

Mixed-stock analysis of Atlantic herring (*Clupea harengus*): a tool for identifying management units and complex migration dynamics

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We developed and validated a mixed-stock analysis (MSA) method with 59 single-nucleotide polymorphisms selected from genome-wide data to assign individuals to populations in mixed-stock samples of Atlantic herring from the North and Baltic seas. We analysed 3734 herring from spawning locations and scientific catches of mixed feeding stocks to demonstrate a “one-fits-all” tool with unprecedented accuracy for monitoring spatio-temporal dynamics throughout a large geographical range with complex stock mixing. We re-analysed time-series data (2002–2021) and compared inferences about stock composition with estimates from morphological data. We show that contributions from the western Baltic spring-spawning stock complex, which is under management concern, have likely been overestimated. We also show that a genetically distinctive population of western Baltic autumn spawners, ascribed low fisheries importance, contributes non-negligible and potentially temporally increasing proportions to mixed-stock aggregations, calling for a re-evaluation of stock definitions. MSA data can be implemented in stock assessment and in a variety of applications, including marine ecosystem description, impact assessment of specific fleets, and stock-rebuilding plans.

Keywords: clupeid, genetic stock identification, genomics, management units, migration, mixed-stock analysis, population structure, SNP.

Introduction

Better-managed fisheries could simultaneously increase yields and decrease risks of overexploitation of ocean resources. Fishery management has recognized for more than a decade that for several managed stocks there is a mismatch between the biological units contributing to local ecosystems and their fishing opportunities and the management units used to regulate the fishery (Reiss *et al.*, 2009). Genomic data are increasingly used to support fisheries and ecosystem management (Bernatchez *et al.*, 2017), hereunder to develop genetic stock identification (GSI) and mixed-stock analysis (MSA) methodologies to assure sustainable management across the full scale from local populations to stock complexes (e.g. Puncner *et*

al., 2022; Hemmer-Hansen *et al.*, 2019; Quintela *et al.*, 2020; Beacham *et al.*, 2021; Bradbury *et al.*, 2021).

Atlantic herring *Clupea harengus* (L.) is a key component in marine food webs in the North Atlantic Ocean (Hjermann *et al.*, 2004) and the target of one of the world's largest fisheries (FAO, 2020). Herring is a schooling, commonly long-distance migrating fish with demographically discrete populations (sometimes referred to as “stocks”) that home to natal locations to spawn (Iles and Sinclair, 1982). Stock identification based on a suite of morphological traits (Clausen *et al.*, 2007; Gröhsler *et al.*, 2013; Berg *et al.*, 2020) and genetic markers (Bekkevold *et al.*, 2015; Kerr *et al.*, 2018; Kongsstovu *et al.*, 2022) has been developed for a subset of

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stocks, each method yielding various degrees of classification accuracy among stocks, management areas, and time periods (Clausen *et al.*, 2007; Berg *et al.*, 2020). Annual herring stock assessment, used to advise managers on sustainable exploitation rates, has until recently been based on either geography or meristic and morphological markers to split catches into biological stocks. These methods, however, have limited value for biological inference (ICES, 2017a, 2021). The advent of genomic characterization of herring populations spanning major spawning areas (Martinez-Barrio *et al.*, 2016; Lamichhane *et al.*, 2017; Pettersson *et al.*, 2019; Han *et al.*, 2020) constitutes a “game-changer” for monitoring stocks (Nielsen *et al.*, 2012). This is timely, given dwindling recruitment of several stocks (e.g. Payne *et al.*, 2013; Toresen *et al.*, 2019) and the need to develop stock-rebuilding plans (Trijoulet *et al.*, 2021).

As an acute example, managers are concerned about the decline in herring spawning in coastal areas spanning the transition zone between the North Sea and the Baltic Sea in the northeast Atlantic (ICES, 2021). These so-called western Baltic spring-spawning (WBSS) herring comprise genetically differentiated populations, believed to be locally adapted to spawning and larval environmental conditions (Gaggiotti *et al.*, 2009; Limborg *et al.*, 2012; Polte *et al.*, 2021). Decreasing recruitment rates of a spawning stock below the revised critical biomass reference point B_{lim} , with no probability of recovery in the short term, have since 2018 led the *International Council for the Exploration of the Seas* (ICES) to advise zero catches for WBSS (ICES, 2021). From age 1, the main spawning components of the WBSS perform long-distance feeding migrations from the western Baltic to the Kattegat and Skagerrak, and as older individuals into the North Sea (Bekkevold *et al.*, 2015 and references herein). Feeding forays are followed by overwintering and back-migration to natal areas for spawning in spring (February–May). During migration, WBSS herring mix with herring from populations straddling the North Sea, English Channel, and Norwegian Sea (e.g. Ruzzante *et al.*, 2006). WBSS herring are exploited in mixed-stock fisheries throughout the eastern North Sea, the Skagerrak–Kattegat, and the western Baltic Sea, where annual WBSS catches have decreased from an estimated 70–100000 to 20–25000 tons over the past two decades (ICES, 2021).

Accurate classifications of the origins of contributing stocks are a prerequisite for precise estimation of fisheries exploitation rates (Cadrin *et al.*, 2020; Kell *et al.*, 2009). We therefore took advantage of comprehensive new genomic data in herring populations spanning major parts of the species’ distribution to develop an MSA tool allowing accurate monitoring of stock distributions in time and space. We validated the accuracy of the method using samples of herring of known origin and analysed time series of samples collected in mixed-stock feeding areas characterized by mixing of several biological units with complex spatial-, temporal-, and life-stage specific distributions. This provided insights into the spatio-temporal dynamics of WBSS herring, as well as of the other genetically distinctive stocks co-occurring in the area. Specific aims of this study were to (1) develop a validated MSA method that accurately classifies individuals of major herring stocks in the eastern North Sea–Skagerrak–Kattegat; (2) assess the method’s applicability for stock identification of catches in neighbouring areas in the Baltic Sea and the Norwegian Sea; (3) evaluate correspondence between genomic and morphological marker-based classifications; and (4) gain a better un-

derstanding of the distributions of smaller stock components, for which there is scarce biological information.

Material and methods

Baseline and mixed-stock samples

A genetic baseline of populations potentially contributing to mixed-stock feeding aggregations was constructed from previous studies and from the analysis of new samples of fin tissue clips from ripe adults or, in two cases, small larvae collected on spawning locations (Table 1). Collections represented all major populations spawning in the area spanning the North Sea to the Baltic Sea (Figure 1, Supplementary Material S1) and included the main stock components WBSS, North Sea autumn-spawners, NSAS, and *Downs* winter-spawners, as well as stocks with smaller expected mixed-stock contributions: central Baltic spring-spawning herring, CBH, Baltic autumn-spawners, BAS, Norwegian spring-spawners, NSS, and North Atlantic autumn-spawners (Faroe Islands, FASH, and Greenland). We included multiple, geographically widespread collections per stock to encompass local sub-stock variation, where appropriate, amounting to 28 collections in total (Table 1). We analysed mixed-stock aggregations from management areas covering the Skagerrak–Kattegat and eastern North Sea, where WBSS herring are targeted by a mixed-stock fishery and where stock dynamics are monitored annually in the *herring acoustic survey* (HERAS). Main sampling effort was in 2019 and 2021, and replicated samples were available for a subset of locations from 2002 to 2018 (Table 2, Figure 2, Supplementary Material S2). To examine MSA’s suitability in neighbouring areas, we analysed four external collections: the Norwegian Sea (66.76°N 1.78°E), northern North Sea (61.94°N 1.94°E), both north of the focal area, and two from the western Baltic Sea (54.26°N 12.12°E, 54.89°N 13.88°E), southeast of the focal area. Sex was determined visually and winter otolith rings were recorded to estimate age, following standardized procedures (ICES, 2017b).

Comparing otolith and MSA classifications

For 624 of 852 HERAS 2019 samples, information was available about visual classification of hatching season using the otolith increment method of Clausen *et al.* (2007). Using this method, fish were classified as hatched in spring, autumn, or winter. In previous protocols for monitoring catches, stocks were separated by assuming that WBSS hatch in spring, NSAS hatch in autumn, and *Downs* hatch in winter. These data allowed for a direct comparison of stock classification with genetic and visual marker-based methods previously applied in stock assessment data.

Genotyping analyses

SNP markers were selected following methods detailed in Supplementary Material (S3). The panel (Supplementary Table S2) consisted of 59 SNPs spanning 20 chromosomes and associated with selective outlier regions from Han *et al.* (2020). The exception was one SNP in strong linkage disequilibrium with the sex determination gene on chromosome 8, where males are heterogametic and females homogametic (Rafati *et al.*, 2020). DNA was extracted from baseline ($N = 1316$) and mixed-stock ($N = 2418$) samples using E.Z.N.A. Tissue DNA kit (Omega Bio-Tek, Norcross, GA, USA) and a Chelex resin protocol (Walsh *et al.*, 1991), respectively. Samples were

Table 1. Atlantic herring spawning samples used as baseline for MSA.

No. in Figure	Collection (locality)	Lat.	Long.	No. of fish	Date of collection	Management unit	GSI stock/reporting group	Sub-stock	SD/MA
1	Bothnian Bay (Oulu) ^A	65.05	24.58	39	Jun. 2009	her.27.3031 (Gulf of Bothnia)	Central Baltic, CBH	CBNC (northern component)	31
2	Gulf of Finland ^A	60.40	26.70	40	May 2009	her.27.25–2932 (central Baltic)		CBNC	32
3	Gulf of Riga (Gulf of Pärnu) ^B	58.16	24.26	45	May 2016	her.27.28 (Gulf of Riga)		CBNC	28–1
4	Gulf of Riga (Saaremaa) ^B	58.02	23.50	36	Sep. 2016	herriga	Baltic autumn spawning, BAS	BAS-East	28–1
5	Curonian Lagoon (Smiltynė) ^{this study}	55.60	21.13	48	Apr.–May 2019	her.27.25–2932 (central Baltic)	CBH	CBSC (southern component)	26
6	Vistula Lagoon (Gdansk) ^A	54.37	19.67	21	Apr. 2009			CBSC	26
7	Baltic proper southwest (Hano) ^A	55.57	15.18	18	Apr. 2002			CBSC	25
8	Bornholm Basin (Christiansø) ^{C, this study}	55.26	15.33	36 §	Oct. 2016	her.27.25–2932 (central Baltic)#	BAS	BAS-West	25
9	Western Baltic Sea (Greifswald Bay, Rügen) ^{this study}	54.21	13.62	83 §	Nov. 2018, Feb. 2019, Mar. 2020			BAS-West	24
9	Western Baltic Sea (Greifswald Bay, Rügen) ^{A, 1, this study}	54.21	13.62	190	Apr. 2009, 2019, 2020, 2021	her.27.20–24 (western Baltic)	Western Baltic spring spawning, WBSS	WBSS-Rügen	24
10	Western Baltic Sea (Warnow estuary) ^{this study}	54.13	12.09	22	Apr. 2021			WBSS-Rügen	24
11	Western Baltic Sea (Lübeck Bight/Trave) ^{this study}	53.92	10.85	29	Apr. 2019			WBSS-W. Baltic	22
12	Western Baltic Sea (Kiel Bight) ^D	54.36	10.16	22	Apr. 2010			WBSS-W. Baltic	22
13	Western Baltic Sea (Schlei) ^C	54.60	09.76	21	Oct. 2012			WBSS-W. Baltic	22

Table 1. Continued

No. in Figure	Collection (locality)	Lat.	Long.	No. of fish	Date of collection	Management unit	GSI stock/reporting group	Sub-stock	SD/MA
13	Western Baltic Sea (Schleg) ^{C, this study}	54.60	09.76	39	Apr. 2010, 2019			WBSS-W. Baltic	22
14	Kattegat (Isefjord) ^{A, this study}	55.73	11.37	49	May 2009, Apr. 2021			WBSS-IDW (Inner Danish Waters)	21/3a
15	Skagerrak East (Öckerö) ^A	57.60	11.40	39	Apr. 2009	her.27.20–24 (western Baltic)#		WBSS-Skagerrak	20/3a
16	Skagerrak West (Höväg) ^D	58.15	08.27	22	Feb. 2009	her.27.20–24 (western Baltic)#		WBSS-Skagerrak	20/3a
17	North Sea/Kattegat (Limfjord) ^{A, this study}	56.96	09.14	68	Apr. 2009, 2021	her.27.3a47d (North Sea)#		WBSS-IDW	4L
18	North Sea (Ringkøbing Fjord) ^{A, this study}	55.97	08.24	59	Apr. 2009, 2021	her.27.3a47d (North Sea)#		WBSS-IDW	4b
19	North Sea (Wadden Sea) ^{A, this study}	55.44	08.54	51	Apr. 2021	her.27.3a47d (North Sea)#		WBSS-IDW	4b
20	North Sea (Askoy) ^{A, this study}	60.46	05.00	68	Mar. 2018, 2019	her.27.1–24a514a (Norwegian)	Norwegian spring spawning, NSS	N.A.	4a(E)
21	North Sea (Karmoy) ^A	59.25	05.17	30	Feb. 2003			N.A.	4a(E)
22	North Sea (Banks) ^{A, this study}	54.20	03.30	56	Aug. 2009, 2018	her.27.3a47d (North Sea)	North Sea autumn spawning, NSAS	N.A.	4b
23	North Sea (Shetland and Orkney) ^{C, this study}	59.21	–02.38	36	Oct. 2016			N.A.	4a(W)
24	North Atlantic (Faroe Islands) ^D	61.02	–06.38	33	Nov. 2009	her.27.3a47d (North Sea)#	North Atlantic autumn spawning	FASH	5b1
25	Southern Bight (Downs) ^{A, this study}	51.63	01.68	76	Dec. 2009, 2020	her.27.3a47d (North Sea)#	Downs winter spawning	N.A.	4c
NA	Labrador Sea (Nanortalik, Greenland) ^{C, this study}	60.79	–47.16	40	Aug. 2015	NAFO area 1E	North Atlantic autumn spawning	Greenland	N.A.

Studies reporting collection details and previous genetic analyses are shown in raised capital letters: respectively, (A) Limborg et al. (2012); (B) Bekkevold et al. (2016); (C) Han et al. (2020); and (D) Bekkevold et al. (2015). SD and MA indicate, respectively, Baltic Sea subdivision and North Sea management area, as used for herring stock assessment (ICES, 2021). Two collections marked § represent larval samples, and the remainder represent mature adults. The grouping of samples by management unit is shown, and instances where there is a mismatch between the biological stock and the management unit are indicated in bold lettering and by a #. Spring spawning herring from the Gulf of Riga constitute a separate management unit but are grouped here into the CBH stock. Details are given in Supplementary Material S1.

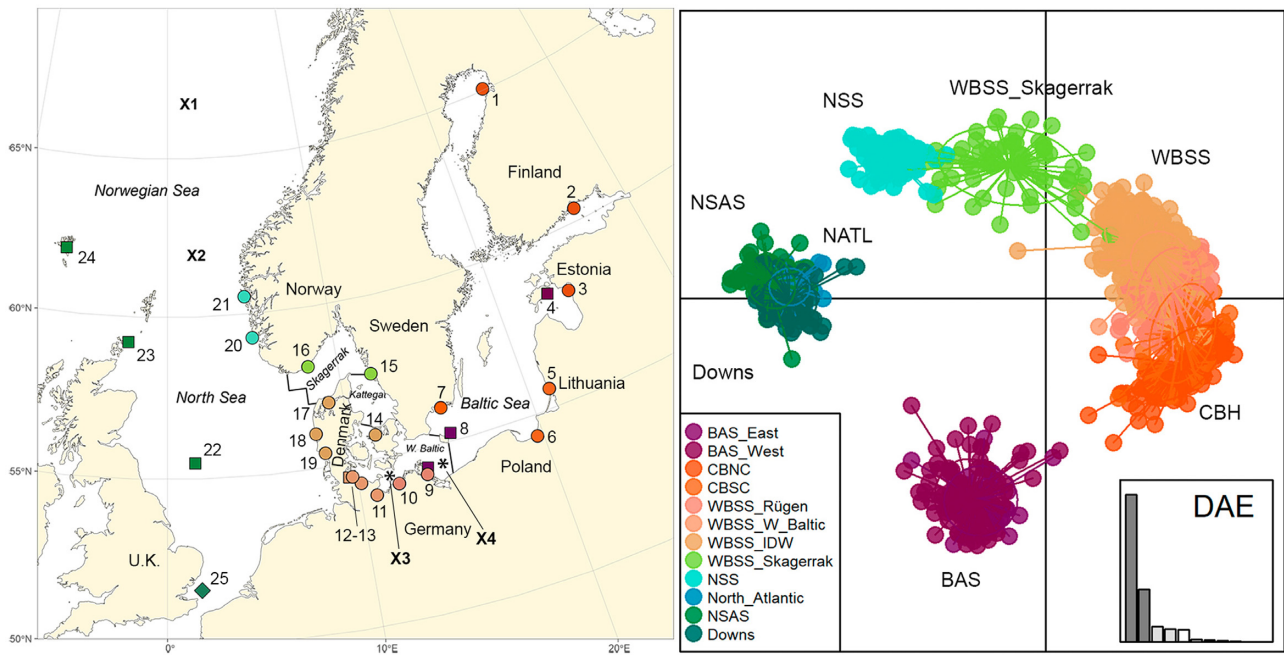


Figure 1. Spawning collections of *C. harengus* used as baseline in MSA of mixed stocks. Symbol colours identify genetic relationships among collections determined using DAPC analysis, where the first three DAs are reflected in colour grading along the red, green, and blue spectra, respectively (i.e. genetically more similar collections show more similar colour shades and vice versa). (A) Collection locations. Numbers refer to Table 1 and symbols indicate spawning season: circles = spring, squares = autumn, and diamond = winter. Locations are indicated for external collections of mixed-stock feeding samples in the Norwegian Sea (X1), the northern North Sea (X2), and the western Baltic Sea (X3–X4). (B) DAPC plot for DA 1–2, where points are individual fish and colours indicate sub-stock specific genetic differentiation. DA eigenvalues (DAE) are shown in inset.

Table 2. Atlantic herring mixed-stock samples in MSA shown by scientific cruise, year, month, and management area.

Cruise	Year	Month	Management area (no. of fish)	Total no. of fish by year
HERAS	2002	June–July	4a (45), 20 (133)	178
	2003		4a (45), 20 (178)	223
	2008	4a (40)	40	
	2018	20 (92)	92	
	2019	4a (37), 4b (200), 20 (356), 21 (259)	852	
	2021	4a (164), 4b (293), 20 (338), 21 (73)	868	
IESNS	2021	May	EX1: 4a (30), EX2: 2a (50)	80
GerAS	2009	October	EX3: 24 (37)	37
Research vessel <i>Solea</i> sample	2012	May	EX4: 24 (48)	48

2a: Norwegian Sea; 4a, b: eastern North Sea; 20: Skagerrak; 21: Kattegat; 24: western Baltic Sea.

analysed using 96.96 Dynamic Arrays for the Fluidigm IFC thermal cyclers and the BioMark™ HD System. Genotypes were determined using the BioMark Genotyping Analysis software (Fluidigm, San Francisco, CA, USA). Fish were excluded if <85% of the loci were genotyped.

Population clustering analyses

Segregation of genotypes according to Hardy–Weinberg expectations was explored by locus and collection for baseline samples, and pairwise F_{ST} s were estimated for the 28 baseline collections using the R-package *genetics*. The most likely number of population clusters was estimated using the Discriminant Analysis of Principal Components, DAPC (Jombart *et al.*, 2011) implemented in the *adegenet* R-package (Jombart *et al.*, 2010), as described in Supplementary Material (S4). Genetic relationships among baseline samples were visualized using *adegenet*'s *colorplot* function.

MSA baseline

We grouped baseline data into seven stocks (in MSA, sometimes called “reporting groups”) based on genetic clustering and predefined stock units (Table 1). Genetically distinctive populations at smaller geographical scales (sometimes called “conservation units”) were also identified and grouped into 13 geographically.

Individual assignment accuracy (cross-validation simulation and leave-one-out, LOO, analysis) and mixed-stock composition (summing individual assignments within collections) were estimated with the R-package *rubias* (Moran and Andersson, 2018) as detailed in Supplementary Material (S5–6). We also compared assignment performance between stocks in a pairwise manner, where stock splitting was limited to two locally mixing populations and used density plots of Rannala and Mountain's (1997) genotype (log) likelihood ratios (Supplementary Material S5) to visualize assignment probabilities between stocks.

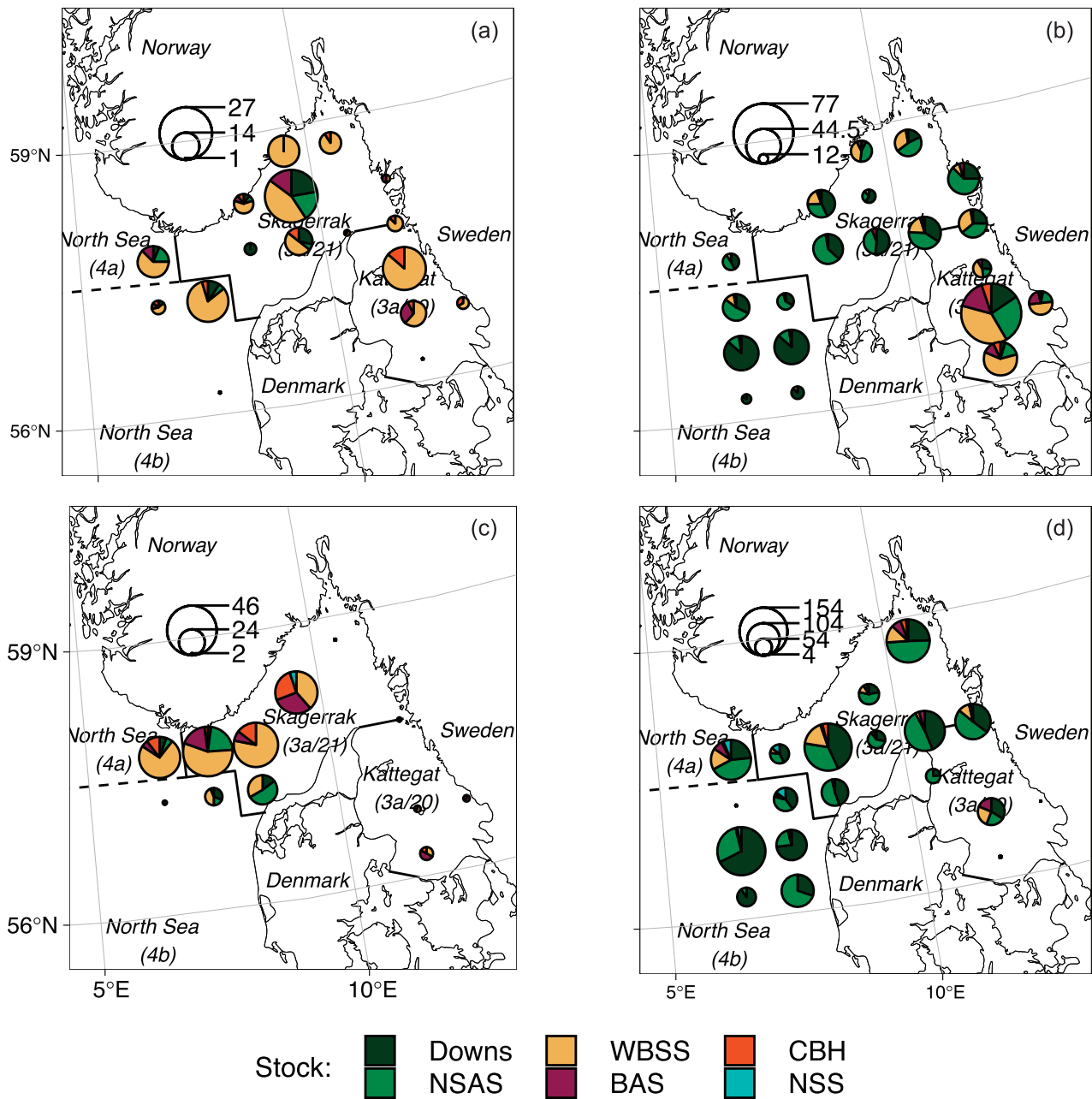


Figure 2. MSA of Atlantic herring from HERAS samples of (A and C) adults (>2 winters), and (B and D) juveniles (<3 winters) in 2019 and 2021, respectively. Pie colours show stocks and pie sizes are scaled to reflect sample sizes, as indicated in legends inside plots.

Results

Baseline collections

Baseline samples were genotyped for 97.0% SNPs on average with individual call rates > 85%. Re-typing of 96 fish showed high (99.86%) genotyping consistency. Pairwise F_{st} between collections ranged from 0 to 0.75, with global $F_{st} = 0.48$ (Supplementary Table S3). Most pairwise comparisons between collections showed statistically significant differentiation at $p < 0.05$, corrected using false discovery rate. Sixteen tests of pairwise sample differentiation were not significant, all between collections within (sub-)stock. Statistically significant F_{st} s included comparisons between *BAS* in the eastern (Gulf of Riga) vs. the western (Greifswald Bay; $F_{st} = 0.030$) and central

(Bornholm; $F_{st} = 0.025$) Baltic Sea, respectively, where the latter two conversely showed small, statistically non-significant F_{st} (0.005). *BAS* collections were distinct from *WBSS* populations (pairwise $F_{st} > 0.39$), as well as from autumn-spawning populations in the North Sea ($F_{st} > 0.45$). Two collections of *WBSS* representing populations spawning in Norwegian and Swedish Skagerrak coastal waters showed strong divergence from other *WBSS* ($F_{st} > 0.17$), and from spring-spawners from the Norwegian continental shelf, *NSS* ($F_{st} > 0.21$).

In DAPC, 40 principal components, PC, and 4 discriminant axes, DA, returned the best fit, resulting in baselines generally grouping by geography, with maximal differentiation (DA1, explaining 60% variation) between spring-spawning populations in the Baltic–western Baltic Sea vs. autumn-spawning

Table 3. Cross-validation mean squared error (MSE) and LOO self-assignment to stock and sub-stock of Atlantic herring.

Stock	% correct stock LOO	Stock most frequently misassigned to	Stock cross-validation MSE	% correct GSI to sub-stock LOO	Sub-stock cross-validation MSE (average)
1. WBSS	98.76	CBH	1.38×10^{-4}	WBSS-Skagerrak 95.08; WBSS-IDW 83.62; WBSS-W. Baltic 79.76; WBSS-Rügen 77.05	8.59×10^{-4}
2. CBH	98.10	WBSS	7.33×10^{-5}	CBNC 88.03; CBSC 76.47	9.81×10^{-4}
3. BAS	100.00	-	9.30×10^{-6}	BAS-W 81.08; BAS-E 75.00	2.22×10^{-3}
4. NSS	98.53	WBSS	7.00×10^{-5}	-	3.99×10^{-5}
5. NSAS	100.00	-	1.87×10^{-5}	-	1.70×10^{-5}
6. Downs	100.00	-	2.02×10^{-5}	-	1.70×10^{-5}
7. North Atlantic	98.63	NSAS	9.88×10^{-6}	FASH 78.79; Greenland 77.00	5.84×10^{-3}
All	98.88	-	4.85×10^{-5}	86.37	9.37×10^{-4}

populations the North Sea–Atlantic Ocean, and, second, by geography, respectively, the North Sea vs. the Baltic Sea and basins (DA2, explaining 25% variation; Figure 1b). DA3 (explaining 9% variation) separated CBH from WBSS, BAS-west from BAS-east, and resolved stock differences among Downs, NSAS, and North Atlantic (Supplementary Material S4). DA4 (explaining 6% variation) mainly separated collections along a north–south axis. Delineation of four WBSS sub-stocks was supported by correspondence analysis with largest separation between northern WBSS-Skagerrak and southern WBSS-W. Baltic (Supplementary Material S4). These results thus supported the MSA baselines (Table 1).

MSA accuracy

Both cross-validation simulation study and LOO analysis showed that MSA had high accuracy (Table 3, Supplementary Material S5). There was slight variation in accuracy among individual stocks but overall 99% of all baseline fish assigned to their stock of collection. Misassigned fish always assigned to geographically neighbouring stocks. Estimates to sub-stock exhibited slightly larger MSE and lower overall accuracy (86%) than estimates to stock. Exceptions included WBSS-Skagerrak herring, which were distinctive from other WBSS and showed high sub-stock MSA accuracy (>95%). Northern CBH (CBNC) could also be statistically split from southern CBH, CBSC, with high sub-stock accuracy > 88% (Table 3). The distributions of assignment likelihood ratios overlapped little when assignment was performed in a pairwise stock manner, supporting that MSA was unambiguous for the majority of baseline stocks (Supplementary Material S5).

MSA in mixed catches

The 2418 mixed-stock fish were genotyped for 97.1% SNPs on average. Five fish were discarded due to low genotyping success (<85%). The remaining 2413 fish were assigned to a stock (average posterior probability = 0.99; 95% fish assigned at high probability; $p > 0.95$) and to a sub-stock (average posterior probability = 0.96; 83% assigned at high probability).

Composition of HERAS catches 2019–2021

In 2019–2021, WBSS were abundant in feeding aggregations in the North Sea–Skagerrak–Kattegat, making up on

average 25% of sampled fish (range 0–64% per haul). Downs/NSAS made up 64% and NSS/BAS/CBH combined made up 11%. WBSS contributions were smallest in southern North Sea, estimated at 15 and 4% in 2019 and 2021, respectively. When data were partitioned by life stage (juvenile/adult), there was a clear separation in stock contributions in both years (Figure 2). Thus, NSAS/Downs were largely juveniles and WBSS, BAS, and CBH were largely adults. BAS herring were encountered in most areas (purple pies in Figure 2), contributing <10% to most hauls and being most frequent in the Kattegat, which is closest to natal origins in the western Baltic area. Contributions from CBH were overall small, with a north–south trend from the North Sea (1%) to the Skagerrak (4%) and the Kattegat (6%). NSS herring were rare and not encountered in HERAS collections prior to 2021. In 2021, they made up 4% in North Sea collections, all of which were juveniles.

Time-series data

Temporal samples in the North Sea and Skagerrak showed increasing contributions from BAS and decreasing contributions from WBSS between 2002/2003 and 2019/2021 (Figure 3). Although MSA to sub-stock was more prone to erroneous assignment, several results emerged. For instance, across 2002–2021 the WBSS-Rügen sub-stock made up 41%, and was thus the most abundant WBSS sub-stock in the dataset. The WBSS-W. Baltic sub-stock was the second largest contributor at 32%, whereas WBSS-Skagerrak (14%) and WBSS-IDW (12%) contributed least overall. Between 2002/2003 and 2019/2021, contributions of the WBSS-Rügen sub-stock to North Sea collections decreased 53%, and 20% to Skagerrak collections.

MSA to sub-stock showed that all 117 BAS in HERAS data belonged to the western sub-stock. The only eastern sub-stock identified were three fish collected in the western Baltic Sea (X3 in Figure 3). For CBH, MSA estimates to sub-stock showed that the majority (72 of 74 fish; 93%) belonged to the southern sub-stock CBSC.

External collections

The northernmost collections X1–X2, showed the largest proportions of the local NSS stock (Figure 3). As the only two

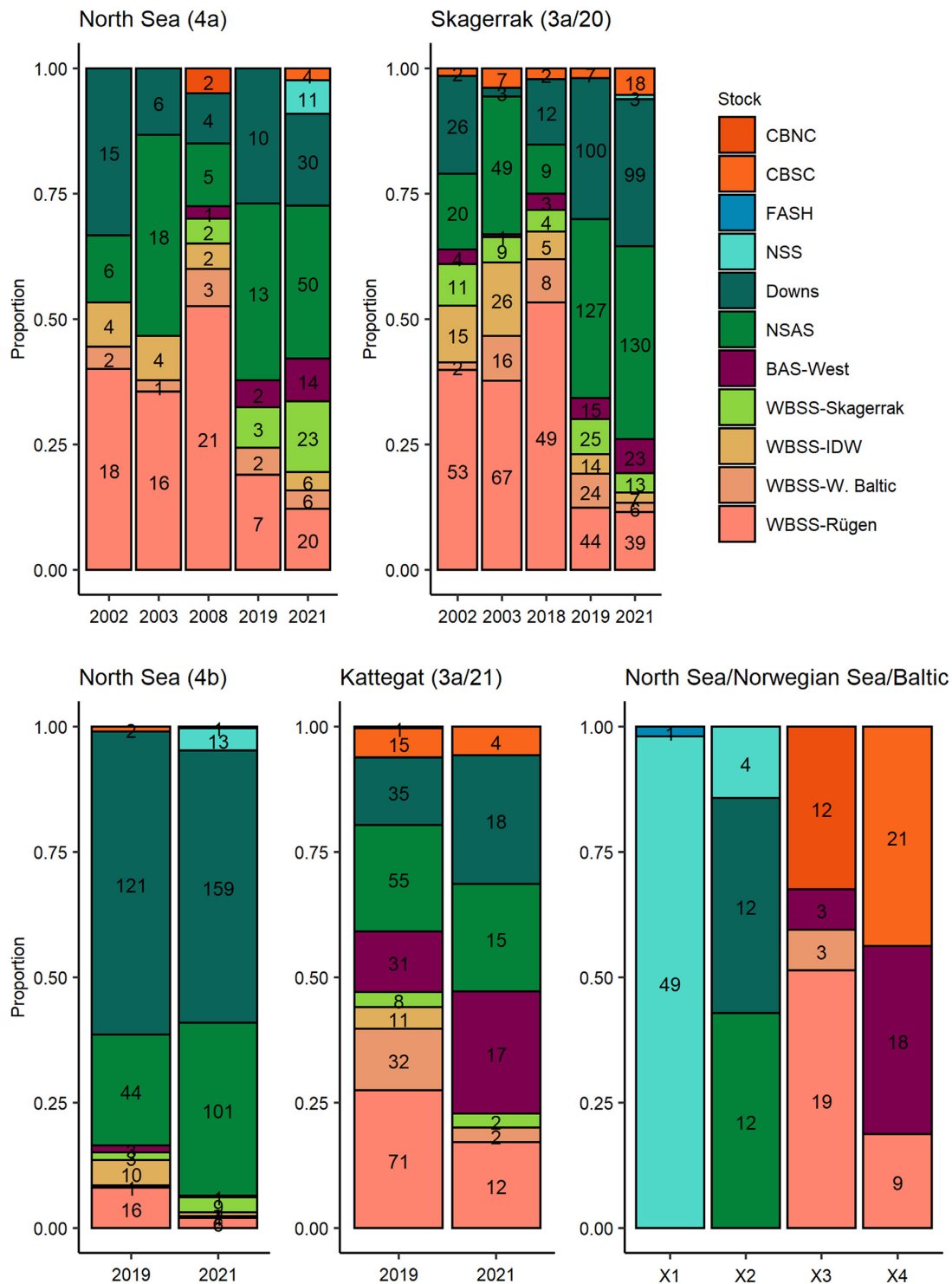


Figure 3. Atlantic herring MSA to sub-stock for mixed feeding collections shown by management area and year. Numbers inside bars show numbers of fish. Individual (sub)stocks are identified by colours reflecting DAPC clustering as in Figure 1.

collections in the analysis, none contained WBSS. A single representative of the North Atlantic stock (assigned to *FASH*) was caught at X1, as expected for a North Atlantic distribution. The two collections from the western Baltic Sea (X3–X4) included only *CBH* and *WBSS* fish; the latter represented by the local sub-stocks *WBSS-Rügen* (82%) and *WBSS-W. Baltic* (18%) (Figure 3).

MSA estimates and otolith-based classification

Stock classifications with genetic and otolith data showed correspondence in that most fish (228 of 234; 97%) originating from the spring-spawning stocks (*WBSS*, *NSS*, *CBH*) also had spring-spawned otoliths (Table 4). Conversely, 166 of 210 (89%) fish originating from autumn-spawning stocks (*NSAS*, *BAS*) had autumn otoliths, and 67% fish from

Table 4. Stock classification of 624 Atlantic herring based on visual assessment of otolith hatch month (down) compared to genetic classification (across).

Otolith classification (inferred stock)	Genetic classification					N
	<i>Downs</i>	<i>NSAS</i>	<i>BAS</i>	<i>CBH</i>	<i>WBSS</i>	
4 (<i>WBSS</i>)	41	6	10	23	<u>205</u> (72%)	285
9 (<i>NSAS</i>)	18	<u>144</u> (77%)	22	0	3	187
12 (<i>Downs</i>)	<u>121</u> (80%)	21	7	0	3	152

Correspondence between methods (underlined cells) is shown in parentheses. According to genetic results, 25% of individuals were erroneously classified with the otolith-based method.

winter-spawning *Downs* had winter otoliths. The otolith-based approach for splitting mixed-stock samples into three stocks (*NSAS*, *Downs*, *WBSS*) failed to assign 25% of fish to their correct genetic stock. In the total dataset classified using both marker types, the proportion *WBSS* was estimated at 33% (MSA) and 47% (otoliths), resulting in a ~27% over-estimation of the *WBSS* contribution with otolith data in this particular sample.

Genetic and visual sex determination

Genetic and visual sex determination largely corresponded. Thus, 90% visually determined males had heterogamic genotypes, and 87% visually determined females had homogamic genotypes. This minor discrepancy is likely explained by the sex-linked SNP not being in complete LD with sex-determining genes (Rafati *et al.*, 2020) and visual classification error.

Discussion

A robust stock separation tool

We applied a stock separation tool showing exceptionally accurate individual assignment across a considerable part of the distributional range of Atlantic herring. We sampled extensively from spatially widespread spawning aggregations and mixed-origin feeding aggregations and demonstrated that the approach can monitor complex mixed-stock catches throughout the transition area connecting the North and Baltic seas.

Spatial genetic structuring of baseline collections agreed with previous analyses of herring population structure based on other markers (Table 1). For the main focal stock, *WBSS*, our extensive spatial coverage of spawning grounds shows that genetic sub-stock differences follow a clinal pattern in the transition area between the saline North Sea and the brackish Baltic Sea that may be imposed by local adaptation along the environmental gradient (Gaggiotti *et al.*, 2009; Limborg *et al.*, 2012; Han *et al.*, 2020). Spatially explicit temporal replicates in all cases grouped together by stock and sub-stock, demonstrating that the marker panel was robust for MSA at decadal time scales, thus agreeing with observations in other marine species (Jorde *et al.*, 2018; Pinsky *et al.*, 2021) and in north-west Atlantic herring populations (Kerr *et al.*, 2018).

Biological stocks and mismatch with management units

Atlantic herring represents a model for marine organisms displaying long-range migrations and complex mixing of stock

components on shared feeding grounds, while simultaneously maintaining distinct populations that in some cases may consist of divergent ecotypes. In other aspects, Atlantic herring populations are more consistent with a meta-population concept (McQuinn, 1997). Spawning-site samples collected for the current analysis improved the understanding of the distributions of sub-stocks by showing that herring spawning in estuaries bordering the eastern North Sea (collections #17–19 in Table 1) are part of the *WBSS* stock complex (sub-stock *WBSS-IDW*). They are thus demographically unconnected with other stocks spawning in the North Sea area (*NSAS*, *Downs*, *NSS*). This mismatch between biological and management units is currently unrecognized in Danish national fisheries management (Bekendtgørelse om regulering af fiskeriet, 2020).

We found strong genetic divergence between herring spawning along the Norwegian–Swedish Skagerrak coast and all other *WBSS* herring, as also demonstrated by whole-genome analyses (Han *et al.*, 2020). We included this Skagerrak stock in the *WBSS* stock complex for the comparison with the current stock classification, but levels of genetic divergence from other *WBSS* and from *NSS* justify a separate biological unit for management. It is assumed that the commercial fishery in the North Sea–Skagerrak–Kattegat catches these local coastal components to a limited extent; hence, the stock is not formally assessed. Our results support a limited contribution of coastal Skagerrak herring to mixed stocks in the focal area. However, time-series analysis indicates a recent increase in this sub-stock's contribution to catches that imply the need to monitor this stock within an assessment framework.

Our study provided novel information about the genetically unique *BAS* spawning in the western Baltic Sea and inner Danish waters. Local contingents of autumn-spawning herring using different spawning substrates and depth preferences have long been acknowledged (Weber, 1971) but were not expected to contribute significantly to aggregations in other basins. Shifting dynamics in the relative strength of locally sympatric spring- and autumn-spawning stocks occurs in the west and east Atlantic and may respond to changes in fisheries exploitation and to climate-induced changes that alter the relative fitnesses of the two ecotypes (Melvin *et al.*, 2009; Mackenzie and Ojaveer, 2018). Importantly, our study shows that *BAS* from the western Baltic Sea migrate out of natal areas and represent a non-negligible and potentially increasing component in Kattegat–Skagerrak–North Sea mixed stocks. This calls for redefining the biological units considered in herring stock assessments in these areas, including the *BAS* as a separate biological unit. *BAS* in the Baltic Sea, here represented by herring from the Gulf of Riga, were not identified in collections outside the Baltic Sea, indicating that they feed mainly in natal gulf areas.

Finally, MSA proved robust for distinguishing between the winter-spawning *Downs* and the autumn-spawning *NSAS*, which are currently assessed as a single stock of North Sea herring. These two stocks have long been considered to show separate population demographics (Iles and Sinclair, 1982), but stock separation has until now depended on the analysis of morphological variation of larval phenology and otolith growth patterns. The latter was here shown to have a large error rate. As predicted for other small pelagics (Lima *et al.*, 2022), it can be hypothesized that (current) southern herring populations are more adapted to warmer temperature regimes than are northern populations (Lyashevskaya *et al.*, 2020).

Alternatively, southern populations may be more at risk from environmental changes because they may have a narrower thermal optimum (Payne *et al.*, 2021). Either way, our MSA method is expected to be a powerful tool for monitoring temporal dynamics in these stocks. The method may also prove useful for tracing shifts in specific genetic markers associated with functional variants underlying adaptation to climate variability (also see Pinsky *et al.*, 2021).

Complex stock mixing resolved with MSA

Our goal was to demonstrate the applicability of MSA in a management area characterized by complex stock mixing dynamics in variations in numbers and relative importance of the biological stock units on feeding grounds. We conclude that the accuracy and resolution offered by genetic markers can improve both the identification of stock units for a better representation of population diversity and the identification of spatial boundaries that better capture the spatio-temporal stock dynamics. Our results pave the way for estimating more solid biological reference points, the main objective in stock assessment for fisheries regulation, and for monitoring sub-stock dynamics to support better stock-rebuilding plans, as needed for WBSS herring (Trijoulet *et al.*, 2021). An important implication of our study is that accurate MSA data can be used to alleviate a need for predefined assumptions about where and when stocks migrate, as applied in current management and enforcement. For instance, it is currently assumed in stock assessment that only WBSS and NSAS were caught in the Kattegat, but we estimated that 32% (2019) and 48% (2021) of collected fish were from other stocks.

Our analyses yield improved insights into distributions of specific sub-stock units. Assignment to sub-stock was often associated with a larger error rate than to stock level, as is common in MSA estimation (e.g. Beacham *et al.*, 2021). A self-assignment accuracy >80% is considered sufficient for MSA estimates to be robust in a management context (Beacham *et al.*, 2021). Here, this was the case for all stocks and for the majority of the sub-stocks, but excluded two sub-stocks WBSS-Rügen and WBSS-W. Baltic, which nonetheless showed accuracies close to 80% (respectively, 77.0% and 79.8%). Although our approach provides information at the sub-stock level, these results should be interpreted cautiously at present. Further exploration of additional SNP data (Han *et al.*, 2020) may provide increased statistical resolution for monitoring dynamics of specific sub-stocks. With this caveat, results indicated different quantitative and spatial distributions of sub-stocks. We corroborated that WBSS-Rügen is ubiquitous and the main WBSS sub-stock in most feeding collections. Conversely, the assumption (Hoffman, 1996) that herring spawning in Danish sounds and estuaries (WBSS-IDW) mainly feed in the Kattegat was not supported, as this sub-stock was consistently encountered also in collections from the North Sea and Skagerrak. The WBSS-W. Baltic sub-stock was likewise feeding in most examined areas but was most prevalent in the Kattegat-Skagerrak. Longer time series will indicate whether de-coupled migratory behavior is a driver of reproductive isolation among WBSS sub-stocks. WBSS herring rely on inshore transitional waters for spawning and larval development (e.g. Polte *et al.*, 2021). The environmental variables determining reproductive success thus differ from other stocks recruiting from coastal shelf areas and may further differ among WBSS sub-stocks. If demographics and feeding distributions

are more or less de-coupled among these sub-stocks, this adds an extra layer of complexity to stock prediction that is not incorporated in current assessment models. We did not evaluate temporal changes in sub-stock size but identified trends consistent with a stock complex under harvest pressure, as also indicated by general stock assessment trends (ICES, 2021).

Spring spawners in the central Baltic Sea and associated basins (CBH) were identified with high accuracy with MSA. CBH are expected to feed mainly within the Baltic Sea but may emigrate out of the Baltic Sea, via the Skagerrak-Kattegat to the North Sea to feed (Gröhsler *et al.*, 2013; ICES, 2021). We corroborated the presence of (small numbers of) CBH throughout the Kattegat-Skagerrak-North Sea. Data supported the notion (ICES, 2018) that mainly the southern component (CBSC) moves out of the Baltic Sea to feed, while the northern component (CBNC), which grows more slowly (Gröhsler *et al.*, 2013), was rarely encountered outside the Baltic Sea.

Biological inference about fish stocks is safeguarded by an understanding of population distributions at local to ocean-wide scales. Our study adds one of the world's most economically important marine fishes to the list of organisms for which a robust MSA is available across major parts of the species' distribution in the northeast Atlantic, in areas characterized by complex variations in stock mixing in space and time. We envisage that coupled with stock modelling approaches that fully integrate MSA results (including associated error rates), there is potential to improve both the accuracy of stock assessment and the quality of management actions, and to alleviate concerns associated with the mismatch between biological stocks and geographically defined management units (Reiss *et al.*, 2009). Genetic classification has also recently been implemented for assessment of herring stocks west of Ireland and Britain (Farrell *et al.*, 2022). Our approach is validated and fully transferrable across users through a publicly available data repository, and has been implemented in routine scientific monitoring of mixed-stock catches in management areas Kattegat-Skagerrak and partly in the North Sea under the European Union *Common Fisheries Policy* data collection framework.

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Supplementary material

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

Supplementary file: Details on samples, SNP selection, and MSA methods.

Supplementary Table S1: Mixed-stock samples with MSA results.

Supplementary Table S2: SNP loci.

Supplementary Table S3: Pairwise F_{st} matrix and p -values for tests of deviation from Hardy-Weinberg proportions.

Conflict of interest statement

The authors declare no conflicts of interest.

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Data availability statement

The data underlying this article are available as online Supplementary Material and SNP genotypes are found in the DTU Data repository at <https://data.dtu.dk/10.11586/DTU.21756236>.

Author contributions

D.B.: conceptualization; A.F., L.A., D.B., P.P., and H.M.: funding acquisition; D.B., P.P., T.G., F.B., J.F., B.H., E.D.F., H.O., T.J., and H.M.: sampling and data collection; D.B., E.D.F., J.H.-H., M.P., and A.F.-P.: molecular data generation and analysis support; D.B., C.M.A., V.B., H.M., and V.T.: data analysis and support; D.B., J.H.-H., and A.F.-P.: data analysis and visualization; and all authors: writing, review and editing.

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