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Original Article

The genetic composition of feeding aggregations of the Atlantic mackerel (*Scomber scombrus*) in the central north Atlantic: a microsatellite loci approach

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The impacts of climate change on marine ecosystems can be seen in the changing distribution, migration, and abundance of species in the oceans. For some species this changing environment may be beneficial and can support population expansions. In the northeast Atlantic (NEA), the Atlantic mackerel (*Scomber scombrus*) is undergoing an increase in stock size accompanied by changing summer migration patterns, which have resulted in an expansion further north and north west than previously recorded. This study uses microsatellite loci to confirm the differentiation among NEA and northwest Atlantic (NWA) mackerel spawning populations and to assess the level of structuring within these populations. In addition, to enable population-specific exploitation rates to be factored into fisheries management, we identified the origin of individuals composing the expanding feeding aggregations in the central north Atlantic (Greenland, Iceland, Faroes), with all aggregations tested originating from spawning populations in the NEA. This study showed that microsatellite loci were useful to assess the contribution of NEA and NWA populations to mixed feeding aggregations across the north Atlantic for large pelagic fish stocks but were not powerful enough to evaluate the specific contribution of known stocks within NEA and NWA.

Keywords: Atlantic mackerel, feeding grounds composition, microsatellite loci, migration, population structure

Introduction

There is increasing concern over the consequences of climate change for marine ecosystems and the effects on fisheries production. It is now accepted unequivocally that anthropogenic climate change is occurring (IPCC, 2014), with measurable hydrographic changes registered in recent decades (Perry *et al.*, 2005; Gamito *et al.*, 2015). The results of this are evident with impacts on the production and species composition of marine ecosystems, and the distribution, migration, and abundance of species in the oceans (Cheung *et al.*, 2008, 2009; Hare *et al.*, 2010). However, for some species this changing environment seems to be supporting or even facilitating population expansion.

Atlantic mackerel (*Scomber scombrus*) in the northeast Atlantic (NEA) is both undergoing a spatial expansion and demonstrating changing migration patterns (Astthorsson *et al.*, 2012; Berge *et al.*, 2015; Nøttestad *et al.*, 2016). Atlantic mackerel occupies an important ecological niche, feeding on a variety of zooplankton, phytoplankton, and the pelagic larval and juvenile stages of several commercially important fish species (Engelhard *et al.*, 2014; Trenkel *et al.*, 2014; Pinnegar *et al.*, 2015; Skaret *et al.*, 2015). They are also an important food source for marine mammals and other fish and are a commercially important species with annual landings of 500 000–1 400 000 tonnes (ICES, 2015). Atlantic mackerel occurs on both sides of the north Atlantic and is traditionally classified into five spawning components. In the northwest Atlantic (NWA), mackerel is found from Cape Hatteras, NC, to the Gulf of St Lawrence in Canada and is defined as two distinct components: the southern, which spawns off the East Coast of the United States in March and April north of Cape Hatteras, and the northern, which spawns around the Gulf of St. Lawrence in June and July (Gregoire *et al.*, 2010). Both components of the NWA have been suggested to display spawning site fidelity (Studholme *et al.*, 1999) and are thought to winter along the Mid-Atlantic Bight (Sette, 1950), with summer feeding migrations moving offshore and north as far as Newfoundland and Labrador (Studholme *et al.*, 1999; Radlinski *et al.*, 2013). In the NEA, mackerel spawn from Hatton Bank in the west to Kattegat in the east, and from Portugal in the south to the Faroe Islands in the north (with an additional, isolated spawning population in the Mediterranean Sea). Spawning starts in early February off the Portuguese coast and ends in July north of Scotland and in the North Sea (ICES, 2015). The spawning appears to be a single large spatiotemporal continuum, although there are local variations in spawning (Bakken, 1977; Iversen, 1981; Jansen, 2014). Despite the lack of complete spatial or temporal separation, NEA mackerel has traditionally been divided into three distinct entities: the southern (Portugal to Bay of Biscay) and western (north of Bay of Biscay to North Sea) components (Molloy, 2004) and a third within the North Sea that is separated from the western and southern components by the relatively low levels of spawning in the English and Fair Isle Channels (Johnson, 1977). However, this classification of stocks has been questioned, with the status of the individual stocks within the eastern regions disputed (Jansen and Gislason, 2013). The spawning intensities (approximated by larval abundances) between the North Sea and Celtic Sea have been shown to be negatively correlated indicating that the two spawning components may be connected (Jansen, 2014). This is in accordance with the lack of solid evidence for stock separation from previous analyses such as tagging data and ectoparasite infections (Jansen and Gislason, 2013). This straying of individuals between the spawning components is thought to be driven by environmental factors and cohort size; conversely, a tendency for homing has also been identified (Jansen *et al.*, 2013). The population structure of NEA mackerel has consequently been described by Jansen and Gislason (2013) as: "A dynamic cline, rather than as connected contingents". Although the stock structure is thought to be complex, NEA mackerel has been managed as a single stock since 1995 (ICES, 2015, 2019). Very few genetic studies have been published on mackerel but analysis of mtDNA (Nesbø *et al.*, 2000) and single-nucleotide polymorphisms (SNPs, Rodríguez-Ezpeleta *et al.*, 2016) suggest that gene flow was restricted between the eastern and western Atlantic samples. Nesbø *et al.* (2000) also recommend that the NEA mackerel should be managed as at least three stocks (southern, western, and North Sea). For mackerel it is also of particular importance to confirm the differences between the eastern and western stocks suggested by other methods (e.g. tagging, parasites).

The dynamic migration behaviour of Atlantic mackerel has been demonstrated by large historic shifts in their distribution, thought to be driven by environmental factors, population size, and prey abundance (Pitois *et al.*, 2015). Recently, the feeding migration of NEA mackerel has expanded further to the north and north west than previously recorded (Astthorsson *et al.*, 2012; Berge *et al.*, 2015). In the NWA, the distribution of mackerel also seems to be changing, with a northward shift of 0.5–0.8° north, with each 1°C increase in average water temperature (Murawski, 1993). A more recent study found an increase in mean catch latitude and a decrease in mean catch depth over the last four decades, equating to a shift of 250 km northeast (Overholtz *et al.*, 2011). However, NWA and NEA mackerel exhibited different fates during the period of the present study. NEA mackerel exhibited a sudden increase in stock abundance and a drastic expansion in both its distribution range and its migration path (Astthorsson *et al.*, 2012; Berge *et al.*, 2015; Nøttestad *et al.*, 2016). While the changes in NEA mackerel distribution range were thought to be linked to climate changes, evidence suggested that a combination of factors, such as stock size, food availability, herring abundance, and temperature/longitude, could possibly explain the observed changes (Nikolioudakis *et al.*, 2019; Olafsdottir *et al.*, 2019). In contrast, the NWA mackerel stock has considerably decreased in abundance since 2005 reaching an historical low level (Fisheries and Oceans Canada, 2019) and has slightly changed its distribution towards the north as a possible response to temperature changes (Overholtz *et al.*, 2011).

The northwestern expansion into Icelandic and Greenlandic waters has appeared as a gradual expansion of the summer distribution of NEA mackerel (Astthorsson *et al.*, 2012; Nøttestad *et al.*, 2016). However, the observations around Iceland and especially around Greenland are geographically so close to the summer distribution of NWA mackerel that it has been suggested that mixing may be occurring between these populations during the feeding migration. It is also crucial to determine if mackerel shows levels of differentiation within the eastern stock and western stocks that would support established populations with a high degree of natal homing to spawning grounds or would support a more dynamic utilization of the available spawning grounds. Once this is accomplished, the composition of mixed summer feeding aggregations, as well as overwintering aggregations, can be assessed to provide accurate data on the population identity of harvested fish that would maximize long-term fisheries yield at minimal risk to population viability.

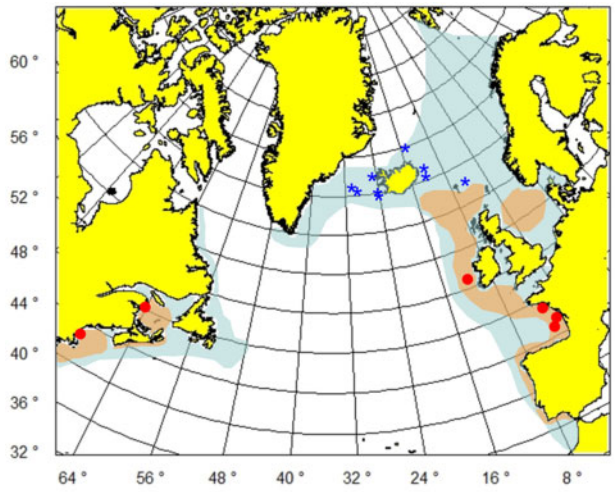

Figure 1. Map of the north Atlantic with location of the Atlantic mackerel samples collected for the present study. Spawning samples (red) and feeding aggregations (blue) are indicated, with the approximate extent of the spawning areas shaded orange, and the area covered by the summer feeding migration shaded pale blue (based on Studholme *et al.*, 1999; Radlinski *et al.*, 2013; ICES, 2015; Nøttestad *et al.*, 2016).

This study focuses on the application of newly developed microsatellite markers to mackerel from across the suggested spawning components in the NWA and NEA. Our aims were threefold: (i) to assess the level of genetic differentiation between NEA and NWA mackerel spawning populations, (ii) to assess the level of differentiation within the NEA and NWA mackerel populations, and (iii) to determine the origin of individuals composing the feeding aggregations in the central north Atlantic region.

Material and methods

Sampling

Samples of Atlantic mackerel were collected in eight locations from scientific surveys and commercial fishing vessels between 2010 and 2012, representing the majority of the species' Atlantic distribution (Figure 1). Populations were targeted during the spawning season at known spawning areas in coastal waters off Canada (CAN) (northern component, region 4T), United States (USA) (southern component, region 5Z), France (FRA), and Ireland (IRE). These samples mainly comprised spawning individuals as collected individuals were at stage 3 of standard maturity scale ICES (2007). Samples from potentially mixed feeding aggregations were collected from Greenland (GRE), Iceland (ICE), and the Faroe Islands (FAR) (Table 1). Samples were predominantly fin clips (some samples were of gill or muscle tissue) and were preserved in 96% ethanol and stored at −20°C until analysed.

Molecular methods

DNA was isolated from all samples using the AGOWA mag Midi DNA Isolation Kit (AGOWA Gmbh) following the manufacturer's protocol. DNA quality and quantity was determined with a NanoDrop Spectrophotometer (Thermo Fisher Scientific Inc.) and agarose gel electrophoresis prior to genotyping. A total of 14 microsatellite loci were genotyped (*Sscom04*, *Sscom07*, *Sscom08*, *Sscom10*, *Sscom25*, *Sscom43*, *Sscom48*, *Sscom49*, *Sscom50*, *Sscom52*, *Sscom55*, *Sscom57*, *Sscom62*, and *Sscom66*; Olafsdottir *et al.*, 2013).

Table 1. Sample information indicating classification as spawning or feeding, year and location of the sample, and the number (*n*) of individuals included in the analyses.

Sample name	Acronym	Type	Latitude/ longitude	Year	*n*
Canada	CAN	Spawning	48.2; −64.8	2011	165
United States	USA	Spawning	42.6; −70.8	2012	98
Ireland	IRE	Spawning	52.9; −11.9	2012	188
France	FRA—FRA01[a]	Spawning	45.0; −2.3	2012	204
	FRA02[a]		45.7; −1.4		
	FRA03[a]		47.0; −3.2		
Greenland	GRE	Feeding	64.8; −30.7	2011	88
Iceland	ICE-10	Feeding	64.9; −11.1	2010	77
			63.7; −24.4		
Iceland	ICE-11	Feeding	63.7; −23.6	2011	317
			64.4; −29.5		
			65.6; −25.0		
			67.9; −14.7		
			63.9; −11.7		
Faroe Islands	FAR	Feeding	62.1; −4.6	2011	94

[a]See Supplementary Table S1 for pairwise comparisons of samples from FRA.

Polymerase chain reactions (PCRs) were performed in a 10-µl volume containing 10–50 ng of DNA, 200 µM of each dNTP, 0.75 U of Taq polymerase (New England Biolabs Ltd.), 1 µl of 10× Standard Buffer (New England Biolabs Ltd.), and 0.3–2.5 µl of a 50:50 ratio of labelled forward (100 µM) and reverse (100 µM) primers tagged on the 5′-end with a GTTTCTT PIG-tail (Brownstein *et al.*, 1996). One microliter of betaine (500 mM) was added to enhance DNA amplification if needed. PCRs were performed on a Tetrad2 Peltier thermal cycler (BioRad), and cycle conditions followed those described in Olafsdottir *et al.* (2013). Samples were analysed on an ABI PRISM 3730 sequencer using the GeneScan-500 LIZ size standard and genotyped with GeneMapper v4.1 (Applied Biosystems).

Statistical analyses

All markers were checked for null alleles, large allele dropout, and potential genotype scoring errors with Microchecker (Van Oosterhout *et al.*, 2004). Genetic diversity indices including the number of alleles (n_a), observed (H_O) and expected (H_E) heterozygosities, and departure from Hardy–Weinberg equilibrium (HWE) and linkage equilibrium within each samples were calculated in Arlequin (Excoffier and Lischer, 2010) using a Markov Chain length of 10^6 and 100 000 dememorizations. A false discovery rate (FDR) was calculated to correct for multiple testing using the approach by Benjamini and Yekutieli (2001). Statistical significance was assessed using Fisher's exact probability test implemented in GENEPOP'007 (Rousset, 2008).

Two independent methods were used to identify putative loci under selection. First, coalescent-based simulation methods (Beaumont and Nichols, 1996) were performed with the software Lositan (Antao *et al.*, 2008) with samples size equal to the collected samples assuming an island model of 100 islands. A total of 100 000 independent loci were generated with the infinite allele mutation model. Simulated distribution of F_{ST} values conditional to heterozygosity under a neutral model was obtained and thus compared with observed F_{ST} values to identify potential outlier

loci. BAYESCAN v2.01 (Foll and Gaggiotti, 2008) was used to measure the discord between global and population-specific allele frequencies (based on F_{ST} coefficients). While this method does not take into account the population structure, simulations have shown BAYESCAN to have lower type I and II errors than coalescent-based methods (Narum and Hess, 2011). Log10 values of the posterior odds (PO) >0.5 and 2.0 were taken as "substantial" and "decisive" evidence for selection (Jeffreys, 1961). The false detection rate was set at 0.05 and 0.01, adjusting the log10(PO) significance thresholds corresponding to 0.5 and 2.0 considered before correction.

Population differentiation was estimated between pairs of samples and overall using the unbiased F_{ST} estimator (θ of Weir and Cockerham, 1984) and statistical significance assessed using Fisher's exact probability test implemented in GENEPOP'007 (Rousset, 2008). Two independent approaches were then used to determine the population structure within the spawning samples; first, a Bayesian cluster analyses approach was performed as implemented in STRUCTURE 2.3.4 (Pritchard *et al.*, 2000). This software groups all individuals into a predefined number of clusters (K) by minimizing overall deviation from HWE and linkage equilibrium within clusters. Considering the likelihood of high levels of gene flow in this highly migratory pelagic species, the admixture model with correlated allele frequencies was used to reflect the most likely pattern of population connectivity. Since the observed level of differentiation was low among spawning samples, the STRUCTURE model was allowed to include prior information on sampling location (LOCPRIOR, see Hubisz *et al.*, 2009). Five independent runs were carried out for each predefined value of K, with $K = 1$–4. A burn-in period of 400 000 steps and 600 000 Markov Chain Monte Carlo (MCMC) simulations were used. As STRUCTURE is likely to only detect the highest level of differentiation among the spawning samples (Evanno *et al.*, 2005), a subsequent STRUCTURE analysis was performed on each identified cluster (K) containing multiple samples, to identify finer scale population structure within these clusters (Vähä *et al.*, 2007). Finally, a similar STRUCTURE run was performed with both spawning and feeding samples.

The genetic mixture analysis software ONCOR (Kalinowski *et al.*, 2007) was used for mixed fishing analysis. First, we used the leave-one-out test to evaluate how well fish in the reference collection can be assign to their population of origin. Second, to assess assessment accuracy, we used the 100% fisheries simulation option in ONCOR in which fisheries samples are simulated based on the same population. We used the same sample size as in the baseline to simulate mixture genotypes with 1000 bootstraps using the method of Anderson *et al.* (2008). Lastly, we used ONCOR to assign individuals coming from the feeding aggregation samples to the most likely population of origin (spawning), based on their genotypes.

Discriminant analysis of principal components (DAPC) (Jombart *et al.*, 2010) was also conducted using ADEGENET (Jombart, 2008; Jombart and Ahmed, 2011) implemented in R (R Development Core Team, 2009). Rather than considering global diversity (as a traditional PCA would), this multivariate approach uses synthetic variables to maximize differences between groups, while minimizing variation within groups (Jombart *et al.*, 2010). DAPC relies on data transformation using principal components analysis (PCA) as a first step before discriminant analysis (DA), which makes the variables that are submitted to DA perfectly uncorrelated (Jombart *et al.*, 2010). To avoid over-fitting the model, the α-score was determined in DAPC. The α-score is the difference between the observed discrimination and discrimination based on random groups and identifies the optimal number of principal components (PCs) to retain. DAPC analysis was carried out on the spawning populations only and then on spawning populations and feeding aggregation together.

Results

A total of 1231 fish were successfully genotyped for the 14 microsatellite loci (Table 1). The number of alleles per locus ranged from 8 (*Sscom62*) to 47 (*Sscom55*) (Table 2). No null alleles or scoring errors were identified. Departure from HWE was identified in two of the 160 exact tests, neither of which remained significant after FDR correction for multiple tests. No linkage disequilibrium was identified between the 14 loci, and no outlier loci were identified with either BayeScan or Lositan (Supplementary Figure S1). All loci were therefore used in all further analyses.

The observed level of genetic differentiation among each pair of spawning samples was relatively low (Table 3). The three samples from FRA were tested for pairwise genetic differentiation using the unbiased F_{ST} estimator (θ of Weir and Cockerham, 1984), to enable pooling of these samples for further analyses (Supplementary Table S1). Significant differences were detected between the NWA (CAN and USA) and NEA (FRA and IRE) samples, but no significant difference was observed within them (i.e. between CAN and USA and FRA and IRE). The genetic diversity of samples collected from feeding aggregations is presented in Supplementary Table S2. Samples collected from feeding aggregation were not significantly different from spawning samples collected in NEA but were different from those collected in NWA (Supplementary Table S3).

Bayesian cluster analyses using STRUCTURE software suggested that the most likely number of populations present in our spawning samples was $K = 2$ [$\ln(K) = -20\ 945.0 \pm 17$ *SD*;

Table 2. Genetic diversity of spawning Atlantic mackerel collected at four geographical locations.

Samples		CAN	USA	IRE	FRA
Locus	n_a	H_O (H_E)	H_O (H_E)	H_O (H_E)	H_O (H_E)
Sscrom04	27	0.703 (0.757)	0.701 (0.740)	0.803 (0.814)	0.789 (0.800)
Sscrom07	10	0.794 (0.796)	0.825 (0.764)	0.757 (0.783)	0.826 (0.800)
Sscrom08	16	**0.409 (0.463)**	0.480 (0.446)	0.596 (0.660)	0.667 (0.668)
Sscrom10	11	0.731 (0.744)	0.684 (0.723)	0.711 (0.698)	0.700 (0.712)
Sscrom25	29	0.732 (0.777)	0.714 (0.807)	0.888 (0.887)	0.873 (0.864)
Sscrom43	11	0.752 (0.718)	0.735 (0.754)	0.777 (0.764)	0.711 (0.740)
Sscrom52	13	0.703 (0.696)	0.694 (0.699)	0.681 (0.703)	0.770 (0.714)
Sscrom55	47	0.939 (0.938)	0.948 (0.934)	0.926 (0.932)	0.926 (0.931)
Sscrom57	11	0.685 (0.694)	0.633 (0.669)	0.707 (0.669)	0.667 (0.699)
Sscrom66	14	0.661 (0.677)	0.541 (0.590)	0.707 (0.678)	0.695 (0.669)
Sscrom50	35	0.915 (0.922)	0.918 (0.926)	0.952 (0.938)	0.868 (0.941)
Sscrom49	11	**0.497 (0.516)**	0.459 (0.480)	0.505 (0.509)	0.512 (0.518)
Sscrom48	17	0.848 (0.836)	0.840 (0.821)	0.786 (0.816)	0.788 (0.837)
Sscrom62	8	0.457 (0.493)	0.529 (0.498)	0.556 (0.606)	0.522 (0.598)

For each locus, the number of alleles (n_a) and expected heterozygosity (H_E) and observed heterozygosity (H_O) are shown. HWE tests that were significant are shown in bold. No tests were significant after correction for multiple tests.

Figure 2a and Table 4a] and clearly discriminated samples collected at the spawning grounds collected in NEA from those collected in NWA. Subsequent hierarchical analysis within these clusters did not show any further population structure (Table 4b and c).

ONCOR leave-one-out tests indicated that the individual's assignment to correct spawning population reached >80% for both NEA and NWA populations (see Table 5). The 100% fisheries simulation indicated that there is good assessment strength for NEA and NWA populations. For NWA the simulation showed that fish were assigned to this population on average 93.35% of the time (95% *CI* = 86.13–98.24), and for the NEA population the average was 97.29% (95% *CI* = 93.89–1.0). Individual assignment of feeding samples was unequivocal and indicated that the majority of the fish in the feeding aggregation was of NEA origin (Table 5). Individuals in the feeding samples were assigned at 0.95% to the NWA population and at 99.05% to the NEA population.

For the discriminant analysis of PCs, 40 PCs and three discriminant factors (DA eiginvalues) were retained (Supplementary Figure S2 and S3). Results were in agreement with other analyses, with two main groupings identified (Supplementary Figure S2 and S3): NWA and NEA. Greater difference was identified within the NWA samples than within the NEA samples (Figure 3). The inclusion of the feeding aggregations in the analyses gives a clear indication of the origin of these migrating fish, with both structure (Figure 2b) and DAPC (Figure 3a and b) clustering these samples with the NEA spawning samples.

Table 3. Pairwise F_{ST} (below diagonal) and *p*-values (above diagonal) between samples collected at spawning locations.

Samples name	CAN	USA	FRA	IRE
CAN	–	0.26	0.00	0.00
USA	0.00048	–	0.00	0.00
FRA	**0.01193**	**0.01348**	–	0.49
IRE	**0.01624**	**0.01793**	−0.00002	–

Significant values are shown in bold.

Discussion

Climate change has been recognized as one of the most important threats to biodiversity in the future, and at present, mounting evidence shows that a variety of species are already responding to these changes. In the ocean, marine fish face fewer constraints and barriers to movement than terrestrial species and many species undertake long migrations both at juvenile and adult stages. Consequently, modern range shifts towards the poles have been documented in marine fishes (Perry *et al.*, 2005; Hiddink and ter Hofstede, 2008; Last *et al.*, 2011). However, marine species and marine ecosystems still received less attention than terrestrial ecosystems, even though evidence suggests that the velocity of climate change and the associated changes in phenology will be more complex in the ocean than on land (Burrows *et al.*, 2011). The recent expansion of the Atlantic mackerel reflects this complexity, as both the spawning ranges and the annual feeding migrations have undergone expansions towards northern latitudes. The effects of this large expansion in the migration pattern of this species to the north have had ecological impacts (Óskarsson *et al.*, 2016) and caused socio-economic, fisheries, and political issues (Hannesson, 2013). This study assessed the level of genetic differentiation between and within the NEA and NWA mackerel spawning populations and assessed the potential origin of individuals composing the expanding feeding aggregations in the central north Atlantic (Greenland, Iceland, Faroes), which can assist the population-specific exploitation rates to be factored into fisheries management.

Divergence among spawning populations

The discrimination of spawning stocks and the consequent determination of their contributions to feeding aggregations are vital to enable population-specific exploitation rates to be taken into consideration in fisheries science and management (Kell *et al.*, 2009; Kerr *et al.*, 2010). The inference of spatial distributions and the exploitation rates of individual populations is particularly complex when fisheries occur on aggregations of fish of mixed origin, because some populations may then be exploited disproportionately over time and space (Bekkevold *et al.*, 2015). To assess the contributions of spawning stocks to feeding aggregations, the

Figure 2. Bayesian cluster analysis carried out in STRUCTURE using (a) only spawning populations and (b) the spawning and feeding aggregations for $K = 2$. Within each plot, each vertical bar represents an individual while colours indicate the different clusters detected. All individuals show admixture, but spawning individuals are clearly differentiated into northwestern (CAN and USA; predominantly red) and northeastern (FRA and IRE; predominantly green) Atlantic components. Individuals from the feeding aggregations (b) cluster with the northeastern spawning component (FRA and IRE).

Table 4. Hierarchical Bayesian cluster analysis carried out in STRUCTURE [*K* and associated mean and standard deviation (*SD*) for ln *P*(*K*)] using all spawning populations (a) and subsequent detected group analyses using eastern (b) and western (c) populations.

	ln *P*(*K*)		ln *P*(*K*)		ln *P*(*K*)	
	(a)		(b)		(c)	
K	Mean	*SD*	Mean	*SD*	Mean	*SD*
1	−21 198.0	10.5	**−20 101.4**	10.6	**−12 553.5**	10.1
2	**−20 945.0**	17.0	−20 135.6	18.4	−12 557.9	14.3
3	−20 961.9	18.2	−20 165.1	20.3	−12 675.5	21.0
4	−20 988.7	21.6	–	–	–	–

A total of five independent runs were performed for $K = 1$–4 with a 400 000 burn-in and 600 000 iterations. Bold values indicate the most likely number of *K* groups detected in our samples collection.

Table 5. Leave-one-out test and individual assignment tests for feeding samples performed in ONCOR.

Population	NEA	NWA
NEA	84.1%	15.9%
NWA	13.0%	87.0%
Feeding samples	99.05% (92.1–99.8)	0.95% (0.2–7.9)

Leave-one-out test for spawning samples showing percentage of individuals from each of the reference populations assign to populations. Grey shade shows correct assignment to population. Individual assignment test of feeding samples with 95% confidence interval is indicated in the last line of the table.

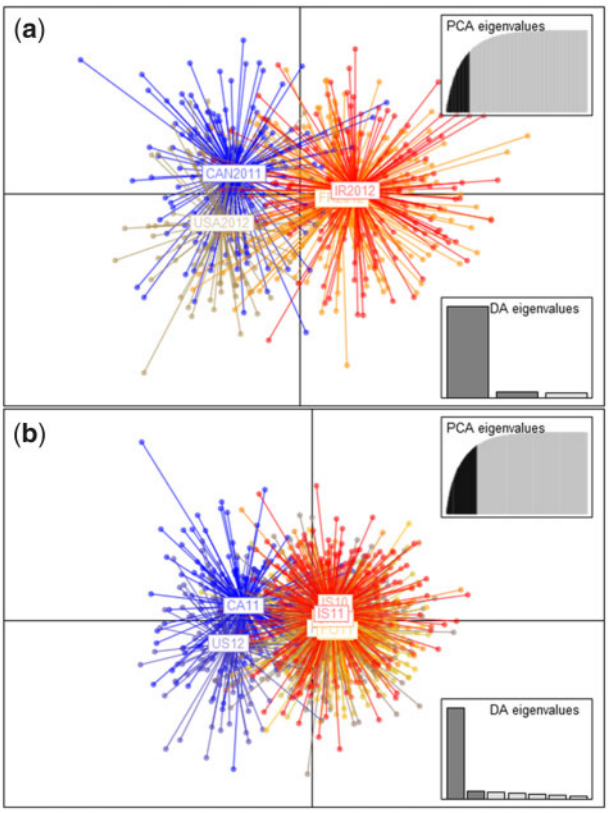

Figure 3. DAPC for (a) the spawning samples and (b) the spawning samples and all feeding aggregations combined. The number of PCs retained was determined by α-score in DAPC. Each circle represents an individual, with the centroid denoting the mean of the population.

potential genetic differences between the suspected spawning populations must be evaluated.

This study shows a clear genetic differentiation between the eastern and western Atlantic components, suggesting that contemporary gene flow might be limited across the Atlantic. This is supported by tagging studies carried out in the eastern Atlantic, where from ∼1 million fish tagged, none were recaptured in the western Atlantic (Iversen, 2002).

Within the NEA, no evidence was found for discrete spawning populations between the two main spawning locations: The Bay of Biscay and the Irish Shelf. No significant genetic differentiation was found with any of the methods used. This suggested that rather than there being natal philopatry to discrete spawning locations, there may be a more dynamic utilization of spawning grounds, perhaps including fish repeat spawning along the continental shelf, following favourable spawning conditions (for example sea surface temperatures). While there was no North Sea sample included in this analysis, the western and southern stocks in the NEA are the largest and so contribute more to the feeding aggregations, hence it is unlikely that the exclusion of this region will affect the identification of the source of the feeding aggregations. The results from this study supported previous suggestions by Jansen and Gislason (2013) that the mackerel spawning stock is a dynamic cline. This was in accordance with the lack of solid evidence for stock separation from previous analyses of tagging data, mtDNA, ectoparasite infections, otolith shape, and blood phenotypes (MacKenzie, 1990; Nesbø *et al.*, 2000; Uriarte *et al.*, 2001; Tenningen *et al.*, 2011; Jansen *et al.*, 2013). While not significant, greater differences were indicated within the western Atlantic than within the eastern Atlantic (see Figure 2). However, it was not possible to determine if these small differences were due to geographical barriers and reduced levels of gene flow, or cohort effects (samples were from 2 different years) at present. NWA mackerel stocks abundance has been decreasing in the last decade and also moved towards north-eastern areas as a possible response to an increase in temperatures (Overholtz *et al.*, 2011). These differences in stock abundance might explain why spawning samples from NWA were slightly more different from each other than their NEA counterparts.

Origin of individuals in feeding aggregations

Mixed stock analyses clearly indicated that all the samples collected at feeding aggregations located in the central north Atlantic originated from the NEA populations rather than from the western Atlantic ones. The observed results showing that all mackerel samples collected in the central north Atlantic feeding grounds were of NEA origin might be explained by the differences in stock abundance and dynamics between the NEA and NWA mackerel populations. While the NEA stock exhibited a large increase in population size, the NWA stock size was drastically declining, which might have facilitated the feeding expansion of the former but not the latter.

Fisheries management

The Atlantic mackerel is currently managed as three spawning components, with the southern and northern components in the

NWA and a single stock in the NEA. This study supports the current management, in that the NEA and NWA stocks were found to be genetically distinct. However, there is no support for smaller management units: while there are indications that there may be some difference within the NWA stock, this is not significant with this marker set. In addition, there is no support for the separate management of the southern and western NEA stocks as suggested by Nesbø *et al.* (2000). However, the lack of detection of genetic structure within the two main components only highlights the limits of the genetic markers used in this study, rather than asserting that none exists. The level of genetic differentiation identified here is comparable to that found in studies of herring using a similar number of microsatellite loci (Shaw *et al.*, 1999; Mariani *et al.*, 2005). However, more recent studies of herring utilizing optimized panels of SNPs have identified further biocomplexity and evidence of local adaptation (Limborg *et al.*, 2012; Bekkevold *et al.*, 2015, 2016) and these methods should be applied to the Atlantic mackerel to improve our ability to successfully manage the stocks. A recent study including samples from the Bay of Biscay and samples from CAN using SNPs already revealed that NWA and NEA mackerel populations were highly differentiated (Rodríguez-Ezpeleta *et al.*, 2016), thus supporting the results of the present study. In addition, the inclusion of further samples (e.g. North Sea) combined with a more powerful SNP marker set may identify further differences within the NEA.

Nevertheless, this study contributes significant important results for the management of this stock, which requires international cooperation for quota allocation: To date, none of the samples from the feeding aggregations from Greenland, Iceland, or the Faroe Islands show any evidence of originating from the NWA.

Data accessibility

The data used during the present study were deposited in the OSF open-access database and are available at: https://osf.io/cta85/?view_only=4ccbc1019b7c4ab28083079731f93d5e

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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