



## Contribution to the Symposium: 'Gadoid Fisheries: The Ecology of Management and Rebuilding' Original Article

# Linking tagging technology and molecular genetics to gain insight in the spatial dynamics of two stocks of cod in Northeast Atlantic waters

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The Northeast Arctic cod (*Gadus morhua* L.: NEAC) remains the most abundant cod stock in the North Atlantic, while the catches of the partially co-occurring Norwegian coastal cod (NCC) stocks have dramatically decreased in recent years. To ensure effective management of the two stocks, it is necessary to know if the population genetic structure is associated with any pattern in the spatial dynamics or whether it is affected by any distinct environmental factors. By combining information from electronic data storage tags (DST) and molecular genetics methods with statistical tools, we have been able to associate spatial dynamics and distinct environmental factors to the two cod stocks. In general, adult NEAC migrate between deep, warm overwintering grounds and shallow summer feeding grounds where water temperatures maybe low. In contrast, NCC do not undertake large-scale seasonal migrations, show little seasonal variation in depth distribution, and experience the opposite seasonal change in temperature compared with NEAC. However, within the NCC group, some individuals did conduct longer horizontal movements than others. Even though the distances calculated in this study represent the shortest distance between release and recapture positions, they are far higher than previously reported by NCC. Distinctive depth profiles indicate that this migrant NCC have moved out of the area, passing the deep trenches outside Lofoten while more stationary NCC occupies shallower depths throughout the year. The temperature profiles also indicate that migrant and stationary NCC has occupied different areas during the year. We demonstrate that the combination of information from DSTs and molecular genetics offers a deeper understanding of individual cod behaviour, provides an insight in the spatial dynamics of the species, and ultimately, improves the scientific basis for management of a complex mixed fishery of Atlantic cod.

**Keywords:** behaviour, data storage tags (DST), distribution, environmental conditions, fishery management, identification of cod types, molecular genetics, Northeast Arctic cod, Norwegian Coastal Cod.

## Introduction

Management of Atlantic cod (*Gadus morhua*) is administered through the International Council for the Exploration of the Seas (ICES) system. Life history parameters play a key role in assessment and monitoring of the species. In the ICES assessments, cod in the Barents Sea and along the Norwegian coast north of 62°N are treated as two distinct stocks: the Northeast Arctic cod (NEAC) and the Norwegian coastal cod (NCC; ICES, 2013). While the abundance of the NEAC stock is all time high, the NCC stock has been dramatically reduced in recent years. Though ICES has, since 2004, recommended no catch of NCC, limited quotas continue to be given mainly for socio-economic reasons (ICES, 2013). This is because the fishery occurs at the spawning grounds where there is spatial overlap between the

target species, NEAC, and NCC. In the resulting mixed stock fishery, a no-catch quota for NCC will be both unrealistic and impossible to enforce in practice. The present state of NCC coupled with high quotas for NEAC can easily result in genetic changes in NCC that could make recovery of the population difficult, even after periods with reduced or cessation of fisheries (Hutchings, 2004, 2005). In addition, climate change may affect the distribution and growth of the cod stock (ICES, 2013; Johansen *et al.*, 2013), and thus defining the constraints under which fisheries may safely operate in the long run (Nakken, 1994). It is therefore of considerable importance that, for each stock, there is adequate understanding of the stocks genetic structure, spatial dynamics, and response to possible changes in the environmental conditions characterizing its habitat.

The terms stocks or populations are both used to describe NEAC and NCC in the literature. Stock might be used for defining everything from a coherent unit in a population-genetic sense (evolutionary paradigm) to representing a group of fish that is fished at a specific location and time (ecological paradigm, Waples and Gaggiotti, 2006). The separation of NEAC and NCC into stocks dates back to the early studies of otolith structure and life history characteristics (Rollefesen, 1933, 1934). Later, it has been argued that distinction in cod types based on otolith morphology could be a reflection of the environmental conditions (Campana, 1999; Stransky et al., 2007). However, the stock separation method developed by Rollefesen (1933, 1934) is still routinely used in current fisheries assessment to distinguish between fish from the two cod stocks. Fish that do not show the typical otolith morphology for NEAC or NCC are classified either as “uncertain NCC” or “uncertain NEAC” (Jakobsen, 1987), recognizing that otolith-based inference may be subjective; depending on the degree of reader experience. The genetic differentiation between NEAC and NCC has been tested by using different genetic markers, such as haemoglobin and blood types (Frydenberg et al., 1965; Møller, 1966; Dahle and Jørstad, 1993; Fyhn et al., 1994), the DNA marker *Pan I* (Pogson et al., 1995; Fevolden and Pogson, 1997), allozymes (Mork and Gæver, 1999), microsatellites (Skarstein et al., 2007; Westgaard and Fevolden, 2007), and lately using single-nucleotide polymorphism (SNP) markers (Nielsen et al., 2009; Hemmer-Hansen et al., 2013; Karlsen et al., 2013). Most of these markers are assumed to be under some kind of selection which could imply that also the genetic structure we observe could be of more of “environmental” origin (Nordeide et al., 2011), although the differentiation is consistent over years (Skarstein et al., 2007; Hemmer-Hansen et al., 2013). The most potent single DNA marker studied in detail by the Fevolden’s group (Fevolden and Pogson, 1997; Skarstein et al., 2007; Westgaard and Fevolden, 2007) is the *Pan I* (Panthophysin) which shows the highest differentiation between NEAC and NCC. While samples of NEAC are almost fixed for the *Pan I<sup>B</sup>* allele ( $p_B = 0.90$ ), samples of NCC exhibit high frequencies of the *Pan I<sup>A</sup>* allele (Fevolden and Pogson, 1997; Sarvas and Fevolden, 2005). This differentiation is in good correlation with the otolith structure observed by Rollefesen (1933), Berg et al. (2005), and Wennevik et al. (2008). However, the mode of selection is not quite understood (Westgaard and Fevolden, 2007). Other studies also indicate that the coastal cod may be structured into several different local populations (Knutsen et al., 2003; Pogson and Fevolden, 2003; Skarstein et al., 2007). It has also been questioned whether heterozygote individuals with the *Pan I<sup>AB</sup>* are hybrids, as a result from interbreeding between NEAC and NCC (Berg et al., 2005).

There is clear evidence that NEAC and NCC also differ with respect to life history characteristics and a summary is given in Høyen et al. (2008). While NEAC is mainly found in the Barents Sea and displays substantial migratory behaviour both within the Barents Sea and also during its spawning migrations to the Norwegian coast, NCC is more typically found in coastal areas and within fjords all along the coast of Norway and displays less migratory behaviour. However, the distribution of the two stocks overlaps, especially during the spawning season in the area around the Lofoten Archipelago. Since 1912, several large-scale tagging programmes have been conducted along the coast of Northern Norway. The goal of these programmes has been to identify seasonal migratory behaviour of spawning cod tagged off the Lofoten Islands and recaptured in summer, hundreds of kilometres away in the

Barents Sea (Hjort, 1914). The development of the migration triangle theory was actually based on these early tagging experiments (Secor, 2002). It is worth noting that none of the above-mentioned tagging experiments included analysis of the genetic identity of the cod. An overview of further tagging and migration analysis of cod in the northeast Atlantic is given in Neuenfeldt et al. (2013). The first tagging experiment with data storage tags (DSTs) of cod in the Barents Sea and along the coast of Norway revealed two distinct temperature patterns and variable depth profiles experienced by the recaptured fish (Godø and Michalsen, 2000). The variance in the temperature–depth profiles was considered to be reflective of the large variability in individual cod behaviour; being larger during summer/autumn and less so during the spawning period. In a more recent study (Righton et al., 2010), the temperatures and depth experienced by wild cod from five different northeast Atlantic ecosystems were described based on a DST tagging programme. The study showed that cod is an adaptable and tolerant species, capable of surviving and growing in a wide range of temperatures, but that there are differences in average temperature exposures within different ecosystems. Neither of these studies included genetic markers nor was there any attempt to link variation in spatial dynamics (distance, depth, and temperature) with the genetic identity or the origin of the cod.

Of particular importance for management is whether this particular commercial species should be managed as a single or as a composite stock, and how much intermingling there is between the oceanic migratory components and stationary coastal components of cod. Previous studies on NEAC and NCC have either focused on the genetic or the demographic aspect of population/stock structure. By combining the two techniques, we aim at understanding more about the individual behaviour of cod, gain insight in the spatial dynamics, and improve the scientific basis for management of a complex mixed fishery of Atlantic cod in the Lofoten area. Questions addressed in this study are: (i) Do NEAC and NCC experience characteristically distinct temperature conditions throughout the year? (ii) Are their spatial dynamics, including the extent of horizontal migration, sharply defined? (iii) Based on the migration pattern observed in the present project, do the NEAC and NCC belong to the same stock or population?

## Material and methods

### Study area and water masses

The area under focus is the most important spawning grounds for cod, i.e. the traditional fishing area off the Lofoten Archipelago, Northern Norway. The area is characterized by steep slopes both above and below the water surface (Sælen, 1967). From the coastline, the depth increases gradually down to 300 m at the coastal shelf. From the offshore shelf, the depth increases rapidly down to 2000 m. Fresh coastal water occupies the surface layers, with saltier Atlantic water below (Orvik et al., 1995). During winter, surface cooling makes the coastal water colder than the Atlantic water (Eggvin, 1938). The thickness and depth of the transition layer between cold coastal fjord water and warm saline Atlantic water also vary during the spawning season and depend on the direction of the wind (Furnes and Sundby, 1981). The Barents Sea is a shelf sea with an average depth of 230 m. It is characterized by an inflow of relatively warm and highly saline Atlantic waters in the southern area (6–8°C) and cold low-saline Arctic water in the north (down to 0°C or even –1°C along the Polar Front). The ocean circulation pattern in the

**Table 1.** Overview of the data at different release sites showing the number of cod tagged, tag types, number of recaptured tags, as well as number of genetic samples taken.

Release site	Release site name	Release date	No tag deployed				No. of genetic samples
			DST	Conv. tag	Total	Per cent per area (%)	
A	Barents Sea	February 2003	89	16	105	6.89	36
B	Bear Island	August 2003	186	14	200	13.13	42
C	Lofoten, North	March 2004–2007	163	581	744	48.85	612
D	Lofoten, South	March 2004–2006	68	114	182	11.95	149
E	Lofoten, East	March 2004–2007	33	233	292	19.17	258
		November 2004	19	7			
	Sum		558	965	1523	100	1 097

Barents Sea is well described in the literature (see Jakobsen and Ozhigin, 2011, for further details).

### Capture, tagging, and release of the fish

Between 2003 and 2007, 1523 tags were deployed on cod caught in the Barents Sea, at the Bear Island and the coast of Norway (mainly around the Lofoten peninsula; Table 1). The cod were tagged with conventional tags ( $n = 965$ ) and Star-Oddi electronic DSTs ( $n = 558$ ). Usually, a fin clip was collected and resulted in a collection of 1097 tissue samples for genetic analysis (Table 1). The release sites of the tagged fish were grouped into five main site clusters, depicted as coloured rectangles on the maps (Figure 3a–h).

The fish were captured by bottom trawl (<200 m depth), which was slowly brought to the surface. Trawl duration was limited to 15 min. See Godø and Michalsen (2000) and Righton *et al.* (2010) for full details about handling of the fish and the tagging process. The tags were programmed to record depth and temperature at intervals of 10 min, for as long as the storage capacity permitted or until the fish was caught. The tagging was conducted under licence from the Norwegian Animal Research Authority (reference no S-2536/02) and complied with the 1974 Animal Welfare Act (supplemented by the provisions of the EU Directive 86/609/CEE).

The Star-Oddi Data Storage Tag (DST-centi) is small, representing 0.084–0.009% of the weight in water of the smallest and largest fish, respectively. The tags record depth ( $0–780 \pm 2.0$  m) and water temperature ( $-3$  to  $40^\circ\text{C} \pm 0.003^\circ\text{C}$ , see the Star-Oddi website for further details, <http://www.star-oddi.com/>).

Upon recapture via the commercial fishery, fishers returned the tags and information on the physical condition of the fish, date, depth, and position of the recapture.

The recapture sites are depicted as coloured triangles or circles on the maps (Figure 3a–h).

### Genetic methods and assignment of individual cod

The 1097 fin clips (dorsal fin) were stored in 96% ethanol for later extraction of DNA and further genetic analysis. The samples were stored ( $4^\circ\text{C}$ ) in the laboratory until DNA extraction, which was carried out by using Qiagen DNeasy 96 Tissue kit (Qiagen, <http://www.qiagen.com/>) or Omega (Omega Bio-Teck, Inc., USA).

For the study, we selected six microsatellites in the analysis; Gmo2, Gmo3, Gmo34, Gmo35, Gmo132, and Tch11, together with the pantophysin loci *Pan I*. For the *Pan I* locus, we followed the procedures described by Fevolden and Pogson (1997) with modified primers (Stenvik *et al.*, 2006; Nielsen *et al.*, 2007) and for the microsatellites, we followed the description in Westgaard and Fevolden (2007). The genetic analyses were performed in the

laboratory at the Norwegian Institute of Marine Research, Tromsø, and were run on an ABI sequencer (Applied Biosystems). Genotyping of the microsatellites and *Pan I* were performed with GeneMapper v4.0 (Applied Biosystems), and every individual scoring was manually checked and corrected.

For assigning individual cod to NEAC or NCC, we made use of baseline samples of cod of known origin from Lofoten. In the present project, we selected samples of NEAC and NCC from Wennevik *et al.* (2008) collected in 2003. The NEAC and NCC had previously been analysed for otolith morphology and the genetic markers, microsatellites, allozymes, and haemoglobin (Wennevik *et al.*, 2008) and later by SNP markers (Nielsen *et al.*, 2009; Hemmer-Hansen *et al.*, 2013). In addition, one NEAC was collected from the Barents Sea and one NCC from Porsangerfjord (Table 2).

For the assignment of cod to subpopulations, we only selected the most informative genetic markers (GMO34, Gmo132, and *Pan I*; Westgaard and Fevolden, 2007; Wennevik *et al.*, 2008). The two microsatellites show clear differentiation between the two types of cod and are assumed under stabilizing selection (Nielsen *et al.*, 2006; Westgaard and Fevolden, 2007). They show lower heterozygosity in NEAC compared with NCC (Westgaard and Fevolden, 2007) and GMO34 seems to be linked to *Pan I*, which could be an advantage in an assignment test. We tried out the free-ware computer programs “TESS” (Chen *et al.*, 2007, for tess 1.1, François *et al.*, 2006) and “STRUCTURE” (Pritchard *et al.*, 2000). These programs implement a Bayesian clustering algorithm to assign individuals to populations. Several running conditions were tested (admixture and non-admixture models). In the runs, the burn-in length was tested from 100 000 to 500 000, and the run length from 500 000 to 1 000 000. While STRUCTURE presents graphs for each run, the results from TESS are based on 50 runs, which are averaged by the program CLUMP (Jakobsson and Rosenberg, 2007).

The recaptured individuals were assigned to NCC and NEAC based on genetic markers and, whenever otoliths were available, compared with the assignment of cod based on otoliths morphology (Rollefson, 1933).

### Mapping tools and statistical analysis

We created maps over release and recapture sites using free and open source GIS software (<http://qgis.org>) and freely available background mapping data (<http://www.naturalearthdata.com>).

We then used the “haversine” formula to calculate the great-circle distance between two points, i.e. the shortest distance over

**Table 2.** Phenotypic variation in the Panthophysin (*Pan I*) is shown for the tagged cod (fin clip DNA) collected at the release sites and from the baseline samples.

		Phenotype distribution								Microsatellites		
		Pan1*aa		Pan1*ab		Pan1*bb		Allele frequency		GMO34 H obs.	GMO132 H obs.	
		<i>n</i>	Obs	Exp	Obs	Exp	Obs	Exp	qa			qb
Release site												
A	Barents Sea	36	1	1	7	8	28	28	0.12	0.88		
B	Bear Island	42	1	0	4	6	37	36	0.07	0.93		
C	Lofoten, North	612	78	42	164	236	370	334	0.26	0.74		
D	Lofoten, West	149	69	50	35	73	45	26	0.58	0.42		
E	Lofoten, East	258	152	128	60	107	46	22	0.71	0.29		
	Sum	1 097	301	173	270	525	526	398	0.40	0.60		
Baseline samples												
	NEAC Barents Sea	65	0	0	8	8	57	57	0.06	0.94	0.243	0.086
	NEAC Lofoten W	76	0	0	8	8	68	68	0.05	0.95	0.405	0.122
	NCC Lofoten E	62	40	40	19	20	3	3	0.80	0.20	0.644	0.534
	NCC Porsanger	80	45	45	30	30	5	5	0.75	0.25	0.758	0.636

Data for cod tagged 2003–2007, as well as for the baseline samples used in individual assignment of cod. The baseline NEAC and NCC samples are also analysed in [Wennevik et al. \(2008\)](#) and [Hemmer-Hansen et al. \(2013\)](#). Observed heterozygosity (H obs.) for the two microsatellites show lower genetic variation in the baseline samples of NEAC compared with baseline NCC samples. Observed (obs) and expected (exp) genotype variation, as well as allele frequency is only shown for *Pan I*.

the earth's surface ([Shumaker and Sinnott, 1984](#));

$$a = \sin^2\left(\frac{\Delta\varphi}{2}\right) + \cos(\varphi_1) \times \cos(\varphi_2) \times \sin^2\left(\frac{\Delta\lambda}{2}\right)$$

$$c = 2 \times a \tan 2(\sqrt{a}, \sqrt{1-a})$$

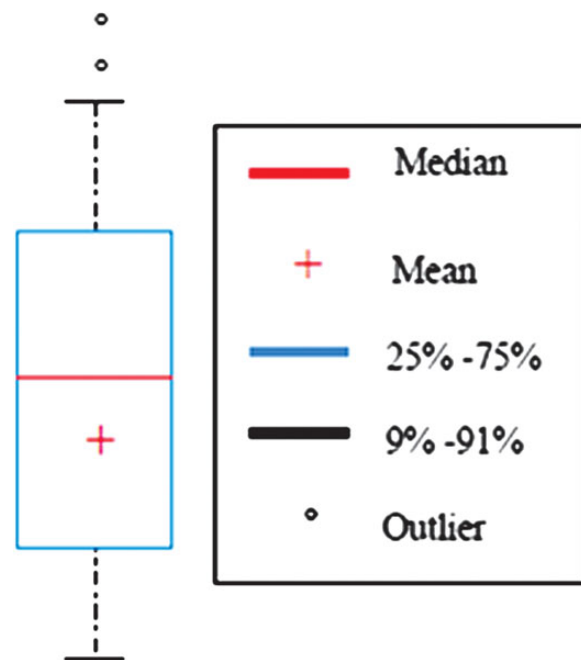
$$d = R \times c,$$

where  $\varphi$  is the latitude,  $\lambda$  the longitude, and  $R$  the earth's radius (mean radius = 6371 km)

To summarize the DST data across several tags and also ease identifying distinct temperature–depth profiles for a given classification, we use box plots (see [Yoav, 1988](#)) and probability density distributions from kernel density estimates (KDE, see [Martinez and Martinez, 2002](#)).

The standard box plot (box-and-whiskers plot) is a graphical summary of a dataset usually showing the lower (Q1) and upper (Q3) quartiles and the median. Data falling outside the Q1–Q3 range are plotted, but are considered as outliers of the data. In this paper, we use box plots for graphical comparisons between datasets pooled on monthly basis and to investigate temperature–depth variations for different classifications. Figure 1 shows the legend for the box-plot type and summary statistics to be presented at the analysis section of this paper.

We also found it prudent to compare the DST data during and outside the spawning period using probability distributions derived from KDE. KDE is a non-parametric method for estimating the probability density function that has generated a random sample set of observations. The kernel is a symmetric function (typically the standard normal density function) that must integrate to one. The KDE is defined as the sum of the weighted kernel function at each data point. This function integrates to unity, and peaks at regions where there is a high density of data points. To illustrate with a one-dimensional case (e.g. only depth), suppose  $x_1, \dots, x_n$  represent  $n$  (not necessarily distinct) observations and  $K$  is a chosen kernel.



**Figure 1.** The legend for the box-plot type and summary statistics for data presented in Figure 6. The lower (Q1) and upper (Q3) quartile, representing observations outside the 9–91 percentile range. The diagram also shows the median and mean observation for a particular month. Data falling outside the Q1–Q3 range are plotted as outliers of the data.

The KDE of the probability function, of the data  $\hat{f}_h(x)$ , is given by

$$\hat{f}_h(x) = \frac{1}{n} \sum_{i=1}^n K_h(x - x_i) = \frac{1}{nh} \sum_{i=1}^n K\left(\frac{x - x_i}{h}\right), \quad (1)$$

where  $h$  is a smoothing parameter known as the bandwidth. For this particular paper, we shall assume  $h = 1$ . The one-dimensional case

is readily extendable to a two-dimensional case. For the temperature–depth data, the result is a three-dimensional temperature–depth–probability surface. A projection of the three-dimensional surface onto a two-dimensional plane would reveal temperature–depth peaks, i.e. with high probability, see, for example, [Martinez and Martinez \(2002\)](#) for computational details.

Results

Of the 1523 tagged fish, 50% were released in the northern part of Lofoten ( $n = 744$ ), 12% ( $n = 182$ ), and 19% ( $n = 292$ ) in the south and east of Lofoten. Nineteen per cent ( $n = 305$ ) of the tags were released in the two open water locations (Barents Sea and Bear Island, Table 1). To obtain optimal information on individual behavioural and environmental conditions, the tags were attached to adult cod ( $>45$  cm). The recapture rate of the tagged cod was close to 7%. Of the recaptures, 45 were DSTs and 58 conventional tags. DNA profiling was conducted for 90 of the 103 recaptured cod.

Genetic identification of cod

The 263 baseline samples of cod from Lofoten and the Barents Seas were analysed for two microsatellites (Gmo34 and Gmo132) and *Pan I* (Table 2). As stated in the introduction, NEAC is almost fixed for the genotype *Pan I*<sup>BB</sup>, while this genotype is quite rare in NCC. In the present study, the tagged and genotyped cod from the Bear Island and the Barents Sea showed similar *Pan I* frequencies as expected for NEAC (Table 2 and see [Fevolden and Pogson, 1997](#); [Skarstein et al., 2007](#)), but the genotype *Pan I*<sup>AA</sup> has not been observed in the Barents Sea before. Among the tagged cod in Lofoten, excess of both homozygotes was observed, which indicates a mechanical mixing of populations ([Wahlund, 1928](#)). None of the recaptured cod with genetic samples was tagged in the Barents Sea or Bear Island (Table 3).

By making use of the clear separation of NCC and NEAC by the three genetic markers and the Monte Carlo simulations, we were able to perform a more objective typing of individual cod. Based on *Pan I* and the two microsatellites Gmo34 and Gmo132, we assigned 1095 cod to either NEAC or NCC. We tested three genetic programs: GeneClass (data not shown), STRUCTURE, and TESS. The two last programs gave best assignment, with TESS giving slightly higher assignment scores compared with STRUCTURE. Both programs showed clear differentiation between NEAC and NCC in the baseline samples (Figure 2). While STRUCTURE presents graphs for each run the results from TESS are based on 50 runs, which are averaged into one figure by the program CLUMP. The best separation for both programs was achieved by no admixture model and 100 000 burn-ins and 500 000 Markov chain Monte Carlo simulations (MCMC). Except for five tagged cod ( $<1\%$ ), the two programs showed similar results. The assignment rate for individual cod to either NEAC or NCC was set in the range 53–100% for the NEAC and 56–100% for NCC. About 70% of the cod showed assignment rate above 83% for NEAC and 96% for NCC. Except for the only five individuals, all recaptured and DNA profiled cod we could assign to either NEAC or NCC (Table 4).

Classification of recaptured cod based on genetic, otoliths, and release site

Of the 103 recaptures, 96 were from fish released close to the coast (Lofoten), while only seven cod from the open ocean release were recaptured (release sites 1 and 2, Table 3). From the results from the assignment program, 54 cod were identified as NCC (40 *Pan I*<sup>AA</sup>, 14 *Pan I*<sup>AB</sup>, Table 4) and 34 cod were assigned to NEAC (29 *Pan I*<sup>BB</sup>, 5 *Pan I*<sup>AB</sup>). Five individuals could not be assigned to either and showed the heterozygote genotype *Pan I*<sup>AB</sup>. For ten recaptured cod, no genetic information was available. For three of

Table 3. Number of recaptured fish within different geographic areas, *Pan I*, and tag type.

Release site	No recaptures			Recapture rate (%)		Genetic distribution				
	DST	Conv. tag	Total	Within area	Total	AA	AB	BB	NN	Total no
A. Barents Sea	4	0	4	3.8	3.9				4	0
B. Bear Island	3	0	3	1.5	2.9				3	0
C. Lofoten, North	9	19	28	3.8	27.2	5	6	16	1	27
D. Lofoten, South	18	9	27	14.8	26.2	12	5	10	0	27
E. Lofoten, East	11	30	41	14.0	39.8	23	13	3	2	39
Sum	45	58	103	6.8	100.0	40	24	29	10	93

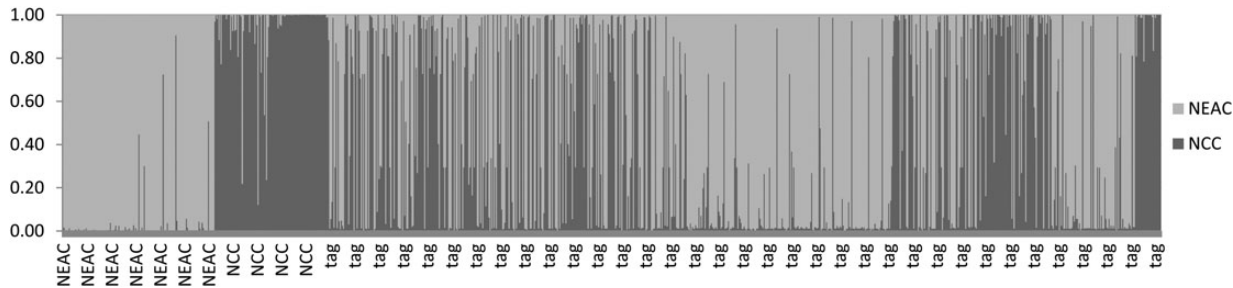


Figure 2. Output from the Assignment test based on the program STRUCTURE is shown. Based on baseline samples of known NEAC and NCC, each bar in the diagram represents one individual cod. The light grey bars show the likelihood of belonging to NEAC and the dark grey bars the likelihood of belonging to NCC. The likelihood is presented in fraction, from 0 to 1. The samples are presented on the x-axis; numbers 1–4 represent the basis samples of NEAC from Barents Sea, NEAC from Lofoten, NEAC from Porsanger, and NCC from Lofoten, respectively. Samples 5–13 represent the individual tagged cod from 2003 to 2007. The assignment is based on *Pan I* and the two microsatellites GMO34 and GMO132.

**Table 4.** Number of recaptured cod classified as NCC, NEAC, or unidentified (NN), based on assignment tests and otoliths, and release site.

Assign method	Cod group		
	NCC	NEAC	NN
DNA	51	32	5
DNA + otolith	3	2	
Otolith	1	2	
No information			7
Release site		5	
Total assigned cod	55	41	12

these individuals, otoliths were retrieved and could be used to classify one as NCC and the other two as NEAC (Table 4). Good correlation was observed between genetic and otolith typing of cod. In total, eight otoliths were retrieved from the recaptured cod. Of these, four otoliths classified the cod to NCC (one of genotype *Pan I<sup>AA</sup>*, two of genotype *Pan I<sup>AB</sup>*, and one without genetic information). The four other otoliths classified the cod as NEAC (one of genotype *Pan I<sup>BB</sup>*, one of genotype *Pan I<sup>AB</sup>*, and two without genetic information). Five cod were released and recaptured from the Barents Sea and were included in the classification analysis as NEAC based on release site.

### Spatial dynamics

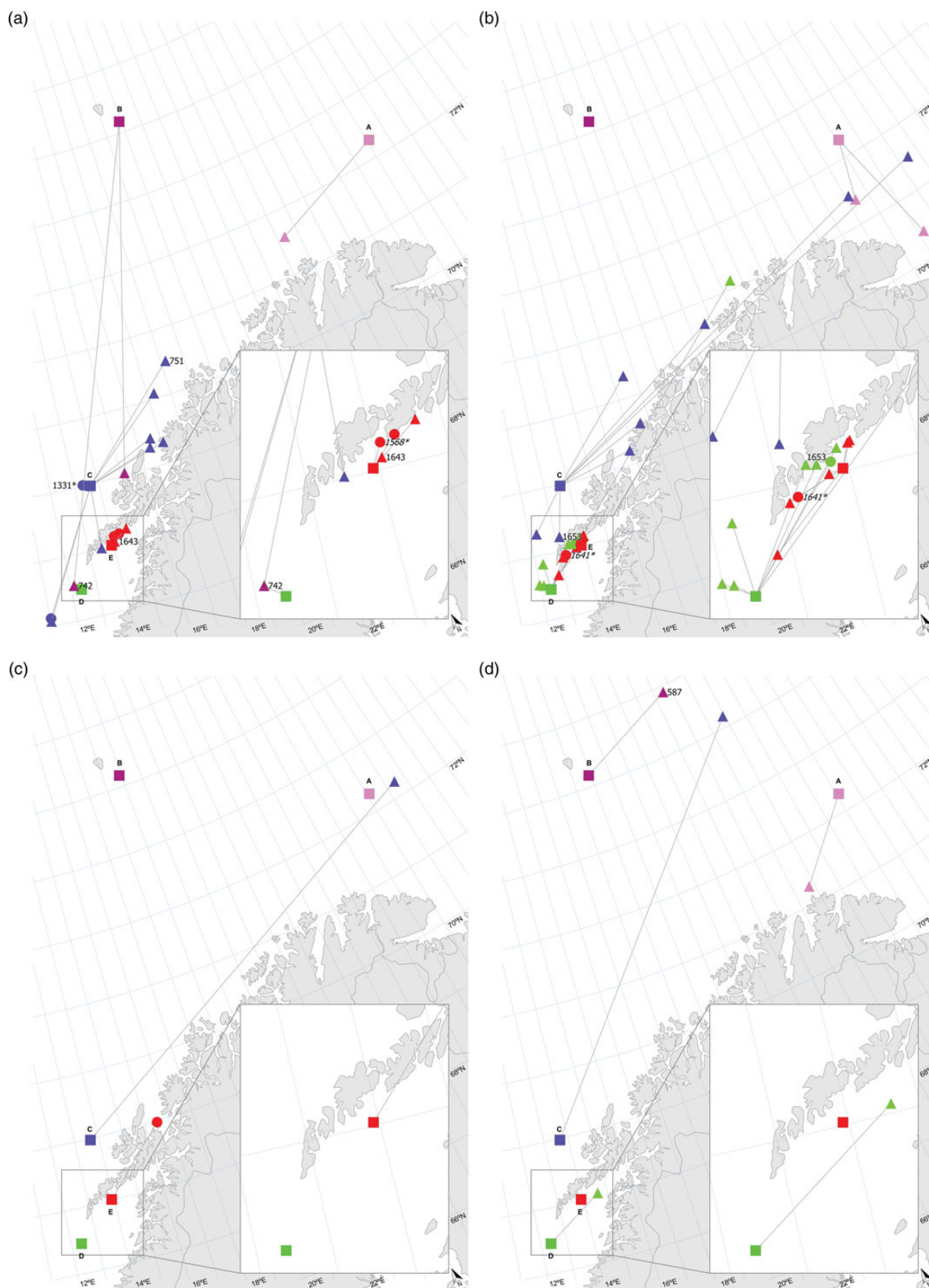
Based on the result of the assignment of individual cod into NEAC and NCC shown in Table 4, the shortest line from release site to the recapture location was calculated (Figure 3). Seven recaptures of NEAC occurred in the Barents Sea, while 47 occurred quite close to the coast (Figure 3a–d). Five of the open water releases were recaptured along the coast, mainly during the first and second quarter of the year (Figure 3a and b), while one (DST 587) was recaptured further east into the Barents Sea in the last quarter of the year (Figure 3d). Nearly all the recaptures of NEAC from Lofoten showed a northward movement after release and in the second quarter of the year, but four individuals from the northern release were recaptured south of the release location, shortly after tagging (Figure 3a and b). Another NEAC (DST 751) was recaptured north of the release location in the first quarter of the year, but this cod had been out for almost 1 year (344 days, Table 5) and was probably on its way back to the spawning area. All NCC were recaptured close to the coast, but some individuals had moved quite far away from the release location (Figure 3e–h). The movement of the seven fish which could not be classified as either NEAC or NCC are presented in Figure 3a–d, as circles. For the geographic presentation of the movements during the year, it is clear that the direction of the movement cannot be used to assist in any further classification.

The shortest distance from release site to the recapture location during the year is shown in Figure 4a and b. To link the genetic variation in *Pan I* to possible variation in migration rate, we have identified this genotype for the individual cod for both NEAC (Figure 4a) and NCC (Figure 4b). The time between release and recapture ranged from 1 to 1460 days (Figure 4). Most of the tags ( $n = 83$ ) were recaptured within a year, while 22 cod were at sea for more than 1 year. NEAC was recaptured either in summer/autumn in the Barents Sea (>600 km from the spawning area) or mainly, at the spawning ground in the first months of the year, the same year, or the year after tagging (Figure 4a). This corresponds to the

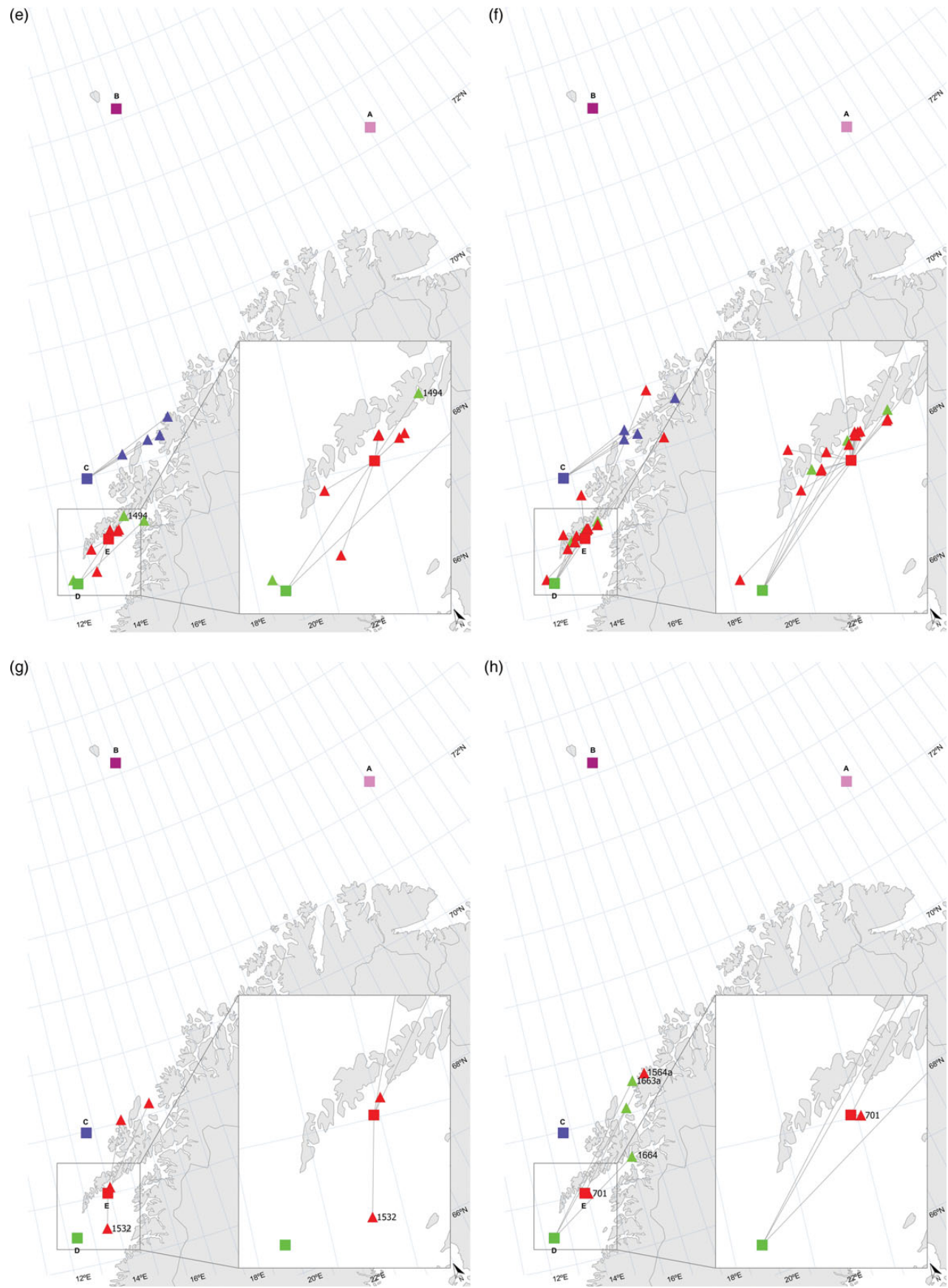
seasonality in the commercial fishery, with high effort during the first 4 months of the year. The longest distance between release site and recapture position was 838 km (Figure 4a, DST 742). This fish was released close to Bear Island in August and was recaptured in November (3 months later) close to Lofoten (Figure 3a). The fastest movement of cod was recorded by an NEAC (DST1653) released in Lofoten (east) and recaptured 126 km further north, 4 days after release (Figure 3b). Also for NCC, most of the recaptures occur in the first and second quarter of the year, but in contrast to NEAC, NCC was also recaptured in the second half of year (Figure 4b). Although movements of more than 300 km from the release site were recorded, all NCC recaptures were close to the coast (Figure 3e–h). Of the cod assigned to either NEAC or NCC, 6 and 15 individuals had genotype *Pan I<sup>AB</sup>*, respectively (Table 3 and Figure 4). Of the genetically unidentified individuals (NN), three showed the genotype *Pan I<sup>AB</sup>*. Figure 4 shows that cod expressing this genotype did not deviate in migration rate compared with homozygote individuals of the same cod type. Cod with tag 1494 and 1532 are highlighted in Figure 4b (see also Figure 3e and f) because, in contrast to the other tagged cod, these were released in November and the number of days at sea will not correspond to the same seasonal pattern as with the other recaptures. Both of these were NCC and were recaptured close to the coast 149 and 692 days after release, respectively (see also Figure 3e and g). Later we will present results indicating that cod with DST 1643 had similar temperature profile as an NCC, although the assignment test classifies it as NEAC (*Pan I<sup>BB</sup>*). The shortest distance between release and recapture for this cod is therefore presented together with NCC in Figure 4b.

### Behaviour of individual cod and environmental conditions experienced

To understand behaviour and environmental conditions experienced by individuals within different cod types, profiles of depth and temperature from the DST were analysed. To reveal seasonal pattern, we selected only DST tag from cod spending more than 60 days at sea. Of the recaptured DST tags listed in Table 5, four cod had been at sea between 60 and 200 days and ten cod had been at sea for more than 200 days. Thirty-one tags were excluded from further analysis either because of too short release–recapture time (<60 days), technical problems with the tags, or that the DST were not retrieved. Since NEAC and NCC are localized in different geographical areas during different times of the year (Figure 3), the temperature profiles rather than the depth profiles turned out to be better diagnostic parameters for distinguishing between the two cod types. The temperature profiles of the 15 DSTs with highest data quality were therefore plotted according to the previous classification of NEAC and NCC and shown in Figure 5a and b. Figure 5 indicates that NEAC and NCC experienced different temperatures during summer and autumn, while experiencing the same temperatures (4–6°C) during the spawning period in January–March. It could be seen that the temperature profiles for two unassigned cods by the DNA markers (Table 5: DST 1641—assignment score of 53%, and DST 742—released at Bear Island in August and no DNA) did fit very well with those assigned to NCC and NEAC, respectively. One deviating pattern was the temperature profile for the cod assigned as NEAC (DST 1643), which show temperature profiles more similar to cod classified genetically as NCC (Figure 5b). This last individual showed up as homozygote for all three genetic markers (*Pan I<sup>BB</sup>*, the common allele for both



**Figure 3.** Spatial distribution of release sites and recapture locations according to recapture quarters of the year. The release sites are symbolized by coloured rectangles and labels. Barents Sea, pink, A; Bear Island, violet, B; Lofoten North, blue, C; Lofoten West, green, D; Lofoten East, red, E. The recapture sites are symbolized with triangles or circles in the same colour as the release site. Circles and tag no were used for recaptures of individuals that could not be assigned to neither NEAC nor NCC, thus named “NN”. Tag no are also included for DST that will be referred to in the text. (a) – (d) combine NEAC and NN recapture locations, in the consecutive quarter of the year. (e) – (h) shows NCC recapture locations, in the consecutive quarter of the year.



**Table 5.** Overview of recaptured DSTs classified as NCC and NEAC or unidentified (NN), based on genetic assignments (*Pan I* analysis and structure), DST profiles, and otoliths morphology.

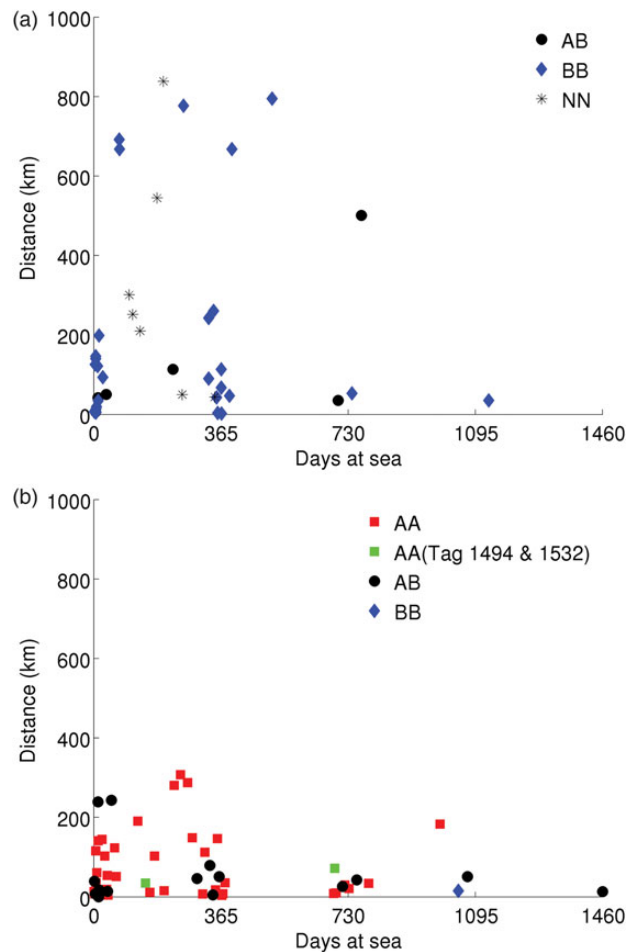
Release date	DST number	Cod type	<i>Pan I</i> allele	Structure	DST profile	Otolith morph.	Release site	Days at sea	Tag quality
01.04.2004	701	NCC	AA	NCC	NCC	NCC	E	202	1
01.04.2004	1564a	NCC	AA	NCC	NCC		E	249	1
02.04.2004	1663a	NCC	AA	NCC	NCC		D	270	1
01.04.2004	1641	NCC	AB	NEAC (53%)	NCC		E	405	1
02.11.2004	1532	NCC	AA	NCC	NCC		E	692	1
01.04.2004	1640	NCC	AA	NCC	NCC		E	733	1
02.04.2004	1664	NCC	AA	NCC	NCC		D	994	1
01.04.2004	1643	NCC	BB	NEAC	NCC		E	1 047	1
03.04.2005	1620	NCC	AA	NCC	NCC		E	127	2
01.11.2004	1494	NCC	AA	NCC	NCC		D	149	2
21.03.2004	751	NEAC	BB	NEAC	NEAC		C	344	1
25.03.2006	2481	NEAC	BB	NEAC	NEAC		D	397	1
19.03.2004	699	NEAC	BB	NEAC	NEAC		C	74	2
26.08.2003	742	NEAC			NEAC		B	200	2
03.04.2006	1564c	NCC	AB	NCC			E	2	3
01.04.2005	1725	NCC	AA	NCC			D	6	3
01.04.2005	1663b	NCC	AA	NCC			D	6	3
03.04.2005	1582	NCC	AA	NCC			E	9	3
03.04.2005	1611	NCC	AB	NCC			D	12	3
01.04.2005	1729	NCC	AA	NCC			D	13	3
02.04.2004	1657	NCC	AA	NCC	NCC		D	283	3
30.03.2004	7615	NCC	AB	NCC			E	755	3
30.03.2005	1564b	NEAC	BB	NEAC			D	2	3
01.04.2005	1653	NEAC	BB	NEAC			D	4	3
01.04.2004	1577a	NEAC	AB	NEAC		NEAC	E	5	3
01.04.2005	1744	NEAC	BB	NEAC			D	6	3
03.04.2005	1577b	NEAC	BB	NEAC			E	6	3
01.04.2005	1728	NEAC	BB	NEAC			D	11	3
03.04.2005	1632	NEAC	BB	NEAC			E	12	3
03.04.2005	1623	NEAC	BB	NEAC			E	13	3
19.03.2004	856	NEAC	BB	NEAC			C	15	3
19.03.2004	721	NEAC	BB	NEAC		NEAC	C	26	3
21.03.2004	739	NEAC	BB	NEAC			C	73	3
08.02.2003	421	NEAC					A	102	3
28.08.2003	587	NEAC					B	112	3
08.02.2003	463	NEAC					A	133	3
28.08.2003	717	NEAC				NEAC	B	182	3
02.02.2003	446	NEAC					A	254	3
02.02.2003	476	NEAC				NEAC	A	347	3
18.03.2004	7608	NEAC	BB	NEAC			C	390	3
21.03.2004	752	NEAC	BB	NEAC			C	512	3
25.03.2004	412	NEAC	BB	NEAC			C	741	3
25.03.2004	409	NEAC	AB	NEAC			C	768	3
01.04.2005	1656	NN	AB	NCC (56%)			D	3	3
01.04.2004	1568	NN	AB	NEAC (63%)		E	707	3	

Numbers of days since release upon recapture are given. The quality of the data from each DST is given from 1 > 180 days in sea, 2 > 60 days in sea, and 3 ≥ data excluded because of few days with data, problems with the DST's or that they have not been received.

microsatellites, Table 5) which should have indicated most likely an NEAC, but can also occur in NCC.

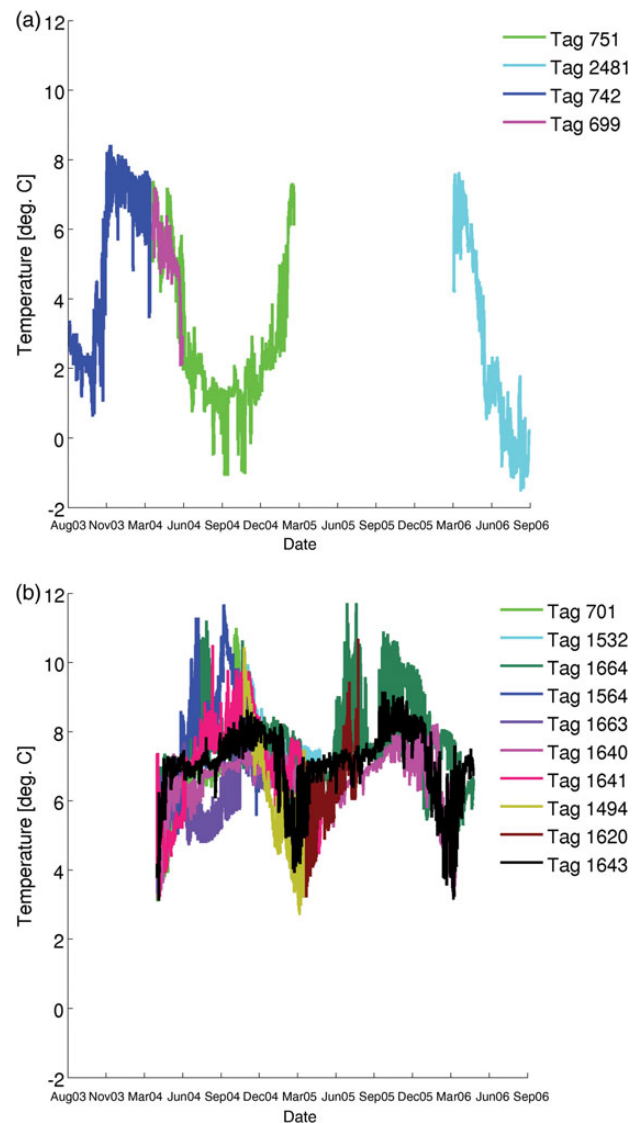
Pooled monthly temperatures and depths throughout the year shown for all recaptured NEAC with DST of quality 1 and 2 (Table 5) is shown in Figure 6a and b, respectively. Observe that the data show high degree of variability across the months, with averages ranging from 0 to 6.5°C. The results also indicate that fish of this classification experience subzero temperatures from July to November (see the box-plot whiskers). In general, and for almost all months, the inter-quartile ranges are comparable with those of NCC (plotted in the same graph). The exception, however, is in December and January, where the inter-quartile

ranges are ~6 and 5°C, respectively. The large variability in temperature (see similar variability in depth) can be attributed to spawning migration over regions with highly variable bathymetry, and temperatures varying from those characterizing Arctic to coastal waters. Figure 6c and d shows the box plots of pooled monthly temperatures and depths, respectively, for NCC. Observe that in general, considering only the first and third quartile, the temperatures from January to December lie within the range of 4–9°C, and that the mean temperature for each month is close to the mode. The inter-quartile range, i.e. Q3–Q1, is very low. Observe that the temperature for NEAC (plotted in the same graph) falls within the inter-quartile range temperature range for NCC, only during



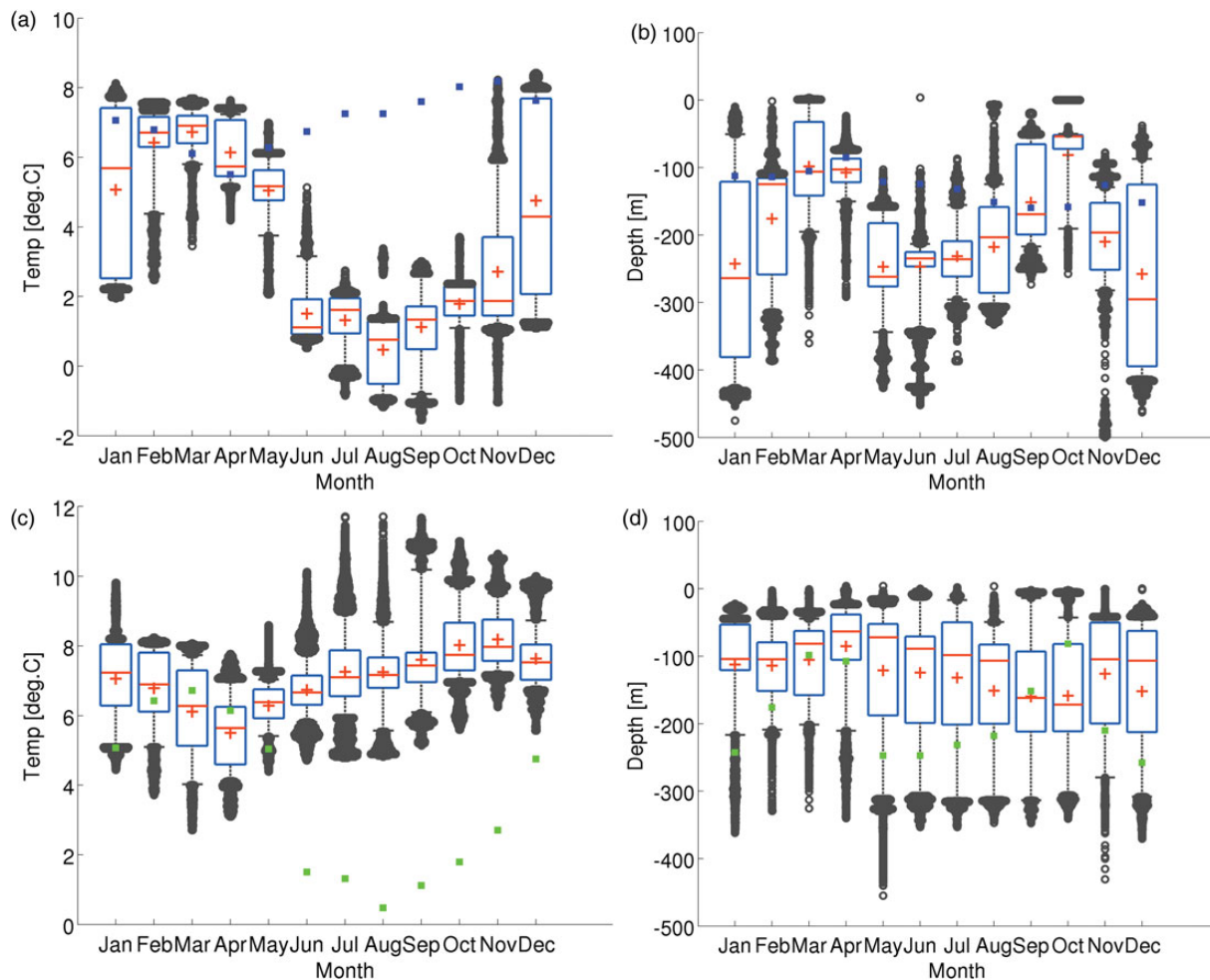
**Figure 4.** Computed shortest distance (in km) between release and recapture sites for cod classified as (a) NEAC ( $Pan I^{BB}$ ,  $Pan I^{AB}$  and genetically unidentified individuals "NN") and (b) NCC, based on genetic assignment, otolith morphology or release site from Tables 3 and 4. The  $Pan I$  alleles are shown with different symbols.  $Pan I^{BB}$ , diamonds;  $Pan I^{AB}$ , circles;  $Pan I^{AA}$ , rectangles; and genetically unidentified individuals "NN", stars. Cod with DST 1494 and 1532 are marked with grey symbols because, in contrast to the other NCC, these were released in November and the number of days at sea will not correspond to the same seasonal pattern as with the other recaptures. The diamond in (b) indicates that one individual had similar temperature profile as an NCC, although the assignment test classifies it as NEAC ( $Pan I^{BB}$ ).

the months February–April. In particular, the mean NEAC temperatures for February–April are close to the mean (and modal) NCC temperatures for these particular months. It is worth noting that outside the time February–April range, the mean temperature profile for NEAC is convex, while that of NCC is concave. The box plot for the depth data indicates little variation in water column usage by NCC. Figure 6d shows a maximum inter-quartile range of ~200 (250–50 m). The depth plot also indicates that only in 1 month is the average NEAC depth recorded, lower than the average depth experienced by NCC in the same month (October). There is strong evidence (by combining the depth and temperature box plots) to suggest that the two stocks share common ambient conditions, at least, during February–April. We later present



**Figure 5.** Temperature profiles from recaptured cod with DST and classified as (a) NEAC and (b) NCC. Note that the tick mark on the x-axis denotes the end of calendar months, over a period of 3 years.

stronger statistical evidence in support of this conjecture, using the KDE results. Due to the closer connection to the coast and lower variation in distribution area, one would expect that the variation in depth and temperature within NCC to be lower than shown in Figure 6c and d. Also between the temperature profiles for NCC shown in Figure 5b, some variation exists. A closer inspection reveals that those tags seem to deviate from the main temperature pattern (DST 1564a, 1663a, and 1664) were all recaptured furthest away from the release site (Figure 3h) and could therefore be defined as a migrating NCC. They all belonged to the  $Pan I^{AA}$  group (Table 5). To illustrate the difference in temperature profile with what could be a stationary (DST 701) and a migrating (DST 1663a) NCC, the depth and temperature profiles are plotted and shown in Figure 7. Though both fish were tagged at the same time of the year in Lofoten, the depth and temperature profiles indicate that one of the individuals stayed within the release area, while the other cod moved through deeper trenches, which characterize



**Figure 6.** Box plots of pooled monthly temperatures and depths for NEAC (a and b) and NCC (c and d), showing the third quartile (Q3) and first quartile (Q1) range of the data and data outliers (legends are explained in Figure 1). For the sake of comparison, we have plotted the average monthly observations (black squares) for NCC in the same diagram and the average monthly observations (grey squares) for NEAC in (c) and (d).

migration out of the Lofoten area (also confirmed by the recapture location shown in Figure 3h).

### Depth and temperature experienced in the spawning period April

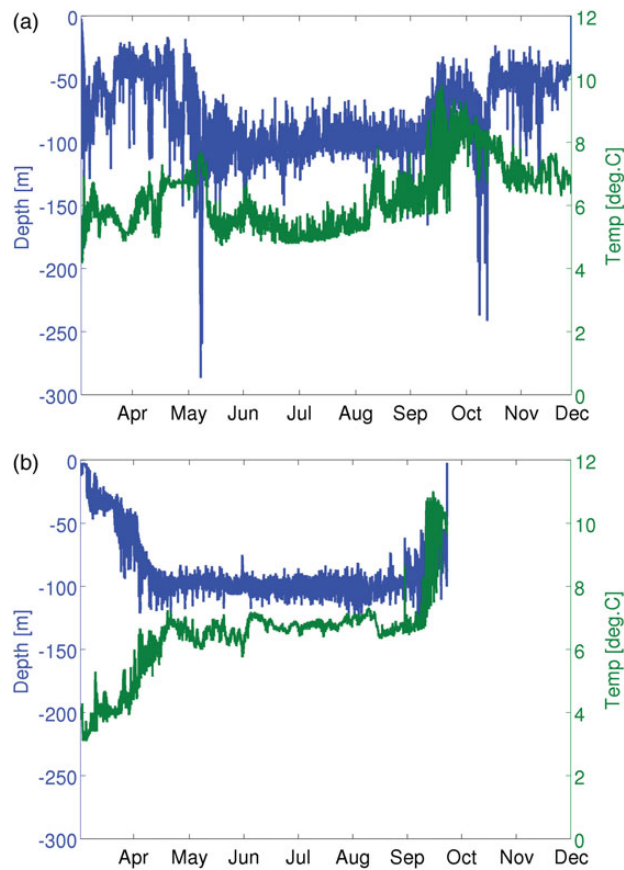
While the box plots give pictorial summaries of the univariate data, we used the KDE approximations of the bivariate (temperature–depth) probability distribution to identify highly probable regions in the temperature–depth space. Figure 8 shows the probability distribution contours for NEAC for January and April. Results for February and March are excluded for the sake of brevity. The January data show a distinct bi-modal probability distribution, with the mode at  $\sim 7^{\circ}\text{C}$ –100 m being coincidental with the average temperature–depth data for NCC. Observe also that for April, the average NCC temperature–depth values lie in the high probability region of the NEAC distribution for this particular month. These observations are also consistent with results for February and March. Figure 9 (in contrast to Figure 8) shows that the probability of NEAC experiencing the average temperature–depth for NEAC is zero for the months of June and September. We have obtained similar results for May–November.

### Discussion

This is the first time a tagging programme has linked genetic markers to gain insight in the spatial dynamics of the two cod stocks belonging to mixed stock fisheries in the Northeast Arctic waters. By combining the methods with statistical tools, we have been able to associate genetic structure with spatial dynamics and distinct environmental factors. In general, NEAC migrate between deep, warm overwintering grounds and shallow summer feeding grounds where water temperatures may be low. In contrast, NCC do not undertake large-scale seasonal migrations, show little seasonal variation in depth distribution, and experience the opposite seasonal change in temperature as conditions become warmer in summer. The NCC seems to stay in shallow and higher temperate waters all year, although we did observe indications of migrating NCC, periodically occupying deeper waters and recaptured more than 300 km from the release site.

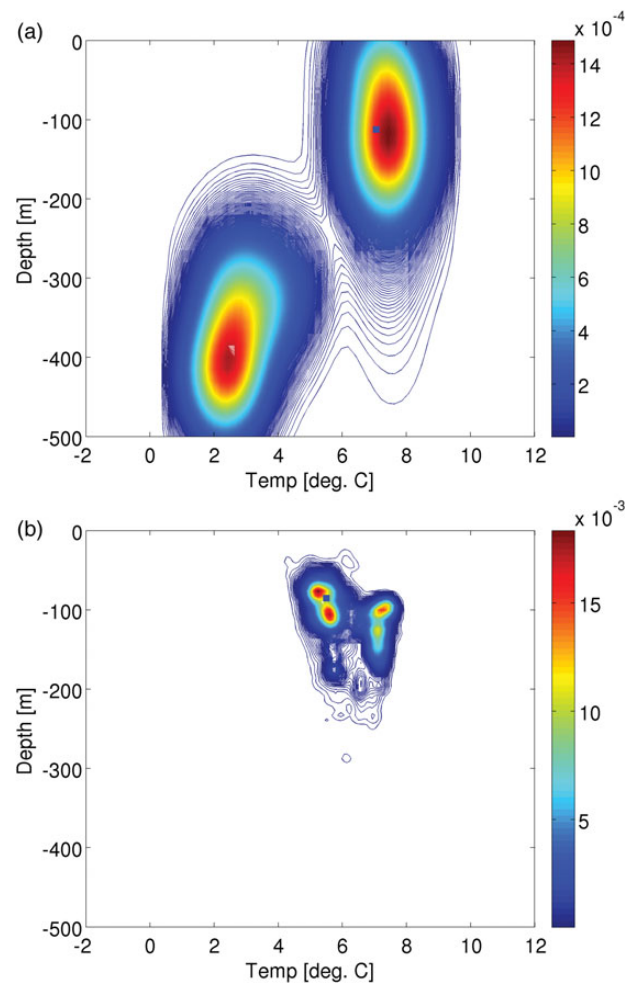
### Genetic identification of cod

We have, in the present project, made use of the selective markers—*Pan I* and two microsatellites (GMO34 and GMO132) to identify the individual tagged cod. This is the first time such an attempt has been



**Figure 7.** Depth and temperature profiles two recaptured NCC with DST, representing (a) migrating NCC with DST 1663a and (b) stationary NCC with DST 701. Note that the tick mark on the x-axis denotes the end of calendar months, over a period of 3 years.

made on individual basis. The pantophysin locus (*Pan I*) is the most powerful locus at the moment to separate NEAC and NCC in a mixed sample (Skarstein *et al.*, 2007; Westgaard and Fevolden, 2007). The *Pan I* locus exhibits two alleles, *Pan I<sup>A</sup>* and *Pan I<sup>B</sup>*, and the genotype *Pan I<sup>BB</sup>* found most frequent in NEAC, while *Pan I<sup>AA</sup>* is the dominating genotype in NCC. In the coastal cod, the *Pan I<sup>B</sup>* allele is present, but at low frequencies as seen for the NCC baseline samples in Table 2. Hence, adding the two microsatellites and application of statistical programs (such as STRUCTURE) offers more objective tools in assigning individuals to either of the two cod stocks. All cod except five of the recaptured cod could be assigned to either NEAC or NCC with more than 70% certainty. This degree of certainty is quite good compared with other studies (Pampoulie *et al.*, 2006), although we are studying population structure where the neutral loci show relatively low differentiation (Skarstein *et al.*, 2007; Westgaard and Fevolden, 2007; Wennevik *et al.*, 2008; Hemmer-Hansen *et al.*, 2013). Pampoulie *et al.* (2008) analysed *Pan I* for DST tagged cod, but did not have available other markers that could separate their coastal and frontal cod which our NEAC and NCC, as the microsatellites showed very low genetic structuring for the two Icelandic cod stock components (Pampoulie *et al.*, 2006). Compared with Pampoulie *et al.* (2008), we have gone one step further and have been able to assign cod expressing *Pan I* heterozygote's to either

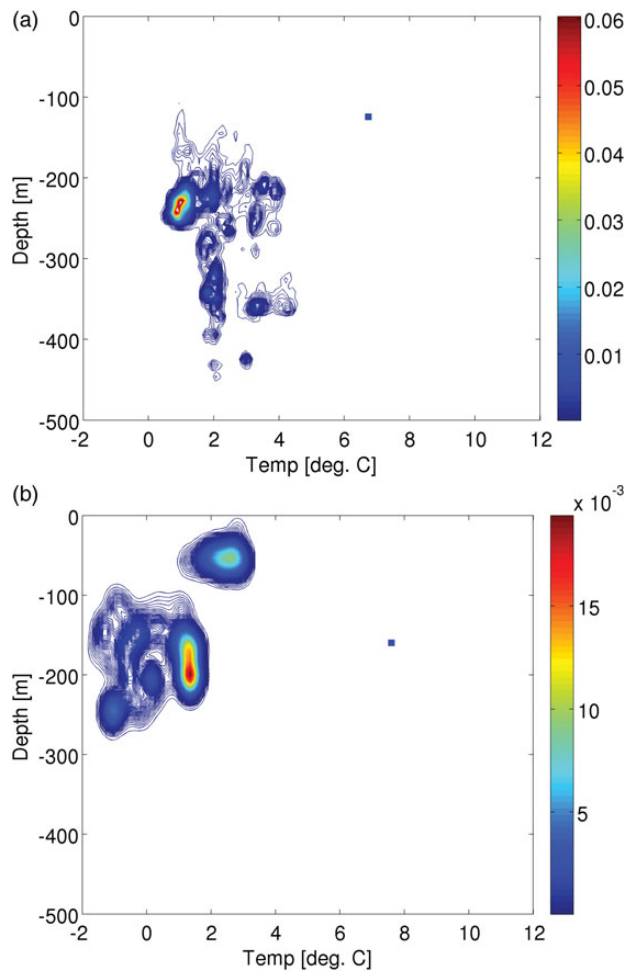


**Figure 8.** Example KDE plots for NEAC covering the months (a) January and (b) April. The black square in each diagram represents the average depth and temperature value for NCC, for the particular month. Observe that for these particular months, the average NCC values lie in the high probability regions of the temperature – depth distribution for NEAC.

NEAC or NCC. Thus, we were able to study behavioural differences compared with the homozygote individuals (Figure 4).

### Classification of cod based on genetic, otolith, and release site

The assignment of cod to NEAC or NCC based on otolith morphology was developed by Rollefson (1933, 1934) and continues to be used in current fisheries assessment. This assignment has later been compared with genetic variation in *Pan I*, indicating good correlation in assignment rate (Berg *et al.*, 2005; Stransky *et al.*, 2007). Nordeide *et al.* (2011) reviewed 80 years of studies of Atlantic cod in the Barents Sea and Norwegian coastal waters. They showed that 70% of the reviewed papers support differentiation of cod into NEAC and NCC based on the morphological, morphometric, and genetic characters. Although there should have been a stronger basis for using otoliths to classify cod, we did receive only eight otoliths from the recaptured cod. Those analysed gave identical classification as the genetic assignments (Table 4). In addition, by assigning some cod based on the release and recapture site in



**Figure 9.** Example KDE plots for NEAC covering the months (a) June and (b) September. The black square in each diagram represents the average depth and temperature value for NCC, for the particular month. Observe that for these particular months, the average NCC values lie far outside the probability distribution contours of temperature–depth for NCC.

Barents Sea and Bear Island, we were able to include even five more fish in our further analysis of cod distribution (Table 4, Figure 3). Further, the way we assigned the recaptured cod seems to group the cod into two main temperature and depth profiles, reflecting the cod types (Figure 5). Only one individual deviated clearly from this pattern and was assigned by genetic methods as NEAC, but the DST temperature-profile suggested an NCC. This individual showed genotype *Pan I<sup>BB</sup>* and was homozygote also for the two microsatellites (DST 1643 in Table 5, Figures 3a and 4b). This combination is also present in coastal cod (Westgaard and Fevolden, 2007). This specimen should be investigated by other genetic markers as such SNP markers (Hemmer-Hansen *et al.*, 2013).

A central question, when analysing different data types derived from a single individual, is whether each data, when viewed in isolation, are in agreement with inference based on other sources. This is often referred to in the literature as cross validation. In the context of our study, we have three independent sources of data. Though each dataset has been analysed independently, the assignments of each individual based on genetics, otoliths, or DST

appear, in general, to be in agreement. By linking methods the classification into NEAC and NCC, we were able to increase the number of recaptured cod that could be used in our analysis on spatial distribution between NEAC and NCC.

### Insight into spatial dynamics of NEAC and NCC

The seasonal differences in habitat associations we observed for cod, as well as the geographic differences between the northerly migratory NEAC and the NCC (Figures 3 and 4), may reflect differences in the factors motivating habitat selection. During winter, the NCC reside in shallow waters of 20–40 m and after spawning in February/March, before they move to deeper waters (Figure 6). NEAC, however, spend June–September in significantly deeper water (50–70 m) both compared with the rest of the year and with NCC during the same summer period (40 m). No clear seasonal patterns were found in the number of movements (ascents and descents combined), for NCC. NEAC however, make fewer and generally longer, vertical movements in the summer (August and September) compared with other months and with NCC during the same months. Although monthly patterns in the temperature exposure are similar for both NEAC and NCC, during the warmest part of summer, there is more variation in temperature experienced by NEAC compared with NCC and the median temperature exposure is considerably lower in September (13.5 and 17.5 °C, respectively). This could suggest that at least part of the motivation for extensive migrations is to head into the Barents Sea for cooler waters due to divergent optima to thermal niches (Righton *et al.*, 2010). However, factors other than temperature preference are likely to influence habitat selection during summer feeding season and both more abundant and higher energy content of the prey could affect the migrations northward during summer (Michalsen *et al.*, 1998; Johannesen *et al.*, 2012; Johansen *et al.*, 2013).

By combining DST profiles with genetic assignment methods, we discover that also within the NCC group, some individuals did conduct longer horizontal movements than others (Figures 3e–h and 4b). Although the distances calculated in this study represent the shortest distance between release and recapture positions (and are probably underestimation of the actual distances covered), they are far higher than previously reported in the literature (Jakobsen, 1987; Høyen *et al.*, 2008). Distinctive “spikes” in the depth profiles for what could be defined as the migrant NCC (Figure 7a) indicate that they have moved out of the area, passing the deep trenches outside Lofoten, while more stationary NCC occupies shallower depths throughout the year (Figure 7b). The temperature profiles (Figure 5b) also indicate that migrant and stationary NCC has occupied different areas during the year. This has to be investigated further, but while DSTs typically provide information about depth and temperature, the direct connection to the actual horizontal position at all times is difficult to obtain. Therefore, a reconstruction of the horizontal migration patterns of all cod tagged with DSTs ought to be made. This would provide a promising basis for further and more detailed studies on spatial differences between individual cod. In addition to new knowledge of migration routes, this model approach can improve our understanding of the factors affecting fish behaviour, the mechanisms behind the migrations, and effects of climate change (Neuenfeldt *et al.*, 2013). As an observed spatial shift in spawning area of cod seems to be a response to climate change, Sundby and Nakken (2008) have indicated that there might a maximum distance feasible for the annual migrations from feeding to spawning areas.

Reconstruction of the migration of cod in the Barents Sea has revealed that to achieve the distance travelled, cod would have required the assistance of directional currents in addition to swimming close to the maximum sustainable swimming speed (Ådlandsvik *et al.*, 2007). The current system (direction and speed) along the coast of Norway might therefore be an important factor, allowing for the long distance migrations conducted by NEAC, to occur (Michalsen *et al.*, 1996).

### Identification of cod on spawning sites

Due to lack of relevant tools, it has until now not been possible to determine whether NEAC and NCC have different environmental preferences as regards water characteristics and the time and place of spawning. Figures 8 and 9 are the first attempt to investigate this. Although NCC and NEA cod intermingle at the spawning grounds, they might not spawn at exactly the same geographical position, at the same time of the day, or at the same depth. This can, together with windforcing at the spawning ground (Jung *et al.*, 2012) and lekking behavior (Nordeide and Folstad, 2000), be one of the mechanism behind population differentiation in Northeast Atlantic cod and have to be studied in more detail.

### Conclusions and management implications

We have demonstrated that the combination of information from DSTs and molecular biology offers a deeper understanding of individual cod behaviour, provides an insight in the spatial dynamics of the species, and ultimately, improves the scientific basis for management of a complex mixed fishery of Atlantic cod in the Lofoten area. The variation in probability of catching NEAC and NCC at certain areas/depths during the year could be used as input to assessment and management plans. This knowledge will have the effect of influencing the interpretation of survey results as well as catch statistics. This is because the variation in vertical water usage and spatial distribution will affect the availability of fish and the catchability pattern for different gear types during the year and in different areas. We have documented that some NCC do also migrate (up to 300 km away from their spawning location). This may pose an extra challenge when marine protected areas (MPAs) are considered. Further, knowledge of arrival/departure times of NEAC is important when considering MPAs.

More detailed knowledge about the actual temperature experienced throughout the year could give more accurate estimates of growth rates and could have implications for establishment of the otolith morphology (hyaline and opaque zonation) and therefore, the age estimation of cod based on otoliths. The present suggested migration pattern, depth, and temperature profiles of NEAC and NCC can further be used to establish a method to identify the type of cod that was tagged in other programmes as Godø and Michalsen (2000 and other studies) where no DNA samples are available (see Subby *et al.*, in prep.).

This study shows that NEAC and NCC do experience characteristically distinct temperature conditions throughout the year. Their spatial dynamics, including the extent of horizontal migration, seem to be well defined. Our findings show distinct migration pattern and temperature profile for the assumed NEAC and NCC which can support the hypothesis that they belong to different stocks. The long migration by some NCC could indicate that NCC might be composed of more than one population. Further studies on spatial dynamics, spawning behaviour, and genetic structure are therefore needed to reach a sound conclusion.

### Acknowledgements

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