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Movement of Atlantic cod around the British Isles: implications for finer scale stock management

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Summary

1. Commercial fisheries risk unintentionally depleting local population components if stock management units do not reflect the population structure of the species. Atlantic cod *Gadus morhua* L. was over exploited in the sea areas around the British Isles in the last century and is struggling to recover. There is an urgent need to define the biological stock structure to improve management.

2. In this study, we used data recovered from temperature and depth loggers attached to 252 Atlantic cod to infer and map their movements around the British Isles. Individual cod showed a range of behaviours including migration, site fidelity and limited home ranging. We estimated home ranges and seasonal movements and test predictions based on data from population genetics. Cod from a northern offshore area in the North Sea did not mix with cod from the central and southern North Sea, which in turn did not mix with those from western areas (the Celtic and Irish Seas).

3. Cod experienced average monthly temperatures between 6 and 17 °C and occupied average depths between 15 and 165 m. Cod that occupied the deeper northern offshore area lived in colder and less variable waters than elsewhere. Differences in thermal experience are likely to underpin variation in physiology and growth rate that will have implications for how the species responds to climate change.

4. This study provides evidence that cod living around the British Isles are comprised of at least one more distinct population unit that is currently recognized for stock management purposes. Failure to recognize this complexity of stock structure in past management plans is likely to have been a contributory factor to the over-exploitation of cod stocks around the British Isles.

5. *Synthesis and applications*. The results of this study and recent genetic research provide a new and more definitive understanding of movement patterns and population structure of cod around the British Isles. The applied implication of this is that spatially explicit adjustment of exploitation strategies, for example setting a maximum sustainable yield for each of the population units, should be considered to ensure sustainable harvesting of cod in the future.

Key-words: cod, electronic tagging, fish, *Gadus morhua*, migration, stock structure, thermal habitat

Introduction

The application of concepts traditionally used in terrestrial ecology, for example, meta-population dynamics are becoming increasingly influential in marine management and fisheries (Lipcius *et al.* 2008). An increasing number of studies suggest that the stock boundaries used to manage marine fish do not necessarily reflect the biological structure underlying population processes (Kritzer & Sale 2004; Reiss *et al.* 2009; Ciannelli *et al.* 2013; Kritzer & Liu 2013). This can become problematic when spatially intensive fisheries lead to local depletion of population

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components that reduce the capacity to withstand exploitation and recover from perturbation (Schindler *et al.* 2010). A crucial element in understanding stock structure is defining movements and home range of the different population units. For example, populations that reside in small geographical areas year round may be the most prone to localized depletion. Conversely, if different populations mix widely outside the spawning period, for example, as do Atlantic blue-fin tuna *Thunnus thynnus*, they can be unwittingly exploited as part of a separate stock (Block *et al.* 2005). A better appreciation of the spatial ecology of the species provides a stronger basis for developing spatially explicit harvesting regimes that maintain each constituent population unit at a safe level of abundance.

Atlantic cod, *Gadus morhua* L., is a commercially valuable fish found throughout the shelf seas of the North Atlantic. Cod has long been thought to be a population-rich species (Sinclair 1988) that exhibits resident, migratory and aggregating behaviours (Rose 1993; Green & Wroblewski 2000; Lawson & Rose 2000; Jónsdóttir, Daníelsdóttir & Naedval 2001; Pálsson & Thorsteinsson 2003; Robichaud & Rose 2004; Neuenfeldt *et al.* 2013) that can be associated with genetically distinct groups (Ruzzante *et al.* 2000; Hutchinson, Carvalho & Rogers 2001; Knutsen *et al.* 2003; Jorde *et al.* 2007; Nielsen *et al.* 2009; Heath *et al.* 2013).

Around the British Isles, cod are managed as four main stock units: the Celtic Sea, the Irish Sea, the west of Scotland and the North Sea (including the English Channel). Cod has been subject to heavy exploitation for many decades, falling to a record low in the North Sea at the end of the last century (Pope & Macer 1996; Cook, Sinclair & Stefansson 1997). In the North Sea, it was apparent that the decline in stock did not occur evenly across the region (Hedger *et al.* 2004; Horwood, O'Brien & Darby 2006), suggesting the presence of spatially discrete populations. To date, there has been no comprehensive study of the movements and spatial dynamics of cod that can provide evidence to underpin a more spatially appropriate management plan.

In the sea areas around the British Isles, molecular evidence for genetic isolation has confirmed that the current management units only partly reflect the population structure; at least two reproductively isolated groups are apparent in the North Sea (Hutchinson, Carvalho & Rogers 2001; Nielsen *et al.* 2009; Heath *et al.* 2013). These genetic studies provide *a priori* expectations regarding cod behaviour and movement; cod from genetically distinct groups should remain spatially isolated during spawning whereas for the cod from areas where there is presently no evidence for genetic segregation, individuals should intermix freely with one another throughout their range. To test these predictions, we present an analysis of inferred movements of 252 individual cod tagged with electronic data loggers from around the British Isles. In the context of understanding possible mechanisms underlying the observed population structure, we also present information on the thermal and depth experience of cod throughout the study area.

Materials and methods

STUDY AREAS

The data were collated from a number of separate studies carried out between 1999 and 2010 and from across nine sea areas (Fig. 1; Table 1): the southern North Sea (ICES area IVc); the central North Sea (ICES area IVb); north-east Scotland (including the Moray Firth and Shetland Isles (ICES area IVa); the Viking Bank (ICES area IVa), the Scottish west coast (ICES area VIa); the Irish Sea (ICES area VIIa); the Celtic Sea (ICES areas VIIb and VIIf); and the western and eastern English Channel (ICES areas VIId and VIIe, respectively). These nine areas covered most of the distribution of cod around the British Isles, although the number of cod tagged and returned in each area varied resulting in some areas being better represented, for example the eastern English Channel, than others, for example the west coast of Scotland. Tagging was carried out mainly during the spawning season (classed here as from 1 January to 30 April).

DATA STORAGE TAG (DST) AND IMPLANTATION

Data storage tags used in this study were either the Centi or Milli (Star-Oddi Marine Device Manufacturing Ltd, Gardabaer, Iceland), the LTD1200 or LTD1110 (Lotek Marine Technologies Inc., Ontario, Canada), or G5 (Cefas Technologies Ltd, Lowestoft, UK). Each DST was programmed to record depth and temperature every 5, 10 or 20 min depending on the memory capacity and battery life of the tag. Cod were captured using a modified commercial bottom trawl or by line in inshore areas where the seabed was too rough to trawl. Cod were anaesthetized in sea water containing MS222 or phenoxyethanol (Sigma-Aldrich Company Ltd, Gillingham, UK). For internal implantation of tags, a small incision was made in the belly along the mid-ventral line and a sterilized DST inserted into the body cavity. A plastic filament (~7 cm long) from the DST remained external and secured with a rubber bead. The incision was then sutured with two stitches using braided nylon (Ethicon Ltd, Johnson & Johnson International). A second conventional fish tag with return details (Floytag Mfg Ltd, Seattle, WA, USA) was sewn through the dorsal musculature. External tags were attached by threading nylon or monofilament line from the attachment points of the DST through the muscles anterior to the first dorsal fin and fastening the ends securely on the other side (Righton *et al.* 2010). The tagged cod were allowed to recover from the procedure in a tank and, provided they showed normal buoyancy control, were released overboard and the position recorded from the ship's GPS. A reward for return was offered to fishermen. In the United Kingdom, this research was carried out by Home Office licensed personnel under a number of Animals (Scientific Procedures) Act project licenses issued by the UK Home Office during the course and across the range of the study.

ESTIMATION OF GEOGRAPHIC POSITION

Hydrostatic (tidal) data, derived from the sinusoidal pressure cycle recorded in the depth data when a fish is at rest on the seafloor, were used to enable the geographical reconstruction of an

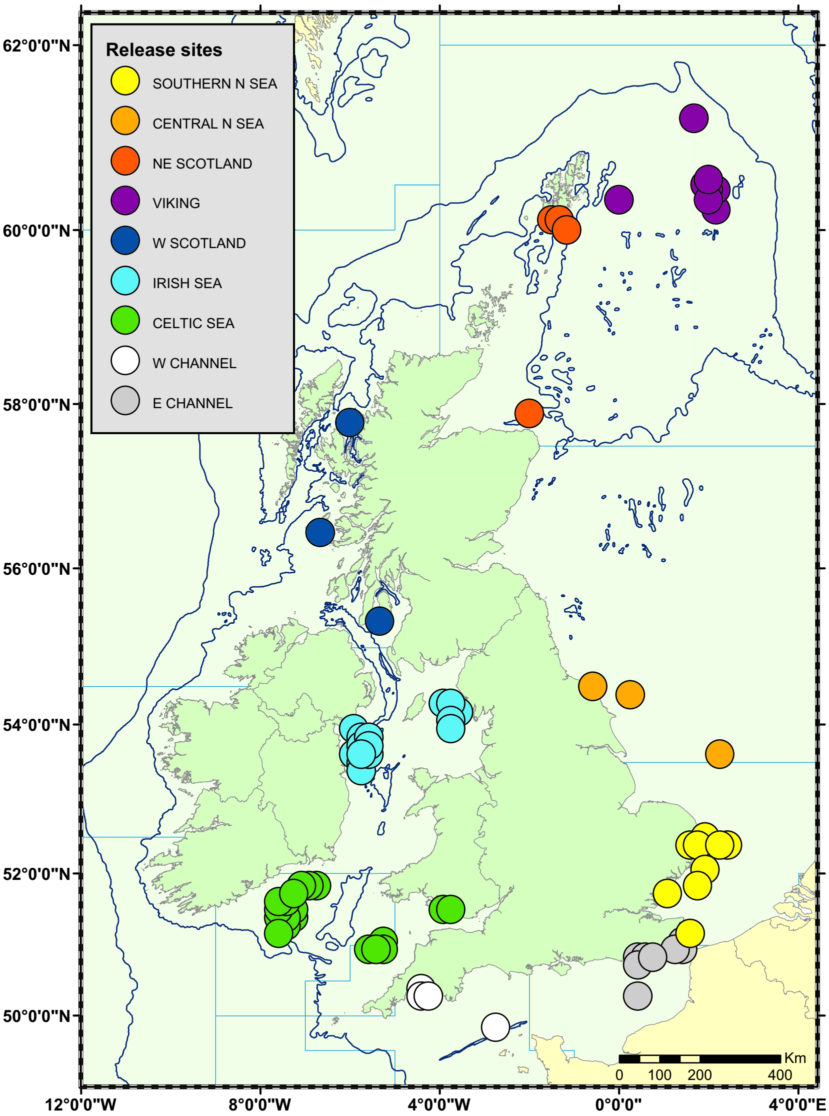

Fig. 1. Release sites of cod tagged with data storage tags.

Table 1. Details of number of cod tagged, released and returned with data storage tags (DSTs) in each of the release areas. Note this does not include cod that were returned without DSTs

Area	Number of cod released	Number of returns	Per cent return, %	Average length (cm)	Fish at liberty during spawning	Migrants/ residents	Mean time at liberty (days)	Total number of days of data
Celtic Sea	323	33	9·0	70·8 ± 7·7	32	23/10	114·8 ± 133·7	3789
Central N Sea	190	22	12·1	53·9 ± 5·7	12	5/17	92·7 ± 69·5	2040
East Channel	187	43	21·9	54·4 ± 12·3	31	25/18	130·8 ± 124	5624
Irish Sea	223	33	17·5	71·6 ± 11·4	33	25/8	195·8 ± 154·2	6461
North-East Scotland	189	27	14·8	52·4 ± 9	27	11/16	220·6 ± 190·6	5955
Southern N Sea	289	59	19·7	61·6 ± 8	58	33/26	79·9 ± 64·1	4715
Viking	86	16	18·6	67·2 ± 23·4	16	5/11	173·2 ± 181·8	2771
West channel	174	15	8·6	72·8 ± 6·6	14	12/3	55·2 ± 47·1	828
West Scotland	13	4	30·8	51·3 ± 7·9	4	2/2	108·3 ± 58·4	433
Overall	1674	252	15	62·1 ± 13·0	227	141/111	129·4 ± 133·4	32 616

individual cod's movements. This method of geolocation is referred to as the tidal location method (Metcalfe & Arnold 1997). We used a novel Fokker–Planck-based method that combines the tidal location method with a hidden Markov model to estimate, for each day at liberty, the nonparametric probability distribution of geographic position (Pedersen *et al.* 2008). The method was slightly modified for cod in the north-east Scotland, west coast of Scotland and Viking Bank areas to include an

exponential probability density function that decayed as the height above the seabed increased. This was necessary to prevent the model returning geolocations at unrealistic heights above the seabed when the cod were in proximity to deep waters off the continental slope. The uncertainty associated with each daily geolocation mainly varied according to the quality of the tidal signal in the data and the geographical proximity to tidal amphidromic nodes (Pedersen *et al.* 2008).

DATA ANALYSIS

Spatial analysis of the geolocation data was undertaken using ArcGIS 10.0. The data were subset and analysed separately for each release area and for the spawning period (1 January to 30 April) and out with the spawning period (1 May to 31 December). A bounding polygon was created encompassing all geolocation points within each data subset. Directional distribution ellipses were then created for each data subset. Centred on the mean position, these ellipses enabled identification of geolocations falling within one standard deviation from that mean, which were then used to create a second, inner, bounding polygon. For each individual, a measure of the straight-line distance travelled between successive geolocations (used to calculate average monthly movement rates), and between each geolocation and the release location (with the maximum used as a measure of migration distance) was calculated using the great circle equation. Individual movement paths were inspected and visually classified as home ranging or migratory (following the classification of Bunnefeld *et al.* 2011). Since most data sets were <1 year in duration and therefore did not encompass a full migratory cycle, migrations were further classified into feeding migrations (movement >100 km away from release area followed by residency) or spawning migrations (movement away from release area before return or movement to another area). In those cases where data sets were more than 250 days long, and therefore encompassed close to a yearly behavioural cycle, migrations were classified into homing migrations (return to release area at spawning time) or straying migrations (no return to release area at spawning time).

The extent of exchange of cod between areas was assessed by calculating the number of individual fish that were within a rectangle of 1° of longitude by 0·5° of latitude during the spawning period (defined as from 1 January to 30 April) and out with the spawning period (1 May to 31 December). Each cod was classed as being present or absent from a square for each day that it was at liberty. The proportion of cod from each area in each square during the spawning period and out with the spawning period was then calculated. Where only a single individual was recorded in a square, that square was excluded.

The temperature and depth data from each tag were summarized to give daily means and standard deviations for each fish. Mean monthly depth, mean standard deviation of depth and mean monthly temperature were then determined for each area. For those areas for which temperature data were recorded in each calendar month, the average monthly temperature per stock was extrapolated to a full year, to provide an estimate of degree days.

Results

From a total of 1674 cod that were tagged and released, 252 tags (15%) were recovered with data. For each study area, the number of usable data sets returned and the total number of days of data per area is summarized in Table 1. Details of all individuals tagged are given in Table S1 in Supporting Information. In total 32 616, estimates of position with corresponding daily records of temperature and depth were available (the number of temperature records was lower due to occasional sensor malfunction).

The extent of movements of all individual cod, colour-coded for each of the nine areas, is shown in Fig. 2a (out with spawning season) and b (during spawning season). The cod showed a general migratory tendency, with 141 of 252 cod making either a feeding, spawning or homing migration during their time at liberty (Table 1). The average daily movement was greater during the spawning season for eight of the nine release areas (Table 2). In consequence, the home range of each stock during the spawning season was often as large, or larger, than the home range during the feeding season (Table 2; Fig. 3a and b). The degree to which cod of different stocks intermingled out with and during the spawning period is summarized in Fig. 4a and b, respectively. The general patterns of migration for each stock can be summarized as follows:

SOUTHERN NORTH SEA

Thirty-three of 59 cod from this area showed migratory behaviour (Table 1). The maximum migration distance travelled from the release position was 578 km, with the average migration distance at 177 km (±145 km). Of the migratory cod, nine moved westward into the English Channel, three moved eastward across the North Sea towards the Danish coast (for example Fig. S1, Supporting information), and ten moved northward into the central North Sea (for example Fig. S2, Supporting information) where they probably mixed with cod from that area (Fig. 3a,b). The 26 resident individuals remained within the southern North Sea, many within their immediate release area (37·3 ± 15·6 km). The extent of migrations gave the stock a latitudinal range of 5°. Home range was the greatest of all the stocks and was larger out with the spawning season (Table 2). The contraction in range at spawning time appeared to be even, and so the centres of gravity of spatial distribution were similar for both seasons. There was no evidence to suggest that southern North Sea cod migrated far enough north to mix with cod from the northern North Sea or far enough west to mix with those from the western English Channel or beyond.

CENTRAL NORTH SEA

Only five cod out of 22 released in this area showed migratory behaviour. One individual moved towards the Danish coast during the spawning season, and several cod moved into the nearby southern North Sea once the spawning period was over. This brought the centre of

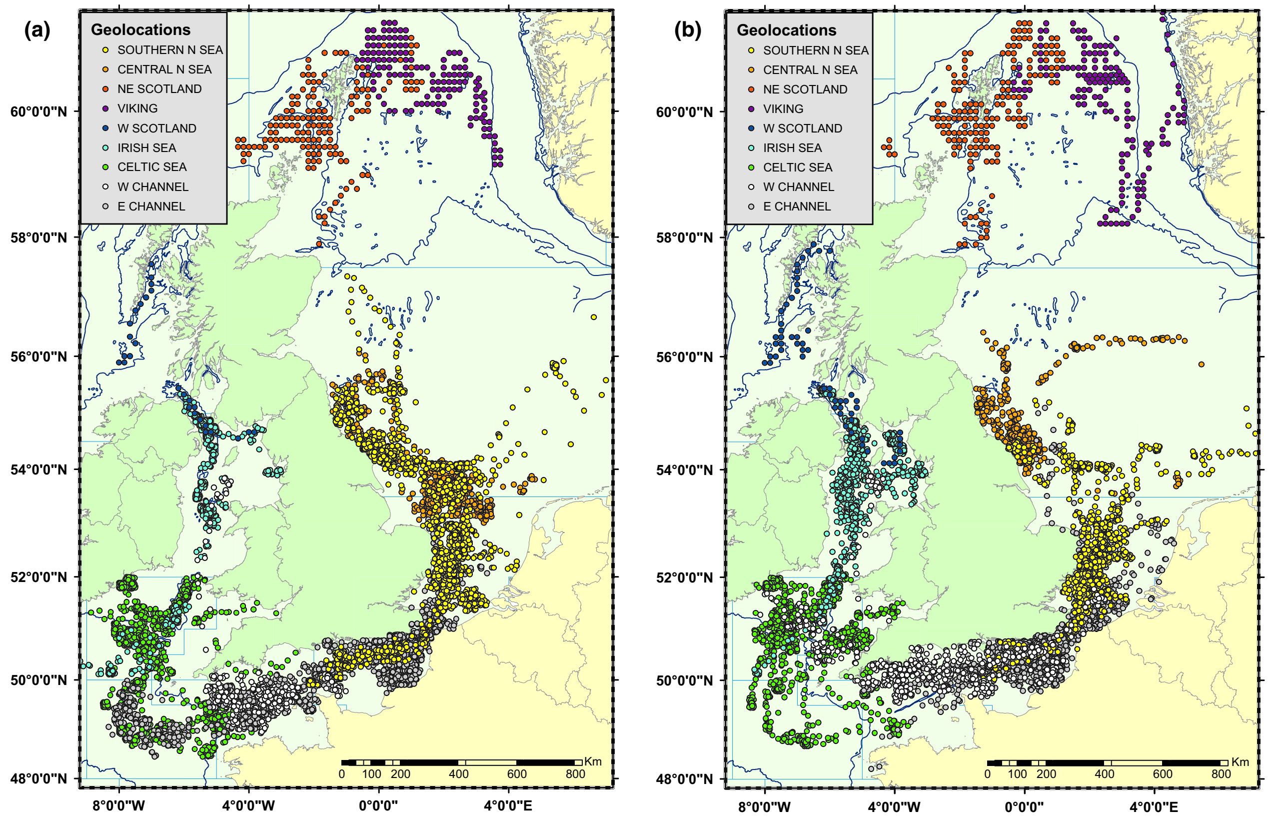

Fig. 2. (a) Estimated positions (geolocations) of individual cod during their time at liberty out with the spawning period (1 May to 31 December). All individuals released in a single area colour-coded the same. (b) Estimated positions (geolocations) of individual cod during their time at liberty during the spawning period (1 January to 30 April). All individuals released in a single area colour-coded the same.

Table 2. Spatial statistics summarizing movement of cod in each of the areas. Average migration distance was calculated from the maximum distance from release location reached by each cod in each area. Other averages are calculated from monthly averages for each area based on average monthly values for each tag. Spawning season defined as 1 January to 30 April

Area	Latitude range (degrees)	Average maximum migration distance (km)	Daily distance (km)	Daily distance (spawning)	Daily distance (not spawning)	Total home range (km^2)	Home range (spawning)	Home range (not spawning)
Celtic Sea	48·7–52·1	136·2 ± 75·5	10·1 ± 2·0	11·8 ± 2·2	9·2 ± 1·3	10 9012	106 419	94 975
Central N Sea	53·6–56·4	92·8 ± 76·6	11·6 ± 1·8	11·3 ± 1·4	11·8 ± 2·1	69 770	39 148	39 459
East channel	48·2–55·1	196·6 ± 140·2	12·4 ± 1·6	13·4 ± 1·6	11·9 ± 1·5	115 615	99 278	91 506
Irish Sea	50·1–55·4	155·9 ± 107·8	7·3 ± 1·2	8·2 ± 1·5	6·8 ± 0·7	48 265	19 891	35 316
North-East Scotland	57·9–61·3	96·4 ± 43·6	2·0 ± 0·8	2·8 ± 0·6	1·6 ± 0·6	45 048	41 569	39 074
Southern N Sea	50–55·2	177·1 ± 146·1	12·9 ± 4·0	14·3 ± 3·8	12·2 ± 4·2	141 523	169 333	77 721
Viking	58·2–62·8	103·9 ± 97·1	2·6 ± 1·5	4·2 ± 1·5	1·7 ± 0·4	78 672	57 472	95 135
West channel	49·5–53·9	266·7 ± 146·3	14·5 ± 7·0	16·6 ± 8·9	11·6 ± 2·1	107 965	59 621	96 882
West Scotland	54·1–57·9	136·2 ± 82·8	4·7 ± 2·3	6·6 ± 1·0	3·8 ± 2·3	27 794	15 154	33 124

gravity for the feeding season to the south and east of the spawning location. The movement of this group of cod, together with the northward movement of the southern North Sea stock, resulted in a large overlap in home range between cod from these two areas (Fig. 3a and b). Northward movements extended to 57°N but not as far as the Viking Bank area. There was no evidence of movement into the English Channel. This stock had the narrowest latitudinal range of all stocks (0·8°). Spawning home range was marginally smaller than during the feeding season.

VIKING BANK

Five of 16 cod from the Viking Bank area showed migratory behaviour. Two cod made return north–south movements of over 300 km following the shelf break of the Norwegian trench. One individual crossed the Norwegian

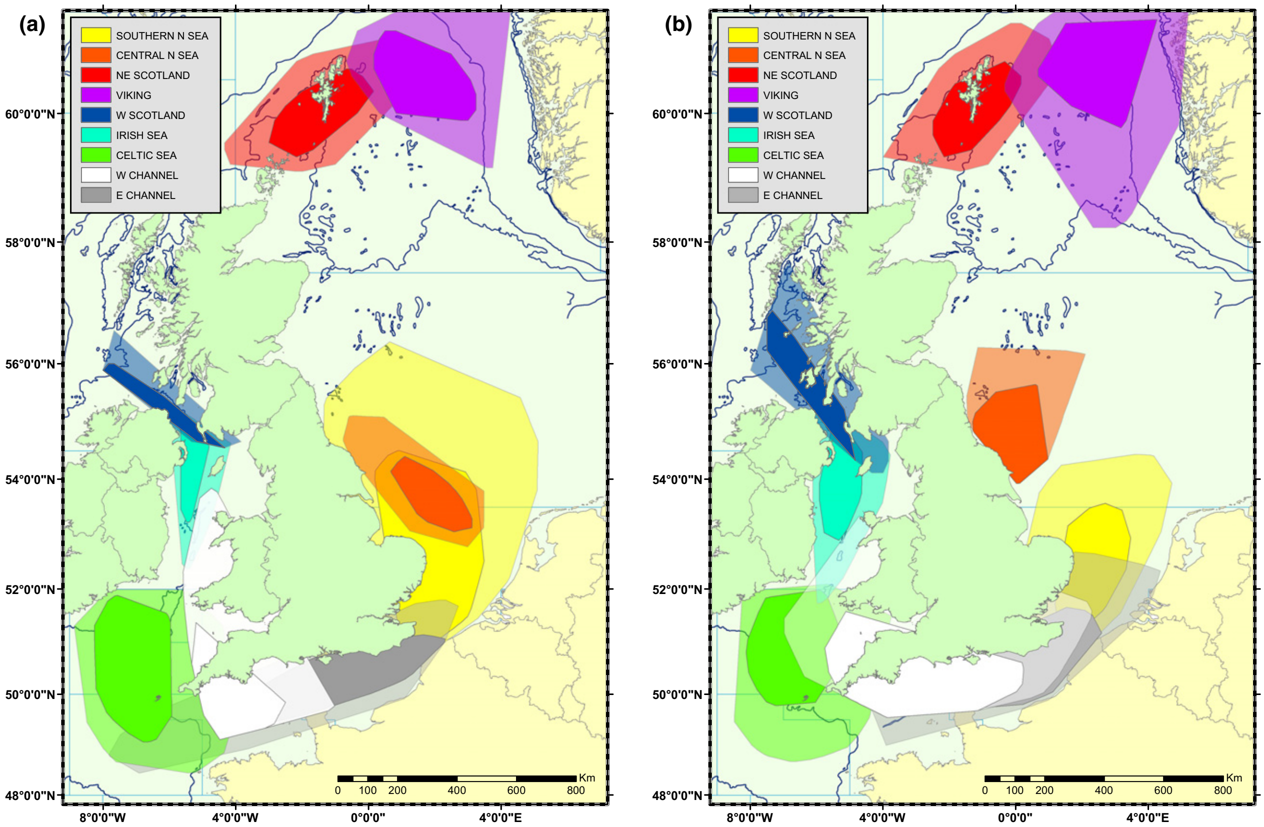

Fig. 3. (a) Home range of cod from each area colour-coded by release area out with the spawning period (1 May to 31 December). Outer areas are full extent of range; inner areas represent one standard deviation. Colour-coded according to release areas. (b) Home range of cod from each area colour-coded by release area during the spawning period (1 January to 30 April). Outer areas are full extent of range; inner areas represent one standard deviation. Colour-coded according to release areas.

trench (Fig. S3, Supporting information) and did not return. It spent its second year at liberty on the Norwegian shelf break having travelled nearly 1000 km from its release site. This group had a latitudinal range of 4°. Two cod moved 150 km west towards the Shetland Isles where they could have mixed with cod tagged and released in that area.

NORTH-EAST SCOTLAND

Cod were released mainly in the waters around the Shetland Isles. Eleven out of 27 cod in this area showed migratory behaviour, three of which returned to the release location to spawn a year later. The cod moved up to 150 km west during the summer. A few immature cod tagged on the east side of Shetland moved offshore after the first year and into areas where cod from the Viking Bank area were present. The latitudinal range was approximately 3°, and the average migration distance for cod in the area was amongst the lowest (Table 2).

SCOTTISH WEST COAST

There were too few cod tagged from the Scottish west coast to infer firm conclusions. Two cod of the four cod showed migratory behaviour, and there was evidence that cod from the Clyde Sea area may mix with cod from the Irish Sea (outside of the spawning season).

IRISH SEA

Twenty-five of 33 cod from the Irish Sea showed migratory behaviour. Five individuals moved north, which could have brought them into contact with cod from the southern part of the Scottish west coast and the firth of Clyde. Four individuals moved sufficiently far south to bring them into contact with cod from the Celtic Sea, and one individual migrated into the western section of English Channel during the spawning season. Latitudinal range was 5·3°, and the migratory distance of this group of cod was amongst the highest (Table 2). Relative to cod from other areas, the home range area of Irish Sea cod during the spawning season or feeding season was quite restricted.

CELTIC SEA

Twenty-three of 33 cod from the Celtic Sea showed migratory behaviour. No cod went north into the Irish Sea, although five individuals moved towards the western section of the English Channel. Individuals showed exten-

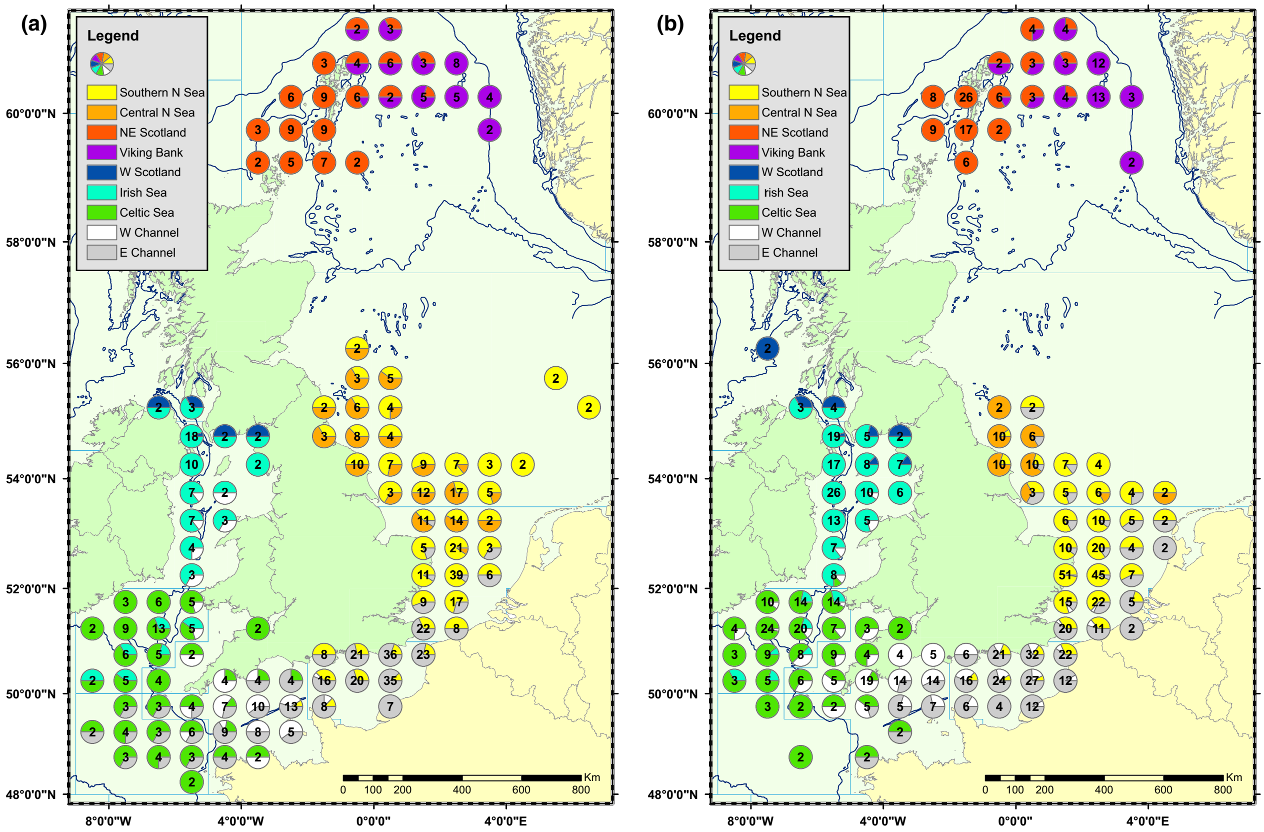

Fig. 4. (a) Extent of mixing of cod from each area out with the spawning period (1 May to 31 December). Pie charts indicate the proportion of cod from each area in an ICES statistical square. Numbers refer to actual number of individuals estimated to be in the square. (b) Extent of mixing of cod from each area during the spawning period (1 January to 30 April). Pie charts indicate the proportion of cod from each area in an ICES statistical square. Numbers refer to actual number of individuals estimated to be in the square.

sive and complex migrations, turning back on themselves numerous times, but returning to roughly the same area during spawning time (Fig. S4, Supporting information). Latitudinal range was approximately 3°, and the home range of these cod was large compared to cod from the neighbouring Irish Sea (Table 2). They overlapped in range with cod from the western and eastern channel and on occasion with cod from Irish Sea (Fig. 3a,b).

WESTERN ENGLISH CHANNEL

Twelve out of 15 cod from the western English Channel were migratory and had a relatively large home range. Those migratory individuals made extensive movements mainly to the west. Five individuals moved into the Celtic Sea area, one of which continued north to the Irish Sea. Others moved east to the Eastern Channel, but none as far as the southern North Sea. The overlap between cod tagged in the western English Channel and eastern English Channel was large and occurred mainly during the feeding season.

EASTERN ENGLISH CHANNEL

Twenty-five out of 43 cod tagged in the eastern English Channel were migratory and moved more than 100 km from release. They moved either west into the western Channel or Celtic Sea during the summer, or east into the southern North Sea. Most returned to near the release location or further east into the North Sea at spawning time. In consequence, this stock had the largest latitudinal range (nearly 7°). This stock had the second largest home range. In one case, a cod spent the summer in the Celtic Sea, before migrating to the southern North Sea in time for spawning (Fig. S5, Supporting information).

ENVIRONMENTAL EXPERIENCE

Cod occupied average monthly depths of between 15 and 165 m. The average monthly depth of each area broadly reflected the local variability in bathymetry within the home range (Table 3, Fig. S6, Supporting information) and was thus generally <100 m in the shallow southern and central North Sea, but frequently greater than 100 m in the deeper northern North Sea and western areas. Cod experienced average monthly temperatures between 6 and 17 °C that clearly differed between areas (Table 3, Fig. S7, Supporting information). Cod from the Irish Sea, English Channel, southern North Sea and central North Sea all experienced strong seasonal cycles in temperature whereas those from the Celtic Sea and Viking Bank areas showed less seasonal variability. At the extremes of the

Table 3. Summary depth and temperature experience for cod in each of the areas. Average values were calculated from monthly averages for each area, which in turn were calculated from average monthly values for each tag. Information on degree days only presented for areas where data were available for a full year

Area	Average depth (m) (normalized monthly values)	Average daily standard deviation of depth (m)	Average temperature (°C) (normalized monthly values)	Total degree days
Celtic Sea	93·4 ± 17·9	3·8 ± 2·2	9·8 ± 0·7	3574
Central N Sea	35·0 ± 6·4	2·3 ± 0·9	11·1 ± 3·9	4056
East channel	44·7 ± 17·0	3·0 ± 0·8	10·7 ± 3·0	3900
Irish Sea	90·6 ± 24·6	6·5 ± 1·4	10·6 ± 2·4	3853
North-East Scotland	75·3 ± 11·2	4·4 ± 0·9	9·6 ± 1·8	3513
Southern N Sea	31·1 ± 10·0	2·9 ± 0·7	11·0 ± 3·8	4007
Viking	130·9 ± 21·7	5·2 ± 2·9	8·4 ± 0·7	3077
West channel	49·2 ± 16·7	5·9 ± 4·1	11·3 ± 1·3	
West Scotland	109·7 ± 25·2	6·1 ± 1·7	9·6 ± 1·5	

thermal range (Table 3), cod from coldest area (the Viking Bank) experienced three-quarters of the annual number of degree days than cod from the warmest area (the central North Sea). Interestingly, however, there was no simple latitudinal gradient in temperature; cod from the Celtic Sea experienced an annual number of degree days lower than cod from the more northerly Irish Sea and central North Sea (Table 3).

Discussion

Environmental and human pressures on fish stocks must be considered at an ecologically appropriate spatial scale if we are to identify the causes of population change and develop sustainable management measures (Holmes *et al.* 2014). This broad-scale and high-resolution study of the movements of cod around the British Isles is a clear case of a commercially exploited fish species being managed at a spatial scale that fails to fully reflect the underlying biological stock structure. Currently, four main cod stocks are recognized and managed around the British Isles, but this study suggests there should be at least five (with the North Sea stock divided in two). This finding is consistent with genetic studies (Nielsen *et al.* 2009; Heath *et al.* 2013) and implies that management and assessment of the current stock units should be revised to better reflect this population structure. The inclusion of ecologically distinct populations into single stock units may contribute to failures in fisheries management by reducing the overall resilience of the species to exploitation (Schindler *et al.* 2010). A failure to consider differing pressures among populations may explain why the decline of North Sea cod was more acute in the south than in the north and may have also been a factor in the collapse of cod stocks in the NW Atlantic (Ruzzante *et al.* 2000). Cod is a species that shows a particularly fine scale of population structuring; other members of the Cod family (Gadoids), such as Whiting *Merlangius merlangus* and Haddock *Melanogrammus aeglefinus,* appear to be less structured, and this is reflected in the less pronounced spatial variation in population trends among these species (Holmes *et al.* 2014). Unlike cod, however, there is little individual-based movement data to estimate home ranges of haddock and whiting, and so, it is difficult to precisely assess the degree of behavioural isolation in these other species.

Although not all cod tagged were at liberty for a full year, the large number of individual records of movement revealed clear patterns in spatial and temporal distribution that were consistent with the results of long-term mark–recapture studies (e.g. Wright *et al.* 2006a,b; Righton *et al.* 2007). The results are therefore likely to represent the behavioural and migratory variation of each population, and they provide insights into the mechanisms that underpin dispersal and stock structure. Like the Atlantic blue-fin Tuna (Block *et al.* 2005), this study thus serves to illustrate how information on individual movements can be used to estimate population-level processes that in turn have implications for the way in which fisheries should be managed.

STOCK STRUCTURE

Three largely discrete groups of cod were evident: (i) cod from the Viking Bank; (ii) cod from the central and southern North Sea; and (iii) cod from the western areas (Irish and Celtic Sea). While cod from the offshore Viking Bank area were isolated from southerly and western groups in the study, there was some overlap in range with cod from the adjacent Shetland Isles. This overlap may arise if the Shetland Isles represent a nursery area used by both local inshore cod and the offshore cod. Interestingly, one cod tagged on the Viking Bank moved into Norwegian coastal water, which raises the possibility that the Viking Bank cod could mix with, or even be the southerly extent of, a northerly population that extends to the Norwegian coast. That the Viking Bank area is home to a distinct population of cod suggests that it should be assessed and managed separately. This population grows more slowly and matures at a larger size and older age than other cod populations (Wright, Millar & Gibb 2011), and

so, even if it is currently abundant (Holmes, Wright & Fryer 2008), it may actually be less resilient to fishing than other populations. Furthermore, it cannot be expected to repopulate the depleted southern or inshore areas, because Viking Bank cod do not range there, are genetically distinct and may even be adapted to a colder, more stable thermal environment.

The other major separation appears to lie between the western areas (Clyde, Irish and Celtic Seas) and the North Sea areas. This is again consistent with the finding of significant genetic distinction between these western groups and the North Sea groups (Heath *et al.* 2013). There were too few data in our study to assess a potential northerly exchange via the west coast of Scotland to the North Sea, and further work is needed to address connectivity of cod found to the north-west of Scotland and those in the North Sea.

Movement of individuals between areas was high among neighbouring areas in coastal areas. Only two individuals (from the western and eastern English Channel) were observed to move beyond a neighbouring area during the spawning period. These individuals, however, were tagged during the winter when they may have been returning to their natal spawning site. Within each of the main population units identified in this study, a small number of individuals made long-distance migrations, but the majority of individuals did not. This suggests an even finer ecological structuring may persist, perhaps similar to the 'bay-scale' population structure described for coastal Atlantic cod off Canada (Ruzzante *et al.* 2000). This type of population structure conforms to the concept of a meta-population (Kritzer & Sale 2004). For species that have a meta-population structure, the assumptions of what constitutes a stock from an assessment and management perspective become questionable. A 'stock' is assumed to be a discrete group of fish that show little mixing with adjacent groups and that have the same growth and mortality parameters across a particular geographical area (Gulland 1983). The present study suggests that the spatial scale at which this assumption remains valid may actually be finer than what even the genetic analyses suggest and further questions whether it is appropriate to apply the concept of a stock to species that exhibit a meta-population structure.

THERMAL ENVIRONMENT

The north-west European shelf represents one of the warmest areas for cod (Brander & Mohn 2004; Righton *et al.* 2010), and there was considerable thermal variation between study areas. This variation reflected depth, latitude and oceanic influence and may act to prevent a uniform cod stock from establishing across all areas. Although cod have been shown to be tolerant and flexible in response to thermal conditions, they may be thermally sensitive at spawning time (Righton *et al.* 2010). It may be that acclimation or adaptation to local thermal conditions constrains ranging and favours a resident strategy, especially if spawning and feeding grounds can be found in close proximity to one another (Neat *et al.* 2006). This may be crucial to the interpretation of reports of habitat shifting in temperate marine fish species (Dulvy *et al.* 2008). Although cod in the southern North Sea experienced summer temperatures considered super-optimal for the species (Neat & Righton 2007), they showed strong site fidelity to spawning grounds. Species like cod that are behaviourally constrained in their range shifting may turn out to be those that are most vulnerable to climate change (Heath *et al.* 2012).

APPLIED IMPLICATIONS AND CONCLUSION

Failure to incorporate information on population structuring of marine fishes into fishery management risks sequentially depleting local population units and eventual stock collapse (Hilborn *et al.* 2003; Kritzer & Sale 2004; Heath *et al.* 2008). This is likely to have happened to cod around the British Isles over the last century where inshore stocks were first depleted and the fleet then moved progressively further offshore (Greenstreet *et al.* 2009). This study suggests that a finer scale of population structure exists in cod around the British Isles than is currently recognized in management and that each population unit experiences different thermal conditions that will affect physiology and growth. The applied implication of this is that local adjustment of exploitation strategies, such as the setting of maximum sustainable yield for each population unit, may be required to ensure sustainable harvesting (Holmes *et al.* 2014). Future management of fisheries should account for this current understanding of population structure and explicitly allow for local population recovery.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Summary details of all tagged and recaptured cod from which a useable dataset was retrieved.

Fig. S1. An example of the migration path of a cod released in the southern North Sea that moved from west to east over the spring period.

Fig. S2. An example of the migration path of a cod released in the southern North Sea that moved north and then back south again during the summer.

Fig. S3. An example of a migration path of a cod released in the Viking Bank that moved south before crossing the Norwegian Trench and then spending the following year on the Norwegian shelf break.

Fig. S4. An example of a migration path of a cod released in the Celtic Sea that showed a complex migratory pathway before returning to the Celtic Sea area at spawning time.

Fig. S5. An example of a migration path of a cod released in the eastern English Channel that migrated west to the Celtic Sea and then returned east to the southern North Sea.

Fig. S6. Mean depth experienced in each month of the year by cod from each of the areas.

Fig. S7. Mean temperature experienced in each month of the year by cod from each of the areas.