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Ágrip

The spawning- and feeding distributions of North-East Atlantic mackerel have been expanding north- and westwards during the last decade. Juvenile mackerel have been observed sporadically in the annual ground fish surveys on the Icelandic shelf, since first recorded in 2004. Further, during the autumn survey of 2010, 0-group mackerel was observed over a wide area south and west of Iceland. Estimation of 0-group hatching date distributions by means of otolith microstructure analysis indicates that the juveniles may originate from spawning in the north-westernmost part of the spawning area in the North-East Atlantic. The possible origin of juvenile mackerel in the area was investigated with the aid of a particle tracking software. It is concluded that juvenile mackerel are overwintering in Icelandic waters and it seems that its nursery areas are expanding.

Lykilorð: *Scomber scombrus, juvenile, otolith, distribution, drift, Iceland, particle tracking*

Undirskrift verkefnisstjóra:	**Undirskrift forstöðumanns sviðs:**

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INTRODUCTION

The distribution and population structures of broad spawning fishes are dictated by offspring origin, dispersal and survival (Hanson 1996). In the Northern hemisphere, recent expansion of fish populations in response to changing climate has resulted in extensive northwards spreading (Drinkwater 2006, Solmundsson et al. 2007, Stefánsdóttir et al. 2010). In the North Atlantic Ocean, changes in geographical distribution due to warming have been documented recently for both commercially exploited fish species and species that are not targeted by fisheries (Brander et al. 2003). These changes have been predicted to lead to a poleward shift in the latitudinal ranges of fish species (Parmesan & Yohe 2003). The quality or availability of habitat used by a species may alter as environmental conditions change or as the population moves to different latitudes (Salinger 2005, Rosa et al. 2011). During the current warm period in the North Atlantic, North-East Atlantic mackerel (NEAM, *Scomber scombrus*) has extended its feeding migration farther to the west and north (ICES 2013).

Until recently, mackerel has been observed only sporadically in Icelandic waters, and its presence during certain periods has been related to a warmer marine climate (Sæmundsson 1934, Astthorsson 2008, Astthorsson et al. 2012). Since 2007, the increased summer presence of feeding mackerel within Iceland's Exclusive Economic Zone (EEZ) has led to an extensive fishery. Results from the ICES coordinated international triennial mackerel egg survey in 2010 showed that the spawning centre of gravity had been moving north- and westward (ICES 2011). In 2013, the results from the triennial mackerel egg survey, however, showed that the spawning centre of gravity had rebounded and moved southward again even though spawning was detected farther north-west than ever before (ICES 2014a).

The most important nursery areas for NEAM are considered to be around Ireland, north and west of Scotland, in the northern North Sea north of 59°N, and, to some extent, also in the Bay of Biscay (Jansen et al. 2014). In 2004 a single one-year old mackerel was recorded for the first time off the south coast of Iceland in the Icelandic spring ground fish survey (Fig. 1). This survey was initiated in 1985 (Björnsson et al. 2007). Since 2004, mackerel juveniles were observed sporadically until the autumn of 2010 when they were observed in higher numbers over a wide area to the south-east, south, south-west, and west of Iceland. These observations were made in the autumn ground fish survey over the Icelandic shelf, which was initiated in 1996.

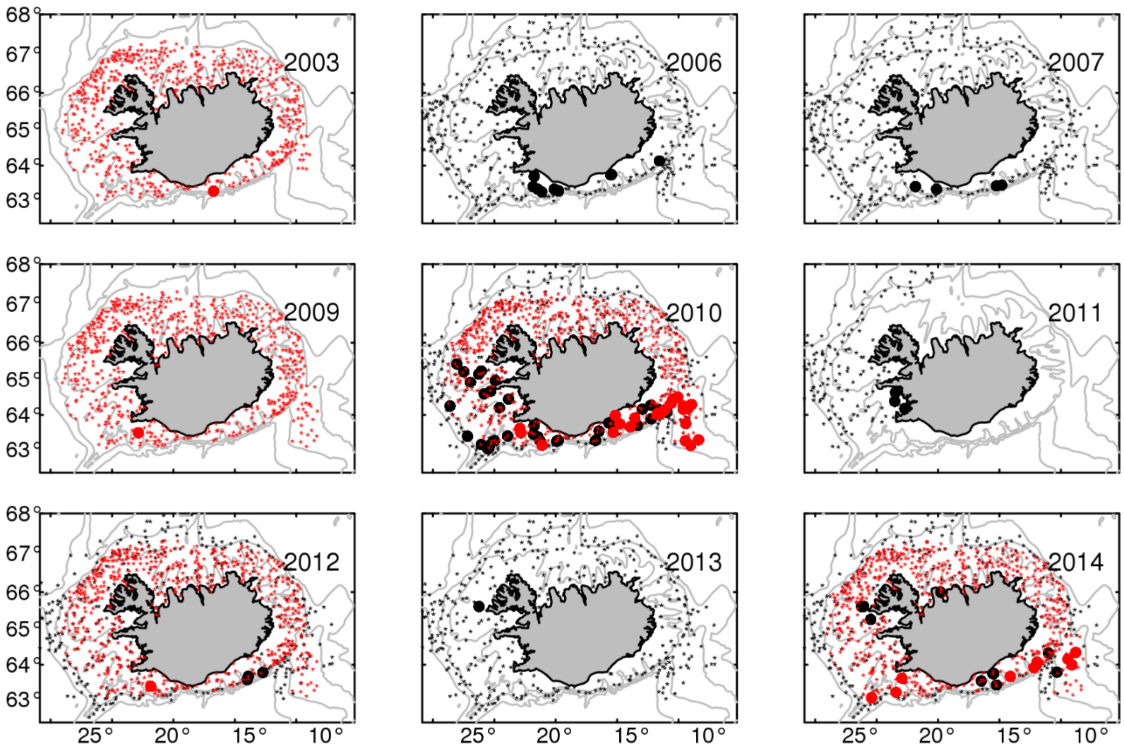

Fig. 1. Occurrence of 0-group and 1-year old mackerel by year classes (between 2003-2015) in the Marine and Freshwater Research Institute's (MFRI) autumn- (black circles) and spring (red circles) ground fish surveys. Small black dots indicate trawl stations in the autumn survey and red dots in the spring survey respectively.

In this study, we present the known geographical distribution of juvenile mackerel in Icelandic waters and the increasing northward and westward extension of spawning mackerel, recorded during the international triennial egg surveys in 2010 and 2013. Our findings are discussed in relation to the possible origin of juvenile mackerel in Icelandic waters. The estimates of the origin were based on hatch date distributions of juveniles sampled in 2010 by means of otolith microstructure as well as by simulating the drift of eggs, larvae and juveniles from the confirmed spawning area within the Icelandic EEZ based on the flow fields of a regional ocean model (Logemann & Harms 2006, Logemann et al. 2013).

MATERIAL AND METHODS

Survey procedures

The data on egg dispersal included outputs from the Marine and Freshwater Research Institute's (MFRI) part of the ICES-coordinated international study in the Northeast Atlantic (see below). The juvenile data included results from MFRI autumn ground fish survey, conducted annually in October from 1996–2012 with on average 405 trawl stations annually, and MFRI spring ground fish survey, conducted annually in March from 1985-2015 with approximately 600 trawl stations (Fig. 1). The surveys are stratified with a mixture of fixed randomly and fisherman selected stations and cover the Icelandic continental shelf and slope, at depths from 20 to 1500 m (Fig. 1). The vertical mouth opening of the bottom trawl is 4–6 m, depending on the towing depth and the mesh size at the cod-end is 40 mm (see Bjornsson et al. 2007, for a detailed gear and method description). It should be noted, that mackerel is a pelagic species and that the bottom trawl used in this study is probably only sampling juveniles on the way up or down. Due to a strike, only one third of the stations were sampled in the autumn survey in 2011 (the western part).

The ICES egg survey is a combined plankton and fishery investigation formed by a series of individual surveys in each sampling year. The surveys have taken place triennially since the late 1970s (Lockwood et al. 1977) and the results have been used in the stock assessment for NEAM. The survey aims to determine annual egg production using the mean annual egg production rates per pre-defined sampling periods for the complete spawning area of NEAM (ICES 2014a). The main objective of the surveys is to estimate the spawning stock biomass from the number of freshly spawned eggs found in the water column. To achieve this, plankton hauls are taken in each half degree by half degree rectangle on every such E-W transects aiming at covering the complete spawning area. An adaptive approach is followed where possible, by continuing sampling to the north, south, east and west until boundaries of egg distribution have been identified. To maximize area coverage, alternate transects were sampled and the remaining time used to fill in the missed transects. The participation of MFRI in the 2010 and 2013 surveys was designed to reach an increased spatial and temporal coverage towards the north and west (Fig. 2). In 2010, MFRI part of the survey was conducted during 9-22 June, collecting samples at 111 plankton stations and monitored four east-west transects between 60°15’ N - 62°50’ N, the northernmost transect stretching from 16° and 2° W and thus the sampling area extended further north than in previous surveys (Fig. 2). In 2013, MFRI monitored 145 stations on 5 transects between 59°45’ N to 63°45’ N and 0°15’ W to 22°15’ W during 10-25 June stretching farther north than ever before (Fig. 2). The sampling of the fish eggs was carried out using a 60 cm diameter “Bongo plankton 60” sampler with a 280 micron mesh size equipped with a calibrated mechanical flow meter mounted in the opening of the net. The net was deployed at 3 knots, towed in double oblique hauls to a maximum depth of 200 m or 5 m above the bottom in shallow water. All plankton samples were sorted for fish eggs on board and identified to the species level. Mackerel eggs were classified into one of six development stages (Lockwood et al. 1981). For further information on methods used in the survey see ICES (2014b).

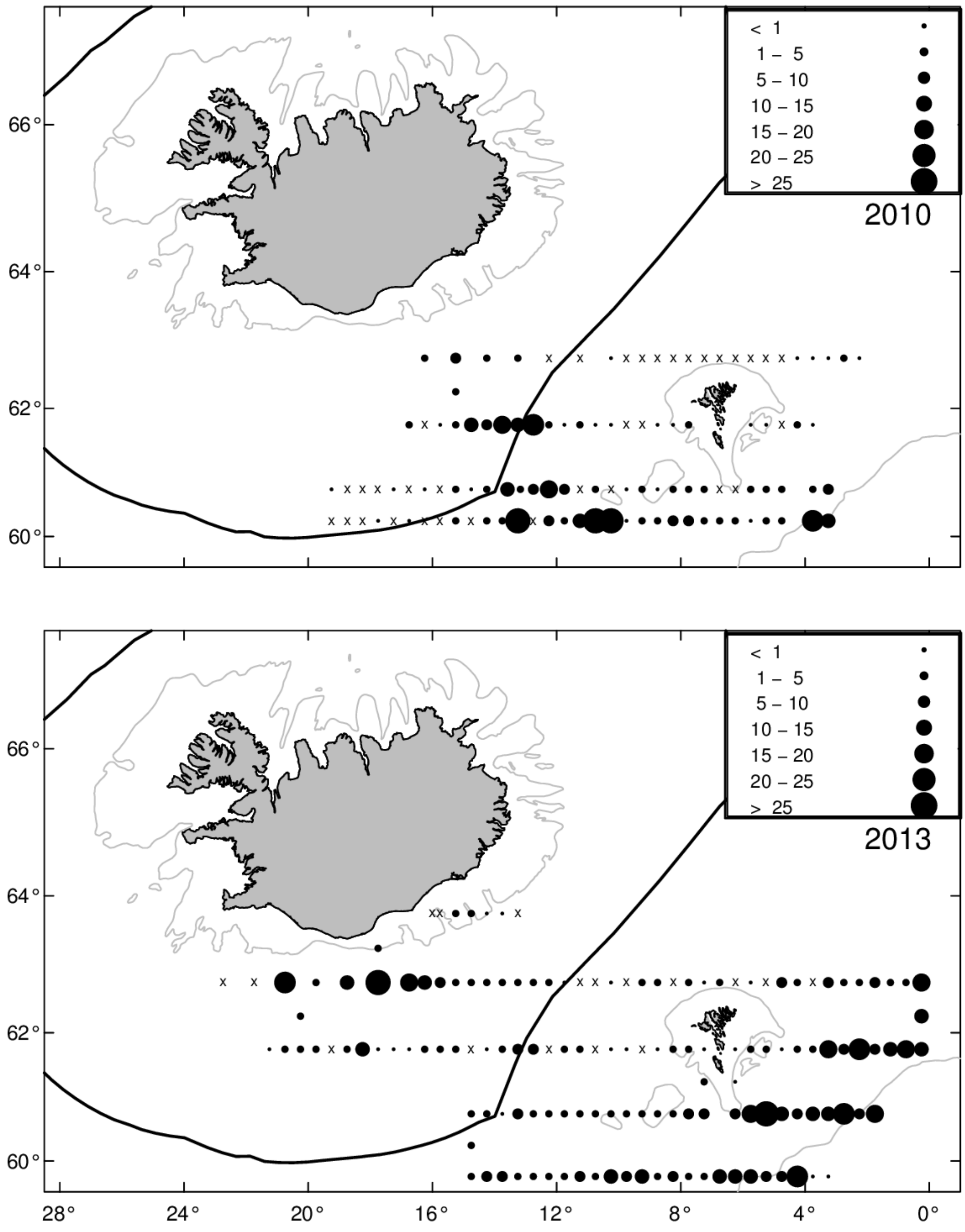

Fig. 2. Distribution of mackerel eggs during the Icelandic participation in the ICES triennial mackerel egg survey in Icelandic, Faroese and UK waters in June 2010 and 2013 respectively. Filled black rings indicate number of mackerel eggs (number/m^2) and black crosses zero catch. Thick black line represents the Icelandic Exclusive Economic Zone (EEZ) and grey lines the 200 m isocline.

Otolith analysis

Daily deposition of increments has been validated for sagittae of Atlantic mackerel larvae and juveniles (D'Amours et al. 1990, Mendiola & Álvarez 2007). Samples of juvenile mackerel for age determination were obtained in 2010 as bycatch in a pelagic herring fishery from two commercial fishing vessels. Routine collection of juvenile mackerel during ground fish surveys initiated later, or in 2012. Approximately 40 individuals were sampled at 63°44′ N and 22°22′ W on 19 October and approximately 120 individuals at 63°59′ N and 14°57′ W on 20 October. The samples were sealed in plastic bags and frozen at – 20° C. In the laboratory, specimens were thawed and measured to the nearest 0.1 mm standard length (SL). Sagittal otoliths were randomly selected from juvenile mackerel in the two samples, extracted, cleaned and mounted on slides using cyanoacrylate glue, under a dissecting microscope. Otoliths were polished on both sides using 30 µm and 3 µm metallurgical lapping films to obtain a thin layer allowing the visualisation of the hatch mark and the initial growth rings. Otoliths from approximately 130 juveniles were analysed. Counts of growth increments were repeated three to five times by an experienced reader until a consistent age was obtained. If any of the counts differed more than +/- 10%, often due to poor sample preparation, the otolith was discarded (16 %).

Growth of juvenile mackerel was estimated using a non-linear fit to the one-cycle Gompertz growth equation (1), which has been used previously to model larvae and juvenile mackerel growth (D'Amour et al. 1990):

$$L_t = L_\infty e^{-e-K(t-t_0)} \qquad (1)$$

where L_t is length in mm at time *t* (days), L_∞ is the asymptotic fork length, *K* is the growth coefficient and t_0 is the point of inflection.

Numerical simulation of egg/larvae drift:

Model description: The basis of our numerical computation regarding the dispersal of mackerel eggs and larvae is formed by the ocean model CODE (Logemann & Harms 2006, Logemann et al. 2013). The model, which includes a Hibler-type sea ice model (Hibler 1979), is applied to the entire North Atlantic/Arctic Ocean. A basic horizontal resolution of 128 km and a vertical resolution from 160 m for the deep sea up to 2.5 m near the surface is used. However, the model's focus is on the waters over the Greenland-Iceland-Scotland Ridge where the used computational mesh increases its spatial resolution up to 1 km near the

Icelandic coast (Fig. 3). This enabled us to simulate the vast majority of the egg/larvae drift trajectories with at least 16 km resolution.

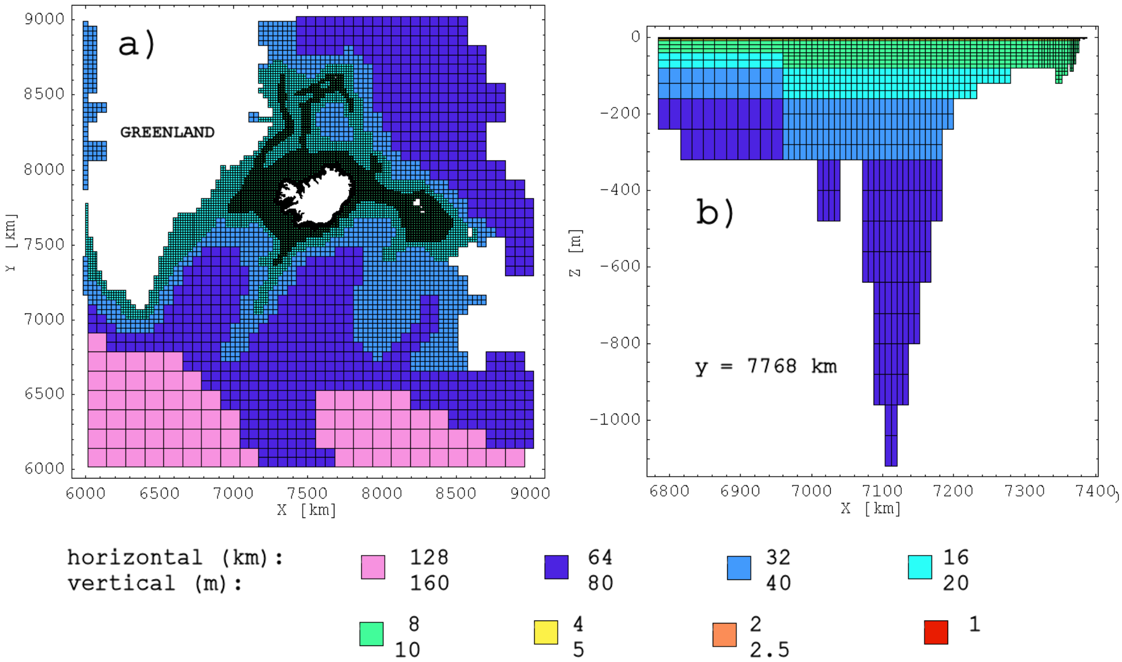

Fig. 3. The computational mesh of the CODE ocean model in Cartesian coordinates. The colours indicate the different resolutions of the a) horizontal and b) vertical mesh structure, (after Logemann et al. 2013).

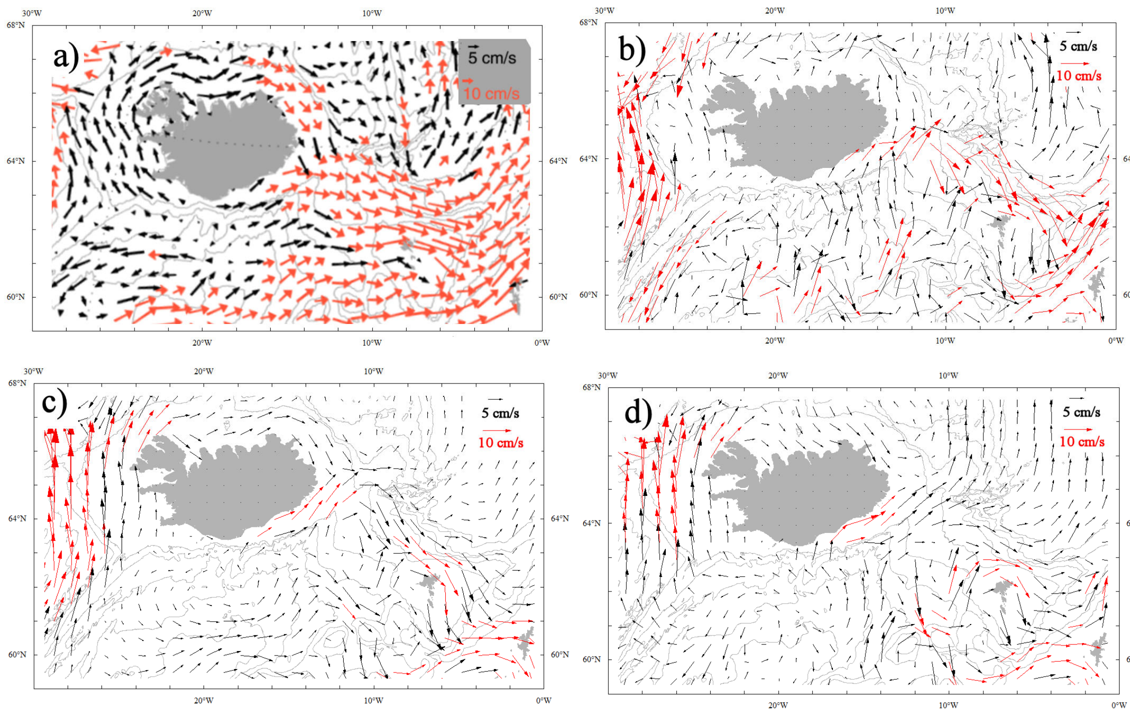

Fig. 4. Flow field south east of Iceland at the depth of 15 m. (a) derived from 387 surface drifter GPS tracks recorded between 1990 and 1999 (after Jakobsen et al. 2003), (b) mean flow during the first half of May 2013 extracted from the Operational Mercator global Ocean analysis data set (Regnier et al. 2015), (c) mean flow between 1990 and 1999 simulated with the CODE ocean model (Logemann et al. 2013), (d) mean flow during the first half of May 2013 simulated with CODE. For all four graphics the underlying data was averaged in overlapping 1° meridional × 2° zonal boxes.

The used flow fields of the years 2010 and 2013, stored with three-hourly resolution, stem from a model run which includes the assimilation of temperature and salinity data. Hereby, all available CTD profiles for the area between 60°N and 70°N and between 30°W and 5°W (on average 93 profiles per month) were used by the technique of incremental analysis updating (Bloom et al. 1996). Logemann et al. (2013) compared the simulated flow at the depth of 15 m with 19 surface drifter GPS tracks resulted from experiments performed by Valdimarsson & Malmberg (1999) in the years 1998 and 1999. After computing 607 low-pass filtered current vectors from both data sources they determined a median model velocity error of -0.64 cm s^{-1} with a standard deviation of 6.54 cm s^{-1} and a median error of the flow direction of 4° with a standard deviation of 67°. Within another validation study we compared the mean simulated flow at the depth of 15 m for the period 1990 to 1999 with the field shown by Jakobsen et al. (2003) which is derived from 387 surface drifters experiments performed during the 1990s (Fig. 4a and 4c). The two flow fields show a great correspondence except at the area south of the Reykjanes Ridge where the drifter data point to a stronger southward recirculation compared to the simulated one. In agreement with the above cited error estimation the simulated flow seems to be slightly too sluggish, which may be at least partially explained by the wind and wave induced force affecting the buoy attached to the drifter (Niiler 1995) and by the fact that drifter velocities are generally biased towards high velocities (Grodsky et al. 2011). In order to expand our flow field comparison to a shorter and more recent period, we extracted the first half of May 2013 from the "COPERNICUS–Operational Mercator global Ocean analysis" data set (Regnier et al. 2015) and compared it with the according field from the CODE simulation (Fig. 4b and 4d). Here, we found a great correspondence regarding the northward path of the Atlantic Water towards the south Icelandic shelf and regarding the strength and shape of the South Icelandic Current (SIC) flowing eastward along the southeast coast. The CODE simulation shows a weaker re-circulation southeast of the Reykjanes ridge and a stronger northward flow over the west Icelandic shelf leading to a stronger North Icelandic Irminger Current (NIIC). Logemann et al. (2013) have demonstrated the precision of the CODE model in simulating the NIIC volume flux when comparing the simulated value of 0.84 Sv (1 Sv = 10^6 $m^3 s^{-1}$) between 1995 and 2006 with the estimated value based on current measurements of 0.85 Sv (Jónsson & Valdimarsson 2012). Regarding the flow southeast of Iceland all four fields shown in Figure 4 contain the basic structure which is schematically outlined in Figure 8. This pattern is also described by other authors, e.g. Valdimarsson & Malmberg (1999) and Orvik & Niiler (2002); i.e. the northward path of Atlantic Water towards Iceland shelf, its division into a weaker westward and a stronger eastward path (SIC) near the southernmost tip of Iceland which further downstream joins the eastward Faroe Current along the Iceland-Faroe Front.

Drift experiment: The simulated flow fields of the years 2010 and 2013 were used by a computer program which computes Lagrangian trajectories and thereby simulates the passive drift of virtual particles through the ocean. The positions of 1507 and 1639 mackerel eggs found in 2010 and 2013 respectively during the MFRI part of each of the surveys in 2010 and 2013 (Fig. 2) were used as starting points of the virtual drifters. Because we were interested in the particles future dispersal from these points covering the short-scale temporal variability of the flow field the release time of each particle was randomly chosen between the 10 and 21 June. Also the initial depth was randomly chosen between 15 and 60 m. The particles vertical movement was made up of three velocity components: (1) the vertical flow; (2) the vertical turbulence (random walk derived from the vertical turbulent viscosity given by the ocean model); and (3) an equilibrium between buoyancy and friction (Stokes' drag caused by molecular viscosity) assuming the particle to be spherical with a radius of 1.3 mm and with the density of the sea water at the depth of 10 m at the particle's current position. This way, the particles were simulated to take up the depth range between 0 and 108 m, with the mean depth of 9.7 m and a standard deviation of 5.3 m. We computed the particle dispersal until the 15 September, hence roughly for 60 days. The particle positions were stored in 6-hourly time intervals.

Motivated by the results from this drifter experiments and an indication for possible insufficient coverage of the egg survey in 2010 (Fig. 2), another 2010 scenario was created. There, the initial positions (i.e. spawning and realising of particles) were assumed to be between 24°-20°W and 60°-63°N, like in 2013, or, further west than the egg survey stations reached.

RESULTS

Since the first record of juvenile mackerel in Icelandic waters during the Icelandic spring ground fish survey of 2004, juveniles have been found sporadically but in increasing numbers. The first record was from the southeast of Iceland, while in 2006 juvenile mackerel were also found south of Iceland (Fig. 1). During 2010 juveniles were caught off the entire south coast and off the west coast up to 65°25 N. From 2009-2015 a total of one up to several hundred individual mackerel juveniles were caught each year at 1-34 trawl stations (Table 1). Usually the catch consisted of juveniles only, except in the autumn 2011 when adult mackerel were also present.

The total length distribution of the juveniles observed in the winter surveys 2006-2014 ranged from 11-25 cm during autumn and 16-24 cm during spring (Table 1). The fish of the 2010 year class were on average per station in same area slightly but not significantly (t-test, p = 0.35) smaller in size when caught in the early spring 2011 (mean 19.7 cm, sd. = 1.4) compared to late autumn 2010 (mean 20.1 cm, sd. = 1.2), suggesting that growth during winter was minimal. The length distribution of the aged juvenile mackerel from the two sampled stations (mean=20.1 cm, sd. = 0.9, range: 18.8-22.8 cm, n = 106) and all the juvenile mackerel measured during the demersal autumn survey in 2010 (mean = 20.3 cm, sd. = 1.1, range: 18.0-23.0 cm, n = 368) did not differ (t-test, p = 0.07). Ageing of juveniles from the 2010 year class showed that the hatch days ranged from the 29 April to the 5 July, with a mean hatch date on the 29 May (sd. = 16). The growth of mackerel described by a Gompertz growth curve (Fig. 5), indicated that the asymptotic length (L_∞) was 212.2 mm, the growth coefficient (*K*) 0.025 and the inflection point (t_0) was 23.0 mm. All the measurements fell on the almost horizontal part of the curve.

Table 1. Overview of juvenile mackerel caught in the autumn- and spring ground fish surveys as from 1984 to 2015. Year class of juvenile mackerel, survey type, number of stations with juvenile mackerel, number of juveniles with s.d, mean length and min. and max. length in each survey. *Due to a strike, only one third of the stations were sampled in the autumn survey in 2011 (the western part).

Year class	Survey	Nr. of stations with juveniles	Nr. of juveniles	Mean length (cm) ± Sd	Min length (cm)	Max length (cm)
2003	Spring 2004	1	1	24.0	24.0	24.0
2006	Autumn 2006	9	316	20.6 ± 0.8	19.0	23.0
2007	Autumn 2007	4	4	23.0 ± 2.8	19.0	25.0
2009	Spring 2010	1	1	22.0	22.0	22.0
2010	Autumn 2010	34	368	20.3 ± 1.1	18.0	23.0
2010	Spring 2011	22	281	19.4 ± 1.3	16.0	23.0
2011*	Autumn 2011	3	105	21.3 ± 0.9	21.0	25.0
2012	Autumn 2012	3	35	17.9 ± 1.4	11.0	19.0
2012	Spring 2013	1	1	19.0	19.0	19.0
2013	Autumn 2013	1	1	12.0	12.0	12.0
2014	Autumn 2014	10	65	23.4 ± 1.1	21.0	26.0
2014	Spring 2015	10	29	24.2 ± 0.8	22.0	26.0

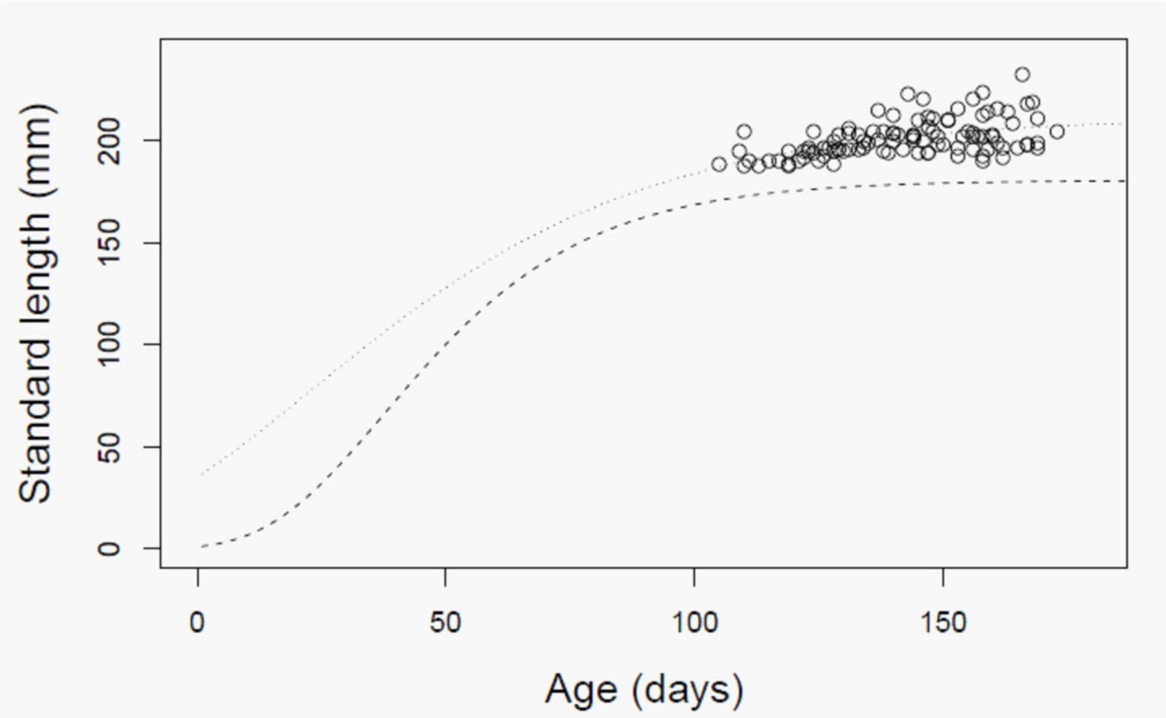

Fig 5. Relationships between standard length and age in days of juvenile mackerel sampled in the autumn ground fish survey in 2010 in Icelandic waters. The dotted line represents the fit of Gompertz growth equation through the points and the broken line the same model for mackerel in Gulf of St. Lawrence (D'Amours & Landry, 1990).

Egg distribution in 2010 and 2013

Since 2004, the boundaries of the international egg survey have steadily stretched further north and west (Fig. 6). The overall results from the international egg survey in 2010 showed that there was a statistically significant north- and westward shift in the centre of the spawning gravity for the western spawning component of the NEAM (ICES 2011). Further, the main spawning period differed markedly from that seen in any egg survey from at least 1998 onwards. 66% of all the egg production in the western area took place between late February and late April. This was in marked contrast to previous years where peak spawning has tended to occur around May or June. Within MFRI's survey area, almost 19 thousand eggs were sorted and identified to the species level. Eggs of pearlside (*Maurolicus mülleri*) were by far most abundant. There were 1507 mackerel eggs found at 54 out of 111 stations sampled, and about 50% of them were at developmental stage 1a (early development lasting for max. ~ 24 h. at 6° C – 10° C, see Geffen & Nash 2012) as defined in Lockwood et al. (1981). The distributional area of eggs stretched to the south and west of the Faroese EEZ and for the first time on record, the distribution was confirmed well into the Icelandic EEZ (Fig. 2). The north-western limit of the spawning area for mackerel could not be determined based on the spatial sampling. Very few eggs belonging to other species were found during this cruise.

The overall results from the international egg survey in 2013 showed that there was a southward shift in the centre of the spawning gravity for the western spawning component of the NEAM compared to the 2010 survey (ICES 2014a). Within MFRI's survey area, the distribution of mackerel eggs was observed to be farther to the north and west than in 2010 (Fig. 2). A total of 145 plankton stations were taken during the cruise with about 17 500 eggs collected and sorted out and identified to the species level. Of these, 3 300 were mackerel eggs, found at 128 stations with approximately 40% at developmental stage 1a. As in the 2010 survey the most abundant species was pearlside, and few eggs from other species were found. Relatively, more mackerel eggs were observed than three years earlier and pockets with relatively high spawning was documented south of Iceland.

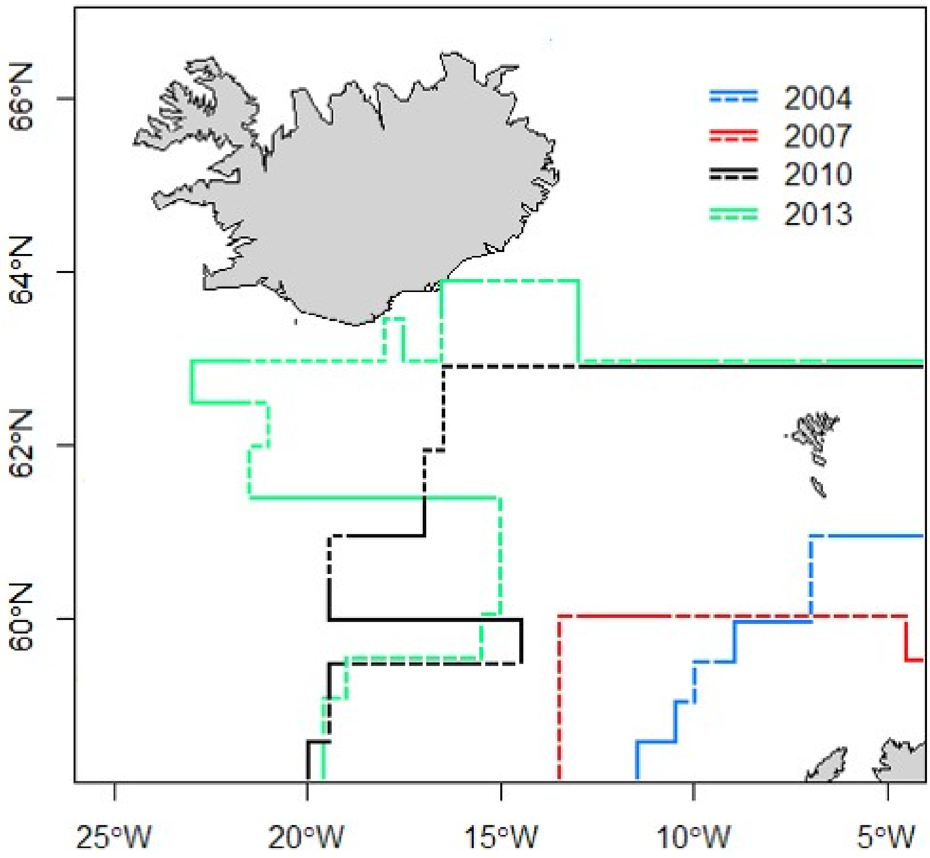

Fig. 6. Representations of the northern and western boundaries of the international mackerel egg surveys in 2004 (blue), 2007 (red), 2010 (black) and 2013 (green). Broken lines indicate where northern or western limits of the egg distribution were probably not reached. Modified from ICES triennial mackerel egg survey 2013.

Drift of particles

The simulated pathways of the released particles were generally directed eastwards (Fig. 7). This is particularly true for the particles originating in stations east of 15°W. However, particles originating west of 15°W often showed an initially northward drift which enabled them to enter the southeast Icelandic shelf. There, they were entrained into the

SIC which carried them along the coast to the north-east and finally into the eastward Faroe Current along the Iceland-Faroe Ridge. A few trajectories reached westward from the starting position. These drift pattern generally agree with the observed mean conditions in that area (Jakobsen et al. 2003, Fig. 8). At the end of the simulated time period in 2010 (late September), only one particle had entered the Icelandic Coastal Current (ICC) close to shore at southwest Iceland. At that time, a second particle had reached the area south-east of the Westman Islands (63°25’ N, 20°17’ W). This means that we simulated two particles entering

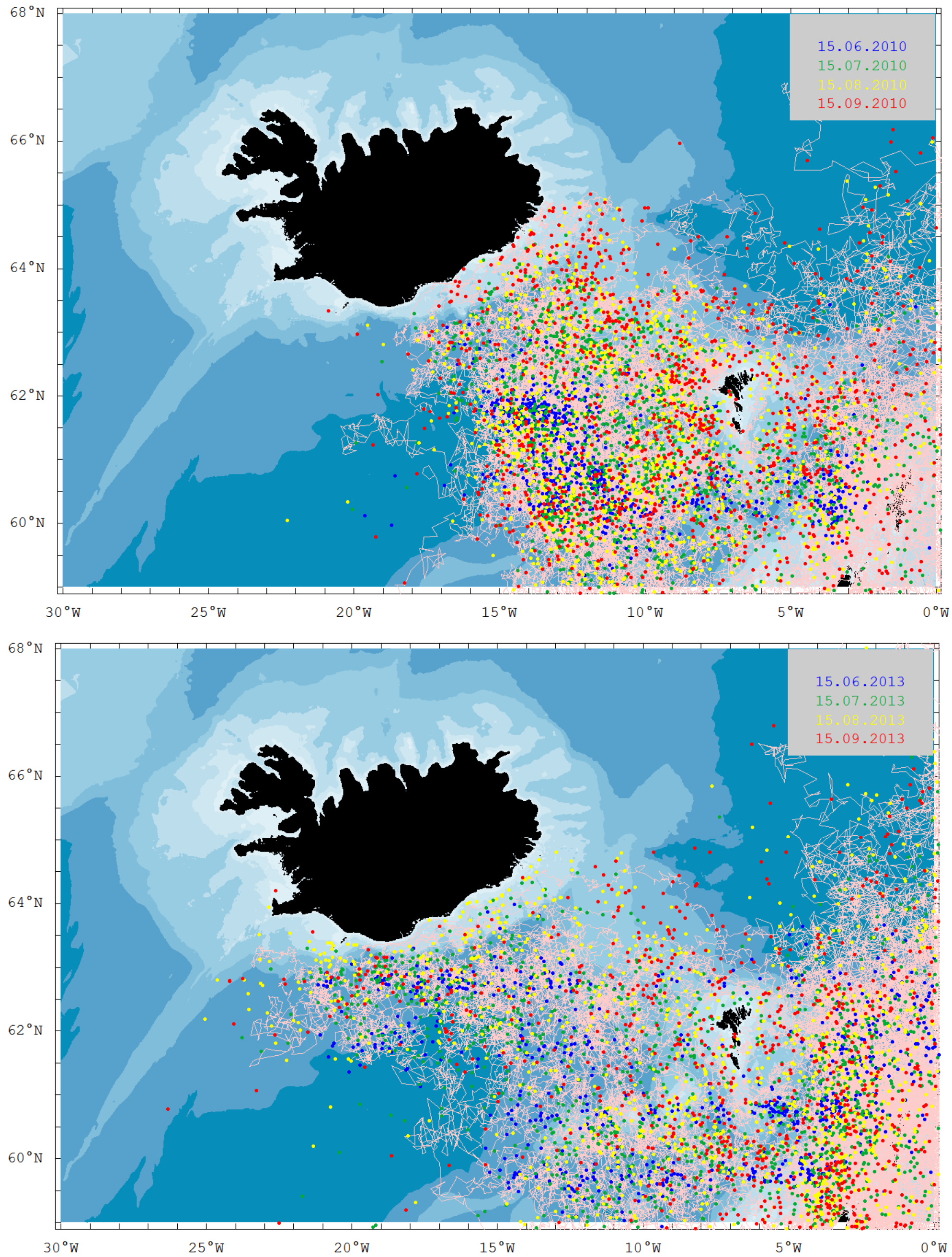

Fig. 7. Simulated dispersal of mackerel egg/larvae in 2010 (above) and 2013 (below) from egg survey stations (see Fig. 2). Drift trajectories of every 10th particle is shown as pink line. The dots show the positions of virtual particles at different dates.

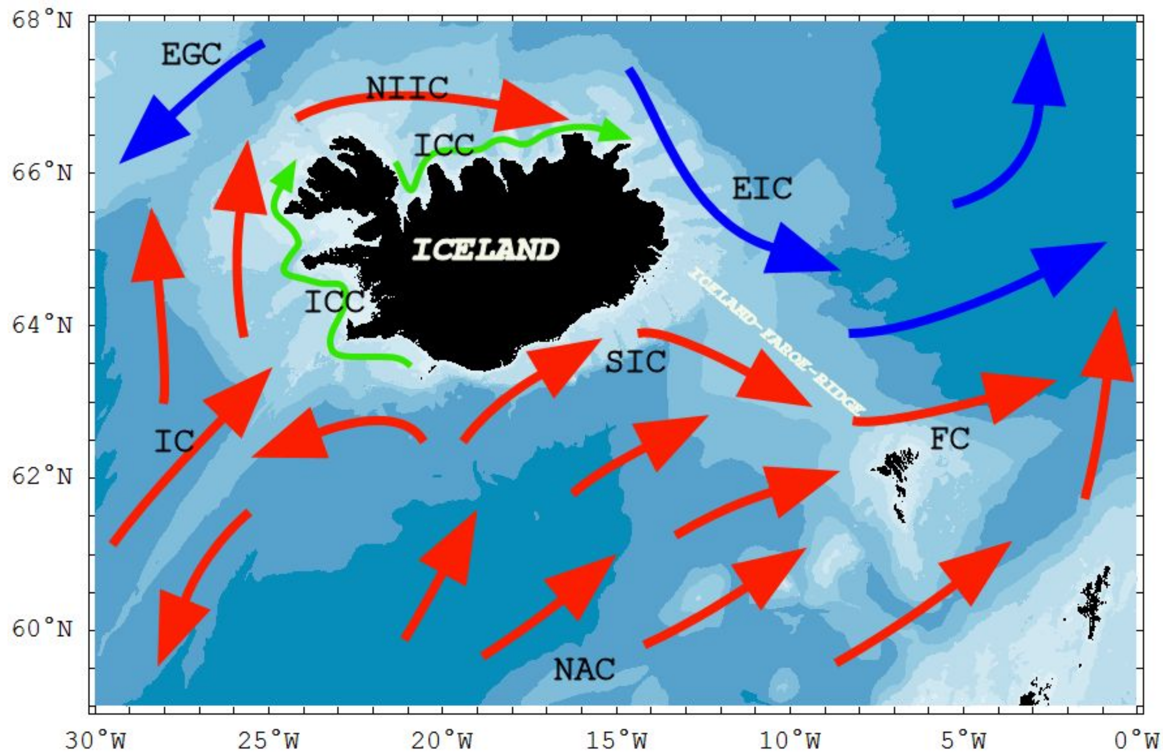

Fig. 8. Scheme of the near-surface circulation around Iceland and the Faroe Islands. Red arrows indicate flow of relatively warm and saline Atlantic Water, blue arrows the flow of cold and less saline Polar or Arctic waters. The abbreviations are: EGC – East Greenland Current, EIC – East Icelandic Current, FC – Faroe Current, IC – Irminger Current, ICC – Icelandic Coastal Current, NAC – North Atlantic Current, NIIC – North Icelandic Irminger Current, SIC – South Icelandic Current.

the north-westward flow regime which would take them over to the west and north Icelandic shelf. It should be highlighted that simulated particle represents much higher number of eggs in reality. Due to different wind field, the particles were carried further eastward during the simulated period in 2013 compared to 2010. Around 10 particles were found west of 20° W in 2013 and only one was found ending within in the ICC.

As no particle entered the western shelf of Iceland, in spite of the number of juveniles caught there in autumn 2010, a different scenario was tested. In this case the location of the spawning areas, i.e. the particle release positions, was allowed to expand to the west, or to the area between 24°-20° W and 60°-63° N. This is a reasonable alternative because the north-western limit of the spawning area was not clearly defined during the survey. A different picture resulted from that drifter experiment (Fig. 9), where a large fraction entered the ICC and were carried to the western shelf off Iceland. The drift was apparently too slow for the juveniles to populate the northern shelf in the autumn.

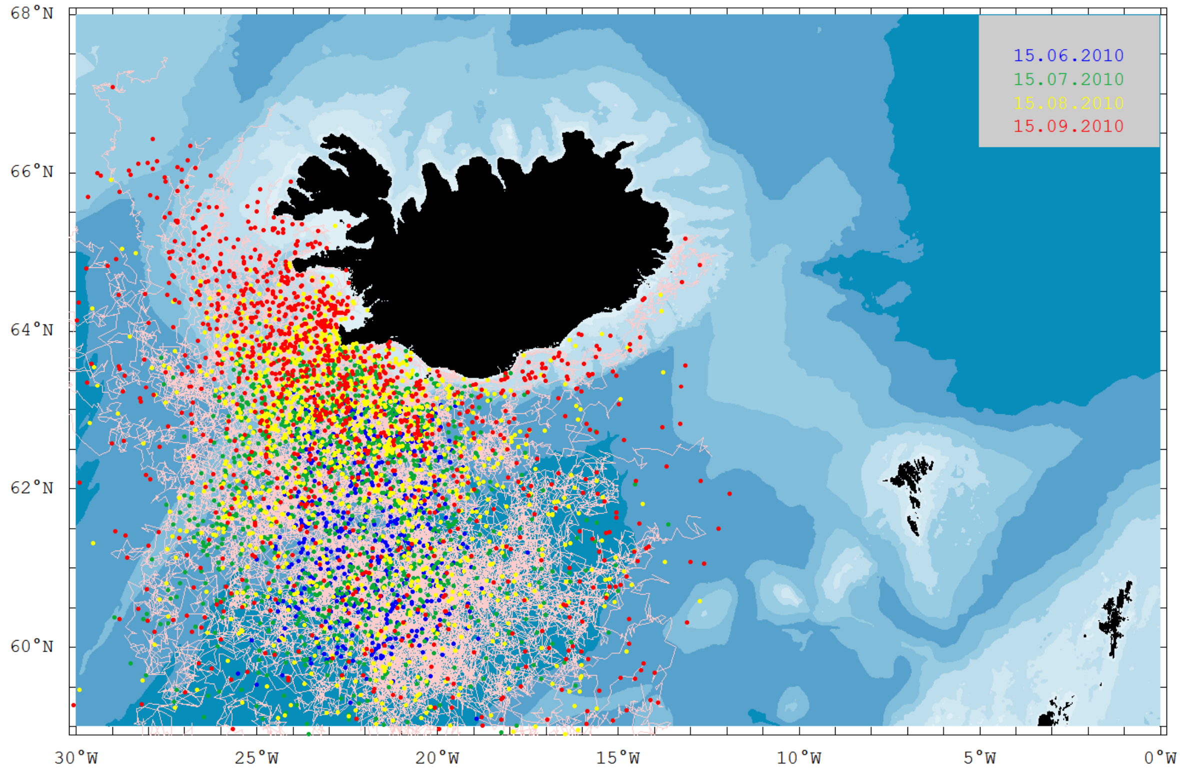

Fig. 9. Results of the alternative 2010 drift experiment, simulating the dispersal of mackerel eggs/larvae which have been released more westerly within the area between 24°-20°W and 60°-63°N. Drift trajectories of every 10th particle is shown as pink line. The dots show the positions of virtual particles at different dates.

DISCUSSION

In this study we present new findings of recently spawned mackerel eggs in the Icelandic region. The distribution of eggs in recent years has expanded considerably north-westwards and model particle tracking suggest that the NEAM are likely spawning in a much wider area along the south coast of Iceland than was previously thought.

The drastic changes in the distribution and feeding migrations of NEAM have co-occurred with rising water temperatures and salinity south and west of Iceland and increasing stock size in the northeast Atlantic (Astthorsson et al. 2012, ICES 2014c, Nøttestad et al. 2015). Starting one decade later, an extensive direct fishery for mackerel within the Icelandic EEZ has developed, with catches increasing from 4 000 tonnes in 2006, to >100 000 t each year 2008-2014 (ICES 2014c). In a swept-area survey carried out as part of the International Ecosystem Survey in the Nordic Seas in July-August 2010, about 23% of the estimated mackerel biomass was found in Icelandic waters (Nøttestad et al. 2014). Since 1996, the waters around Iceland have been relatively warm, yielding a temperature increase of ~1–2°C in these areas (Astthorsson et al. 2012). It has been suggested that the expansion of the stock may possibly be due to increased sea surface temperature in the area (Astthorsson et al. 2012, Hughes et al. 2014). It should be highlighted though that there is continuous spawning of mackerel from Spain to Iceland and the increase is not only seen in the northern part of the distribution but also to the west (ICES 2014c). On the other hand, some studies showed no clear movement or relationship with temperature (Brunel & Boucher 2007). Since the expansion started, stock size of mackerel has been steadily increasing. The increase in numbers may have forced the stock to expand the coverage of the spawning and summer feeding area. The question remains if those changes are permanent or cyclical. The processes involved are likely dynamic with an interaction between stock size and temperature where zooplankton and oceanographic conditions also shape the field.

Our representation of mackerel juveniles may indicate that the nursery area of the NEAM is extending into Icelandic waters. Furthermore, these juveniles may originate from observed spawning areas off the south- and south-east coasts of Iceland. In Icelandic waters, the juveniles appear in the commercial catches first in late August (ICES 2013). The swimming speed of fish is related to its size, and therefore the ability to travel over long distances. Considering the timeframe it is not likely that the juveniles captured off the coast of Iceland have originated from the main nursery areas west of Scotland more than 400 nautical miles away. The incubation period for mackerel eggs is estimated to be approximately 8 days at temperatures most likely experienced in the area of the egg survey (Russell 1976, Geffen & Nash 2012). A study from the Gulf of St. Lawrence (D'Amour et al. 1990) showed that mackerel will grow from ~ 4 mm at hatching to 100 mm in approximately 50 days. The mackerel larvae are mostly in the wind-driven surface Eckman layer to a depth of about 50 m with sub-surface peak of abundance in the depth range of 10-30 m (Coombs et al. 2001). However, with increased size, they will become more active swimmers. The passive drift assumption during the last weeks of the simulation may thus be questioned as it is unknown to what extent the juveniles are able to influence their drift route during this time. It must be noted, that in this study, we had no ability to quantify the distribution of juveniles in Icelandic waters, merely confirm whether they were present or absent. The ground fish survey will therefore, at the best, only give relative information about inter-annual and spatial variation in density of the juvenile mackerel.

The results presented here provide possible explanation for the existence of the mackerel juveniles observed in the winter 2010-2011 in Icelandic waters. The triennial international egg surveys in 2004 and 2007 were carried out further south (Fig. 6), hence one can only speculate, where the eggs had been spawned that the juvenile mackerel found in Icelandic waters in 2004-2007 hatched from. In 2010, however, the area of the egg survey extended much farther to the north and west and even into the Icelandic EEZ. The spawning of mackerel inside the Icelandic EEZ was confirmed there for the first time (ICES 2011). Then in the autumn of the same year juvenile mackerel was observed off the entire south coast and off the west coast of Iceland north to 65°N. The ageing of the juveniles collected in 2010 revealed a hatching distribution stretching from end of April to early July. This indicates that some of these juveniles may have hatched from eggs spawned during the egg survey took place 9-22 June. Thus, the hatch date distributions for the juveniles caught of the south coast of Iceland in October 2010 suggest that they may have originated from the observed spawning grounds southeast of Iceland. During the international hydro acoustic survey for Norwegian spring-spawning herring in the Norwegian Sea in 2010 spawning mackerel was caught on several stations in the area between Iceland and the Faroe Islands in early May (ICES 2010). That coincides with the earlier hatch dates observed in Icelandic waters.

Few studies have looked at the growth of juvenile mackerel. D'Amours et al. (1990) identified and validated daily rings in the sagitta of Atlantic juvenile mackerel from the Gulf of St. Lawrence over the size range 93-170 mm and the age of larval and juvenile mackerel was estimated over the size range 7-192 mm. A one-cycle Gompertz curve was fitted to the length-at-age and the results from that model is included in the graph of current results (Fig. 5). The asymptotic length at the end of the first growing season are larger in the present study, which is an indication of faster growth in Icelandic waters, but the present data were limited to large individuals and consequently the model fit was poor.

Boeuf & Le Bail (1999) asserted that many marine fish species react to photoperiod treatments and long day length stimulates growth. Assuming that feeding of mackerel is light-limited, the very long summer daylight hours at high latitudes is a possible reason for the indicated fast growth in Icelandic waters. Suthers & Sundby (1996) showed that the size-at-age of pelagic juvenile cod from the north-east Atlantic off northern Norway was approximately twice that of cod from off Nova Scotia, Canada. They hypothesized that the size difference was due to difference in light-limited feeding opportunity and the necessity for fast growth in the short northern summer for over-winter survival. This could, at least partially, explain the observed growth difference between the juveniles caught in Icelandic waters and juveniles from the Gulf of St. Lawrence (D'Amours et al. 1990) at lower latitudes.

Examination of the length-at-age of juveniles revealed that there seems to be a very rapid growth during the first summer followed by a slow or no growth during the winter. As an example, the average length of one-year old mackerel in the spring 2011 was the same as juveniles caught in the preceding fall (Table 1). Even though we cannot exclude that this might be related to length-specific catchability or mortality, this is consistent with findings from the Gulf of St. Lawrence where individuals from a northern contingent spawn mainly in late June (Ware 1977) and their progeny reached 200 mm fork length at end of November in the same year (MacKay 1979, Ware and Lambert 1985). Fish from a southern contingent spawn in late April or early May (Morse 1980). Despite earlier spawning, their progeny appear to reach the same terminal length of 200 mm at the end of the first growing season (Sette 1950). In addition to slow or no growth during the winter months, the Icelandic spring ground fish survey in 2011 indicates that the juveniles remain on the nursery grounds south and south-east of Iceland through the winter. This agrees with Lockwood's (1988) suggestion, that during their first winter the juveniles remain within the same general areas as they spent their first summer in, i.e. their nursery grounds.

Particles released in a particle tracking model for the year 2010 at positions where eggs were found in the egg survey the same year, ended only in the eastern part of the juvenile distribution. The juveniles caught off the southeast coast may therefore have originated from the observed spawning grounds in June 2010. The lack of particles ending in the western part is, however, considered to be related to insufficient coverage in the 2010 egg survey towards the west and thereby poorly confined spawning- and particles releasing area. In other words, the spawning may have reached farther west than could be confirmed in 2010 and might have been similar to the egg distribution observed in 2013. Applying that assumption, the CODE ocean model simulated the flow of particles released in 2010 in a way that compared well with the distribution of the juveniles found south-west and west off Iceland in the autumn. This finding suggests both insufficient survey coverage in the egg survey in 2010 and more westerly spawning. Furthermore, the presence of eggs at the outermost stations in 2010 might indicate that the northern and western boundary of the spawning areas had not been reached during the survey. Thus, it is concluded that the juveniles in the western area in 2010 originated most likely from more westerly spawning areas not covered during the egg survey. The simulated releasing of particles from the observed spawning grounds in 2013 resulted in very few particles in the western area in 2013 compared to 2010. Only one mackerel was caught in the autumn survey in 2013 compared to 368 in 2010, which is in agreement with the simulation results. However, other factors influencing the larval survival could also be responsible for this difference between the two years. These factors include prey availability, possibly through mismatch of available prey and feeding mackerel larvae (Cushing 1990) and predation on the larvae (Leggett & Deblois, 1994).

The simulated drift of the released particles indicated a low fraction of drifting (2 of 1500) from the observed spawning areas in 2010 towards south and western Icelandic shelf. How accurate and reliable are these results? There are at least two processes which should be further examined in this context. First, the oceanic flow south and southeast of Iceland is known to be sluggish, wide and eddy-structured (Valdimarsson 1998). In the central Iceland Basin, where the ocean model's resolution is too coarse to resolve most of the eddies, the turbulence closure approach of Smagorinski (1963) is used to estimate horizontal turbulent exchange coefficients. These coefficients are used for the computation of the particle's "random walk", i.e. the chaotic component of its trajectory. When using this approach, several trajectories reached areas west of the starting positions. We assume this spreading opposite to the direction of the mean circulation to be strongly linked to the particle's random walk, though the wind stress variability could also play a role. It is possible that we have under-estimated the turbulent exchange in the central Iceland Basin. A greater random walk component would lead to more particles west of 20° W and finally more particles being entrained into the coastal or Irminger Current west of Iceland. Another possibility that needs to be addressed is the mean depth of the particles which was set to 10 m in our experiments. A greater depth could lead to an enhanced westward spreading of the particles. As mentioned above however, the juveniles found off the southwest and west coasts may possibly originate almost solely from a spawning west of about 19°W.

The main results of the drift studies indicate that the drift probability of near surface particles from the area south-west and west of the Faroe Islands onto the west and north Icelandic shelf is small. Though this may contradict certain traditional circulation schemes our results are supported by modern observational studies (e.g. Perkins et al. 1998, Valdimarsson & Malmberg 1999, Orvik & Niiler 2002, Hunegnaw et al. 2009). A westwards extension of spawning in areas south of Iceland is therefore a plausible explanation of observed mackerel juveniles in southwestern and western Icelandic waters. It would be of general interest to extend the drift studies in the future to include the whole western spawning component of the NEA mackerel.

The spatial distribution of commercial catches (Astthorsson et al. 2012, ICES 2013), the 2010 and 2013 egg distributions (Fig. 6) and the swept-area analysis (Nøttestad et al. 2015) all indicate that the NEAM stock has expanded considerably north-westwards during their spawning and summer feeding migration. Spawning west of 19°W is suggested both by the model simulations and observation in 2013. However, it should be noted that the fraction of the total egg biomass found in Icelandic EEZ in these years was small part of the total spawning of the stock, or ~ 1 % (ICES 2011, ICES 2014c). These recent changes in spawning migration may explain that juvenile mackerel can be found in the autumn, at least in some years, off the south and south-east coast of Iceland. Based on the present study it is concluded that the juvenile mackerel are sporadically overwintering in Icelandic waters.

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