led to an increasing pressure on local food resources and, possibly compounded by small numbers of zooplankton prey in some parts of its traditional habitat (Norwegian Sea, ICES 2013d), is likely to have driven this expansion (Astthorsson *et al.*, 2012; ICES, 2013a, Olafsdottir *et al.*, 2016). As temperatures have increased in the north and northwestern extremities of the species' distribution, where colder temperatures were previously a limiting factor (ICES, 2013a), mackerel have been able to expand their range. The densitydependent effects were corroborated by recent studies which found strong negative correlations between stock size and growth of both juveniles and adults (Jansen & Burns, 2015; Olafsdottir *et al.*, 2016).

Summer mackerel migration and distribution in the North Sea

Mackerel from the western NEA spawning component migrate into the North Sea during summer and mix with those spawning in the North Sea, yet little is known about the extent of this mixing. We speculate about which component of the population is schooling and therefore captured in the acoustic data. The distribution of schooling mackerel in the North Sea appeared to be associated with those areas that are dominated by inflow of Atlantic water: the Fair Isle current between Orkney and Shetland, the East Shetland Atlantic Inflow, and the inflow near the Norwegian Deep (e.g. Reid et al., 1997). The southernmost schools in the west of the North Sea appeared to spatially overlap with the Scottish Coastal water current which runs south along the UK east coast until it meets the mixed waters off Flamborough (Turrell, 1992; Brown et al., 1999). This association with inflow of Atlantic waters from the north could suggest that most schooling mackerel were those from western waters rather than the North Sea.

A comparison between the acoustically derived biomass index with the western and North Sea SSB time series, suggested that the acoustically derived schooling index best resembled the trends in western NEA mackerel SSB. Both show an increase during the study period although for the acoustic index the period of strongest increase is between 2010 and 2013, whereas the western SSB appears to stabilize after 2011. The North Sea SSB shows a different pattern with a strong decrease before 2008 and only a small increase from 2008 to 2011. Due to the limited coincidence of the two time series, and, for the NS SBB, limited resolution, as well as uncertainties in the acoustic index, no further analysis was conducted but these results could be further evidence that the schooling component of mackerel in the North Sea is dominated by specimens that migrated from the western waters after the spawning season, rather than mackerel that spawn in the North Sea.

The continued increase in schooling mackerel biomass after 2011 is not reflected in the western SSB, which instead shows limited change between 2011 and 2013. This increase of mackerel in the North Sea relative to the SSB could be explained by a possible forward shift in timing of southward migrating mackerel that have been feeding in the Nordic seas. A density-dependent effect, demonstrated by observed reductions in mackerel growth and weight at length (Olafsdottir *et al.*, 2016), could have driven a premature migration of mackerel feeding in Nordic waters southward to the northern North Sea, in search of feeding grounds. Although this is possible, in 2013 schooling mackerel biomass in the northern North Sea (IVa) actually showed a decrease in growth, while the increase in mackerel biomass in the central North Sea (IVb) accelerated. This suggests that the same density-dependent processes that

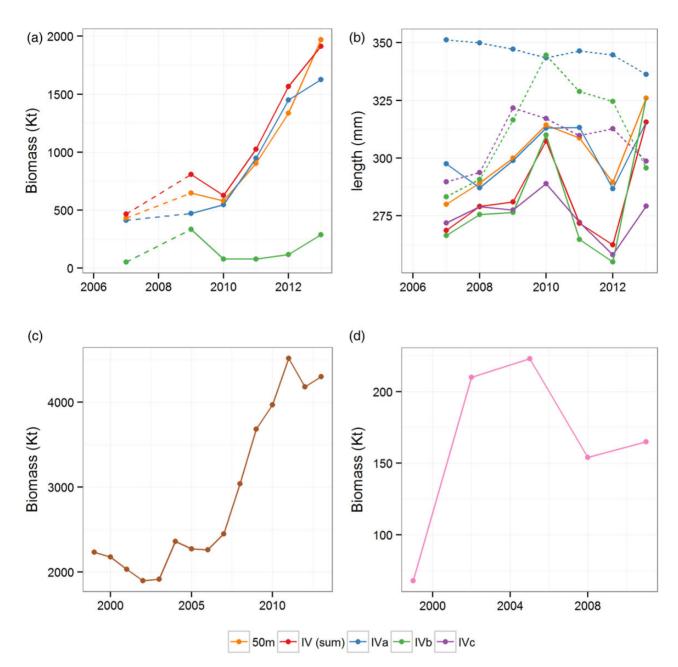


Figure 4. (a) Trends in acoustically derived schooling mackerel biomass collected during English IBTS (2008 was omitted for reasons discussed in the text) using mean mackerel lengths based on IBTS trawl catches (England only). (b) Mean mackerel lengths based on IBTS trawl catches (England only) during Q3 IBTS (solid lines) and from the commercial landings data during Q3 (dashed lines). (c) Annual estimates of SSB of western NEA mackerel (ICES, 2014b). (d) SSB of North Sea Spawning component derived from triennial egg survey, calculated for every third (survey) year (ICES, 2012). Note the different scaling on the *x*- and *y*-axis. North Sea subareas indicated by colours in legend.

forced mackerel to expand north and west ward also could have led mackerel to expand southward in 2013.

Effects of mackerel schooling and phenology

We emphasize that the trends in biomass and patterns in distribution presented here were based on the acoustically derived schooling mackerel only and dispersed mackerel were not included. Previous reports suggested that mackerel in the North Sea were mainly dispersed throughout the water column during summer (Anon., 2009). The presence of significant amounts of schooling mackerel suggests that mackerel feeding behaviour in the north of the North Sea (Misund, 1988, 1993) may instead be more comparable with that in the Norwegian Sea, where mackerel were found schooling, although predominantly in the top 40 m of the water column (Godø *et al.*, 2004). However, mackerel were caught, often in small numbers, at most bottom trawl stations in the North Sea, including in the south (not shown), which confirms that not all mackerel were captured by acoustic methods. Trawl and acoustic methods sample different components of the water column: the acoustic data covered all but the top 13 m below the surface and a small "deadzone" above the seabed. The bottom trawl catches in contrast sampled from the seabed to \sim 4 m above it and previous studies,

Table 2. Mean lengths (cm) and associated biomass (*t*) obtained from trawl survey catches and commercial landings, for ICES Divisions and years where acoustic backscatter was extracted on schooling mackerel.

		Trawl su	rvey	Commercial landings		
Year	ICES Division	Length	Biomass	Length	Biomass	
2007	IVa	29.76	412 929	35.13	498 516	
	IVb	26.65	53 494	28.33	57 334	
2008	IVa	28.71	_	34.99	-	
	IVb	27.50	_	29.08	-	
2009	IVa	29.90	473 045	34.72	560 575	
	IVb	27.65	335 470	31.65	391 116	
2010	IVa	31.88	547 880	34.34	596 171	
	IVb	31.03	78 201	34.47	88 090	
2011	IVa	31.33	949 272	34.64	1 064 015	
	IVb	26.47	77 643	32.89	99 338	
2012	IVa	28.97	1 450 563	34.48	1 767 507	
	IVb	25.44	116 960	32.46	154 201	
2013	IVa	31.59	1 668 182	33.63	1 791 059	
	IVb	32.78	562 175	29.57	500 124	

Biomass estimates in 2008 were not calculated due to interference in the acoustic data.

comparing concurrently collected acoustic and trawl data above the seabed on the North Sea IBTS, found no clear relationship between the two (e.g. Mackinson *et al.*, 2005).

We did not conduct a quantitative analysis on the mackerel caught in the bottom trawl because of the relatively small component of the water column sampled by this gear and, more important, because mackerel exhibit strong avoidance behaviour to most methods of trawling (Slotte et al., 2007). However, in the absence of midwater trawls on acoustically detected mackerel schools, we did use the bottom trawl catches to extract mackerel length data for the biomass calculations and it is likely that the larger faster swimming fish were not well represented in the catch. This is confirmed by the higher mean mackerel lengths in commercial landings and suggests that the presented biomass values were underestimates. However, given the enforced minimum landing size for mackerel in the North Sea, "true" mackerel length values probably lie somewhere in between the two. Despite the higher biomass values using lengths from the commercial catches, the general trends in mackerel biomass remained the same, other than a slight decrease in biomass growth in 2013. Another factor that may have influenced the observed trends in biomass is the fact that a fixed length-weight relationship for mackerel was used, based on ten years of bottom trawl survey data in the North Sea. Recent observations of a reduction in mackerel mean weight at length in the northern North Sea (Olafsdottir et al., 2016) would results in a reduction of the increasing trend in biomass towards the end of the time series. Both these uncertainties would be resolved by conducting pelagic trawls on mackerel schools during the IBTS.

The absence of acoustic data from the surface waters will have led to undersampling of mackerel. A recent case study (ICES, 2014a) compared the vertical distribution of acoustically derived mackerel schools in the northern North Sea from the 2013 North Sea herring survey and from the 2013 IBTS survey, with the swept-area-based mackerel estimates from the surface tows (estimated to sample the top 0-30 m) of the 2013 IESSNS survey which in this year also covered part of the northern North Sea. It concluded that the surface blind-zone was important for mackerel but it also demonstrated that, unlike in the Nordic Seas, the majority of mackerel in the northern North Sea were located below the area sampled by the surface trawl and were therefore available for acoustic sampling techniques. The current study demonstrated that a significant fraction of the stock aggregated in schools in the North Sea during summer which, to our knowledge, extended further south than has previously been reported.

Quality of acoustic data

The acoustic data from which mackerel biomass and distribution data were derived were opportunistically collected as part of an existing bottom trawl survey. Therefore, some of the conditions at which the data were recorded did not necessarily meet those that are aimed to be achieved during dedicated acoustic surveys. This includes the absences of a systematic survey design which is usually applied: as the acoustic densities recorded during steaming are expected to be representative of the mean acoustic densities for a certain area, bias due to over (or under-) sampling of specific habitats, is generally reduced by conducting parallel transects across bathymetrical features. In this study, the surveys' tracks followed a more random approach, resulting from the direct steam from one bottom trawl station to the next. However, as the survey track was conducted without any prior knowledge of mackerel distribution and because the trawl stations were evenly distributed across the North Sea, the resulting survey track covered the ICES rectangles evenly and without bias. Another important factor that could have affected the acoustic results was the absence of a dedicated calibration. However, as calibration settings conducted during other surveys (on the same vessel) were loaded, biofouling was regularly removed from the transducers, and as the Simrad EK60 system has been shown to be stable with minimal changes in transducer gain (Knudsen, 2009), we argue that it was justified to use the biomass estimates as a comparable and relative index. Ongoing theoretical work on the Target Strength of mackerel at 200 kHz will further contribute to more accurate acoustic biomass estimations. Misidentification of mackerel schools was also considered a source of uncertainty in the data. The algorithm has been demonstrated to correctly identify 94% of schools (Korneliussen, 2010) when using six operating frequencies. In this study, the algorithm was based on three frequencies and although that included the most important 38 and 200 kHz, several other schooling species have a frequency response that lies within the permitted error range of those described for mackerel Sandeels (Ammodytes spp.) generally have a stronger backscatter at 120 kHz than at 38 kHz (van der Kooij et al., 2008) although this is size dependent and particularly valid for 1-year-old fish (Johnsen et al., 2009). Because the mackerel algorithm included error bands, in theory some sandeel backscatter could have been (mis)identified as mackerel. However, the visual scrutiny process found no sandeel schools among those automatically classified as mackerel, and the complete absence of schools classified as mackerel (correctly or not) in one of the key sandeel habitats (Dogger Bank) confirmed that erroneous inclusion of sandeels elsewhere was unlikely to have played a significant role. Preliminary results on the frequency response of horse mackerel (Trachurus trachurus) show that the backscatter at 200 kHz is also higher than at 38 kHz (Fernandes et al., 2006), although on average no more than 1.5 times. It is therefore possible that small numbers of schools are misidentified. Addition of more frequencies would reduce the uncertainty, as would the use of pelagic ground-truth hauls. Given the success of the algorithm during other surveys where ground-truth hauls

were available (Peltic survey, ICES 2015; Jansen *et al.*, 2015), we are confident that the overall classification of mackerel was likely to be largely correct.

Recommendations

This study has demonstrated benefits of collecting acoustic data opportunistically on existing surveys, in this case focusing on a species which, due to its expansive distribution, large migrations, and regionally varying behaviour, is difficult and expensive to survey by other means. With increasing focus on more efficient use of costly research vessel time as well as a drive to concurrent sampling of increasing components of the marine environment it can also contribute to policy drivers such as the European Union Marine Strategy Framework Directive, a framework with the overall objective of achieving or maintaining Good Environmental Status in Europe's seas by 2020 (Anon., 2008). The current application is mainly suitable to species with unique acoustic properties, particularly when it is not possible to conduct ground-truth hauls to validate acoustic marks. Inclusion of additional frequencies would improve the confidence of the acoustic species identification, especially when the unique frequency responses of different species are more accurately defined.

The methods presented could be extrapolated to other existing surveys such as the triennial mackerel egg survey. Although acoustics are not recorded as standard, the position of plankton stations along equidistant transects, and the availability of pelagic trawling gear, currently mainly used to collect biological data on spawning mackerel, would make it particularly suitable. Indeed, applications can be found beyond scientific surveys, with most commercial fishing vessels using a range of different frequency echosounders. Although extracting biomass indices from the data will present challenges of a different nature, such as hyper-stability, they could provide a useful addition data source, where information is limited.

Acknowledgements

We are grateful to scientists and crew on the RV Cefas Endeavour during the IBTS surveys, particularly B. Harley, S. McCully, and A. Plirú for facilitating and monitoring the acoustic data acquisition. Peter Robinson is thanked for collating the ICES mackerel landings data and Andrew Campbell for the landing-based mean mackerel length data. This manuscript has benefited from valuable discussions at several ICES Working Groups and workshops, particularly WKPELA and WGFAST. We appreciate the critical and thorough comments of three anonymous reviewers and are particularly grateful for the insightful comments by the editor, Richard O'Driscoll. This study was funded by the UK Department for Environment, Food and Rural Affairs contract MF1112 (POSEIDON), with further contributions from the EU FP7 project FACTS. The template for the Echoview algorithm used in the paper is available on request from S.M.M.F. or J.v.d.K.

References

- Anon. 2008. Directive 2008/56/EC of the European Parliament and the Council of 17 June 2008 Establishing a Framework for Community Action in the Field of Marine Environmental Policy (Marine Strategy Framework Directive). http://ec.europa.eu/environment/water/ marine/index_en.htm.
- Anon. 2009. Report from the international meeting on mackerel distribution and migration in the Northeast Atlantic, Bergen, April 2009. 119 pp.
- 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.

- Barange, M. 1994. Acoustic identification, classification and structure of biological patchiness on the edge of the Agulhas Bank and its relation to frontal features. South African Journal of Marine Science, 14: 333–347.
- Brown, J., Hill, A. E., Fernand, L., and Horsburgh, K. J. 1999. Observations of a seasonal jet-like circulation at the Central North Sea Cold Pool Margin. Estuarine Coastal and Shelf Science, 48: 343–355.
- De Pierrepont, J. F., Dubois, B., Desormonts, S., Santos, M. B., and Robin, J. P. 2005. Stomach contents of English Channel cetaceans stranded on the coast of Normandy. Journal of the Marine Biological Association of the UK, 85: 1539–1546.
- De Robertis, A., and Higginbottom, I. 2007. A post-processing technique to estimate the signal-to-noise ratio and remove echosounder background noise. ICES Journal of Marine Science, 64: 1282–1291.
- Ellis, J. R., and Shackley, S. E. 1995. Notes on porbeagle shark, *Lamna nasus*, from the Bristol Channel. Journal of Fish Biology, 46: 368–370.
- Engelhard, G. H., Pinnegar, J. K., Kell, L. T., and Rijnsdorp, A. D. 2011. Nine decades of North Sea sole and plaice distribution. ICES Journal of Marine Science, 68: 1090–1104.
- Fernandes, P. G. 2009. Classification trees for species identification of fish-school echotraces. ICES Journal of Marine Science, 66: 1073–1080.
- Fernandes, P. G., Korneliussen, R. J., Lebourges-Dhaussy, A., Masse, J., Iglesias, M., Diner, N., Ona, E., *et al.* 2006. The SIMFAMI project: species identification methods from acoustic multifrequency information. Final Report to the EC Number Q5RS-2001-02054.
- Foote, K. G., Knudsen, H. P., Vestnes, G., MacLennan, D. N., and Simmonds, E. J. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report, 144. 69 pp.
- Garthe, S., Montevecchi, W. A., Chapdelaine, G., Rail, J-F., and Hedd, A. 2007. Contrasting foraging tactics by northern gannets (Sula bassana) breeding in different oceanographic domains with different prey fields. Marine Biology, 151: 687–694.
- 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. 61. pp. 1093–1099.
- Gorska, N., Korneliussen, R. J., and Ona, E. 2007. Acoustic backscatter by schools of adult Atlantic mackerel. ICES Journal of Marine Science, 64: 1145–1151.
- Gorska, N., Ona, E., and Korneliussen, R. J. 2005. Acoustic backscattering by Atlantic mackerel as being representative of fish that lack a swimbladder. ICES Journal of Marine Science, 62: 984–995.
- Hannesson, R. 2013. Sharing the Northeast Atlantic Mackerel. ICES Journal of Marine Science, 70: 259–269.
- ICES. 2008. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 21–1 September 2008, ICES Headquarters Copenhagen. Diane. 67 pp.
- ICES. 2009. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 2–8 September 2009, Copenhagen, Denmark. ICES 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 CM 2010/ACOM:15. 612 pp.
- ICES. 2011a. Report of the Working Group on Mackerel and Horse Mackerel Egg Surveys (WGMEGS), 11–15 April 2011, San Sebastian, Spain. ICES CM 2011/SSGESST:07. 109 pp.
- ICES. 2011b. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 23–29 August 2011, ICES Headquarters, Copenhagen, Denmark. ICES 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 CM 2012/ACOM:15. 931 pp.
- ICES. 2013a. Report of the Ad hoc Group on Distribution and Migration of Northeast Atlantic Mackerel (AGDMM). ICES Document CM 2013/ACOM: 58.
- ICES. 2013b. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 27 August–2 September 2013, ICES Headquarters, Copenhagen, Denmark. ICES CM 2013/ACOM:15. 950 pp.
- ICES. 2013c. Manual for the International Bottom Trawl Surveys. Series of ICES Survey Protocols. SISP 1-IBTS IX. 83 pp.
- ICES. 2013d. Interim Report of the Working Group on Integrated Ecosystem Assessments for the Norwegian Sea (WGINOR), 19– 23August 2013, Bergen, Norway. ICES Document CM 2013/ SSGRSP: 07. 94 pp.
- ICES. 2014a. Report of the Benchmark Workshop on Pelagic Stocks (WKPELA), 17–21 February 2014, Copenhagen, Denmark. ICES CM 2014/ACOM: 43. 341 pp.
- ICES. 2014b. 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. 938 pp.
- ICES. 2015. Manual for International Pelagic Surveys (IPS). Series of ICES Survey Protocols SISP 9—IPS. 92 pp.
- Jansen, T. 2014. Pseudocollapse and rebuilding of North Sea mackerel (Scomber scombrus). ICES Journal of Marine Science, 71: 299–307.
- Jansen, T., and Burns, F. 2015. Density dependent growth changes through juvenile and early adultlife of North East Atlantic Mackerel (*Scomber scombrus*).). Fisheries Research, 169: 37–44.
- Jansen, T., Campbell, A., Kelly, C. J., Hátún, H., and Payne, M. 2012b. Temperature, migration and fisheries of North East Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter. PLoS ONE, 7: e51541.
- Jansen, T., and Gislason, H. 2013. Population Structure of Atlantic Mackerel (*Scomber scombrus*). PLoS ONE, 8: e64744.
- Jansen, T., Kristensen, K., Payne, M., Edwards, M., Schrum, C., Pitois, S., et al. 2012a. Long-term retrospective analysis of Mackerel spawning in the North Sea: a New Time Series and modelling approach to CPR data. PLoS ONE, 7: e38758.
- 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.
- Jensen, H., Rindorf, A., Wright, P. J., and Mosegaard, H. 2011. Inferring the location and scale of mixing between habitat areas of lesser sandeel through information from the fishery. ICES Journal of Marine Science, 68: 43–51.
- Johnsen, E., Pedersen, R., and Ona, E. 2009. Size-dependent frequency response of sandeel schools. ICES Journal of Marine Science, 66: 1100–1105.
- Knudsen, F. R., Hawkins, A. D., McAllen, R., and Sand, O. 2009. Diel interactions between sprat and mackerel in a marine lough and their effects upon acoustic measurements of fish abundance. Fisheries Research, 100: 140–147.
- Knudsen, H. P. 2009. Long-term evaluation of scientific-echosounder performance. ICES Journal of Marine Science, 66: 1335–1340.
- Korneliussen, R. J. 2010. The acoustic identification of Atlantic mackerel. ICES Journal of Marine Science, 67: 1749–1758.
- Korneliussen, R. J., Diner, N., Ona, E., Berger, L., and Fernandes, P. 2008. Proposals for the collection of acoustic multifrequency acoustic data. ICES Journal of Marine Science, 65: 982–994.
- Korneliussen, R. J., and Ona, E. 2003. Synthetic echograms generated from the relative frequency response. ICES Journal of Marine Science, 60: 636–640.
- 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: 5–6, 442–460.

- Lockwood, S. J. 1988. The Mackerel its biology, assessment and the management of a fishery. Fishing News Books Ltd. 181 pp.
- Mackinson, S., van der Kooij, J., and Neville, S. 2005. The fuzzy relationship between trawl and acoustic surveys in the North Sea. ICES Journal of Marine Science, 62: 1556–1575.
- Misund, O. A. 1988. Sonar observations of schooling mackerel during purse seining. ICES C.M. 1988/i3, 27 pp.
- Misund, O. A. 1993. Abundance estimation of fish schools based on a relationship between school area and school biomass. Aquatic Living Resources, 6: 235–241.
- Misund, O. A., and Beltestad, A. K. 1996. Target-strength estimates of schooling herring and mackerel using the comparison method. ICES Journal of Marine Science Symposia, 53: 281–284.
- Nesbo, C. L., Rueness, E. K., Iversen, S. A., Skagen, D. W., and Jakobsen, K. S. 2000. Phylogeography and population history of Atlantic mackerel (*Scomber scombrus* L.): a genealogical approach reveals genetic structuring among the eastern Atlantic stocks. pp. 281–292.
- Nesse, T. L., Hobæk, H., and Korneliussen, R. J. 2009. Measurements of acoustic-scattering spectra from the whole and parts of Atlantic mackerel. ICES Journal of Marine Science, 66: 1169–1175.
- Olafsdottir, A. H., Slotte, A., Jacobsen, J. A., Oskarsson, G. J., Utne, K. R., and Nøttestad, L. 2016. Changes in weight-at-length and size at-age of mature Northeast Atlantic mackerel (*Scomber scombrus*) from 1984 to 2013: effects of mackerel stock size and herring (*Clupea harengus*) stock size. ICES Journal of Marine Science, 73: 1255–1265.
- Pepin, P., Pearre, S., Jr, and Koslow, I. A. 1987. Predation on larval fish by Atlantic mackerel, *Scomber scombrus*, with a comparison of predation by zooplankton. Canadian Journal of Fisheries and Aquatic Science. 44: 2012–2018.
- Reid, D. G., Eltink, A., and Kelly, C. J. 2003. Inferences on the changes in pattern in the prespawning migration of the western mackerel (*Scomber scombrus*) from commercial vessel data. ICES CM 2003/Q:19.
- Reid, D. G., Eltink, A., Kelly, C. J., and Clark, M. 2006. Long-term changes in the pattern of the prespawning migration of the Western Mackerel (*Scomber scombrus*) since 1975, using commercial vessel data. ICES CM 2006/B:14.
- Reid, D. G., Turrell, W. R., Walsh, M., and Corten, A. 1997. Cross-shelf processes north of Scotland in relation to the southerly migration of western mackerel. ICES Journal of Marine Science, 54: 168–178.
- Saunders, R. A., O'Donnell, C., Korneliussen, R. J., Fässle, S. M. M., Clarke, M. W., Egan, A., and Reid, D. 2012. Utility of 18-kHz acoustic data for abundance estimation of Atlantic herring (*Clupea haren-gus*). ICES Journal of Marine Science, 69: 1086–1098.
- Silva, J. F., Ellis, J. R., and Ayers, R. A. 2013. Length-weight relationships of marine fish collected from around the British Isles. Science Series Technical Report no. 150. 112 pp.
- Simmonds, E. J., and MacLennan, D. N. 2005. Fisheries Acoustics: Theory and Practice, 2nd edn. Blackwell Publishing, Oxford. 456 pp.
- Slotte, A., Skagen, D., and Iversen, S. A. 2007. Size of mackerel in research vessel trawls and commercial purse-seine catches: implications for acoustic estimation of biomass. ICES Journal of Marine Science, 64: 989–994.
- Spitz, J., Chouvelon, T., Cardinaud, M., Kostecki, C., and Lorance, P. 2013. Prey preferences of adult sea bass Dicentrarchus labrax in the northeastern Atlantic: implications for bycatch of common dolphin *Delphinus delphis*. ICES Journal of Marine Science, 70: 452–461.
- Stevens, J. D. 1973. Stomach Contents of the Blue Shark (*Prionace glauca* L.) Off South-West England. Journal of the Marine Biological Association of the United Kingdom, 53: 357–361.
- Trenkel, V. M., Huse, G., MacKenzie, B.R., Alvarez, P., Arrizabalaga, 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.

- Turrell, W. R. 1992. New hypotheses concerning the circulation of the northern North Sea and its relation to North Sea fish stock recruitment. ICES Journal of Marine Science, 49: 107–123.
- Uriarte, A., Alvarez, P., Iversen, S., Molloy, J., Villamor, B., Martins, M. M., and Myklevoll, S. 2001. Spatial pattern of migration and recruitment of north east Atlantic Mackerel. ICES CM 2001/O:17.
- van der Kooij, J., Scott, B. E., and Mackinson, S. 2008. The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. Journal of Sea Research, 60: 201–209.

Handling editor: Richard O'Driscoll