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Stock structure of Atlantic herring *Clupea harengus* in the Norwegian Sea and adjacent waters

Christophe Pampoulie[1,*], Aril Slotte[2], Guðmundur J. Óskarsson[1], Sarah J. Helyar[3], Ásbjörn Jónsson[3], Guðbjörg Ólafsdóttir[3], Sigurlaug Skírnisdóttir[3], Lísa Anne Libungan[4], Jan Arge Jacobsen[5], Hóraldur Joensen[6], Henrik Hauch Nielsen[7], Sindri Karl Sigurðsson[8], Anna Kristin Daníelsdóttir[3]

[1]Marine Research Institute, Skúlagata 4, 101 Reykjavík, Iceland
[2]Institute of Marine Research, Bergen, Norway
[3]Matís Ltd., Vinlandleið 12, 113 Reykjavík, Iceland
[4]University of Iceland, Faculty of Life and Environmental Sciences, Askja, Sturlugata 7, 101 Reykjavík, Iceland
[5]Faroe Marine Research Institute, Tórshavn, Faroe Islands
[6]University of the Faroe Islands, Tórshavn, Faroe Islands
[7]DTU Food Lyngby, Denmark
[8]Síldarvinnslan hf., Fjarðabyggð, Iceland

ABSTRACT: The genetic structure of Atlantic herring *Clupea harengus* L. was investigated in its north-easterly distribution in the Norwegian Sea and adjacent waters, using 23 neutral and one non-neutral (*Cpa111*) microsatellite loci. Fish from the suspected 2 main populations — the Norwegian spring-spawning herring (NSSH) and the Icelandic summer-spawning herring (ISSH) — were collected at spawning locations in their respective spawning seasons from 2009 to 2012. Samples were also collected from Norwegian autumn spawning locations, from different local Norwegian fjords such as the inner part of Trondheimsfjorden, Lindås pollene, Landvikvannet and Lusterfjorden, as well as from suspected Faroese spawning components. The observed level of genetic differentiation was significant but low (F_{ST} = 0.007) and mostly attributable to the differentiation of the local Norwegian fjord populations. The locus *Cpa111*, which was detected to putatively be under positive selection, exhibited the highest F_{ST} value (0.044). The observed genetic patterns were robust to exclusion of this locus. Landvikvannet herring was also genetically distinguishable from the 3 other fjord populations. In addition, the present study does not support genetic structuring among the ISSH and the NSSH.

KEY WORDS: Atlantic herring · Norwegian Sea · Norwegian fjords · Microsatellite loci · Adaptation · Gene flow

INTRODUCTION

Several approaches have been used to understand the population structuring of marine taxa — from life-history (Einarsson 1951, Ricklefs & Wikelski 2002, Arai et al. 2006, Curtis & Vincent 2006, Clarke et al. 2007, Silva et al. 2013) and tracking studies (Fridriksson & Aasen 1950, Fritsch et al. 2007, Wood et al. 2007, Donaldson et al. 2008, Tamdrari et al. 2012a,b, Thorsteinsson et al. 2012, Whitlock et al. 2012), to population dynamics (Amilhat & Lorenzen 2005, Syrjänen et al. 2008, Jung et al. 2012, Pampoulie et al. 2012). However, one of the most common approaches employed in the last 20 yr is the indirect estimation of gene flow and migration rates as inferred from genetic markers (Carvalho & Hauser 1994, Hauser &

*Corresponding author: chrisp@hafro.is

Carvalho 2008, Reiss et al. 2009). In the marine environment, neutral genetic markers such as microsatellite loci have been extremely useful in complementing other means of inferring population differentiation, such as life-history studies (Smith et al. 2002, Conover et al. 2006, Higgins et al. 2010), and in understanding the complex population dynamics of several marine species (Ruzzante et al. 2006, Bradbury et al. 2010, Pampoulie et al. 2012). Population structure (differentiation) and dynamics are prerequisites for devising sustainable management and conservation measures for exploited species (Hutchinson 2008). Moreover, the discovery of microsatellite loci showing signatures of selection (e.g. Nielsen et al. 2006) has changed our perception about genetic structuring of marine populations. The combined use of neutral and non-neutral loci has potential to yield deeper insights into patterns and degree of genetic structuring of populations (e.g. Beaumont 2005, Conover et al. 2006, Gaggiotti et al. 2009), and introduces an ecological-time scale approach more suitable to conservation and management practices (Hauser & Carvalho 2008).

The Atlantic herring *Clupea harengus* is a typical marine pelagic species that exhibits spatio-temporally separate spawning aggregations across the North Atlantic and the Baltic Sea. These discrete stocks also exhibit large-distance migration from their spawning areas to common feeding grounds (Dragesund et al. 1997, McQuinn 1997, Óskarsson et al. 2009) where mixed fisheries occur. The Atlantic herring fishery has a long history and Atlantic herring has been a commercially important species over nearly 2 centuries (Smylie 2004). The species occurs on both sides of the North Atlantic and has exhibited considerable fluctuations in stock size and spatial distribution in the last hundred years, with drastic concurrent collapses in several stocks in the 1960s (Jakobsson 1980, Toresen & Østvedt 2000, Overholtz 2002, Dickey-Collas et al. 2010). Contrary to the Atlantic cod and other marine resources, most of the herring stocks recovered from collapses over periods of varying length, and are presently subject to intense fishing pressure. Currently, the largest Atlantic herring stock is the Norwegian spring-spawning herring (NSSH), which is distributed from the southern part of Norway to the Barents Sea and from the Norwegian Sea to the Northeast coast of Iceland. Prior to the collapse of the NSSH in the late 1960s, a part of this stock spawned on the banks east of the Faroe Islands, foraged over a wide area in the NE-Atlantic and had wintering grounds off the east coast of Iceland (Jakobsson 1980, Dragesund et al. 1997). It therefore mixed with the Icelandic summer-spawning herring (ISSH) and Icelandic spring-spawning herring (ISPH), the latter not having recovered from its collapse in the late 1960s (Jakobsson 1980). After the collapse of the NSSH, the stock was primarily confined to the coastal areas along the western coast of Norway (Dragesund et al. 1997). Since the 1970s, the stock has slowly recovered, with a maximum level of ~10 million t in 2010 (ICES 2012) and again feeding in the open ocean between Norway, the Faroe Islands and Iceland (Fig. 1). Three different management units are currently considered for stock assessment in the Norwegian Sea and adjacent waters: the Norwegian spring-spawning herring (NSSH), the Icelandic summer-spawning herring (ISSH) and the North Sea autumn spawning herring (NSAH). In addition, the occurrence of a Norwegian local spring-spawning herring (NLSSH) (Johannessen et al. 2009, Silva et al. 2013) mainly spawning in local fjords, and of a Norwegian autumn-spawning (NASH) herring has been mentioned (Husebo et al. 2005). Moreover, the presence of a spring-spawning herring (FSSH) and an autumn-spawning (FASH) herring has been suggested in Faroese waters. So far, the discrimination among these stocks is primarily based on spawning time and location.

The genetic structure of the Atlantic herring has received considerable attention in recent years, as the species has been shown to exhibit a complex population dynamics, life-history variations within the management units (Husebo et al. 2005), and a relatively low level of differentiation among isolated local populations that overlap geographically during feeding migrations (Bekkevold et al. 2005, Jørgensen et al. 2005, Mariani et al. 2005, Ruzzante et al. 2006, Gaggiotti et al. 2009, André et al. 2011, Lamichhaney et al. 2012, Corander et al. 2013, Teacher et al. 2013). However, most of the aforementioned studies that have been performed to genetically discriminate stocks and assess their contribution to mixed fisheries have focused on the southern distribution of the Atlantic herring.

The conservation and sustainable exploitation of the herring stocks in the Norwegian Sea and adjacent waters crucially depend on our understanding of genetic structuring and interactions among the potentially distinct populations in this area. Until now, the genetic differentiation among NSSH and ISSH management units and/or subpopulations has never been investigated, even with already available microsatellite loci (O'Connell et al. 1998, McPherson et al. 2001, Miller et al. 2001, Olsen et al. 2002, Libungan et al. 2012). Hence, it is not currently known if,

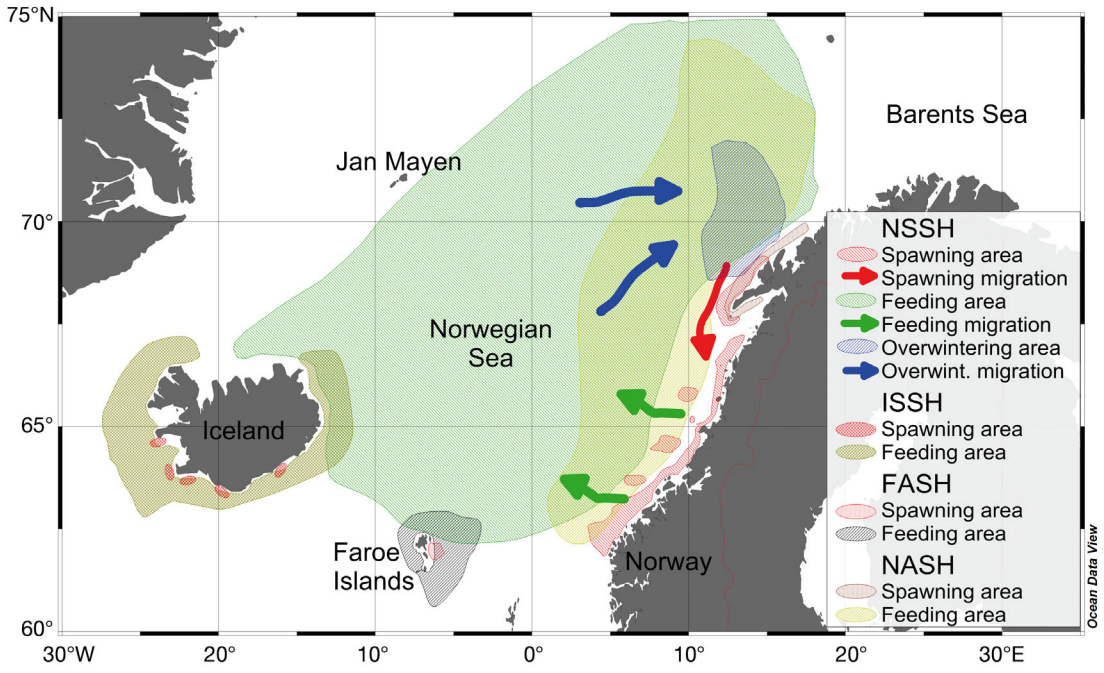


Fig. 1. Current migration pattern of adult Norwegian spring-spawning herring (NSSH) and interactions with other surrounding stocks, i.e. Icelandic summer-spawning herring (ISSH), Faroese autumn-spawning herring (FASH), and Norwegian autumn-spawning herring (NASH)

and which, genetic markers can be used to discriminate stocks occurring in this area, and thereby to assess their respective contributions to the mixed-stock fisheries of this commercially highly important species. Here we present one of the first genetic studies of the herring populations of the Norwegian Sea and adjacent waters, using 24 microsatellite loci, of which several are known to be under selection in other herring populations (Gaggiotti et al. 2009, André et al. 2011, Teacher et al. 2013). Our aims were 3-fold: (1) to attempt to confirm the aforementioned reproductive isolation (spawning time and location) between different herring populations around the Norwegian Sea; (2) to assess the aforementioned uniqueness of the Norwegian fjord spawning herring; and (3) to compare neutral to non-neutral genetic variation in order to detect potential signatures of selective differentiation.

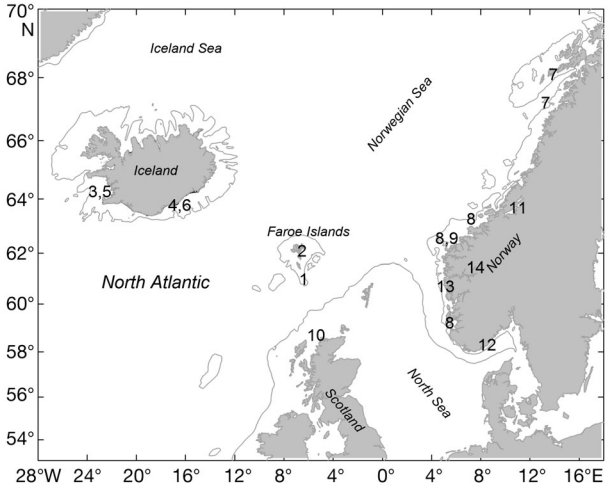


Fig. 2. Sampling locations of Atlantic herring *Clupea harengus* in the Norwegian Sea and surrounding waters. See Table 1 for sample codes

MATERIALS AND METHODS

Sampling areas and protocol

Atlantic herring (n = 1258) were collected at several spawning locations in the Northeast Atlantic from 2009 to 2012 during local spawning seasons (Fig. 2, Table 1); this included samples from different local Norwegian fjords such as Trondheimsfjorden (inner part of Trondheim fjord), Lindås pollene, Landvikvannet and Lusterfjorden, as well as suspected FASH and FSSH. Individual fish were selected for genotyping based on their reproductive status using the following maturity scale (see Table 1 for the percentages of breeding fish per sample): 1–2 immature, 3–5 maturing, 6 spawning, 7 recently

Table 1. Sampling areas and data for 14 samples of North Atlantic herring *Clupea harengus*. The maturity stage of individual fish is expressed in percentage per stage. Numbers in braces refer to maturity scale, while numbers in brackets indicate the specific stages fish were in. NA: data not available

Sample acronym	Sampling area	Stock acronym	Sample code	Date	Coordinates		Sample size	Maturity stage (%) [Scale]				Age range (yr)	Length (mm)	
								Maturing {3–5}	Spawning {6}	Recently spawned {7}	Resting {8}		Mean ± SD	Range
FASH	Faroese Islands	FASH	1	27.11.2009	60°48.00'N	06°10.80'W	119	5 [5]	–	–	95	4–11	373 ± 13	318–396
FSSH	Faroese Islands	FSSH	2	28.3.2011	62°06.06'N	06°45.00'W	40	95 [5]	5	–	–	5–10	333 ± 11	310–350
ISSH403	Iceland	ISSH	3	5.7.2009	64°13.75'N	22°56.29'W	48	2 [3]; 17 [4]; 81 [5]	–	–	–	4–13	325 ± 23	280–360
ISSH411	Iceland	ISSH	4	9.7.2009	63°44.84'N	16°26.80'W	84	99 [5]	–	1	–	2–11	326 ± 22	260–360
ISSH463	Iceland	ISSH	5	2.7.2010	64°05.40'N	23°01.90'W	70	1 [4]; 9 [5]	90	–	–	4–14	329 ± 19	280–370
ISSH473	Iceland	ISSH	6	5.7.2010	63°46.10'N	16°19.40'W	93	15 [4]; 60 [5]	10	–	5	2–11	308 ± 36	190–360
NASH	Lofoten	NASH	7	11.8.2010	67°14.60'N	13°17.00'E	88	–	1	57	33	3–12	338 ± 17	280–370
NSSH12	Norway	NSSH	8	29.1.2012	63°17.50'N	07°14.70'E	87	52 [4]; 30 [5]	18	–	–	3–13	329 ± 15	295–360
NSSH10	Norway	NSSH	9	14.2.2010	62°531.00'N	05°14.00'E	63	13 [4]; 84 [5]	2	1	–	4–15	324 ± 15	295–360
SCOTLAND	Scotland	NASH.S	10	9.1.2010	58°743.80'N	05°22.20'W	105	–	100	–	–	3–12	296 ± 15	267–337
NLSSH	Trondheimsfjorden	NLSSH	11	3.12.2010	63°42.00'N	11°00.00'E	120	NA	NA	NA	NA	3–15	272 ± 12	230–305
NLSSH	Landvikvannet	NLSSH	12	12.5.2010	58°19.20'N	08°30.10'E	149	1 [4]; 62 [5]	36	1	–	2–10	276 ± 17	225–320
NLSSH	Lindås pollene	NLSSH	13	3.2010	60°43.80'N	05°08.00'E	64	13 [4]; 44 [5]	42	2	–	NA	325 ± 14	295–360
NLSSH	Lusterfjorden	NLSSH	14	8.11.2011	61°47.67'N	07°57.33'E	128	77 [46]; 5[5]	–	–	–	2–6	181 ± 14	145–225

spawned and 8 resting (Bowers & Holliday 1961, Anonymous 1962).

Genetic samples were collected from muscle or fin clips that were preserved in 99% ethanol. Samples were genotyped at 24 microsatellite loci: *msild12*, *msild13*, *msild17*, *msild24*, *msild27* and *msild32* (Libungan et al. 2012); *Cha1017*, *Cha 1020*, *Cha1027*, *Cha1059* and *Cha1202* (McPherson et al. 2001); *Cha4* (*Cpa4* in Miller et al. 2001), *Cha17*, *Cha63* and *Cha113* (O'Connell et al. 1998); *Cpa101*, *Cpa102*, *Cpa103*, *Cpa104*, *Cpa 108*, *Cpa111*, *Cpa112*, *Cpa113* and *Cpa114* (Olsen et al. 2002).

DNA was extracted either from muscle or fin clips using the AGOWA mag Midi DNA Isolation Kit (AGOWA) or hot shot DNA extraction method (Montero-Pau et al. 2008). The forward primers of each microsatellite loci were labelled with one fluorescent dye (6-FAM, VIC, NED or PET). PCR assays were performed in multiplexes (Table S1 in the Supplement at www.int-res.com/articles/suppl/m522p219_supp.pdf) as follows: 10 µl volume containing 2–3 µl of DNA (10–100 ng μl^{-1}), 0.80 µl of dNTP (10 mM), 0.6–1.2 U of *Teg* polymerase (Matís, *Taq* comparable, see Ólafsson et al. 2010), 1 µl of 10× buffer (Matís), 0.03–0.25 µl of labelled forward (50:50 ratio, 100 µM) and reverse (100 µM) primer tagged on the 5'-end with a GTTTCTT PIG-tail (Brownstein et al. 1996), adding 1 µl of betaine (5 M) when improvement of DNA amplification was needed. Samples were analysed on an ABI PRISM 3730 sequencer using the GeneScan-500 LIZ size standard and genotyped with GeneMapper v.4.0 (Applied Biosystems).

Genetic analyses

As the neutrality assumption of genetic markers is crucial for conclusions drawn from genetic data, we applied the coalescent-based simulation methods of Beaumont & Nichols (1996) to detect potential outlier loci (loci under selection). Coalescent simulations were performed with the software LOSITAN (Antao et al. 2008), with samples of the same size as the observed samples, assuming an island model with 100 islands. A total of 100000 independent loci were generated with the infinite allele mutation model and the 'neutral' mean F_{ST} function (outlier loci were excluded in calculating the initial mean F_{ST}). Simulated distributions of F_{ST} values conditional to heterozygos-

ity under a neutral model were obtained and then compared to observed F_{ST} values to identify potential outlier loci. In addition, we performed outlier tests in BayeScan (Foll & Gaggiotti 2008), which allows for different demographic histories and drift between populations. BayeScan was run with 50000 burn-in, 50 thinning, a sample size of 1000, 300000 iterations, 20 pilot runs with a length of 5000, and a false discovery rate (FDR) of 0.05. Outliers which were identified with both methods (LOSITAN and BayeScan) were considered to be under selection.

A statistical power analysis of the microsatellite loci was performed to assess whether genetic structure could be detected among the North Atlantic samples with the developed sampling strategy and the genetic markers used. The Norwegian local spring-spawner (NLSSH) samples showed the highest level of differentiation in our sample collection and were therefore excluded from this analysis. The statistical power of the microsatellite loci was estimated using the program POWSIM (Ryman & Palm 2006), which assesses the α (type I) error (the probability of rejecting H_0 when it is true) and the power of the genetic design performed, using information on sample sizes, number of samples, number of loci, and allele frequencies for any hypothetical degree of true differentiation quantified as F_{ST} (Ryman & Palm 2006). The significance of the tests was assessed using Fisher's exact tests as well as χ^2 tests.

Genetic diversity of samples (evaluated using allele frequencies), observed and expected heterozygosities, and deviations from the Hardy-Weinberg equilibrium (HWE) were calculated in GENEPOP'007 (Rousset 2008). Population differentiation was estimated both between pairwise samples and overall, using the unbiased F_{ST} estimator θ of Weir & Cockerham (1984). Statistical significance was assessed using the exact *G*-test implemented in GENEPOP'007. To visualize the level of genetic differentiation among samples, the pairwise estimates of F_{ST} were plotted using the multi-dimensional scale (MDS) function in R (cmdscale, R Core Team 2012).

The number of subpopulations (K) potentially contained in our sample set was assessed using STRUCTURE (Pritchard et al. 2000) with no prior information on sample location. STRUCTURE was run using 350000 burn-in and 500000 iterations, for 10 independent runs for K = 1 to 10, using an admixture model with correlated allele frequencies. The results were scrutinized in STRUCTURE HARVESTER (Earl & vonHoldt 2012) in order to estimate the optimal number of *K*, using Evanno's method (Evanno et al. 2005). DISTRUCT was then used to visualize the data (Rosenberg 2004). As STRUCTURE is likely to detect the highest level of differentiation among the samples, we conducted a hierarchical analysis by performing similar STRUCTURE runs on detected populations (K) containing several samples.

RESULTS

Genetic diversity

Biological data for the samples is listed in Table 1. Except for samples 1 and 14, most of the fish collected were ready to spawn (maturity stage 5) or were spawning (maturity stage 6) (Table 1). The number of alleles per locus was high, ranging from 9 (*Cap111*) to 63 (*msild24*; data not shown). The unbiased expected heterozygosity per sample ranged from 0.813 (NLSSH12) to 0.850 (FSSH) (see H_e in the last row of Table S2 in the Supplement at www.int-res.com/articles/suppl/m522p219_supp.pdf). Genotypic proportions were out of HWE in 26 of 336 exact tests, of which 2 remained significant after the Bonferroni correction for multiple tests, and were not attributable to any loci or samples (Table S2).

Outlier tests

Simulations for detection of outlier loci performed in LOSITAN suggested that 2 loci fell outside the 95% CI; locus *Cpa111* and *msild13* were suggested to be under positive selection (Table S3 in the Supplement). Using the 99% CI, only *Cpa111* was suggested to be under positive selection (Table S3). BayeScan simulations only identified *Cpa111* as putatively under selection (Table S4 in the Supplement). Hence, all subsequent structure analyses were performed with and without the outlier locus (*Cpa111*), except for the statistical power test.

Statistical power of the microsatellite loci

Excluding the Norwegian local spring-spawner (NLSSH) samples, the estimate of the statistical α (type I) error rate (i.e. the probability of rejecting the null hypothesis of genetic homogeneity when it is true) varied from 0.075 with Fisher's exact tests to 0.077 with χ^2 tests (Table S5 in the Supplement; these are slightly higher than the 5% limit for significance, but still at a reasonable level (Ryman & Palm 2006). The simulations on the power analysis of the micro-

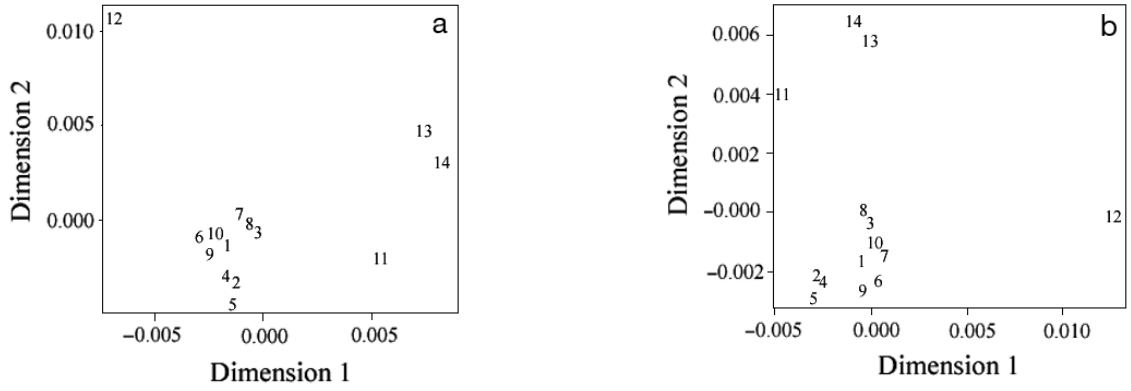


Fig. 3. Multi-dimensional scaling plot of Atlantic herring *Clupea harengus* samples in the Norwegian Sea and surrounding waters: (a) all loci included, (b) without the outlier *Cpa111*. See Table 1 for sample codes; 1–10 = North Atlantic samples, 11–14 = NLSSH samples

satellite loci revealed that the combination of the microsatellite loci and sample sizes used conferred a statistical power that is sufficient to detect any level of differentiation among the North Atlantic samples collected, equal to or above F_{ST} = 0.001 (Table S5).

Population structure

The overall genetic estimates revealed a highly significant F_{ST} (0.007, p < 0.001, 95% CI: 0.005–0.0010) and F_{IS} (0.021, p < 0.001, 95% CI: 0.012–0.031). Locus *Cpa111* exhibited the highest F_{ST} value (0.044), while all other loci exhibited similar lower values. Out of 91 pairwise F_{ST} comparisons, 52 were significantly different from zero (Table S6 in the Supplement), and 45 remained significant after Bonferroni correction. All 45 significant comparisons involved samples from Norwegian local spawning herring (NLSSH). The pattern of significance of pairwise F_{ST} comparisons remained similar when the *Cpa111* locus was removed (Table S7 in the Supplement).

The MDS analysis for all loci confirmed the above results and revealed that all NLSSH samples were highly distinct from the Northeast Atlantic ones. NLSSH samples were also clearly distinct from each other apart from samples 13 and 14 (Fig. 3a). The same pattern was observed when the outlier locus was excluded from the analysis (Fig. 3b).

Using all loci, the Bayesian cluster analysis (STRUCTURE) revealed that the most likely number of populations contained in our samples was K = 2 (Fig. 4a, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m522p219_supp.pdf) for both LnP(K) values and ΔK (Evanno et al. 2005). One cluster was composed of all Northeast Atlantic samples, while the second cluster was composed of the Norwegian fjord samples (NLSSH). The hierarchical analysis of the North Atlantic cluster did not reveal any further structuring (Table S8 in the Supplement), whereas it detected 2 additional clusters in the fjord samples (NLSSH) — one composed of sample 12 (Landvikvannet) and the other composed of the 3 other fjord samples (Fig. 4b, samples 11, 13 and 14; Table S8, Fig. S2 in the Supplement). Further analyses of the second cluster (samples 11, 13 and 14) did not reveal any additional structuring (Table S8, Fig. S3 in the Supplement).

Using only the neutral loci, the most likely number of clusters detected with STRUCTURE was K = 3 (Fig. 5, Fig. S3) for both LnP(K) values and ΔK (Evanno et al. 2005). The first, second and third clusters were respectively composed of all samples from the Northeast Atlantic, the sample collected in Landvikvannet (sample 12), and the samples collected in other fjords (samples 11, 13 and 14). Additional hierarchical analysis of the third cluster (samples 11, 13 and 14) did not reveal any substructuring in these fjords, i.e. the most likely number of clusters was K = 1 (Table S9 in the Supplement). The same result was observed for the Northeast Atlantic cluster (Table S9).

DISCUSSION

Global genetic structure

Genetic markers have been intensively used to assess the genetic structure of the Atlantic herring in its south-eastern distribution, but our study is one of the first (however, see Shaw et al. 1999) to investigate the use of genetic markers on herring caught in the Norwegian Sea and surrounding waters. The results of

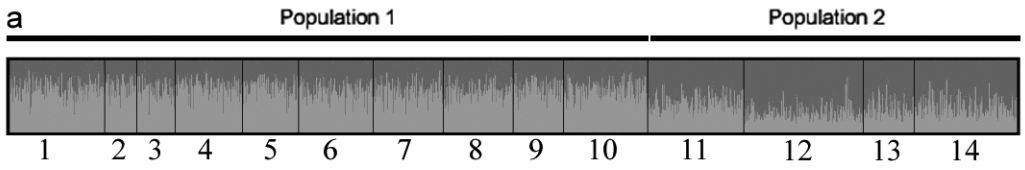
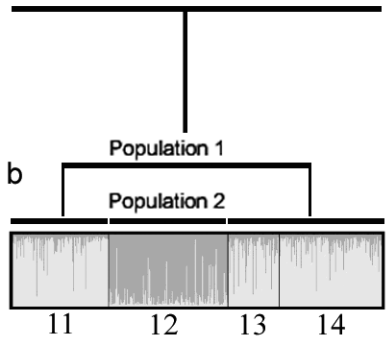


Fig. 4. Hierarchical Bayesian cluster analysis performed in STRUCTURE using all loci and all samples. A total of 10 runs were performed for each *K*, from *K* = 1 to 10 with 350000 burn-in, 500000 MCMC (Monte Carlo Markov Chain), using an admixture model with correlated allele frequencies and no prior information on sample location. (a) The first hierarchical level including all samples. Two clusters were detected, the first one composed of all Northeast Atlantic samples (1–10), and the second composed of the fjord samples (NLSSH, samples 11–14). (b) The second hierarchical level including only the NLSSH samples. Two clusters were detected, the first one composed of sample 12, and the second composed of samples 11, 13 and 14. See Table 1 for sample codes



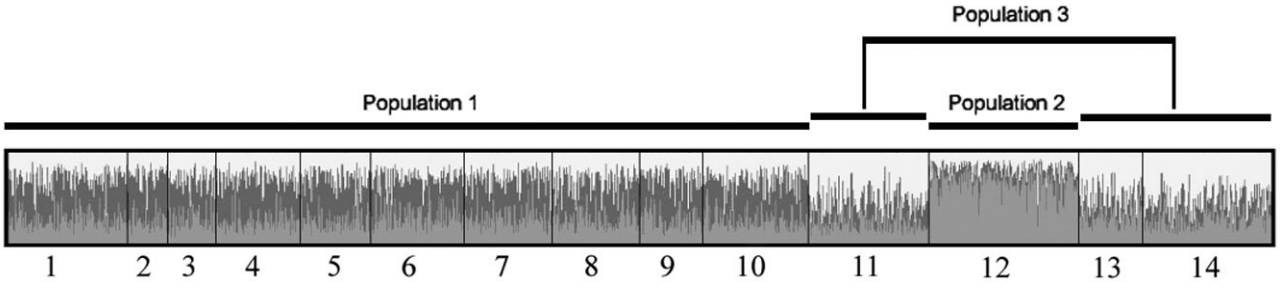


Fig. 5. Bayesian cluster analysis performed in STRUCTURE using neutral loci and all herring samples. A total of 10 runs were performed for each *K*, from *K* = 1 to 10 with 350000 burn-in, 500000 MCMC, using an admixture model with correlated allele frequencies and no prior information on sample location. Additional hierarchical analyses did not detect any additional clusters within the 2 main groups, i.e. the Northeast Atlantic samples (1–10) and the fjord samples (NLSSH, samples 11–14). See Table 1 for sample codes

this study showed that, even with 23 neutral and one non-neutral microsatellite loci, the Atlantic herring did not exhibit any significant genetic differentiation among stocks across the investigated area, even though the Norwegian local-spawning herring samples were genetically differentiated from all other samples. Although one can suggest that STRUCTURE analyses might not correctly uncover genetic patterns due to the observed low level of differentiation, this study presents a robust interpretation of the developed statistical approaches based on a combination of F_{ST} values, MDS and STRUCTURE runs, which strongly support the observed genetic pattern.

The populations of Atlantic herring which have been genetically studied in the southeastern distribution (Jørgensen et al. 2005, Mariani et al. 2005, Ruzzante et al. 2006, Gaggiotti et al. 2009, André et al. 2011) exhibited low levels of differentiation except at some hitchhiking microsatellite loci such as *Cpa112* and *Her14* (Gaggiotti et al. 2009, Teacher et al. 2013). Genetic differentiation is indeed expected to be more pronounced at coding (or linked) loci, especially in large populations in which even weak selection might override effects of genetic drift (Gaggiotti et al. 2009). Microsatellite loci and other genetic markers under selection (e.g. single nucleotide polymorphisms, SNPs) were found to show some striking differentiation among herring populations (Lamichhaney et al. 2012, Nielsen et al. 2012, Corander et al. 2013). In the present study, we failed to detect any genetic structuring among the large Northeast Atlantic herring populations. NSSH is by far the largest and ISSH among the largest herring populations of the Northeast Atlantic, and their effective population size (N_e) is expected to be very large, which could possibly explain the lack of genetic differentiation. The potential combination of high N_e and considerable level of gene flow among herring populations have been suggested to hinder the detection of structure among local populations of this species using neutral mark-

ers (Bekkevold et al. 2005, Mariani et al. 2005). However, an earlier microsatellite loci study has discovered genetic differences between ISSH and NSSH at neutral loci (Shaw et al. 1999), although only a small number (n = 4) of microsatellite loci and a relatively small sample collection were used in that study. The North Atlantic herring exhibits a large effective population size and such a low number of microsatellite loci might not be sufficient to uncover the genetic pattern of this species. For such a species, a higher number of samples and loci are necessary to fully fathom genetic structure (see Ruzzante 1998 for bias and sampling variance when using microsatellite loci).

Another potential explanation for the lack of significant genetic differentiation among Northeast Atlantic populations of herring might be the low power of the microsatellite loci resolving population structuring, as well as the quality of the sampling design (Ryman & Palm 2006). However, the power analysis of the 24 microsatellite loci used in this study revealed that the estimated α (type I error) was reasonably low, and that the sampling design should have been sufficient to detect the level of differentiation of F_{ST} = 0.001 if it were present (see Table S5 in the Supplement at www.int-res.com/articles/suppl/m522p219_supp.pdf). Until now, the distinction between ISSH and NSSH is mainly based on morphological, physiological and biological characteristics (Einarsson 1951, Jakobsson et al. 1969). SNPs have recently been developed and seem to be promising for such marine species with large N_e and complex biodynamics, especially when investigating functionally important genetic loci (Helyar et al. 2012, Limborg et al. 2012, Nielsen et al. 2012, Corander et al. 2013, Teacher et al. 2013).

Most of the local herring populations included in this study (NLSSH, samples 11, 13, and 14) have recently been studied in terms of reproductive investment and growth (Silva et al. 2013). The stationary herring of Trondheimsfjord was described in the early 1900s and suggested to be distinct from NSSH (Broch 1908, Runnstrom 1941, see Silva et al. 2013 for a full description). An allozyme study of samples from ISSH, NSSH and 2 Norwegian fjords (including Trondheimsfjord) also only found significant genetic differentiation between the stationary Trondheimsfjord herring and all other localities (Turan et al. 1998). Recent life-history studies have suggested that Trondheimsfjord herring is 'a few of many potentially genetically unique populations with phenotypic adaptations to a stationary life in well defined environment…' (Silva et al. 2013, p. 78). Trondheimsfjord (Broch 1908, Runnstrom 1941, Sørensen 2012, Silva et al. 2013), Lusterfjord (Aasen 1952), Lindås pollene (Lie et al. 1978, Johannessen et al. 2009, Silva et al. 2013) and Landvikvannet (Eggers 2013, Silva et al. 2013) herrings have long been considered to belong to self-sustaining and rather stationary populations characterized by a lower vertebral count, slower growth, lower length at maturity, shorter life span and a higher relative fecundity than the migratory oceanic NSSH. Since these populations with apparent adaptations to life mostly spent inside fjord areas have been known to exist for up to a century, they may indeed be genetically unique as supported by the present study. In addition, the analysis of the fjord samples revealed that the Landvikvannet sample was genetically distinguishable from all other fjord samples. This is most likely linked to the potential mixture with various life stages of oceanic herring that differ between Landvikvannet herring and the other fjord populations. The herring in Lindås pollene, Lusterfjord and Trondheimsfjord may all mix with NSSH drifting into the fjord areas as larvae from spawning grounds outside the fjord areas. Albeit most of the NSSH grow up in the Barents Sea, some of these fishes always tend to use the fjords as nursery areas until 2 yr of age (Holst & Slotte 1998). Even though the NSSH is genetically tuned to leave the fjords by 2 yr of age to grow further and join the adult spawning stock in the open ocean, one cannot exclude the possibility that some would choose to stay, especially if there is numerical domination of local herring of the same size (Huse et al. 2002). Hence, gene flow might have occurred consistently over time between the NSSH and local fjord populations. Recent studies from Lindås pollene even indicate that gene flow among adult NSSH and local herring might explain the evolution of the fjord population's life history traits from the 1960s to the 2000s towards a regime with higher growth and higher length at maturity (Langård 2013). In Landvikvannet, the link to the NSSH is not clear as this local fjord is outside the observed spawning area of the NSSH. In the latter, local herring might mix with coastal spring spawners or even with Western Baltic spring spawners (WBSS) migrating into the Skagerrak area and feeding close to the Norwegian coast during summer. Landvikvannet was artificially connected to the open sea through a 3 km long canal in 1887, and has been a brackish environment ever since, with anoxic conditions at depths below 4 m. Therefore, the observed genetic differences between Landvikvannet herring and herring from the other fjords are likely due to the fact that Landvikvannet was colonized by stray WBSS herring that were already adapted to low

salinity conditions. In fact, the very low vertebral count in Landvikvannet herring perfectly equals that of WBSS herring (55.7). However, data on vertebral counts and growth from the most recent study in Landvikvannet (2012) indicate that NSSH has also recently visited this area, mixing with a group of coastal spring spawners and what is believed to be Landvikvannet herring (Eggers 2013). The 3 groups occupy this ecological niche at different times with some overlap in spawning stages. NSSH arrive first in March, the coastal spring spawners arrive in March–April, and Landvikvannet herring peak in abundance in May. The genetic samples used in the present study were taken in May, which has been the main sampling period since the 1980s and used as a basis for the suggestion of a local fjord population. Given the results from 2012, further genetic studies of the herring in the area of Landvikvannet are needed to be able to draw firm conclusions.

Neutral versus non-neutral genetic markers

While levels of differentiation (F_{ST}s) and their visual representation (MDS) tend to suggest similar genetic patterns both when all loci are included and when *Cpa111* is excluded, the primary results of the Bayesian cluster analysis would have resulted in fairly different conclusions based on these 2 approaches. The first Bayesian cluster analysis including all loci supported a main differentiation between all fjord samples and all samples collected around the Norwegian Sea, while the neutral loci analysis clearly distinguished one additional cluster — the fjord sample from Landvikvannet (NLSSH, sample 12). In addition, when all loci were used, the Bayesian cluster analysis could not detect differences among the fjord samples without an additional hierarchical analysis. A closer look at *Cpa111* (the locus under selection) allele frequencies (Fig. 6) revealed a clear shift in allele frequencies in the fjord and the Northeast Atlantic populations (the former exhibited a high frequency of allele-275 compared to the latter), but also a slightly different pattern in the Landvikvannet sample (NLSSH, sample 12) compared to the other fjord samples. Indeed, the Landvikvannet sample exhibited a higher frequency of allele-287 than any other fjord and Northeast Atlantic samples, and it also exhibited a lower allele-275 frequency than the other fjord samples; these differences were not detected by the Bayesian cluster analysis except when an additional hierarchical analysis was performed on the fjord samples. As suggested above, these observed genetic differences among the fjord samples might be due to differences in their origin and their respective interactions with the NSSH, but might also reflect potentially different ongoing genetic evolution of the fjord populations.

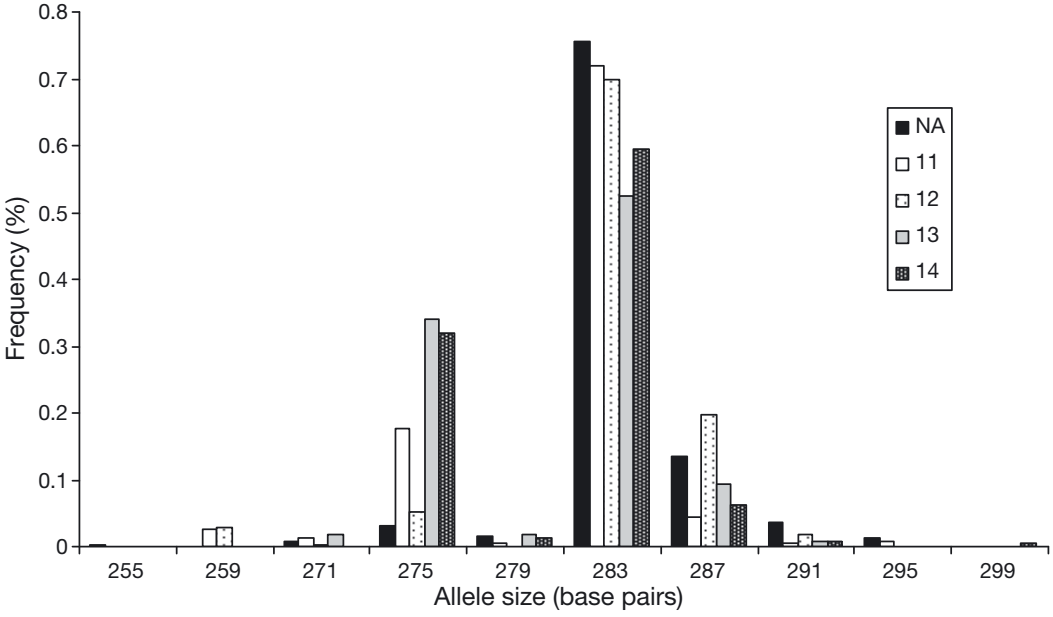


Fig. 6. Allele frequencies at the *Cpa111* locus. All samples of North Atlantic (NA) populations were combined, while allele frequencies of the 4 Norwegian local-spawning herring (NLSSH; samples 11–14) are depicted separately. See Table 1 for sample codes

Fisheries management

In terms of management, although the power analysis performed suggests that a relatively low level of differentiation would be detectable with our research design, we only detected genetic differences between the North Atlantic and the Norwegian local populations. The combination of large effective population size and the relatively short time for divergence since the recovery of the North Atlantic populations might have precluded evolution of genetic differences. However, the herring populations in the investigated area are exhibiting different life-history patterns, which, in the absence of genetic evidence, should be integrated (and are already so) in fisheries management. The observed biological uniqueness of the Norwegian local populations, and especially the exceptionality of Landvikvannet herring should be investigated further to decipher their interactions with the NSSH component and the Western Baltic component to ensure appropriate management of herring stocks in the future.

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