INTRODUCTION

Many fish populations are composed of several stock components that may differ with respect to spatial distribution, morphology, genetic structure, or life-history traits (Robichaud & Rose 2004, Ruzzante et al. 2006, Harrald et al. 2010, McAdam et al. 2012). Spatial structure and degree of population richness are generally thought to be determined in early life stages and shaped by oceanographic processes and various behavioural traits, such as natal homing to spawning grounds (Heath et al. 2008, Svedäng et al. 2010). It is increasingly recognized that fisheries management will need to take more notice of population variation, to maintain viability of different components and preserve diversity within populations (Smedbol & Stephenson 2001, Hutchinson 2008, Zemeckis et al. 2014).

Atlantic cod *Gadus morhua* is among the most important commercial species in the North Atlantic, and cod migration patterns have been studied extensively (Robichaud & Rose 2004, Neuenfeldt et al. 2013). Adult cod have a capacity to migrate over extensive distances, and when considering long-distance drift probabilities of cod eggs and larvae (e.g. Brickman et al. 2007, Vikebø et al. 2007), a weak population structure would be expected. Yet, there is evidence of a subpopulation structure and a high degree of biological diversification within the species (Smedbol & Stephenson 2001, Wright et al. 2006, Hutchinson 2008, Grabowski et al. 2011, Michalsen et al. 2014). Cod spawn at numerous locations around
Iceland, where the most densely populated spawning grounds are located in the south and southwest (Sæmundsson 1926, Jónsson 1996, Jónsson & Pálsson 2013). Eggs and larvae mainly drift clockwise via the Irminger Current, which flows along the southwestern and western shelf and partly branches into North Icelandic waters (Jónsson & Valdimarsson 2005). A freshwater-induced coastal current further enhances the clockwise drift (Valdimarsson & Malmberg 1999).

In recent years, studies have aimed at identifying those biological and behavioural factors that discriminate among spawning components of Icelandic cod and their relative contribution to the surviving juvenile population, by analysing tagging data (Pálsson & Thorsteinsson 2003), otolith variables (Jónsdóttir et al. 2006, 2007, Petursdottir et al. 2006, Thorisson et al. 2011), genetic structure (Jónsdóttir et al. 2002, Jakobsdóttir et al. 2011, Pampoulie et al. 2012), body condition (Fardoe et al. 2008), morphology (McAdam et al. 2012) and back-calculated birthdates of juveniles (Marteinsdottir et al. 2000b, Begg & Marteinsdottir 2002). There appears to be a genetic difference between spawning groups in the northeastern and southwestern parts of the country (Pampoulie et al. 2006), and both groups have been shown to include 2 behavioural types of fish that occupy distinct seasonal thermal and bathymetric niches (Grabowski et al. 2011, Thorsteinsson et al. 2012). Despite accumulating knowledge of subpopulation structure, the cod fishery in Iceland is, in general, managed on a single-stock basis (Marine Research Institute 2014).

In earlier mark-recapture studies on spawning Icelandic cod, little attempt was made to quantify the connectivity of spatially distinct spawning components. The main purpose of our study was to investigate home range patterns and the degree of spatial association among cod spawning components, to provide information on stock structure. The study is based on conventional mark-recapture data collected over 2 decades. Due to potential sources of bias inherent in conventional tagging and recapture data (Bolle et al. 2005), they were validated with data from more recently employed electronic data storage tags.

**MATERIALS AND METHODS**

**Terminology**

Here, terms regarding population structure are defined following Smedbol & Stephenson (2001, p. 110): ‘A population is a self-reproducing group of conspecific individuals that inhabit the same range at the same time, are affected by similar environmental factors and are reproductively isolated from other populations’. ‘A subpopulation is a semi-independent, self-reproducing group of individuals within a larger population that undergoes some measurable but limited exchange of individuals with other areas within the population’ (Smedbol & Stephenson 2001, p. 110). A spawning component is here simply defined, based on Smedbol & Stephenson (2001), as a segment of a population comprised of mature individuals that occupy discrete spawning grounds interannually. From the data presented here, we cannot conclude whether spatially segregated subpopulations or spawning components are genetically distinct or not.

**Conventional tags**

The tag-recapture database of the Marine Research Institute (MRI) was explored for cod tagged with conventional tags (CTs) on spawning grounds in Icelandic waters during spawning seasons since 1991. In total, date and position of tagging for 7318 recaptured cod are available for this period, of which 5987 include information on date and position of recapture and were considered to be spawners (Table 1). These cod were mainly caught with bottom seines and gillnets, and they were tagged with T-bar anchor tags as described in Schopka et al. (2010) and Björnsson et al. (2011).

In the analysis, recaptures were divided between 2 seasons. The main feeding season was defined as June to February, whereas the period March to May includes the main spawning season, with the height of spawning in April (Jónsson 1982, Jónsson 1996, Pálsson & Thorsteinsson 2003, Grabowski et al. 2011). Cod spawn at many locations around Iceland (Fig. 1), and tagging data are available for the main spawning grounds south and west of Iceland and a few areas in the north and east. Grouping into spawning components and delineation of spawning grounds was based on Marteinsdottir et al. (2000b) and Jónsdóttir et al. (2010), with the exception that adjacent sites off the southeast, with relatively low sample sizes, were merged (Fig. 1). Stock sizes of different spawning components are not known, but their relative importance in the cod fishery in April varies substantially, i.e. from only 72 t on average in the eastern spawning area (E) to approximately 2700 t in the southwestern spawning area (SW) (Table 2). Sexual maturity of cod at tagging could be reliably confirmed for 1278 actively spawning (running) fish,
which were included in the analysis. Remaining cod larger than the length at 50% maturity (46 to 58 cm, depending on spawning ground; see Table 2) were included in the analyses, with the exception of a few fish determined as immature at recapture.

### Kernel density estimation

To estimate the main distributional area of the group of fish in each spawning component, we used kernel density estimation (KDE), where the 95 and 50% volume density contours were taken as estimates for 2-dimensional ‘home ranges’ and ‘core areas’, respectively (Worton 1989, Seaman & Powell 1996). The home range of a group of cod is defined here, based on Burt (1943), as the area traversed by the bulk of individuals in their normal activities of food gathering and mating. KDE is carried out by substituting each position with a probability distribution and summing all distributions to create an overall probability distribution. Smoothing parameters used in KDE analyses were 70 to 90% of the ‘reference bandwidth’ (Worton 1989, Kie et al. 2010, Kie 2013), calculated as:

\[
h_{\text{ad}} = \sigma \times n^{-1/6}
\]  

where \(\sigma\) is the standard deviation of the x- and y-coordinates of recapture locations for each group and \(n\) is the number of locations. Reducing the reference bandwidth is important when locations are clumped, to avoid the data being over-smoothed and the areal estimate of the home range estimate being too large, with excess space around the outermost points (Kie et al. 2010, Kie 2013). A fixed proportion of 0.7 to 0.8 has been suggested to reduce over-smoothing (Kie et al. 2010), and here the reference bandwidth was sequentially reduced in increments of 0.10 following Kie (2013) to select an ad hoc bandwidth \((h_{\text{ad, hoc}})\). Kernel estimators are robust to autocorrelation (De Solla et al. 1999, Barg et al. 2005), but tend to overestimate home range size at small sample sizes (Seaman & Powell 1996).
In the KDE analysis, home ranges and core areas were estimated separately for the spawning and feeding seasons. Home ranges were not estimated for spawning components with fewer than 300 recaptures in total, but core areas were estimated for all components. Due to high numbers of recaptures for the SW, E and NE spawning components, both home ranges and core areas were estimated for each month of the spawning season. Home ranges were restricted to depths of <800 m and, for obvious reasons, not allowed to enter the land mass of Iceland. The 800 m depth criterion was based on depth profiles from DST tags and data from the annual MRI Autumn Groundfish Survey (10 to 1500 m), where only 0.01% of cod >54 cm are caught below depths of 800 m. The size (km²) of the home range of each spawning component was calculated, and the area of home range overlap was calculated for each pair.

## Fidelity

Here, following Robichaud & Rose (2004), fish that stay year-round within a spawning area are said to display site fidelity, whereas those that leave the spawning area but return in subsequent spawning seasons display homing. CT recaptures do not allow for distinguishing between these 2 behavioural patterns, and therefore we use the phrase 'fidelity' to identify fish that were recaptured within the area of tagging.

Rates of fidelity to spawning grounds (Fig. 1) were estimated based on tag returns from April (the height of spawning and the month of tagging for the majority of fish), excluding the season of tagging. Total catch of cod at each spawning ground (Table 2) was used to standardize the observed recaptures. Catch weight from fishing logbooks was converted to numbers using the mean weight of cod by areas in the spawning season, from samples collected routinely by MRI from the landed catch (Table 2). We used an equation from Bayliff (1979), where the proportional distribution of tagged fish ($P_i$) located in area $i$ is estimated from the number of recaptures ($R_i$) weighted by total catch ($C_i$) and size of the area ($A_i$), as follows:

$$P_i = \frac{R_i / (C_i / A_i)}{\sum(R_j / (C_j / A_j))}$$

The method assumes that the probability of a tag recapture is related linearly to the catch. Tag reporting rate and catchability of cod among areas, and tag reporting rates from different gear types, are assumed to be equal. Rate of spawning ground fidelity for each component was estimated as the proportion of standardized recaptures in April, recaptured within the spawning ground of tagging. Straying rate was estimated as the percentage of standardized recaptures within other spawning grounds in April.

## Data storage tags

Depth and temperature data were extracted from 235 returned data storage tags (DSTs) surgically implanted in the abdominal cavity of cod at several spawning locations around Iceland (Table 1). All DSTs were produced by Star Oddi. Four types of DSTs were used, depending on the period. From 1995 to 1999, ‘DST 200’ and ‘DST 300’ types were used, followed by ‘DST milli’ in 2002. From 2003 to 2005 both ‘DST milli’ and ‘DST centi-ex’ were used. Characteristics of the tags and tagging procedure are described on the website: www.hafro.is/skrar/flokkar/merkingar_thorskur.pdf (accessed 19 January 2015).

As part of earlier studies, recaptured cod with DSTs were classified into ‘coastal’ or ‘frontal’ behavioural
types (hereafter referred to as frontal and coastal cod) on the basis of their depth and temperature association outside the spawning season (for details see Pálsson & Thorsteinsson 2003, Pampoulie et al. 2008, Grabowski et al. 2011). Within a given year, coastal cod show a clear seasonal temperature signal, with a maximum in September/October and a minimum in February/March, and reside mostly at depths above 200 m. In contrast, frontal cod are mostly found below 200 m outside the spawning season and tend to carry out frequent vertical migrations. Temperature signals from frontal cod are highly variable, indicative of thermal fronts.

DST depth and temperature recordings from 162 coastal cod and 73 frontal cod (Table 3), each providing data for at least 90 d, were used to compare spawning components and to validate the depth distribution of CTs. Following Wright et al. (2006) and Le Bris et al. (2013), we assume that cod spend at least some time during every 24 h at or close to the seabed, and we therefore took the maximum depth recorded on each calendar day as indicative of bottom depth in the area where the fish resided. Temperature at maximum daily depth was taken as indicative of near-bottom temperature.

As a part of an earlier study (Thorsteinsson et al. 2012), a tidal location model was applied to depth recordings of 35 DSTs from cod tagged at 5 spawning grounds to determine geographical locations. From the model, 460 locations are available for the spawning season and 479 locations for the feeding season (Table 4). A description of the tidal location method and the criteria for selecting DSTs for that analysis are found in Thorsteinsson et al. (2012).

### Parallel distance and distance from shore

Orthogonal projection was used to analyse spatial overlap of 5 spawning components through time, excluding components with a low number of recaptures. Position (latitude and longitude) of each CT recapture was projected onto a curve drawn around Iceland, outside the main headlands. The calculated value used was the distance (km) from the start/end position of the curve, hereafter referred to as the parallel distance. Constraining each recapture position orthogonally to a single position on a curve provides a method to analyse the degree of overlap of different spawning components. The validity of the method is supported by the fact that migration of Icelandic cod tends to follow the shelf (Jónsson 1996, Schopka et al. 2010). A disadvantage of the method is the discontinuity where the curve begins and ends, and therefore the start/end position of the curve had to be located in areas with a low number of recaptures. For that reason, spawning grounds in the south and west were analysed separately from those in the north and east.

To compare offshore/inshore movements among spawning components, the minimum distance (km) between each CT recapture position and the main coast of Iceland was estimated. The distance to every location of the coastline was calculated, and the lowest value was used to represent the distance from shore.

### Statistical analysis

The statistical program R Version 3.0.1 (R Core Team 2013) was used for statistical analyses and plotting, and for calculating parallel distance and minimum distance from shore. Two-factor ANOVAs were used to compare mean parallel distance and mean distance from shore between spawning components (factor area; 5 levels) and seasons (factor season; 6 levels). Prior to analysing distance from shore, the data were log-
transformed in order to approach the normal distribution. In the ANOVAs, recaptures in the first 2 seasons were excluded to allow time for cod to disperse from the tagging sites.

RESULTS

Number of recaptures

Tagging sites of cod *Gadus morhua* were distributed around Iceland, but most recaptures originated from nearshore tagging experiments in the southwest, southeast, east, northeast and west (Table 5). From 6764 recaptured CTs for which fishing gear was known, 45% were caught with gillnets, 20% with longlines, 14% with bottom trawls, 13% with bottom seines and 8% with handlines. The median value for time from tagging to recapture was 9.7 mo (1st quartile = 2.5 mo, 3rd quartile = 14.7 mo). Most tagged cod were recaptured within 20 mo (81%), but 13% were recaptured at least 2 yr after tagging.

Recaptures in the spawning season

Core areas of 7 spawning components in the spawning season were completely segregated (Fig. 2a–g). Furthermore, the spawning home range of the W spawning component was almost completely segregated from the SE, E and NE components. A considerable overlap in home ranges was observed between the SW and SE spawning components (55%), and the E component was largely overlapped by the NE component (Table 6). Home ranges and core areas of the SW spawners were larger in March, and especially in May, than during the peak time of spawning in April (Fig. 3a). For the E and NE components, home ranges and core areas were less extensive in April and May than in March (Fig. 3b,c).

Fidelity rates of spawning components to the spawning ground of tagging ranged from 53 to 97%; these were highest for the E spawning component and lowest for the NE component (Table 7). Average straying rate between adjacent spawning grounds was 8.6% (median = 8%), but straying to more distant spawning grounds was rare.

Recaptures in the feeding season

The recaptures were more widely distributed in the feeding season than in the spawning season, and consequently home ranges and core areas were larger (Fig. 2h–n). There were substantial differences in recapture positions and feeding home ranges among spawning components (Fig. 2h–n). The recaptures suggest that all the components include both migratory and relatively sedentary individuals. Cod belonging to the SW spawning component were recaptured in areas from the southeast to the

<table>
<thead>
<tr>
<th>Area</th>
<th>Season</th>
<th>S1</th>
<th>F1</th>
<th>S2</th>
<th>F2</th>
<th>S3</th>
<th>F3</th>
<th>S4+</th>
<th>F4+</th>
</tr>
</thead>
<tbody>
<tr>
<td>SW</td>
<td></td>
<td>528</td>
<td>579</td>
<td>426</td>
<td>368</td>
<td>138</td>
<td>77</td>
<td>63</td>
<td>40</td>
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<tr>
<td>SE</td>
<td></td>
<td>92</td>
<td>134</td>
<td>104</td>
<td>65</td>
<td>23</td>
<td>29</td>
<td>31</td>
<td>14</td>
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<tr>
<td>E</td>
<td></td>
<td>220</td>
<td>138</td>
<td>227</td>
<td>131</td>
<td>60</td>
<td>61</td>
<td>56</td>
<td>41</td>
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<td></td>
<td>200</td>
<td>309</td>
<td>228</td>
<td>212</td>
<td>91</td>
<td>97</td>
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<td>8</td>
</tr>
<tr>
<td>W</td>
<td></td>
<td>35</td>
<td>198</td>
<td>32</td>
<td>106</td>
<td>29</td>
<td>53</td>
<td>26</td>
<td>21</td>
</tr>
<tr>
<td>WSW</td>
<td></td>
<td>43</td>
<td>58</td>
<td>23</td>
<td>35</td>
<td>11</td>
<td>5</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>883</td>
<td>909</td>
<td>780</td>
<td>599</td>
<td>232</td>
<td>172</td>
<td>156</td>
<td>101</td>
</tr>
</tbody>
</table>

Table 5. *Gadus morhua*. Numbers of recapture positions for different tagging areas and seasons. S1 is the spawning season of tagging; F1 is the feeding season following tagging, etc. S4+: fourth and later spawning seasons combined; F4+: fourth and later feeding seasons combined

<table>
<thead>
<tr>
<th>Spawning component</th>
<th>a (km²)</th>
<th>b (km²)</th>
<th>Overlap</th>
<th>a (%)</th>
<th>b (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SW</td>
<td>124.9</td>
<td>77.6</td>
<td>40.6</td>
<td>52</td>
<td>33</td>
</tr>
<tr>
<td>SE</td>
<td>124.9</td>
<td>25.0</td>
<td>18.7</td>
<td>75</td>
<td>15</td>
</tr>
<tr>
<td>E</td>
<td>124.9</td>
<td>72.2</td>
<td>24.1</td>
<td>33</td>
<td>19</td>
</tr>
<tr>
<td>NE</td>
<td>124.9</td>
<td>69.4</td>
<td>54.2</td>
<td>78</td>
<td>43</td>
</tr>
<tr>
<td>SE</td>
<td>77.6</td>
<td>25.0</td>
<td>23.7</td>
<td>95</td>
<td>31</td>
</tr>
<tr>
<td>E</td>
<td>77.6</td>
<td>72.2</td>
<td>43.3</td>
<td>60</td>
<td>56</td>
</tr>
<tr>
<td>NE</td>
<td>77.6</td>
<td>69.4</td>
<td>0.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>W</td>
<td>25.0</td>
<td>25.0</td>
<td>23.1</td>
<td>32</td>
<td>92</td>
</tr>
<tr>
<td>N</td>
<td>72.2</td>
<td>69.4</td>
<td>5.1</td>
<td>7</td>
<td>7</td>
</tr>
</tbody>
</table>

Table 6. *Gadus morhua*. Pairwise comparison of 95% kernel density estimation home range sizes (×1000 km²) and spatial overlap between spawning components during the spawning and feeding seasons
Fig. 2. Recapture positions of cod *Gadus morhua* from tagging conducted within 7 spawning grounds from 1991 to 2008. Left (a−g): spawning season; right (h−n): feeding season. Orange dots indicate recapture positions for conventional tags, red polygons denote estimated 95% kernel home ranges and black polygons denote 50% core areas (or black lines where core areas are overlapped by dots). Green triangles show tidal locations from data storage tags. The 800 m depth contour is shown 

(Fig. continued on next page)
northwest of the country but were not found to migrate to the northern or northeastern areas (Fig. 2h). Fish from the SE spawning grounds were recaptured at feeding areas off the southern and eastern coasts but rarely migrated to areas west or north off Iceland (Fig. 2i). Cod from the E spawning area were mainly recaptured in relatively shallow waters in the east and southeast (Fig. 2j), but feeding migrations of the NE spawners were both to inshore and offshore areas off the eastern part of Iceland (Fig. 2k). Fish in the N spawning area rarely migrated to the southern and eastern feeding grounds, but several fish were recaptured west and northwest of Iceland (Fig. 2l). In contrast to the SE, E and NE spawners, cod from the W component were mainly recaptured in the west and northwest in the feeding season (Fig. 2m). The recapture data suggest high site fidelity in the WSW spawning component, although several fish were recaptured in the northwest and southeast (Fig. 2n).

The home range sizes in the feeding season, estimated for 5 spawning components, ranged from 25 000 (E) to 125 000 km² (SW) (Table 6). Home range overlap was relatively high for the SW and W components, the SE and E components, and the E and NE components. The home range of the W spawning component during the feeding season was completely segregated from the SE and E components.
Similarly, a relatively low overlap was found between the SW/W components and the NE component despite large home ranges (Table 6, Fig. 2h,k,m). Overlap in core feeding areas was minimal, except for the WSW component that was overlapped extensively by the SW component (Fig. 2h,n).

Tidal locations

Most DST tidal locations were positioned within the home ranges estimated with CT recaptures, and usually they were distributed throughout the areas (Fig. 2). However, for the SW component, tidal locations in the feeding season (from only 2 DSTs, see Table 4) were restricted to nearshore areas in the south and southwest (Fig. 2h). For the SE component, offshore feeding areas east and southeast of Iceland had no tidal locations (Fig. 2i), and, for the NE spawners, locations were lacking in the southern part of the home range (Fig. 2k).

Parallel distance and distance from shore

Year-to-year stability was observed in parallel distance of recaptures of each spawning component, and the different components were found to have different parallel distributions (Fig. 4a,b). For example, the median parallel distances of the SE spawners were around 400 to 430 km in the spawning seasons but 320 to 400 km in the feeding seasons (Fig. 4a), reflecting anticlockwise feeding migrations. In contrast, the median parallel distances of cod spawners from the SW and W were found to be in the ranges of 650 to 750 and 900 to 960 km, respectively, with weak indications of clockwise feeding migrations (Fig. 4a). A weak clockwise shift from spawning to feeding grounds was observed for the NE spawning component, but the E component showed no annual or seasonal variation in parallel distribution (Fig. 4b). Significant main effects were found for the factors ‘area’ and ‘season’ on mean parallel distance of recaptures, when examined with 2-factor ANOVAs (Table 8). The F-values for the factor ‘area’ were high, thus suggesting that spawning components were highly spatially distinct. The interactions be-

Table 7. *Gadus morhua*. Fidelity (bold) and straying rates (%) for different spawning components according to standardized tag recaptures in different spawning areas (see Fig. 1) during the peak of the spawning season (April)

<table>
<thead>
<tr>
<th>Spawning component</th>
<th>Number of recaptures</th>
<th>Spawning areas (% standardized recaptures)</th>
<th>Total straying rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SW</td>
<td>193</td>
<td>SW 78, SE 15, E 0, NE 0, N 0, W 7, WSW 0</td>
<td>22</td>
</tr>
<tr>
<td>SE</td>
<td>54</td>
<td>SE 11, SW 78, E 85, NE 0, N 1, W 0, WSW 1</td>
<td>15</td>
</tr>
<tr>
<td>E</td>
<td>155</td>
<td>E 0, SW 0, SE 85, NE 97, N 1, W 0, WSW 1</td>
<td>3</td>
</tr>
<tr>
<td>NE</td>
<td>128</td>
<td>NE 1, SW 3, SE 9, N 53, W 30, WSW 30, Other 4</td>
<td>47</td>
</tr>
<tr>
<td>N</td>
<td>16</td>
<td>N 0, SW 10, SE 82, E 0, NE 10, W 0, WSW 0</td>
<td>18</td>
</tr>
<tr>
<td>W</td>
<td>17</td>
<td>W 0, SW 0, SE 0, E 0, NE 0, WSW 0, Other 86</td>
<td>14</td>
</tr>
<tr>
<td>WSW</td>
<td>9</td>
<td>WSW 21, SW 0, SE 0, E 0, NE 0, W 0, WSW 0</td>
<td>21</td>
</tr>
</tbody>
</table>
between the 2 factors were also significant, indicating that the parallel distances were not consistent among spawning components over time.

All spawning components analysed showed offshore movements from spawning grounds to feeding areas, where cod from the SE component tended to migrate farther offshore than the other components (Fig. 4c,d). In the feeding season, 42% of SE spawners were recaptured farther than 30 km from shore, compared with 8 to 29% for the other components. The E spawners exhibited the shortest offshore feeding migrations; these were generally <15 km from shore. In a 2-factor ANOVA, the main effects and interaction term of the factors ‘area’ and ‘season’ on mean distance of recaptures from shore were statistically significant (Table 8).

There was a shift from predominantly anticlockwise to both clockwise and anticlockwise feeding migration when moving from spawning grounds in the southeast to the southwest (Fig. 5a). The shift occurred at a parallel distance of approximately 600 km (start position in the northeast), corresponding to longitudes of about 20°W. East of 20°W only 7 to 19% of the recaptured fish conducted clockwise feeding migrations, compared with 63 to 88% for fish spawning west of 20°W. On average, spawning com-
ponents in the north and east did not show strong clockwise or anticlockwise movements, although more fish migrated in a clockwise direction (Fig. 5b).

### Depth and temperature association

The recapture depths of CTs (Fig. 6a) were lower than the maximum daily depths of the DSTs, particularly in the feeding season (Fig. 6b). Depth distributions of CTs resembled those of DST-tagged coastal cod (Fig. 6c), usually ranging from 50 to 100 m in the spawning season and 50 to 200 m in the feeding season. Although recapture depths of CTs of >400 m were observed for all spawning components during the feeding season (Fig. 6a), they constituted only 1.4% of the total recaptures, compared with 6.8% for the DSTs combined.

As integrated into the behavioural type classification of DST-tagged cod, there were substantial differences in bottom depths and bottom temperatures occupied by coastal and frontal cod in the feeding season. Coastal cod mainly inhabited feeding areas with depths of 50 to 200 m (Fig. 6c) and bottom temperatures of 6 to 9°C (Fig. 7a), except for the NE component that was found in shallower waters at lower temperatures. Frontal cod foraged mainly in waters with bottom depths of 200 to 500 m (Fig. 6d) and at temperatures of 1 to 6°C (Fig. 7b). Frontal cod from the NE spawning component were found in shallower waters than other components, but at similar temperatures.

In the spawning season, DST-tagged cod mainly occupied areas with bottom depths of 50 to 200 m (Fig. 6b). However, frontal cod (Fig. 6d) were usually associated with deeper areas than their coastal counterparts (Fig. 6c), and the NE component was found in shallower waters than other components. There were no clear differences in temperatures experienced by frontal versus coastal cod for any of the spawning components during spawning (Fig. 7). On the contrary, there were substantial differences among spawning components, with the NE component spawning at 2 to 4°C, the W component at 4 to 6°C, and the more southerly components at 6 to 8°C (Fig. 7).
DISCUSSION

The study revealed migration patterns, home ranges and depth/temperature associations that differed among spawning components of cod *Gadus morhua*. Some home ranges were almost completely segregated, during both the spawning and feeding seasons, and spawning components concentrated in different areas around the country and at different distances from shore. The results complement earlier studies indicating genetic, morphological, or behavioural distinction between some of the spawning components.
components (Jónsdóttir et al. 2002, Pampoulie et al. 2006, McAdam et al. 2012). Although the question remains open as to what extent this complexity promotes resilience of the cod population, a greater diversity in temporal, spatial and biological aspects of spawning is likely to aid fish populations in adjusting to anthropogenic and climatic pressure (Hilborn et al. 2003, Hutchinson 2008). Spatially segregated groups of spawning Icelandic cod are exposed to variable environmental conditions, which seem to affect their relative spawning success (Begg & Marteinsdottir 2000, 2002, Marteinsdottir et al. 2000b, Thorisson et al. 2011, Pampoulie et al. 2012). These studies suggest a substantial inter-annual variation, characterized typically by the largest contributions from southwestern spawning components, but occasionally with larger contributions from smaller and more northerly spawning components.

Both spawning and feeding home range sizes varied greatly, reflecting the relative abundance of the spawning components. Within the distribution range of Atlantic cod, the area occupied by different cod groups is strongly related to their biomass (Robichaud & Rose 2004), in line with the hypothesis that high migratory activity is an adaptation to cope with high abundance (Harden-Jones 1968). Earlier studies, analysing mark-recapture data (e.g. Jónsson 1996) and otolith chemistry (Campana et al. 1999) show that cod from segregated spawning grounds may mix seasonally at productive feeding areas. However, according to the present study, cod aggregations on important feeding grounds northwest and east of Iceland are essentially of different origins, and only the large SW spawning component conducted significant migrations both to the northwest and east. Cod in these 2 feeding areas have been shown to differ with respect to liver and body condition (Pardoe & Marteinsdóttir 2009). Although this variation may lend support to our findings, it may mainly be due to regional differences in prey availability and temperature.

Despite year-round spatial distinction between some components, we observed straying of up to 30% across adjacent spawning grounds. Cod do exhibit distinct prey preferences (Link & Garrison 2002), and prey availability and prey movements are factors likely to affect migratory behaviour and the structure of predator populations. In most years, just prior to the spawning period of cod, dense schools of capelin *Mallotus villosus* arrive at the southeastern shelf and migrate to spawn in shallow areas south and west of Iceland (Vilhjálmsson 1994). The capelin is heavily preyed upon by cod and other predators as it migrates westward along the south coast (Magnússon & Pálsson 1991, Vilhjálmsson 1997). The ‘capelin run’ is likely to affect spatial structure in the cod population and could promote straying of cod between spawning grounds south and southwest of Iceland. Abiotic environmental fluctuations could also be a driving force for straying between spawning grounds, e.g. in the north where temperature variability is high due to variable inflow of Atlantic water via the North Icelandic Irminger Current (Jónsson & Valdimarsson 2005). In these areas spawning may be constrained by suboptimal temperatures, as suggested for Northeast Arctic cod spawning off northern Norway (Höffle et al. 2014). There are other factors that could stimulate straying, including social transmission of migratory behaviour (Dodson 1988, Corten 2002) in areas where feeding home ranges overlap.

Although core areas rarely overlapped, there was a considerable overlap in home ranges even during the spawning season. A drawback of the analysis of spawning home ranges is that a period of 3 mo (March to May) was taken to represent the spawning season, to include spawning activity of most fish and obtain a reasonable number of recaptures. However, the actual spawning period of individual cod is generally only about 3 to 4 wk (Jónsson 1982), and therefore some fish recaptured in March may have been on migration to spawning grounds, and in May fish may have already initiated feeding migrations. In support of this argument, home ranges and core areas of the SW spawning component were less extensive in April than in March and May. The main spawning of the E and NE components may take place in April and May, judging from less extensive home ranges than those found in March. Using a shorter time period adjusted to match the peak spawning period would therefore result in smaller home ranges and less overlap.

The observed spatial demography of cod seems to match well with the metapopulation concept. A metapopulation is a set of local non-autonomous subpopulations connected by a variable degree of movement and gene flow, where the subpopulations may potentially undergo extinction and recolonization (Hanski & Gilpin 1997, McQuinn 1997). Metapopulation theory has been applied as a framework to describe the population structure of marine fish such as Atlantic herring *Clupea harengus* (McQuinn 1997) and cod (Smedbol & Wroblewski 2002). In Newfoundland waters, cod are believed to have achieved a balance between homing and straying that maintains population stability, but considering meta-
population theory, would allow for recolonization and recovery of depleted subpopulations (Robichaud & Rose 2001). Yet, in line with Robichaud & Rose (2001) and Wright et al. (2006), it seems likely that spawning grounds with high levels of fidelity but low levels of immigration from other areas, e.g. the inshore grounds in East Iceland, would rebuild slowly following collapse. Although the small spawning components in the north and east are of relatively low importance in the current fishery for cod, their significance could become greater under different environmental conditions.

The pronounced anticlockwise feeding migration of the SE spawning component to the areas east of Iceland suggest a different pattern compared with other spawning components. Presuming that post-spawning migration of cod is denatant and linked to drift of eggs and larvae from the spawning grounds (Harden-Jones 1968), the anticlockwise movement could be related to larval advection by ocean currents towards the east. This proposition is supported by near-surface drifter experiments (Valdimarsson & Malmberg 1999) and drift probability models (Brickman et al. 2007), and recent current models demonstrate an intense eastward flow from the southern and southeastern shelf of Iceland to the areas between Iceland and the Faroes (Logemann et al. 2013). In light of this, the connectivity between the SE spawning grounds and the eastern feeding areas could be facilitated by larval drift via the eastward current, later followed by natal homing migrations. Evidence for natal homing in cod has been presented by Svedäng et al. (2007a), although their conclusions are not without dispute (Bradbury & Laurel 2007, Svedäng et al. 2007b). More information is needed on oceanographic processes, larval drift, and juvenile and adult migrations to understand the connectivity between the SE spawning grounds and the eastern feeding aggregation area.

Geographical tidal locations from DSTs demonstrate migration patterns similar to those found by CTs. Still, for some components, only parts of the home ranges had tidal locations, usually in cases where tidal locations were based on only a few individuals. Potentially, tidal locations could reveal migrations outside fished areas and, consequently, outside home ranges estimated from CT recaptures. This was rarely the case. A disadvantage of the tidal location method is that geographical locations are only available for periods when tagged fish stay at the seafloor for several hours, i.e. a time sufficient to detect the phase and amplitude of the tidal wave (Thorsteinsson et al. 2012). Cod foraging at offshore thermal fronts exhibit frequent vertical migrations and are therefore unlikely to provide geographical tidal locations during the feeding period. Neither DST tidal locations nor CT methods would therefore reveal offshore migrations of frontal cod outside fishing grounds.

Foraging migrations of frontal cod to the outer parts of the continental shelf (400 to 800 m) were underrepresented by CT recaptures. This could be due to lower fishing effort in these areas and/or lower catchability of frontal cod with bottom gear due to greater vertical swimming activity. The actual proportions of coastal and frontal cod on the spawning grounds could also play a role. Analysis of the Panto-physin locus (PanI) indicates that coastal cod primarily carry the PanIAA genotype (94%, n = 32), but frontal cod carry the PanIBB genotype (88%, n = 8) (Pampoulie et al. 2008). According to PanI genotype frequencies on the spawning grounds (Pampoulie et al. 2008, Jakobsdóttir et al. 2011, McAdam et al. 2012), and using genotype as a proxy for behaviour, coastal cod may have been much more abundant than frontal cod on the main spawning grounds in the study period. Underestimating off-slope migrations could affect home range estimates, but these effects are probably minor, firstly because the migrations are conducted by only a part of the population, and more importantly because KDE tended to stretch the outer parts of home ranges outside the slope areas to depths of around 800 m.

Our results have implications for fisheries management. From 1993 onwards, cod spawning grounds within Icelandic waters have been closed for all fishing for 2 to 3 wk at the height of spawning (Schopka 2007). Although Icelandic cod is, in general, assessed and managed on a single-stock basis (Schopka 1994, Marine Research Institute 2014), these closures aim at promoting spawning in all known spawning areas. Spawning ground closures, however, may not be sufficient to protect all spawning components, owing to fishing activities at other times of the year. Total allowable catch is set for the whole population, and disproportionate fishing mortality in the feeding season could have detrimental effects on small and vulnerable subpopulations. Indeed, changes in genotype frequencies in spawning cod have been observed and related to intense and disproportionate fishing (Árnason et al. 2009, Jakobsdóttir et al. 2011). Networks of marine protected areas (MPAs) have been put forward as a tool for conserving marine biodiversity and fish stocks (Gell & Roberts 2003, Jennings 2009), although MPAs can rarely be relied upon as a sole solution (Kaiser 2005, Jones 2007). In fisheries management, e.g. in Iceland, MPAs are
most often used in conjunction with other measures (Jaworski et al. 2006), where they may serve as a buffer against control errors and uncertainty (Hilborn et al. 2004, Stefansson & Rosenberg 2005). Yet, effective MPA design would require thorough knowledge of stock structure, larval drift, adult migration and oceanographic processes that drive the system.

Here, we analysed migration of cod from spawning areas ranging from approximately 1000 to 7000 km², covering various depth intervals and/or fjord systems. Some of these areas comprise at least 2 groups of cod that differ with respect to fine-scale spawning habitat selection and foraging strategies outside the spawning season (Grabowski et al. 2011). Furthermore, there is considerable spatial variation in size and age of cod spawners among adjacent locations, even within areas referred to as single spawning grounds (Marteinsdottir et al. 2000a). Hence, the areas outlined here are most likely too coarse to reflect the fine-scale subpopulation structure of Icelandic cod. Currently, however, a transition from single-stock management to fine-scale management of numerous subpopulations does not seem to be a feasible option, given the state of knowledge and practical constraints within the management system.

The Icelandic cod population consists of several spawning components, some of which are separated from each other throughout the year. This subpopulation structure is maintained by site fidelity, but the spawning components are interconnected by relatively low levels of straying. Our study contributes to the growing knowledge of the within-population diversity and demographic structure of cod and further emphasizes the need for considering these factors in stock assessment and fishery management. We suggest that properly designed area closures in feeding and nursery areas, temporary spawning ground closures and precautionary fishing mortality rates are the most practical measures to preserve diversity within cod populations and minimize the risk of over-exploitation and recruitment failure. All of these management strategies have already been adopted for the Icelandic cod but could be adjusted based on accumulating knowledge of the stock’s structure.

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