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

Pampoulie, C., Slotte, A., Óskarsson, G. J., Helyar, S. J., Jónsson, Á., Ólafsdóttird, G., ... Daníelsdóttir, A. K. (2015). Stock structure of Atlantic herring Clupea harengus in the Norwegian Sea and adjacent waters. Marine Ecology: Progress Series, 522, 219-230. DOI: 10.3354/meps11114

Published in:
Marine Ecology: Progress Series

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
Link to publication record in Queen's University Belfast Research Portal

Stock structure of Atlantic herring (*Clupea harengus* L.) 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 Reykjavik, 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.

**Corresponding author: tel: +354 575 2038; fax: +354 575 2001; email: chrisp@hafro.is*

ABSTRACT: The genetic structure of Atlantic herring *Clupea harengus* was investigated in its north-easterly distribution at the Norwegian Sea and adjacent waters, using 23 neutral and one non-neutral (Cpa111) microsatellite loci. Fish from the two main suspected populations, the Norwegian spring-spawning herring (NSSH) and the Icelandic summer-spawning herring (ISSH), were collected at spawning locations/seasons from 2009 to 2012. Samples were also collected from Norwegian autumn spawning locations and from different local Norwegian fjords such as 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, (F_{ST} = 0.044). The observed genetic patterns were robust to exclusion of this locus. Landvikvannet herring was also genetically distinguishable from the three other fjord populations. In addition, the present study does not support genetic structuring among the Icelandic summer-spawning herring and the Norwegian spring-spawning herring.

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, Tamdrari et al. 2012b, 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, in the last 20 years one of the most common approaches employed to understand population structuring has been the indirect estimation of gene flow and migration rates as inferred from genetic markers (Carvalho & Hauser 1994, Hauser & Carvalho 2008, Reiss et al. 2009). In the marine environment, neutral genetic markers such as microsatellite loci have been extremely useful to complement other means of inferring population differentiation such as life-history studies (Smith et al. 2002, Conover et al. 2006; Higgins et al. 2010), as well as to understand the complex population dynamics of several marine species (Ruzzante et al. 2006, Bradbury et al. 2010, Pampoulie et al. 2012). Yet, such information 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, Cano et al. 2008, 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 which 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. Atlantic herring has, indeed, a long history of fishing and has been a commercially important species over nearly two centuries (Smylie 2004). It occurs on both side of the North Atlantic and has exhibited considerable fluctuations in stock size and spatial distribution in the last hundred years, marked by drastic concurrent collapses in several stocks in the 1960's (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 today subject to intense fishing pressure. Today, 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 NSSH in the late 1960s, a part of this stock spawned on the banks east of the Faroe Islands, fed over a wide area in the NE-Atlantic and had wintering grounds off the east coast of Iceland (Jakobsson 1980, Dragesund et al. 1997), therefore mixing with the Icelandic summer-spawning herring (ISSH) and Icelandic spring-spawning herring (ISPH), the latter which has not recovered from it's collapse in the late 1960s (Jakobsson 1980). After the collapse of 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 in 2010 of around 10 million tons (ICES 2012) and again feeding in the open ocean between Norway, 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 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 have been suggested in Faroese waters. So far, the discrimination of 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 and life-history variations within the management units (Husebo et al. 2005), as well as a relatively low level of differentiation among isolated local populations overlapping 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 these studies performed to genetically discriminate stocks and assess their contribution to mixed fisheries have been focusing 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 depends on our understanding of genetic structuring and interactions of 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'Connel 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 and which genetic markers can be used to discriminate stocks occurring in this area, and thereby to assess their respective contributions to mixed-stock fisheries of this commercially highly important species. Here we present one of the first genetic studies of the Norwegian Sea and adjacent waters herring populations 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 three-fold- First, to attempt to confirm the aforementioned reproductive isolation (spawning time and location) between different herring populations around the Norwegian Sea. Second, to assess the aforementioned uniqueness of the Norwegian fjord spawning herring, and third, to compare neutral to non-neutral genetic variation in order to detect potential signatures of selective differentiation.

MATERIALS AND METHODS

Sampling areas and protocol

In all, 1258 Atlantic herring were collected at several spawning locations in the Northeast Atlantic from 2009 to 2012 during local spawning seasons (Fig. 2, Table 1) including 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. Individuals fish were selected for genotyping owing to their reproductive status using the following maturity scale (see Table 1 for the percentage of breeding fish per sample): 1–2 immature, 3–5 maturing, 6 spawning, 7 recently spawned and 8 resting (Bowers & Holliday 1961, Anonymous 1962).

Genetic samples were collected from muscle or fin clips preserved in 99% ethanol. Samples were genotyped at 24 microsatellite loci: msild12, msild13, msild17, msild24, msild27 and msild32 (Libungan et al. 2012), Cha1017, Cha1020, Cha1027, Cha1059 and Cha1202 (McPherson et al. 2001), Cha4 (Cpa4 in Miller et al., 2001), Cha17, Cha63 and Cha113 (O'Connel et al. 1998), Cpa101, Cpa102, Cpa103, Cpa104, Cpa108, Cpa111, Cpa112, Cpa113 and Cpa114 (Olsen et al. 2002).

DNA was extracted either from muscle, or fin clips by AGOWA mag Midi DNA Isolation Kit (AGOWA Gmbh) 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). Polymerase chain reactions (PCR) were performed in Multiplexes (Supplementary Table S1) as follows: 10 µl volume containing 2-3 µl DNA (10-100 ng/µl), 0.80 µl of dNTP (10mM), 0.6-1.2 U Teg polymerase (Matís Ltd., Taq comparable, see Ólafsson et al. 2010), 1 µl of 10x buffer (Matís Ltd.), 0.03-0.25 µl of a 50:50 ratio of labelled forward (100 µM) and reverse (100 µM) primer tagged on the 5´-end with a GTTTCTT PIG-tail (Brownstein et al. 1996) adding 1 µl 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 v4.0 (Applied Biosystems).

Genetic analyses

As the neutrality assumption of genetic markers is crucial for the conclusion drawn from genetic data, we applied the coalescent-based simulation methods of Beaumont and Nichols (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 100,000 independent loci were generated with the infinite allele mutation model and the "neutral" mean F_{ST} function (outlier loci were excluded to calculate the initial mean F_{ST}). Simulated distribution of F_{ST} values conditional to heterozygosity under a neutral model were obtained and thus compared to observed F_{ST} values to identify potential outlier loci. In addition, we performed outliers' tests in BayeScan (Foll & Gaggiotti 2008), which allows for different demographic histories and drift between populations. BayeScan was run with 50,000 Burn-in, 50 thinning, a sample size of 1,000, 300,000 iterations, 20 pilot runs with a length of 5,000 and a FDR of 0.05. Outliers which were identified with both methods (LOSITAN and BayeScan) were considered to be under selection.

170 A statistical power analysis of the microsatellite loci was performed to assess whether
171 genetic structure could be detected among the North Atlantic samples with the developed
172 sampling strategy and the genetic markers used. The Norwegian local spring-spawners
173 samples which showed the highest level of differentiation in our samples' collection were
174 therefore excluded for this analysis. The statistical power of the microsatellite loci was
175 estimated using the program POWSIM (Ryman & Palm 2006), which assesses the α (type I)
176 error (the probability of rejecting *H*o when it is true) and the power of the genetic design
177 performed using information on sample sizes, number of samples, number of loci, and allele
178 frequencies for any hypothetical degree of true differentiation quantified as F_{ST} (Ryman &
179 Palm 2006). The significance of the tests was assessed by Fisher's exact tests as well as by χ^2
180 tests. These tests were performed without the NLSSH samples.
181 Genetic diversity of samples (evaluated using allele frequencies), observed and expected
182 heterozygosities. and deviations from Hardy-Weinberg equilibrium (HWE) were calculated in
183 GENEPOP'007 (Rousset 2008). Population differentiation was estimated both between
184 pairwise samples and overall using the unbiased F_{ST} estimator θ of Weir & Cockerham
185 (1984). Statistical significance was assessed using the exact G-test implemented in
186 GENEPOP'007.
187 To visualize the level of genetic differentiation among samples, the pairwise estimates of
188 F_{ST} were lotted using the multidimensional scale (MDS) function in R (cmdscale, Team RC
189 2012).
190 The number of subpopulations (*K*) potentially contained in our samples set was assessed
191 using STRUCTURE (Pritchard et al. 2000) with no prior information on sample location.
192 STRUCTURE was run using 350,000 burn-in and 500,000 iterations for 10 independent runs
193 for $K = 1$ to 10 using an admixture model with correlated allele frequencies. The results were
194 scrutinized in STRUCTURE HARVESTER (Earl & vonHoldt 2012) in order to estimate the

optimal number of *K* using the Evanno's method (Evanno et al. 2005). DISTRUCT was then used to visualise 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 information retrieved from the samples is listed in Table 1. Except sample 1 and 14, most of the fish collected were ready to spawn (maturity stage 5) or 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 0.836 (NSSH4) to 0.850 (FSSH) (Supplementary Table S2). Genotypic proportion were out of HWE in 26 of 336 exact tests, of which two remained significant after the Bonferroni correction for multiple tests, and were not attributable to any loci or samples (Supplementary Table S2).

Outlier tests

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

220

221 **Statistical power of the microsatellite loci**

222 Excluding the Norwegian local spring-spawners samples, the estimate of the statistical α
223 (type I) error rate (i.e. the probability of rejecting the null hypothesis of genetic homogeneity
224 when it is true), varied from 0.075 with Fisher's exact tests to 0.077 with χ^2 tests
225 (Supplementary Table S5), which is slightly higher than the 5% limit for significance, but still
226 at a reasonable level (Ryman & Palm 2006). The simulations on the power analysis of the
227 microsatellite loci revealed that the combination of the microsatellite loci and sample sizes
228 used, conferred a statistical power sufficient to detect any level of differentiation among the
229 North Atlantic samples collected, equal to or above F_{ST} = 0.001 with a maximum power
230 (Supplementary Table S5).

231

232 **Population structure**

233 The overall genetic estimates revealed a highly significant F_{ST} (F_{ST} = 0.007, $p < 0.001$,
234 95% CI: 0.005-0.0010) and F_{IS} (F_{IS} = 0.021, $p < 0.001$, 95% CI: 0.012-0.031). Locus Cpa111
235 exhibited the highest F_{ST} value (F_{ST} = 0.044), while all other loci exhibited lower similar
236 values. Out of 91 pairwise F_{ST} comparisons, 53 were significantly different from zero
237 (Supplementary Table S6), and 50 remained significant after Bonferroni correction. All
238 significant 50 comparisons involved samples from Norwegian local spawning herring
239 (NLSSH). The pattern of significance of pairwise F_{ST} comparisons remained similar when the
240 Cpa111 locus was removed (Supplementary Table S7).

241 The multidimensional scale analysis (MDS) for all loci confirmed these results and
242 revealed that all NLSSH samples were highly distinct from the Northeast Atlantic ones.
243 NLSSH samples were also clearly distinct from each other apart from sample 13 and 14 (Fig.

244 3a). The same pattern was observed when the outlier locus was excluded from the analysis
245 (Fig. 3b).
246 Using all loci, the Bayesian cluster analysis (STRUCTURE) revealed that the most likely
247 number of populations contained in our samples was for $K = 2$ (Fig. 4a, Supplement Fig. S1),
248 both with LnP(k) values and ΔK (Evanno et al. 2005). One cluster was composed of all
249 Northeast Atlantic samples while the second one was composed of the Norwegian fjord
250 samples (NLSSH). The hierarchical analysis of the North Atlantic cluster did not reveal any
251 further structuring (Supplementary TableS8) while it detected two additional clusters in the
252 fjord samples (NLSSH), one composed of sample 12 (Landvikvannet) and one composed of
253 the three other fjord samples (samples 11, 13 and 14: Supplementary Table S8, Fig. S2).
254 Further analyses of the second cluster (samples 11, 13 and 14) did not reveal any additional
255 structuring (Supplementary Table S8, Fig. S3).
256 Using the neutral loci only, the most likely number of cluster detected with STRUCTURE
257 was for $K = 3$ (Fig. 4b, Supplement Fig. S3) both with LnP(k) values and ΔK (Evanno et al.
258 2005). The first cluster was composed of all samples from the Northeast Atlantic, the second
259 of the sample collected in Landvikvannet (sample 12), and the third one of samples collected
260 in other fjords (samples 11, 13 and 14). Additional hierarchical analysis of the third cluster
261 (samples 11, 13 and 14) did not reveal any substructure in these fjords, i.e. the most likely
262 number of cluster was $K = 1$ (Supplementary Table S9). The same result was observed for the
263 first cluster, i.e. the samples collected in Northeast Atlantic (Supplementary Table S9).
264
265 **DISCUSSION**
266 **Global genetic structure**
267 Genetic markers have been intensively used to assess genetic structure of the Atlantic
268 herring in its south-eastern distribution, but we are among the first ones (but see: Shaw et al.

1999) to investigate it in the Norwegian Sea and surrounding waters, including the Norwegian local spawning herring. The results of 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, although the Norwegian local-spawning herring samples were indeed genetically differentiated from all other samples. Although one can suggest that STRUCTURE analyses might not correctly uncover genetic pattern 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 STRUTURE runs, which strongly support the observed genetic pattern.

The populations of Atlantic herring which have been genetically studied in the south-eastern distribution (Jørgensen et al. 2005, Mariani et al. 2005, Ruzzante et al. 2006, Gaggiotti et al. 2009, André et al. 2011), exhibited low level of differentiations 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 (like 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 current 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, and hence, provides a probable explanation for 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 markers (Bekkevold et al. 2005, Mariani et al. 2005). However,

294 an earlier microsatellite loci study has discovered genetic differences between ISSH and
295 NSSH at neutral loci (Shaw et al. 1999), but only a small number (n = 4 loci) of microsatellite
296 loci and a relatively small sample collection were used in that study. The North Atlantic
297 herring exhibits large effective population size and such a low number of microsatellite might
298 not be sufficient to uncover the genetic pattern of this species. For such a species, a higher
299 number of samples and loci are necessary to fully fathom genetic structure (see Ruzzante
300 1998 for bias and sampling variance when using microsatellite loci).
301 Another potential explanation for the lack of significant genetic differentiation among
302 Northeast Atlantic populations of herring might be found from the low power of the
303 microsatellite loci resolving population structuring, as well as the quality of the sampling
304 design (Ryman & Palm 2006). However, the power analysis of the 24 microsatellite loci used
305 revealed that the estimated α (type I error) was reasonably low, and that the sampling design
306 should have been sufficient to detect level of differentiation of F_{ST} = 0.001 if it was present
307 (see Table 5). Until now, the distinction of ISSH *vs*. NSSH is mainly based on morphological,
308 physiological and biological characteristics (Einarsson 1951, Jakobsson et al. 1969). Single
309 nucleotide Polymorphisms (SNPs) have recently been developed and seem to be promising
310 for such marine species with large N_e and complex biodynamic, especially when investigating
311 functionally important genetic loci (Helyar et al. 2012, Limborg et al. 2012, Nielsen et al.
312 2012, Corander et al. 2013, Teacher et al. 2013).
313 Most of the local populations of herring included in this study (NLSSH, samples 11, 13,
314 and 14) have recently been studied in terms of reproductive investment and growth (Silva et
315 al. 2013). The stationary herring of Trondheimsfjord was described in the early 1900's and
316 suggested to be distinct from NSSH (Broch 1908, Runnstrom 1941, see Silva et al. 2013 for a
317 full description). An allozyme studiy of samples from ISSH, NSSH and two Norwegian fjords
318 (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 was "a few of many potentially genetically unique populations with phenotypic adaptations to a stationary life in well defined environment…" (Silva et al. 2013). Trondheimfjord (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 herrings (Silva et al. 2013, Eggers 2013) 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. The fact that these populations with apparent adaptations to life mostly spent inside fjord areas have been known to exist for up to a century suggests that they may be genetically unique as supported by the present study. In addition, the analysis of the fjord samples revealed that Landvikvannet sample was genetically distinguishable from all other fjord samples. This is most likely linked to the potential mixture with oceanic herring at various life stages that differ between Landvikvannet herring and the other fjord populations. The herring in Lindås pollene, Lusterfjord and Trondheimfjord may all mix with NSSH herring drifting into the fjord areas as larvae from spawning grounds outside the fjord areas. Albeit most of NSSH grow up in the Barents Sea, portions always tend use the fjords as nursery areas until age of two years (Holst & Slotte 1998). Even though the NSSH is genetically tuned to leave the fjords by two years age to grow further and join the adult spawning stock in the open ocean, one cannot exclude the possibility that some choose to stay, especially if there is numerical domination of the local herring of the same size (Huse et al. 2002). Hence, over time gene flow might have occurred consistently 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 NSSH is not clear as this local fjord is outside the observed spawning area of 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 condition at depths below 4 m. Therefore, the observed genetic differences among Landvikvannet herring and the other fjords is likely due to the fact that Landvikvannet was colonized by straying of WBSS herring already being adapted to low salinity conditions. In fact the very low vertebral count in Landvikvannet herring perfectly equals that of WBSS (55.7). However, data on vertebral counts and growth from the most recent study in Landvikvannet (2012) indicate that NSSH herring 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 three groups occupy this ecological niche at different times with some overlap in spawning stages. NSSH arrive first in March, while the coastal spring spawners arrive in March-April and finally Landvikvannet herring peaks in abundance in May. The genetic sample used in the present study was taken in May, which has been the main sampling period since 1980s used as a basis for the suggestion of a local fjord population. Given the results from 2012 further genetic studies are needed of the herring in the area of Landvikvannet to be able to draw firm conclusions.

Neutral vs. non neutral genetic markers

While levels of differentiation (F_{ST}'s) and their visual representation (MDS) tend to suggest similar genetic patterns when all loci are included or when excluding Cpa111, the primary results of the Bayesian cluster analysis would have resulted in fairly different

conclusions based on these two approaches. In fact, the first Bayesian cluster analysis including all loci supported a main differentiation between all fjords 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). On the contrary, 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 into Cap111 (the locus under selection) allele frequencies (Fig. 6) revealed a clear shift in allele frequencies among the fjords 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 Landvikvannet "sample" (NLSSH, sample 12) compared to the other fjord samples. Indeed, it exhibited a higher frequency at allele-287 than any other fjords and Northeast Atlantic samples, and did exhibit a somehow lower allele-275 frequency than the other fjord samples, differences that the Bayesian cluster analysis did not catch 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 interaction with NSSH but might also reflect potential different ongoing genetic evolution of the fjords populations.

Fisheries management

In term of management, although the power analysis performed suggested that a relatively low level of differentiation would be detectable with our research design, we only detected genetic differences among 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

394 different life-history patterns, which, in the absence of genetic evidence, should be integrated
395 (and are already) in fisheries management. The observed biological uniqueness of the
396 Norwegian local populations, and especially the exceptionality of Landvikvannet herring
397 should be investigated further to decipher their interactions with the NSSH component and
398 Western Baltic component to ensure appropriate management of herring stocks in future.
399
400 *Acknowledgements.* This research was supported by grants from the Working Group for
401 Fisheries Co-operation (AG-Fisk) of the Nordic Council of Ministers (HerMix project number
402 45-2011), the Icelandic Fisheries Research Fund (HerMix project number R007), the
403 Fisheries Research Fund of the Faroe Islands (Fiskivinnuroyndir, HerMix project number
404 201000742), the Icelandic Research Fund for Graduate Students RANNIS (Project number
405 100710001) and the Icelandic Student Innovation Fund RANNIS (project number
406 903100862). The FRS Marine Laboratory in Aberdeen, Scotland, UK, is acknowledged for
407 the provision of a herring sample west of Shetland. Bergur Poulsen, Havsbrún P/F, Faroe
408 Islands for their support and view from the industry. Sigurjón Arason at Matis is
409 acknowledged for his valuable contribution to the construction of the project and scientific
410 input.
411
412

413 LITERATURE CITED

414 Aasen O, (1952) The Lusterfjord Herring and its environment. Fiskeridirektoratets Skrifter
415 Serie Havundersøkelser 10:1-63
416 Amilhat E, Lorenzen K (2005) Habitat use, migration pattern and population dynamics of
417 chevron snakehead *Channa striata* in a rainfed rice farming landscape. J Fish Biol
418 67:23-34
419 André C, Larsson LC, Laikre L, Bekkevold D, Brigham J, Carvalho GR, Dahlgren TG,
420 Hutchinson WF, Mariani S, Mudde K, Ruzzante DE, Ryman N (2011) Detecting
421 population structure in a high gene-flow species, Atlantic herring (*Clupea harengus*):
422 direct, simultaneous evaluation of neutral vs putatively selected loci. Heredity
423 106:270-280
424 Anonymous (1962) Recommendations adopted by the Herring Committee. Rapp P.-V. Réun
425 Cons Int Explor Mer 1:1-73 [Append.].
426 Antao L, Lopes A, Lopes RJ, Beja-Pereira A, Luikart G (2008) LOSITAN: a workbench to
427 detect molecular adaptation based on a FST-outlier method. BMC Bioinfo 9:323-327
428 Arai T, Yang J, Miyazaki N (2006) Migration flexibility between freshwater and marine
429 habitats of the pond smelt *Hypomesus nipponensis*. J Fish Biol 68:1388-1398
430 Beaumont M, Nichols RA (1996) Evaluating loci for use in the genetic analysis of population
431 structure. Proc Roy Soc Lond B Biol Sci 263:1619-1626
432 Beaumont MA (2005) Adaptation and speciation: what can FST tell us? TREE 20:435-440
433 Bekkevold D, André C, Dahlgren TG, Clausen LA, Torstensen E, Mosegaard H, Carvalho
434 GR, Christensen TB, Norlinder E, Ruzzante DE (2005) Environmental correlates of
435 population differentiation in Atlantic herring. Evolution 59:2656-2668
436 Bowers AB, Holliday FGT (1961) Histological changes in the gonad associated with the
437 reproductive cycle of the herring (*Clupea harengus* L.). Mar Res 5:1-16
438 Bradbury IR, Hubert S, Higgins B, Borza T, Bowman S, Paterson IG, Snelgrove PlVR,
439 Morris CJ, Gregory RS, Hardie DC, Hutchings JA, Ruzzante DE, Taggart CT,
440 Bentzen P (2010) Parallel adaptive evolution of Atlantic cod on both sides of the
441 Atlantic Ocean in response to temperature. Proc Roy Soc B Biol Sci 277:3725-3734
442 Broch H (1906) Foreløpig meddelelse om sildeundersøgelserne. Aarsberetning vedkommende
443 Norges fiskerier for 1905:442-451
444 Broch H (1908) Norwegische heringsuntersuchen wahrend der jahre 1904-1906. Bergen
445 Museums Årbok 1:1-9
446 Brownstein MJ, Carpten JD, Smith JR (1996) Modulation of non-templated nucleotide
447 addition by Taq DNA polymerase: primer modifications that facilitate genotyping.
448 Biotechniques 20:1004-1006, 1008-1010

449 Cano JM, Shikano T, Kuparinen A, Merilä J (2009) Genetic differentiation, effective
450 population size and gene flow in marine fishes: implications for stock management. J
451 Integrat Field Biol 5:1-10
452 Carvalho GR, Hauser L (1994) Molecular genetics and the stock concept in fisheries. Rev
453 Fish Biol Fish 4:326-350
454 Clarke AD, Lewis A, Telmer KH, Shrimpton JM (2007) Life history and age at maturity of an
455 anadromous smelt, the eulachon *Thaleichthys pacificus* (Richardson). J Fish Biol
456 71:1479-1493
457 Conover DO, Clarke LM, Munch SB, Wagner GN (2006) Spatial and temporal scales of
458 adaptive divergence in marine fishes and the implications for conservation. J Fish Biol
459 69:21-47

460 Corander J, Majander KK, Cheng L, Merilä J (2013) High degree of cryptic population
461 differentiation in the Baltic Sea herring *Clupea harengus*. Mol Ecol 22:2931-2940
462 Curtis JMR, Vincent ACJ (2006) Life history of an unusual marine fish: survival, growth and
463 movement patterns of *Hippocampus guttulatus* Cuvier 1829. J Fish Biol 68:707-733
464 Dickey-Collas M, Nash RDM, Brunel T, van Damme CJG, Marshall CT, Payne MR, Corten
465 A, Geffen AJ, Peck MA, Hatfield EMC, Hintzen NT, Enberg Ka, Kell LT, Simmonds
466 EJ (2010) Lessons learned from stock collapse and recovery of North Sea herring: a
467 review. ICES J Mar Sci 67:1875-1886
468 Donaldson MR, Arlinghaus R, Hanson KC, Cooke SJ (2008) Enhancing catch-and-release
469 science with biotelemetry. Fish Fish 9:79-105
470 Dragesund O, Johannessen A, Ultang O (1997) Variation in migration and abundance of
471 Norwegian spring spawning herring (*Clupea harengus* L.). Sarsia 82:97-105
472 Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for
473 visualizing STRUCTURE output and implementing the Evanno method. Cons Genet
474 Res 4:359-361
475 Eggers F (2013) Metapopulation dynamics in Atlantic herring (*Clupea harengus* L.) along the
476 coast of southern Norway and in the local area of Landvikvannet. Master of Science in
477 Fisheries Biology and Fisheries Management. University of Bergen, 92 pp.
478 Einarsson H (1951) Racial analysis of Icelandic herrings by means of the otoliths. Rapports et
479 Procés Verbaux des Réunions du Conseil Interntational pour l'Exploration de la Mer
480 128:55-74
481 Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using
482 the software STRUCTURE: a simulation study. Mol Ecol 14:2611-2620
483 Foll M, Gaggiotti OE (2008) A genome-scan method to identify selected loci appropriate for
484 both dominant and codominant markers: A Bayesian Perspective. Genetics 180:977-
485 993
486 Fridriksson A, Aasen O (1950) The Norwegian-Icelandic herring tagging experiments. Rep
487 No 1. Fisk Dir Skr Ser Havunders 9:1-43
488 Fritsch M, Morizur Y, Lambert E, Bonhomme F, Guinand B (2007) Assessment of sea bass
489 (*Dicentrarchus labrax*, L.) stock delimitation in the Bay of Biscay and the English
490 Channel based on mark-recapture and genetic data. Fish Res 83:123-132
491 Gaggiotti OE, Bekkevold D, Jørgensen HBH, Foll M, Carvalho GR, Andre C, Ruzzante DE
492 (2009) Disentangling the effect of evolutionary, demographic, and environmental
493 factors influencing genetic structure of natural populations: Atlantic herring as a case
494 study. Evolution 63:2939-2951
495 Hauser L, Carvalho GR (2008) Paradigm shifts in marine fisheries genetics: ugly hypotheses
496 slain by beautiful facts Fish Fish 9:333-362
497 Helyar SJ, Limborg MT, Bekkevold D, Babbucci M, van Hout JKJ, Maes G, Bargelloni L, Nielsen
498 RO, Taylor MI, Carvalho GR, FishPopTrace Consortium, Panitz F. (2012) SNP discovery
499 using next generation transcriptomic sequencing in Atlantic Herring (*Clupea harengus*). PLoS
500 ONE **7**: e42089
501 Higgins RM, Danilowicz BS, Balbuena JA, Daníelsdóttir AK, Geffen AJ, Meijer WG, Modin
502 J, Montero FE, Pampoulie C, Perdiguero D, Schreiber A, Stéfansson MÖ, Wilson B
503 (2010) Multi-disciplinary fingerprints reveal the harvest location of cod (*Gadus*
504 *morhua*) in the Northeast Atlantic. Mar Ecol Prog Ser 404:197-206
505 Holst JC, Slotte A (1998) Effects of juvenile nursery on geographic spawning distribution in
506 Norwegian spring spawning herring (*Clupea harengus* L.). ICES J Mar Sci 55:987-
507 996
508 Huse G, Railsback SF, Fernø A (2002) Modelling changes in the migration pattern of herring:
509 collective behaviour and numerical domination. J Fish Biol 60:571-582

510 Huse G, Railsback SF, Fernø A (2002) Modelling changes in the migration pattern of herring:
511 collective behaviour and numerical domination. J Fish Biol 60:571-582.
512 Husebo A, Slotte A, Clausen LAW, Mosegaard H (2005) Mixing of populations or year class
513 twinning in Norwegian spring spawning herring? Mar Fresh Res 56:763-772
514 Hutchinson WF (2008) The dangers of ignoring stock complexity in fishery management: the
515 case of the North Sea cod. Biol Lett 4:693-695
516 ICES (2012) Report of the Working Group on Widely Distributed Stocks (WGWIDE), 21-27
517 August 2012, Lowestoft, United-Kingdom. ICES CM 2012/ACOM:16
518 Jakobsson J (1980) Exploitation of the Icelandic spring- and summer-spawning herring in
519 relation to fisheries management. Rapports et Procès Verbaux des Réunions du
520 Conseil International pour L'Exploration de la Mer 177:23-42
521 Jakobsson J, Vilhjlmsson H, Schopka SA (1969) On the biology of the Icelandic herring
522 stock. Rit Fiskideildar 4:1-18
523 Johannessen A, Nottestad L, Fernö A, Langard L, Skaret G (2009) Two components of
524 Northeast Atlantic herring within the same school during spawning: support for the
525 existence of a metapopulaion? ICES J Mar Sci 66:1740-1748
526 Jung K-M, Folkvord A, Kjesbu OS, Agnalt A, Thorsen A, Sundby S (2012) Egg buoyancy
527 variability in local populations of Atlantic cod (*Gadus morhua*). Mar Biol 159:1969-
528 1980
529 Jørgensen HBH, Hansen MM, Bekkevold D, Ruzzante DE, Loeschcke V (2005) Marine
530 landscapes and population genetic structure of herring (*Clupea harengus* L.) in the
531 Baltic Sea. Mol Ecol 14:3219-3234
532 Lamichhaney S, Barrio AM, Rafati N, Sundström G, Rubin C-J, Gilbert ER, Berglund J,
533 Wetterbom A, Laikre L, Webster MT, Grabherr M, Ryman N, Andersson L (2012)
534 Population-scale sequencing reveals genetic differentiation due to local adaptation in
535 Atlantic herring. Proc Natl Acad Sci USA 109:19345-19350
536 Langgård L (2013) Metapopulation dynamics in Atlantic herring (*Clupea harengus* L.) in a
537 small semi-enclosed coastal marine ecosystem. PhD in Fisheries Biology. University
538 of Bergen.
539 Libungan LA, Ólafsdóttir G, Skírnisdóttir S, Pálsson S, Pampoulie C, Björnsdóttir SH,
540 Ólafsson K, Óskarsson G, Daníelsdóttir AK (2012) Fourteen new microsatellite
541 markers for Atlantic herring *Clupea harengus*. J Fish Biol 81:1422-1426
542 Lie U, Dahl, O, Østvedt, OJ (1978). Aspects of the life history of the local herring stock in
543 Lindåspollene, western Norway. Fiskeridirektoratets Skrifter Serie Havundersøkelser
544 16:369-404
545 Limborg MT, Helyar SJ, de Bruyn M, Taylor MI, Nielsen EE, Ogden R, Carvalho GR,
546 Consortium F, Bekkevold D (2012) Environmental selection on transcriptome-derived
547 SNPs in a high gene flow marine fish, the Atlantic herring (*Clupea harengus*). Mol
548 Ecol 21:3686-3703
549 Mariani S, Hutchinson WF, Hatfield EMC, Ruzzante DE, Simmonds EJ, Dahlgren TG, Andre
550 C, Brigham J, Torstensen E, Carvalho GR (2005) North Sea herring population
551 structure revealed by microsatellite analysis. Mar Ecol Prog Ser 303:245-257
552 McQuinn IH (1997) Metapopulations and the Atlantic herring. Rev Fish Biol Fish 7:297-329
553 McPherson AA, O'Reilly PT, McParland TL, Jones MW, Bentzen P (2001) Isolation of nine
554 novel tetranucleotide microsatellites in Atlantic herring (*Clupea harengus*). Mol Ecol
555 Notes 1:31-32
556 Montero-Pau J, Gómez A, Muñoz J (2008) Application of an inexpensive and high-
557 throughput genomic DNA extraction method for the molecular ecology of
558 zooplanktonic diapausing eggs. Limnol Oceanogr Methods 6:218-222

559 Nielsen EE, Hansen MM, Meldrup D (2006) Evidence of microsatellite hitch-hiking selection
560 in Atlantic cod (*Gadus morhua* L.): implications for inferring population in nonmodel
561 organisms. Mol Ecol 15:3219-3229
562 Nielsen EE, Cariani A, Aoidh EM, MAes GE, Milano I, Ogden R, Taylor M, Hemmer-
563 Hansen J, Babbucci M, Bargelloni L, Bekkevold D, Diopere E, Grenfell L, Helyar S,
564 Limborg MT, Martinsohn JT, McEwing R, Panitz F, Patarnello T, Tinti F, Van Houdt
565 JKJ, Volckaert FAM, Waples RS, FishPop Trace consortium, Carvlho GR (2012) Gene-
566 associated markers provide tools for tackling illegal fishing and false eco-certification.
567 Nat Commun 3:851
568 O'Connel M, Dillon MC, Wright JM (1998) Development of primers for polymorphic
569 microsatellite loci in the Pacific herring (*Clupea harengus pallasi*). Mol Ecol 7:358-
570 360
571 Olsen JB, Lewis CJ, Kretschmer EJ, Wilson SL, Seeb JE (2002) Characterization of 14
572 tetranucleotide microsatellite loci derived from Pacific herring. Mol Ecol Notes 2:101-
573 103
574 Overholtz WJ (2002) The Gulf of Maine-Georges Bank Atlantic herring (*Clupea harengus*):
575 spatial pattern analysis of the collapse and recovery of a large marine fish complex.
576 Fish Res 57:237-254
577 Óskarsson GJ, Gudmundsdottir A, Sigurdsson T (2009) Variation in spatial distribution and
578 migration of Icelandic summer-spawning herring. ICES J Mar Sci 66:1762-1767
579 Ólafsson K, Hjörleifsdóttir S, Pampoulie C, Hreggviðsson GÓ, Guðjónsson S (2010) Novel
580 set of multiplex assays (SalPrint15) for efficient analysis of 15 microsatellite loci of
581 contemporary samples of the Atlantic salmon (*Salmo salar*). Mol Ecol Res 10:533-537
582 Pampoulie C, Daníelsdóttir AK, Thorsteinsson V, Hjörleifsson E, Marteinsdóttir G, Ruzzante
583 DE (2012) The composition of adult overwintering and juvenile aggregations of
584 Atlantic cod (*Gadus morhua* L.) around Iceland using neutral and functional markers:
585 a statistical challenge. Can J Fish Aquat Sci 69:307-320
586 Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using
587 multilocus genotype data. Genetics 155:945-959
588 Reiss H, Hoarau G, Dickey-Collas M, Wolff WJ (2009) Genetic structure of marine fish:
589 mismatch between biological and fisheries management units. Fish Fish 10:361-395
590 Ricklefs RE, Wikelski M (2002) The physiology/life history nexus. Trends Ecol Evol 17:462-
591 468
592 Rosenberg NA (2004) Distruct: a program for the graphical display of population structure.
593 Mol Ecol Notes 4:137-138
594 Rousset F (2008) Genepop'007: a complete re-implementation of the genepop software for
595 Windows and Linux. Mol Ecol Res 8:103-106
596 Runnstrom S (1941) Racial analysis of the herring in Norwegian waters. Fiskdir Skr Ser
597 Havunders 6:5-10
598 Ruzzante DE (1998) A comparison of several measures of genetic distance and population
599 structure with microsatellite data: bias and sampling variance. Can J Fish Aquat Sci
600 55:1-14
601 Ruzzante DE, Mariani S, Bekkevold D, André C, Mosegaard H, Clausen LAW, Dahlgren TG,
602 Hutchinson WF, Hatfield EMC, Torstensen E, Brigham J, Simmonds EJ, Laikre L,
603 Larsson LC, Stet RJM, Ryman N, Carvalho GR (2006) Biocomplexity in a highly
604 migratory pelagic marine fish, Atlantic herring. Proc Roy Soc London B Biol Sci
605 273:1459-1464
606 Ryman N, Palm S (2006) POWSIM: a computer program for assessing statistical power when
607 testing for genetic differentiation. Mol Ecol 6:600-602

608 Shaw PW, Turan C, Wright JM, O'Connel M, Carvalho GR (1999) Microsatellite DNA
609 analysis of population structure in Atlantic herring (*Clupea harengus*), with direct
610 comparison to allozyme and mtDNA RLFP analyses. Heredity 83:490-499
611 Silva FFG, Slotte A, Johannessen A, Kennedy J, Kjesbu OS (2013) Strategies for partition
612 between body growth and reproductive investment in migratory and stationary
613 populations of spring-spawning Atlantic herring (*Clupea harengus* L.). Fish Res
614 138:71-79
615 Smith JP, Robertson SG, Horn PL, Bull B, Anderson OF, Stanton BR, Oke CS (2002)
616 Multiple techniques for determining stock relationships between orange roughy,
617 *Hoplostethus atlanticus*, fishereies in the eastern Tasman Sea. Fish Res 58:119-140
618 Smylie M (2004) Herring. A history of the silver darlings. Tempus, Tempus publishing, The
619 Mill, Brimscombe Port, Gloucestershire:224pp
620 Sørensen, Ø. 2012. Comparative biology and population dynamics between Trondheimsfjord
621 herring and Norwegian Spring Spawning herring-Implications for management.
622 Master of Science in Fisheries Biology and Fisheries Management. University of
623 Bergen, 58 pp.
624 Syrjänen J, Kiljunen M, Karjalainen J, Eloranta A, Muotka T (2008) Survival and growth of
625 brown trout *Salmo trutta* L. embryos and the timing of hatching and emergence in two
626 boreal lake outlet streams. J Fish Biol 72:985-1000
627 Tamdrari H, Brêthes JC, Castonguay M, Duplisea DE (2012a) Homing and group cohesion in
628 Atlantic cod *Gadus morhua* revealed by tagging experiments. J Fish Biol 81:714-727
629 Tamdrari H, Castonguay M, Brêthes JC, Galbraith PS, Duplisea DE (2012b) The dispersal
630 pattern and behaviour of Atlantic cod (*Gadus morhua*) in the northern Gulf of St
631 Lawrence: results from tagging experiments. Can J Fish Aquat Sci 69:112-121
632 Teacher AGF, André C, Jonsson PR, Merilä J (2013) Oceanographic connectivity and
633 environmental correlates of genetic structuring in Atlantic herring in the Baltic Sea.
634 Evol Appl 6:549-567
635 Team RC (2012) R: A language and environment for statistical computing. R Foundation for
636 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://R-
637 project.org/.
638 Thorsteinsson V, Pálsson ÓK, Jónsdóttir IG, Pampoulie C (2012) Consistency in the
639 behaviour types of the Atlantic cod: repeatability, timing of migration and geo-
640 location. Mar Ecol Prog Ser 462:251-260
641 Toresen R, Østvedt OJ (2000) Variation in abundance of Norwegian spring-spawning herring
642 (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of
643 climatic fluctuations. Fish Fish 1:231-256
644 Turan C, Carvalho GR, Mork J (1998) Molecular analysis of Atlanto-Scandian herring
645 (Clupea harengus) populations using allozymes and mitochondrial DNA markers. J
646 Mar Biol Assoc UK 78:269-283
647 Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population
648 structure. Evolution 38:1358-1370
649 Whitlock RE, McAllister MK, Block BA (2012) Estimating fishing and natural mortality rates
650 for Pacific bluefin tuna (*Thunnus orientalis*) using electronic tagging data. Fish Res
651 119-120:115-127
652 Wood AD, Collie JS, Kohler NE (2007) Estimating survival of the shortfin mako *Isurus*
653 *oxyrinchus* (Rafinesque) in the north-west Atlantic from tag-recapture data. J Fish Biol
654 71:1679-1695
655

Table 1. Sampling areas and information for 14 samples of North Atlantic herring *Clupea harengus*. The maturity stage of individual fish is expressed in percentage per stages.

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

* numbers between brackets indicates the specific stage in which fish were. na, non available data.

700 **Figure legends**

701

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

706

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

709

710 Fig. 3. Multi-dimensional scaling plot of Atlantic herring *C. harengus* in Norwegian Sea and
711 surrounding waters: a) all loci included, b) without the outlier Cpa111. See Table 1 for sample
712 codes.

713

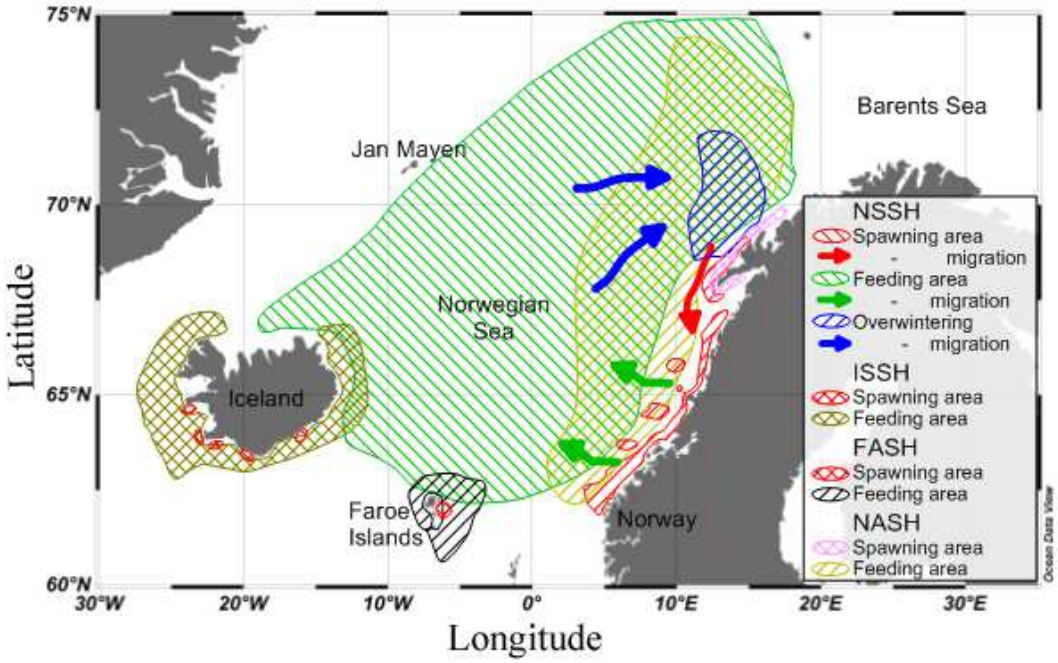
714 Fig. 4. Hierarchical Bayesian cluster analysis performed in STRUCTURE using all loci and
715 all samples. A total of 10 runs were performed for each K, from K = 1 to 10 with 350,000
716 Burn-in, 500,000 MCMC, using an admixture model with correlated allele frequencies and no
717 prior information on sample location. (a) Represents the first hierarchical level including all
718 samples. Two clusters were detected, the first one composed of composed of all Northeast
719 Atlantic samples, and the second of the fjord samples (NLSSH), (b) represents the second
720 hierarchical level only including the NLSSH samples. Two clusters were detected, the first
721 one composed of composed of sample 12, and the second of samples 11, 13 and 14. See Table
722 1 for sample codes.

723

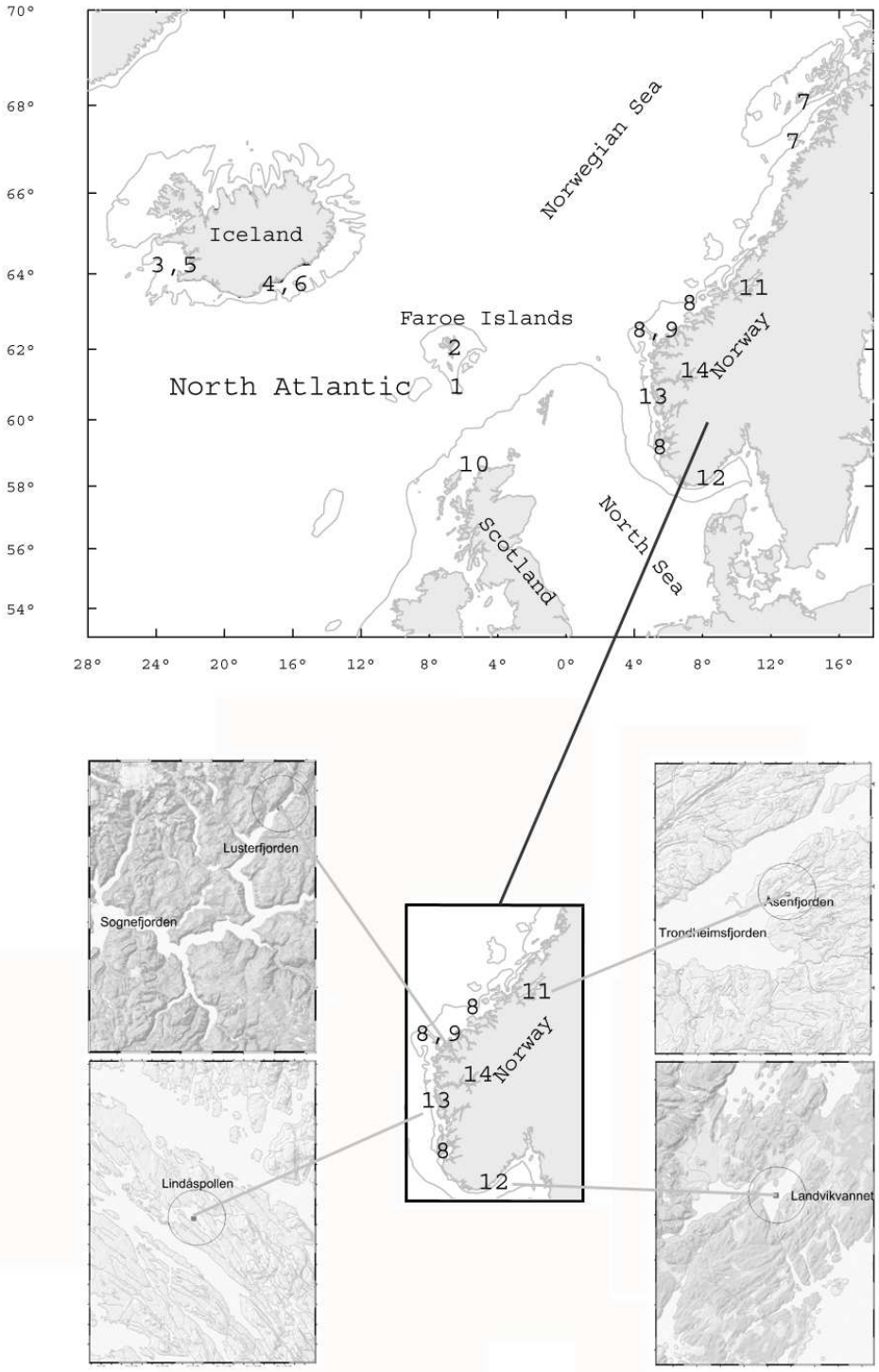
Fig. 5. Bayesian cluster analysis performed in STRUCTURE using neutral loci and all herring samples. A total of 10 runs were performed for each *K*, from *K* = 1 to 10 with 350,000 Burn-in, 500,000 MCMC, using an admixture model with correlated allele frequencies and no prior information on sample location. Additional hierarchical analyses did not detect any additional clusters within the two main groups, i.e. the Northeast Atlantic samples and the fjords samples (NLSSH). See Table 1 for sample codes.

Fig. 6. Allele frequencies at Cpa111 locus. All samples of North Atlantic populations were combined while allele frequencies of the four Norwegian local-spawning herring are depicted separately. NA, North Atlantic population; See Table 1 for sample codes.

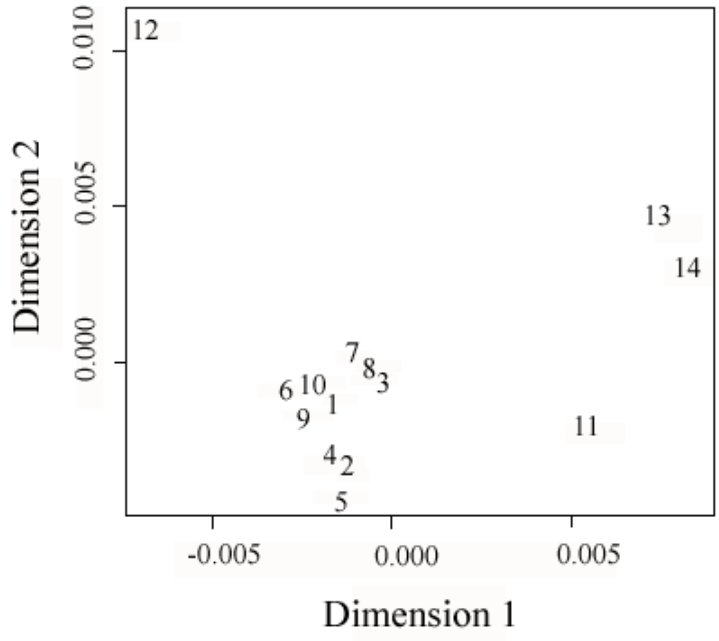
735



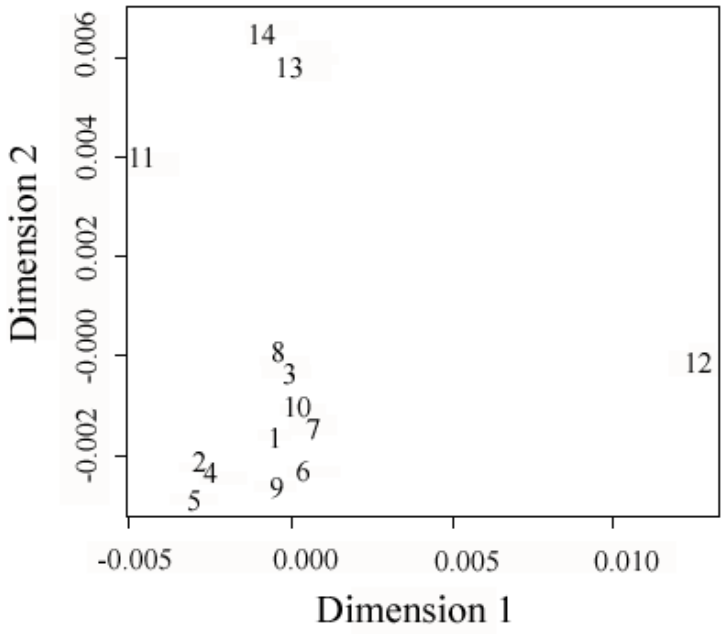
736
737 Fig. 1.
738
739



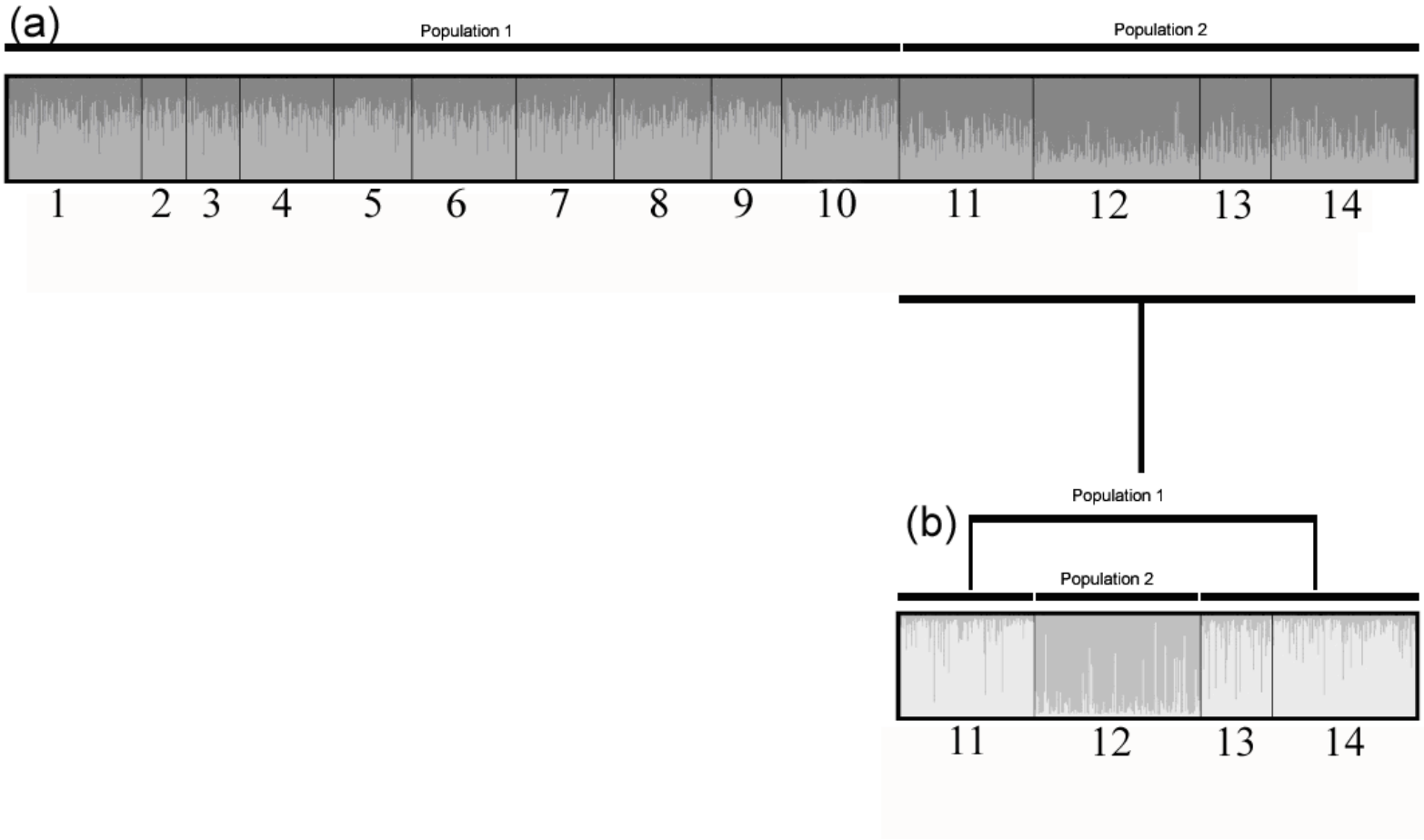
740
741 Fig. 2.
742



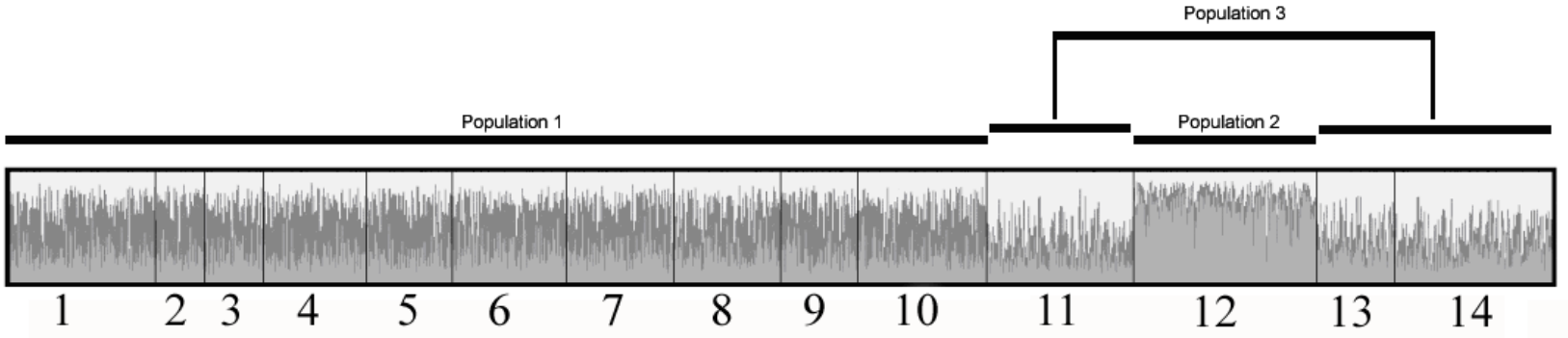
743
744 Fig. 3a.



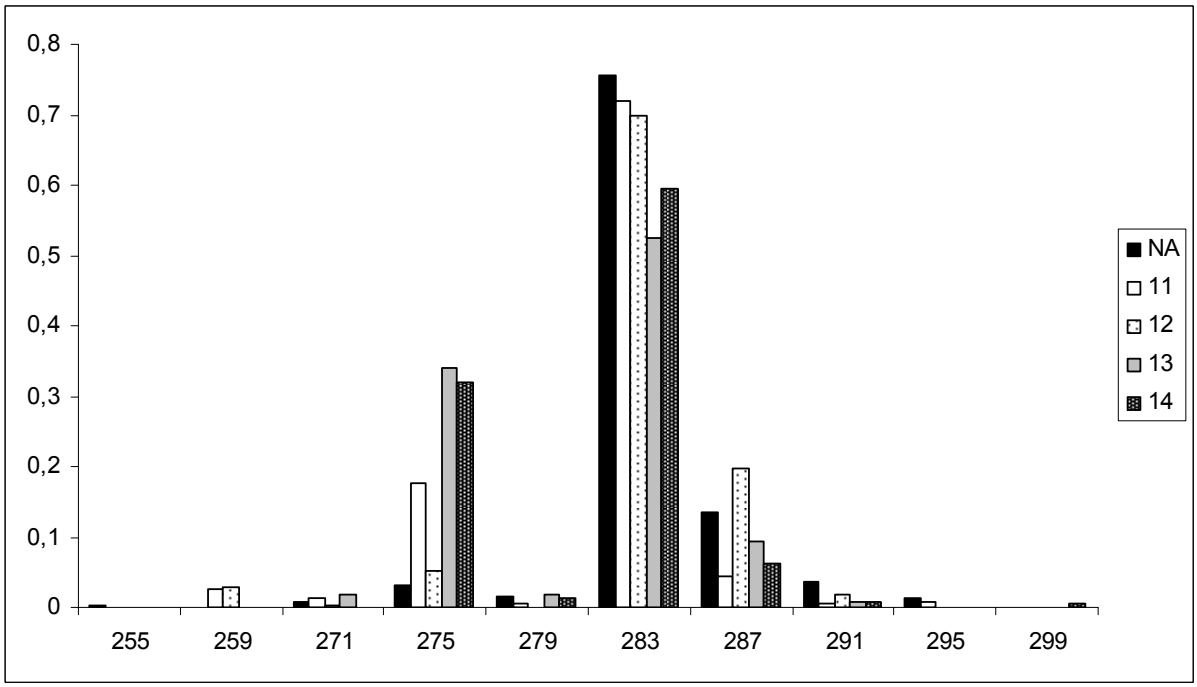
745
746 Fig. 3b.



747
748 Fig. 4.
749
750


Population 3
Population 1
Population 2
1
2
3
4
5
6
7
8
9
10
11
12
13
14

751
752 Fig. 5.


0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
255
259
271
275
279
283
287
291
295
299
NA
11
12
13
14
Fig. 6.

Supplementary Table S1: Characteristics of multiplexes for 24 microsatellite loci of Atlantic herring *C. harengus*. *Tm* stands for annealing temperature and *µl* for micro-litres of primer used. Genotyping quality reports the percentage of individuals which were correctly genotyped at a specific microsatellite loci.

Multiplex	Loci	µl	Tm	Dye	Allele range	Genotyping quality
SildPrint2	Cha113	0.10	58	PET	104-156	97
	Cha17	0.18	58	6FAM	85-189	99
	Cha1059	0.03	58	NED	63-127	98
	Cha1020	0.14	58	VIC	153-245	90
	Cpa111	0.16	58	VIC	256-295	91
SildPrint4	Cpa113	0.06	57	PET	118-230	93
	Cha1017	0.15	57	VIC	161-213	98
	Cpa103	0.13	57	6FAM	163-263	93
	Cpa112	0.14	57	VIC	232-416	92
	Cpa108	0.10	57	NED	233-275	96
SildPrint6	msild12	0.03	58	VIC	73-139	97
	Cha1027	0.10	58	PET	113-213	100
	Cha63	0.10	58	NED	137-181	100
	Cpa101	0.06	58	VIC	169-321	98
SildPrint7	Cpa104	0.08	60	NED	180-506	97
	Cpa114	0.08	60	VIC	178-282	98
	Cha1202	0.10	60	6FAM	97-173	100
SildPrint9	Cha4	0.07	58	VIC	106-194	99
	Cpa102	0.06	58	NED	128-420	99
	msild13	0.16	58	6FAM	176-251	99
SildPrint13	msild17	0.10	58	VIC	336-420	95
	msild24	0.15	58	PET	165-351	96
	msild27	0.06	58	6FAM	185-233	99
	msild32	0.10	58	VIC	172-272	99

Supplementary Table S2: Genetic diversity of the 24 microsatellite loci. Expected heterozygosity (H_e) and deviation from HWE (F_{IS}) for 24 microsatellite loci in 14 samples of Atlantic herring *C. harengus*. See Table 1 for sample codes.

Sample	1		2		3		4		5		6		7		8		9		10		11		12		13		14	
Locus	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}	H_e	F_{IS}
Cha4	0.874	**0.091**	0.884	-0.031	0.862	**0.098**	0.856	0.037	0.889	0.076	0.875	-0.025	0.853	0.020	0.858	0.020	0.865	0.058	0.868	0.074	0.884	0.034	0.852	0.012	0.854	0.060	0.882	**0.020**
Cha17	0.941	0.025	0.937	0.002	0.929	0.025	0.944	0.010	0.941	0.023	0.944	0.026	0.943	0.019	0.949	**0.036***	0.945	0.024	0.941	0.015	0.942	0.006	0.928	0.007	0.941	-0.055	0.940	0.025
Cha63	0.862	0.010	0.878	0.136	0.862	**0.019**	0.868	**0.005**	0.860	-0.054	0.858	0.005	0.851	0.044	0.855	-0.060	0.847	-0.024	0.841	0.014	0.846	0.021	0.816	-0.083	0.859	-0.022	0.863	0.053
Cha113	0.891	-0.003	0.875	0.016	0.893	0.026	0.884	-0.017	0.883	0.039	0.872	-0.005	0.877	0.091	0.866	-0.036	0.863	-0.003	0.889	0.010	0.881	0.036	0.861	0.023	0.905	0.010	0.881	-0.014
Cha1017	0.793	0.018	0.788	0.054	0.839	0.066	0.834	0.095	0.843	0.051	0.798	0.134	0.825	0.008	0.797	0.098	0.833	0.124	0.815	0.047	0.802	0.050	0.778	-0.015	0.762	0.084	0.812	0.035
Cha1020	0.926	0.008	0.931	-0.003	0.920	-0.004	0.918	-0.042	0.923	**0.028**	0.923	-0.017	0.914	0.026	0.915	0.013	0.921	0.004	0.920	0.036	0.917	-0.036	0.881	-0.055	0.871	-0.073	0.901	-0.044
Cha1027	0.934	-0.012	0.923	0.096	0.907	-0.022	0.936	**0.052**	0.923	0.032	0.930	0.058	0.939	-0.023	0.938	0.139	0.929	**-0.022**	0.930	0.061	0.922	0.028	0.917	0.023	0.908	0.033	0.914	0.008
Cha1059	0.670	0.035	0.695	0.257	0.708	0.132	0.674	0.065	0.666	**0.020**	0.663	0.061	0.660	**0.130***	0.679	0.059	0.663	**-0.043**	0.729	0.091	0.693	0.123	0.668	**0.035**	0.787	0.080	0.680	0.143
Cha1202	0.701	0.057	0.744	0.082	0.676	-0.007	0.709	-0.048	0.763	-0.056	0.722	0.023	0.750	0.060	0.761	**0.097**	0.761	0.009	0.750	-0.085	0.753	0.002	0.704	-0.008	0.760	0.027	0.752	0.065
Cpa101	0.919	0.000	0.916	0.006	0.909	0.033	0.915	0.047	0.910	0.119	0.915	0.028	0.913	-0.039	0.914	-0.036	0.912	0.044	0.926	-0.006	0.918	-0.011	0.900	0.054	0.912	0.040	0.916	0.032
Cpa102	0.923	-0.024	0.927	-0.038	0.912	0.034	0.929	-0.031	0.922	0.050	0.924	0.028	0.927	0.062	0.928	**-0.001**	0.923	0.048	0.930	0.002	0.939	-0.007	0.913	-0.003	0.913	-0.053	0.919	0.060
Cpa103	0.874	0.045	0.880	0.162	0.878	0.085	0.891	0.086	0.878	0.034	0.885	**0.130**	0.884	**0.025**	0.883	0.096	0.870	0.047	0.874	0.144	0.874	-0.018	0.884	0.077	0.865	0.039	0.839	**0.045**
Cpa104	0.836	0.022	0.840	0.120	0.823	0.049	0.870	0.041	0.834	0.073	0.878	**0.040**	0.823	0.155	0.810	0.0182	0.847	0.101	0.832	0.024	0.739	0.071	0.830	0.067	0.719	-0.023	0.699	0.057
Cpa108	0.481	0.070	0.535	0.103	0.492	0.121	0.540	0.135	0.447	0.024	0.461	-0.043	0.424	**-0.093**	0.543	0.072	0.448	0.059	0.457	0.025	0.627	-0.018	0.396	-0.083	0.533	0.020	0.576	0.082
Cpa111	0.434	-0.003	0.389	-0.028	0.331	0.003	0.372	-0.001	0.397	0.021	0.402	0.033	0.502	0.009	0.464	0.0138	0.402	0.140	0.349	0.041	0.447	-0.085	0.468	-0.010	0.600	0.019	0.541	-0.065
Cpa112	0.904	-0.027	0.882	0.066	0.879	-0.078	0.889	0.003	0.886	0.033	0.887	-0.020	0.860	0.038	0.904	**-0.092**	0.878	0.085	0.885	-0.017	0.901	-0.019	0.791	-0.065	0.872	-0.050	0.880	-0.017
Cpa113	0.937	0.030	0.921	-0.044	0.919	-0.025	0.935	-0.025	0.925	0.035	0.929	0.016	0.928	0.010	0.919	0.035	0.926	0.030	0.929	0.011	0.935	0.010	0.886	0.022	0.930	0.035	0.924	-0.020
Cpa114	0.917	0.043	0.903	-0.038	0.902	0.087	0.905	0.049	0.905	0.111	0.908	0.013	0.913	0.089	0.918	0.038	0.910	-0.013	0.905	0.016	0.912	-0.010	0.908	0.044	0.903	0.048	0.909	0.008
msild12	0.883	0.042	0.849	-0.075	0.892	0.036	0.873	-0.040	0.874	0.004	0.877	0.016	0.876	**-0.007**	0.893	-0.032	0.883	0.011	0.881	0.005	0.881	0.086	0.860	0.044	0.873	0.015	0.879	0.025
msild13	0.898	0.012	0.898	0.011	0.899	0.014	0.884	-0.004	0.898	-0.026	0.901	-0.057	0.894	0.005	0.881	0.051	0.907	0.021	0.895	0.028	0.865	0.003	0.845	-0.006	0.838	-0.003	0.851	**0.012**
msild17	0.895	0.055	0.898	0.042	0.881	-0.045	0.887	0.024	0.884	0.030	0.888	0.056	0.878	0.002	0.878	0.023	0.894	0.057	0.896	0.058	0.857	-0.034	0.811	0.005	0.847	0.123	0.821	-0.029
msild24	0.957	0.023	0.943	-0.021	0.943	**0.039**	0.956	**0.053**	0.951	**0.062**	0.951	**0.034**	0.953	0.041	0.955	-0.006	0.951	-0.016	0.961	0.004	0.949	-0.014	0.925	-0.018	0.945	-0.048	0.952	**0.030**
msild27	0.816	0.013	0.790	0.007	0.811	0.040	0.786	0.033	0.791	-0.015	0.823	0.054	0.801	-0.013	0.787	-0.039	0.753	0.020	0.806	0.032	0.816	0.067	0.782	-0.015	0.808	0.010	0.811	0.004
msild32	0.910	-0.028	0.899	**0.178**	0.904	-0.025	0.905	0.047	0.891	0.022	0.907	-0.026	0.902	-0.053	0.904	0.056	0.903	0.041	0.908	0.061	0.893	-0.020	0.897	0.040	0.890	-0.037	0.913	-0.028
Overal all loci	0.844	0.020	0.850	0.042	0.841	0.028	0.845	0.022	0.843	0.032	0.843	0.024	0.841	**0.025***	0.847	0.031	0.842	0.032	0.842	0.028	0.845	0.012	0.813	0.007	0.838	0.010	0.836	0.019

Values in bold indicate significant deviations from HWE (Exact tests, $p < 0.05$).
*Values remaining significant after Bonferroni correction ($\alpha = 0.05/168 = 0.0003$).

Supplementary Table S3: Results from Lositan outlier tests for the 24 microsatellite loci in 14 samples of Atlantic herring *C. harengus*. Expected heterozygosity (H_E) and F_{ST} are given. The loci in bold were identified as 95% outliers, while those marked with asterix were identified as significant outliers at a false discovery rate of 0.01.

Locus	Heterozygosity	F_{ST}	P(Simul F_{ST} < Sample F_{ST})
Cha4	0.881	0.008	0.824
Cha17	0.948	0.002	0.113
Cha63	0.863	0.003	0.344
Cha113	0.889	0.003	0.358
Cha1017	0.816	0.003	0.389
Cha1020	0.927	0.008	0.882
Cha1027	0.935	0.004	0.480
Cha1059	0.695	0.004	0.471
Cha1202	0.742	0.001	0.293
Cpa101	0.922	0.002	0.236
Cpa102	0.935	0.006	0.706
Cpa103	0.885	0.004	0.483
Cpa104	0.824	0.007	0.691
Cpa108	0.504	0.005	0.547
Cpa111*	**0.457**	**0.040**	**0.998**
Cpa112	0.894	0.011	0.940
Cpa113	0.936	0.006	0.694
Cpa114	0.916	0.002	0.209
msild12	0.884	0.002	0.269
msild13	**0.899**	**0.012**	**0.986**
msild17	0.889	0.012	0.972
msild24	0.960	0.003	0.234
msild27	0.805	0.001	0.239
msild32	0.910	0.003	0.298

Supplementary Table S4: Outlier tests performed in BAYESCAN for the 24 microsatellite loci in 14 samples of Atlantic herring *C. harengus*. The posterior probability for the model including selection (p), the log10 of the Posterior Odds for the model including selection (log10(PO)), and the estimated alpha coefficient indicating the strength and direction of selection (alpha; positive values indicate positive selection, while negative values indicate putative balancing selection) are given for each locus. It should be noted that the power to detect loci under putative balancing selection is low. The loci in bold were identified as significant outliers under a false discovery rate of 0.05.

Locus	p	log10(PO)	alpha	F_{ST}
Cha4	1	1000	-1.40	0.006
Cha17	1	1000	-2.36	0.002
Cha63	1	1000	-2.19	0.003
Cha113	1	1000	-1.77	0.004
Cha1017	1	1000	-2.46	0.002
Cha1020	1	1000	-1.14	0.006
Cha1027	1	1000	-1.81	0.004
Cha1059	1	1000	-2.30	0.003
Cha1202	1	1000	-2.04	0.003
Cpa101	1	1000	-2.71	0.002
Cpa102	1	1000	-1.60	0.005
Cpa103	1	1000	-1.48	0.006
Cpa104	1	1000	-2.03	0.003
Cpa108	1	1000	-1.65	0.005
Cpa111	**0.046**	**-1.23**	**-0.007**	**0.024**
Cpa112	1	1000	-1.17	0.008
Cpa113	1	1000	-1.78	0.004
Cpa114	1	1000	-2.38	0.002
msild12	1	1000	-2.60	0.002
msild13	1	1000	-1.11	0.009
msild17	1	1000	-0.96	0.010
msild24	1	1000	-2.23	0.003
msild27	1	1000	-2.31	0.003
msild32	1	1000	-2.35	0.003

Supplementary Table S5: Power of the 24 microsatellite loci in 10 samples of Atlantic herring *C. harengus*. The Norwegian local spring-spawning herring were excluded from the analysis. Estimate of the resolution power of the microsatellite loci were performed using POWSIM (Ryman & Palm 2006).

Expected F_{ST}	Average F_{ST}	χ^2-test	Fisher's test	N_e	Generation (t)	**Runs**
0.0000	0.0000	0.077	0.075	1,000	0	1,000
0.0000	0.0000	0.089	0.076	5,000	0	1,000
0.0010	0.0010	1.000	1.000	500	1	1,000
0.0010	0.0010	1.000	1.000	1,000	2	1,000
0.0010	0.0010	1.000	1.000	5,000	10	1,000
0.0025	0.0025	1.000	1.000	1,000	5	1,000
0.0050	0.0050	1.000	1.000	1,000	10	1,000

The resolution power is assessed by simulating different expected level of F_{ST} according to the effective population size (N_e) and generations (t) and to Nei (1987) formula: $F_{ST} = 1 - (1 - 1/2N_e)^t$. The significance, evaluated using Fisher's exact tests as well as χ^2 tests, reflects the power to detect any given level of differentiation (Average F_{ST}) with the sampling design developed during our study. N_e values used during the test are based on estimates calculated from fisheries data. "Runs" denotes the number of simulation performed. The setting $F_{ST} = 0$ and t = 0 estimates α (type I error; in the absence of genetic drift).

Supplementary Table S6: Genetic differentiation among samples. Pairwise F_{ST} (above diagonal) and p-values (below diagonal) among 14 samples of Atlantic herring *C. harengus* based on allelic frequencies at 24 microsatellite loci. See Table 1 for sample codes.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0	-0.0010	-0.0008	-0.0003	0.0006	-0.0007	-0.0003	0.0003	0.0008	0.0007	**0.0074***	**0.0127***	**0.0106***	**0.0110***
2	0.998	0	-0.0006	-0.0004	-0.0002	0.0001	-0.0005	-0.0001	0.0012	-0.0004	**0.0082***	**0.0154***	**0.0117***	**0.0115***
3	0.907	0.850	0	-0.0002	-0.0009	-0.0008	-0.0014	0.0001	0.0007	-0.0013	**0.0064***	**0.0124***	**0.092***	**0.0010***
4	0.494	0.803	0.490	0	0.0005	-0.0001	-0.0001	**0.0003**	0.0011	**0.0024**	**0.0087***	**0.0150***	**0.0122***	**0.0116***
5	0.127	0.808	0.598	0.117	0	**-0.0005**	-0.0001	**0.0011**	**0.0012**	**0.0015**	**0.0088***	**0.0160***	**0.0130***	**0.0115***
6	0.928	0.929	0.916	0.639	0.038	0	0.0009	-0.0003	0.0001	0.0002	**0.0082***	**0.0115***	**0.0122***	**0.0122***
7	0.972	0.951	0.986	0.590	0.310	0.957	0	-0.0007	-0.0001	0.0003	**0.0073***	**0.0113***	**0.0093***	**0.0101***
8	0.138	0.811	0.720	0.024	0.038	0.912	0.972	0	-0.0001	0.0008	**0.0067***	**0.0120***	**0.0090***	**0.0092***
9	0.097	0.766	0.549	0.122	0.018	0.332	0.497	0.014	0	-0.0001	**0.0074***	**0.0127***	**0.0121***	**0.0122***
10	0.112	0.783	0.989	0.001	0.006	0.359	0.155	0.416	0.083	0	**0.0075***	**0.0119***	**0.0115***	**0.0107***
11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0	**0.0182***	**0.0079***	**0.0069***
12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0	**0.0160***	**0.0169***
13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0	**0.0022**
14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0

Emboldened values differ significantly from zero (Fisher's exact test. $p < 0.05$).
***** Values remaining significant after Bonferroni correction ($\alpha = 0.05/91 = 0.0005$).

Supplementary Table S7: Genetic differentiation among samples. Pairwise F_{ST} (above diagonal) and p-values (below diagonal) among 14 samples of Atlantic herring *C. harengus* based on allelic frequencies at Cpa111. See Table 1 for sample codes.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	0	-0.0066	0.0013	-0.0020	-0.0021	-0.0038	-0.0004	0.0011	-0.0048	0.0023	0.0300	0.0054	0.1196	0.0965
2	0.791	0	-0.0087	-0.0070	-0.0067	-0.0077	0.0018	0.0018	-0.0102	-0.0067	0.0282	0.0060	0.1234	0.1000
3	0.636	0.891	0	-0.0048	-0.0024	0.0004	0.0137	0.0155	-0.0052	-0.0050	0.0266	0.0162	0.1367	0.1053
4	0.616	0.313	0.445	0	-0.0049	-0.0022	0.0091	0.0109	-0.0042	-0.0002	0.0308	0.0135	0.1389	0.1078
5	0.744	0.871	0.586	0.652	0	-0.0020	0.0091	0.0137	-0.0024	0.0035	0.0288	0.0177	0.1325	0.1041
6	0.691	0.587	0.162	0.111	0.405	0	0.0044	0.0021	-0.0050	-0.0006	0.0427	0.0086	0.1435	0.1176
7	0.756	0.566	0.408	0.136	0.164	0.083	0	-0.0035	0.0010	0.0134	0.0263	-0.0003	0.0836	0.0715
8	0.424	0.483	0.217	0.124	0.110	0.261	0.517	0	-0.0014	0.0084	0.0468	-0.0038	0.1112	0.1002
9	0.750	0.893	0.923	0.492	0.646	0.342	0.465	0.698	0	-0.0048	0.0301	0.0031	0.1233	0.0998
10	0.097	0.480	0.770	0.066	0.051	0.118	**0.018**	0.270	0.884	0	0.0440	0.0122	0.1620	0.1277
11	**0.000***	**0.000***	**0.007**	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	0	0.0371	0.0580	0.0334
12	**0.001**	**0.015**	**0.052**	**0.004**	**0.000***	**0.000***	**0.002**	**0.027**	**0.019**	**0.001**	**0.000***	0	0.1042	0.0890
13	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.001**	**0.000***	0	-0.0004
14	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	**0.000***	0.320	0

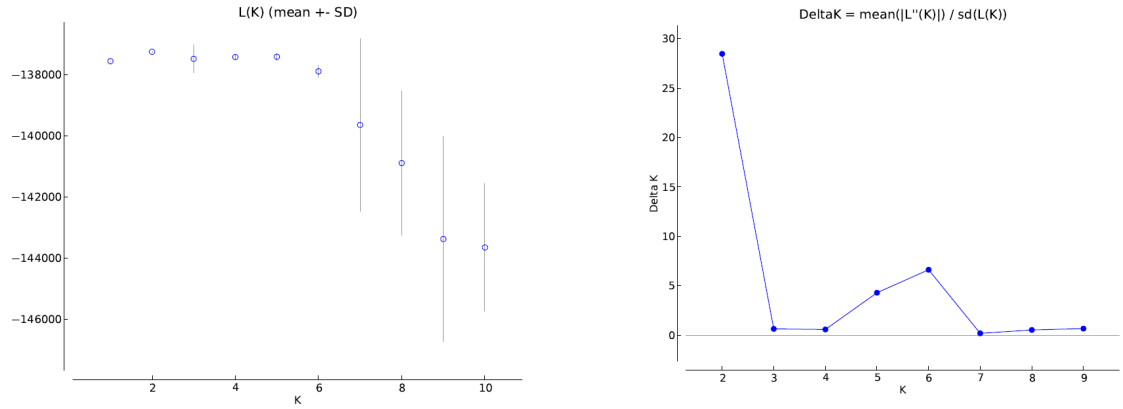
Emboldened values differ significantly from zero (Fisher's exact test. $p < 0.05$).
* Values remaining significant after Bonferroni correction ($\alpha = 0.05/91 = 0.0005$).

Supplementary Table S8: Results from the hierarchical Bayesian cluster analysis (STRUCTURE) based on all 24 microsatellite loci and all samples. STRUCTURE was run using 350,000 burn-in and 500,000 iterations for 10 independent runs for K = 1 to 10 for the North Atlantic samples and from K = 1 to 4 for the local Norwegian fjords (samples 11, 12, 13 and 14). An admixture model with correlated allele frequencies without prior information on sample location was implemented. Bold values indicate the most likely number of clusters.

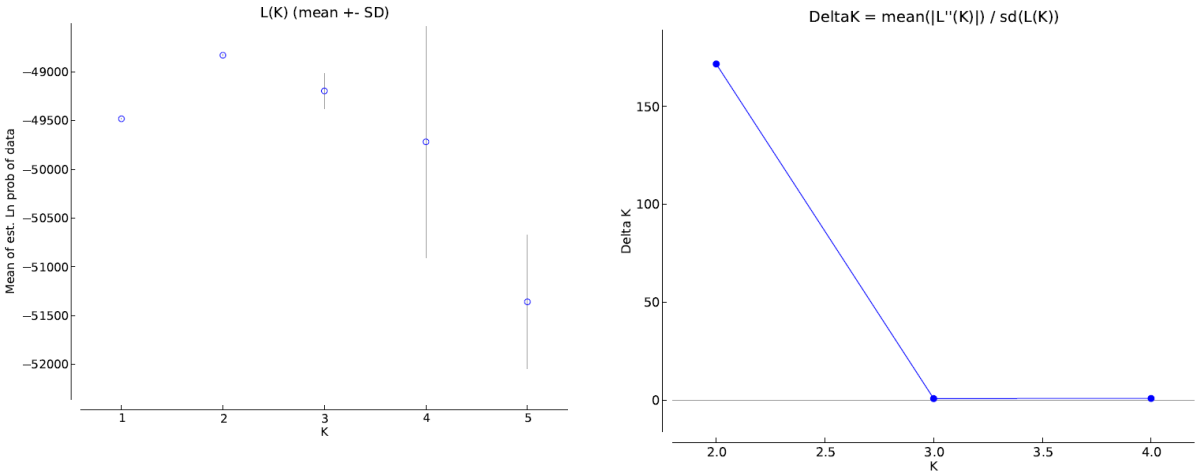
	K	Mean LnP(K)	StDev LnP(*K*)
North Atlantic	**1**	**-87102**	**0.2898**
	2	-87261	12.7600
	3	-87740	91.5819
	4	-88410	95.0116
	5	-89562	271.3621
	6	-91281	799.5722
	7	-93083	1390.0332
	8	-95410	1819.3528
	9	-95538	2152.4678
	10	-95920	1641.7548
Local fjords (all)	1	-49481	2.0991
	2	**-48829**	**5.9326**
	3	-49195	180.2179
	4	-49718	1186.7621
Local fjords (samples 11, 13 and 14)	**1**	**-33530**	**1.0390**
	2	-33627	23.2868
	3	-34463	254.8380

Supplementary Table S9: Results from the hierarchical Bayesian cluster analysis (STRUCTURE) based only on neutral microsatellite loci and all samples. STRUCTURE was run using 350,000 burn-in and 500,000 iterations for 10 independent runs for $K = 1$ to 10 for the North Atlantic samples and from $K = 1$ to 3 for the local Norwegian fjords (samples 11, 13 and 14). An admixture model with correlated allele frequencies without prior information on sample location was implemented. Bold values indicate the most likely number of clusters.

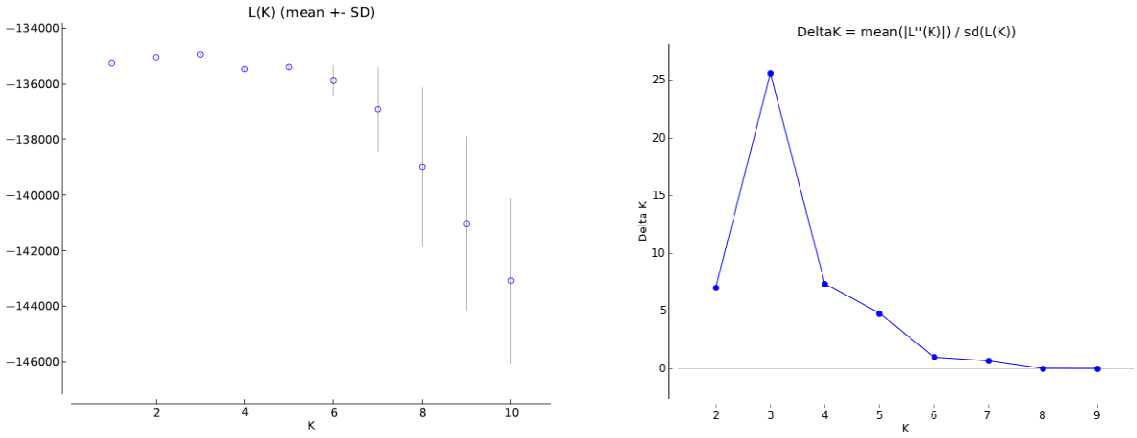
	K	Mean LnP(K)	StDev LnP(K)
North Atlantic	**1**	**-85817**	**0.1871**
	2	-85981	25.6621
	3	-86425	74.1802
	4	-87096	124.9924
	5	-88564	489.7930
	6	-90622	1073.9283
	7	-92667	2955.3703
	8	-94162	2935.9272
	9	-96560	3065.5698
	10	-97251	3204.5460
Local fjords	**1**	**-32919**	**0.6579**
	2	-32999	21.2130
	3	-33709	251.2843



Supplementary Fig. S1: Results of the Bayesian cluster analysis performed in Structure for all microsatellite loci and all samples. Two clusters were detected both at the LnP(*K*) (left figure) and Δ*K* levels (Right figure). STRUCTURE was run using 350,000 burn-in and 500,000 iterations for 10 independent runs for *K* = 1 to 10 using an admixture model with correlated allele frequencies. No prior information on sample location was implemented.



Supplementary Fig. S2: Results of the Bayesian cluster analysis performed in Structure for all microsatellite loci and the fjord samples. Two clusters were detected both at the LnP(*K*) (left figure) and Δ*K* levels (Right figure). STRUCTURE was run using 350,000 burn-in and 500,000 iterations for 10 independent runs for *K* = 1 to 5 using an admixture model with correlated allele frequencies. No prior information on sample location was implemented.



Supplementary Fig. S3: Results of the Bayesian cluster analysis performed in Structure for neutral microsatellite loci only and all samples. Three clusters were detected both at the LnP(*K*) (left figure) and Δ*K* levels (Right figure). STRUCTURE was run using 350,000 burn-in and 500,000 iterations for 10 independent runs for *K* = 1 to 10 using an admixture model with correlated allele frequencies. No prior information on sample location was implemented. No additional clusters were detected.