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Stock structure of Atlantic herring (*Clupea harengus* L.) in the Norwegian Sea and adjacent waters

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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,

145 VIC, NED or PET). Polymerase chain reactions (PCR) were performed in Multiplexes
146 (Supplementary Table S1) as follows: 10 µl volume containing 2-3 µl DNA (10-100 ng/µl),
147 0.80 µl of dNTP (10mM), 0.6-1.2 U Teg polymerase (Matís Ltd., Taq comparable, see
148 Ólafsson et al. 2010), 1 µl of 10x buffer (Matís Ltd.), 0.03-0.25 µl of a 50:50 ratio of labelled
149 forward (100 µM) and reverse (100 µM) primer tagged on the 5´-end with a GTTTCTT PIG-
150 tail (Brownstein et al. 1996) adding 1 µl betaine (5 M) when improvement of DNA
151 amplification was needed. Samples were analysed on an ABI PRISM 3730 sequencer using
152 the GeneScan-500 LIZ size standard and genotyped with GeneMapper v4.0 (Applied
153 Biosystems).
154
155 **Genetic analyses**
156 As the neutrality assumption of genetic markers is crucial for the conclusion drawn from
157 genetic data, we applied the coalescent-based simulation methods of Beaumont and Nichols
158 (Beaumont & Nichols 1996) to detect potential outlier loci (loci under selection). Coalescent
159 simulations were performed with the software LOSITAN (Antao et al. 2008) with samples of
160 the same size as the observed samples assuming an island model with 100 islands. A total of
161 100,000 independent loci were generated with the infinite allele mutation model and the
162 "neutral" mean F_{ST} function (outlier loci were excluded to calculate the initial mean F_{ST}).
163 Simulated distribution of F_{ST} values conditional to heterozygosity under a neutral model were
164 obtained and thus compared to observed F_{ST} values to identify potential outlier loci. In
165 addition, we performed outliers' tests in BayeScan (Foll & Gaggiotti 2008), which allows for
166 different demographic histories and drift between populations. BayeScan was run with 50,000
167 Burn-in, 50 thinning, a sample size of 1,000, 300,000 iterations, 20 pilot runs with a length of
168 5,000 and a FDR of 0.05. Outliers which were identified with both methods (LOSITAN and
169 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

195 optimal number of *K* using the Evanno's method (Evanno et al. 2005). DISTRUCT was then
196 used to visualise the data (Rosenberg 2004). As STRUCTURE is likely to detect the highest
197 level of differentiation among the samples, we conducted a hierarchical analysis by
198 performing similar STRUCTURE runs on detected populations (*K*) containing several
199 samples.
200

201 **RESULTS**

202 **Genetic diversity**

203 Biological information retrieved from the samples is listed in Table 1. Except sample 1
204 and 14, most of the fish collected were ready to spawn (maturity stage 5) or spawning
205 (maturity stage 6) (Table 1). The number of alleles per locus was high, ranging from 9
206 (Cap111) to 63 (msild24; data not shown). The unbiased expected heterozygosity per sample
207 ranged from 0.836 (NSSH4) to 0.850 (FSSH) (Supplementary Table S2). Genotypic
208 proportion were out of HWE in 26 of 336 exact tests, of which two remained significant after
209 the Bonferroni correction for multiple tests, and were not attributable to any loci or samples
210 (Supplementary Table S2).
211

212 **Outlier tests**

213 Simulations for detection of outlier loci performed in LOSITAN suggested that two loci
214 fell outside the 95% confidence interval; locus Cpa111 and msild13 were suggested to be
215 under positive selection (Supplementary Table S3). Using a 99% confidence interval, only
216 Cpa111 was suggested to be under positive selection (Supplementary Table S3). BayeScan
217 simulations only identified Cpa111 as putatively under selection (Supplementary Table S4).
218 Hence, all following structure analyses were performed with and without the outlier locus
219 (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.

269 1999) to investigate it in the Norwegian Sea and surrounding waters, including the Norwegian
270 local spawning herring. The results of this study showed that, even with 23 neutral and one
271 non-neutral microsatellite loci, the Atlantic herring did not exhibit any significant genetic
272 differentiation among stocks across the investigated area, although the Norwegian local-
273 spawning herring samples were indeed genetically differentiated from all other samples.
274 Although one can suggest that STRUCTURE analyses might not correctly uncover genetic
275 pattern due to the observed low level of differentiation, this study presents a robust
276 interpretation of the developed statistical approaches based on a combination of F_{ST} values,
277 MDS and STRUTURE runs, which strongly support the observed genetic pattern.

278 The populations of Atlantic herring which have been genetically studied in the south-
279 eastern distribution (Jørgensen et al. 2005, Mariani et al. 2005, Ruzzante et al. 2006, Gaggiotti
280 et al. 2009, André et al. 2011), exhibited low level of differentiations except at some
281 hitchhiking microsatellite loci such as Cpa112 and Her14 (Gaggiotti et al. 2009, Teacher et al.
282 2013). Genetic differentiation is indeed expected to be more pronounced at coding (or linked)
283 loci, especially in large populations in which even weak selection might override effects of
284 genetic drift (Gaggiotti et al. 2009). Microsatellite loci and other genetic markers under
285 selection (like SNPs) were found to show some striking differentiation among herring
286 populations (Lamichhaney et al. 2012, Nielsen et al. 2012, Corander et al. 2013). In the
287 current study, we failed to detect any genetic structuring among the large Northeast Atlantic
288 herring populations. NSSH is by far the largest and ISSH among the largest herring
289 populations of the Northeast Atlantic, and their effective population size (N_e) is expected to be
290 very large, and hence, provides a probable explanation for lack of genetic differentiation. The
291 potential combination of high N_e and considerable level of gene flow among herring
292 populations have been suggested to hinder the detection of structure among local populations
293 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

319 stationary Trondheimsfjord herring and all other localities (Turan et al. 1998). Recent life-
320 history studies have suggested that Trondheimsfjord herring was "a few of many potentially
321 genetically unique populations with phenotypic adaptations to a stationary life in well defined
322 environment…" (Silva et al. 2013). Trondheimfjord (Broch 1908, Runnstrom 1941, Sørensen
323 2012, Silva et al. 2013), Lusterfjord (Aasen 1952), Lindås pollene (Lie et al. 1978,
324 Johannessen et al. 2009, Silva et al. 2013) and Landvikvannet herrings (Silva et al. 2013,
325 Eggers 2013) have long been considered to belong to self-sustaining and rather stationary
326 populations characterized by a lower vertebral count, slower growth, lower length at maturity,
327 shorter life span and a higher relative fecundity than the migratory oceanic NSSH. The fact
328 that these populations with apparent adaptations to life mostly spent inside fjord areas have
329 been known to exist for up to a century suggests that they may be genetically unique as
330 supported by the present study. In addition, the analysis of the fjord samples revealed that
331 Landvikvannet sample was genetically distinguishable from all other fjord samples. This is
332 most likely linked to the potential mixture with oceanic herring at various life stages that
333 differ between Landvikvannet herring and the other fjord populations. The herring in Lindås
334 pollene, Lusterfjord and Trondheimfjord may all mix with NSSH herring drifting into the
335 fjord areas as larvae from spawning grounds outside the fjord areas. Albeit most of NSSH
336 grow up in the Barents Sea, portions always tend use the fjords as nursery areas until age of
337 two years (Holst & Slotte 1998). Even though the NSSH is genetically tuned to leave the
338 fjords by two years age to grow further and join the adult spawning stock in the open ocean,
339 one cannot exclude the possibility that some choose to stay, especially if there is numerical
340 domination of the local herring of the same size (Huse et al. 2002). Hence, over time gene
341 flow might have occurred consistently between the NSSH and local fjord populations. Recent
342 studies from Lindås pollene even indicate that gene flow among adult NSSH and local herring
343 might explain the evolution of the fjord population's life history traits from the 1960s to the

344 2000s towards a regime with higher growth and higher length at maturity (Langård 2013). In
345 Landvikvannet the link to NSSH is not clear as this local fjord is outside the observed
346 spawning area of NSSH. In the latter, local herring might mix with coastal spring spawners or
347 even with Western Baltic spring spawners (WBSS) migrating into the Skagerrak area and
348 feeding close to the Norwegian coast during summer. Landvikvannet was artificially
349 connected to the open sea through a 3 km long canal in 1887, and has been a brackish
350 environment ever since with anoxic condition at depths below 4 m. Therefore, the observed
351 genetic differences among Landvikvannet herring and the other fjords is likely due to the fact
352 that Landvikvannet was colonized by straying of WBSS herring already being adapted to low
353 salinity conditions. In fact the very low vertebral count in Landvikvannet herring perfectly
354 equals that of WBSS (55.7). However, data on vertebral counts and growth from the most
355 recent study in Landvikvannet (2012) indicate that NSSH herring has also recently visited this
356 area, mixing with a group of coastal spring spawners and what is believed to be
357 Landvikvannet herring (Eggers 2013). The three groups occupy this ecological niche at
358 different times with some overlap in spawning stages. NSSH arrive first in March, while the
359 coastal spring spawners arrive in March-April and finally Landvikvannet herring peaks in
360 abundance in May. The genetic sample used in the present study was taken in May, which has
361 been the main sampling period since 1980s used as a basis for the suggestion of a local fjord
362 population. Given the results from 2012 further genetic studies are needed of the herring in
363 the area of Landvikvannet to be able to draw firm conclusions.
364

365 **Neutral vs. non neutral genetic markers**

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

369 conclusions based on these two approaches. In fact, the first Bayesian cluster analysis
370 including all loci supported a main differentiation between all fjords samples and all samples
371 collected around the Norwegian Sea, while the neutral loci analysis clearly distinguished one
372 additional cluster, the fjord sample from Landvikvannet (NLSSH, sample 12). On the
373 contrary, when all loci were used, the Bayesian cluster analysis could not detect differences
374 among the fjord samples without an additional hierarchical analysis. A closer look into
375 Cap111 (the locus under selection) allele frequencies (Fig. 6) revealed a clear shift in allele
376 frequencies among the fjords and the Northeast Atlantic populations (the former exhibited a
377 high frequency of allele-275 compared to the latter), but also a slightly different pattern in
378 Landvikvannet "sample" (NLSSH, sample 12) compared to the other fjord samples. Indeed, it
379 exhibited a higher frequency at allele-287 than any other fjords and Northeast Atlantic
380 samples, and did exhibit a somehow lower allele-275 frequency than the other fjord samples,
381 differences that the Bayesian cluster analysis did not catch except when an additional
382 hierarchical analysis was performed on the fjord samples. As suggested above, these observed
383 genetic differences among the fjord samples might be due to differences in their origin and
384 their respective interaction with NSSH but might also reflect potential different ongoing
385 genetic evolution of the fjords populations.
386
387 **Fisheries management**
388 In term of management, although the power analysis performed suggested that a relatively
389 low level of differentiation would be detectable with our research design, we only detected
390 genetic differences among the North Atlantic and the Norwegian local populations. The
391 combination of large effective population size and the relatively short time for divergence
392 since the recovery of the North Atlantic populations might have precluded evolution of
393 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

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411
412

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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)	99 (5)	1 (4)	15 (4)		52 (4)	13 (4)		na	1 (4)	13 (4)	77 (4)
			17 (4)		9 (5)	60 (5)		30 (5)	84 (5)			62 (5)	44 (5)	5 (5)
			81 (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	62°06.06'N	64°13.75'N	63°44.84'N	64°05.40'N	63°46.10'N	67°14.60'N	63°17.50'N	62°531.00'N	58°743.80'N	63°42.00'N	58°19.20'N	60°43.80'N	61°47.67'N
	06°10.80'W	06°45.00'W	22°56.29'W	16°26.80'W	23°01.90'W	16°19.40'W	13°17.00'E	07°14.70'E	05°14.00'E	05°22.20'W	11°00.00'E	08°30.10'E	05°08.00'E	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

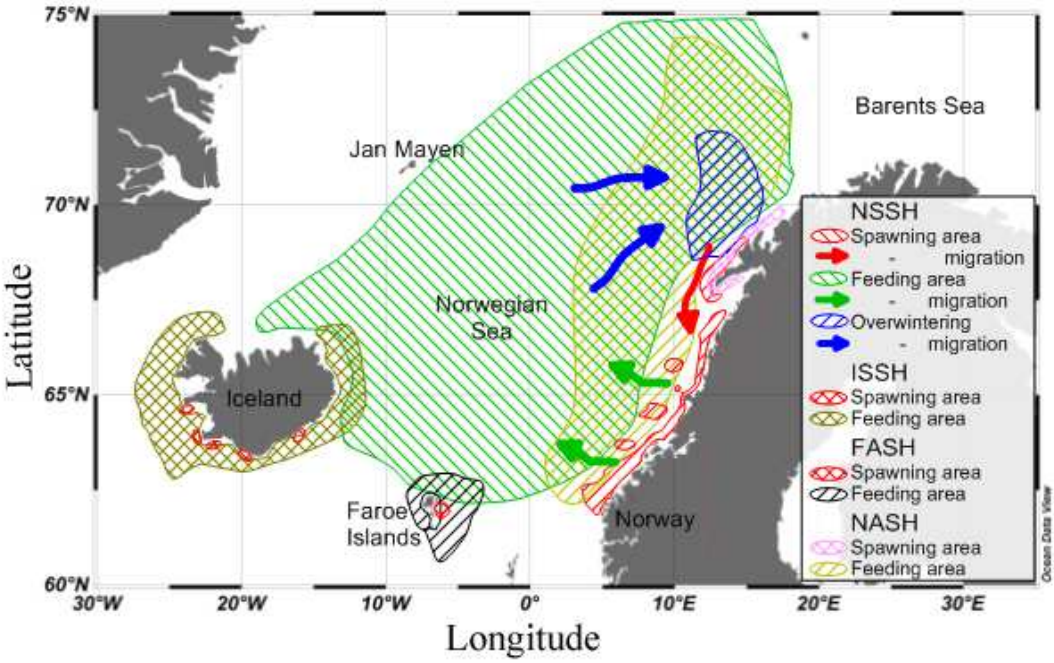
710 Fig. 3. Multi-dimensional scaling plot of Atlantic herring *C. harengus* in Norwegian Sea and
711 surrounding waters: a) all loci included, b) without the outlier Cpa111. See Table 1 for sample
712 codes.

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

724 Fig. 5. Bayesian cluster analysis performed in STRUCTURE using neutral loci and all herring
725 samples. A total of 10 runs were performed for each *K*, from *K* = 1 to 10 with 350,000 Burn-
726 in, 500,000 MCMC, using an admixture model with correlated allele frequencies and no prior
727 information on sample location. Additional hierarchical analyses did not detect any additional
728 clusters within the two main groups, i.e. the Northeast Atlantic samples and the fjords
729 samples (NLSSH). See Table 1 for sample codes.
730
731 Fig. 6. Allele frequencies at Cpa111 locus. All samples of North Atlantic populations were
732 combined while allele frequencies of the four Norwegian local-spawning herring are depicted
733 separately. NA, North Atlantic population; See Table 1 for sample codes.
734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Jan Mayen
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Faroe Islands
Norway
NSSH
Spawning area
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Feeding area
- migration
Overwintering
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ISSH
Spawning area
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FASH
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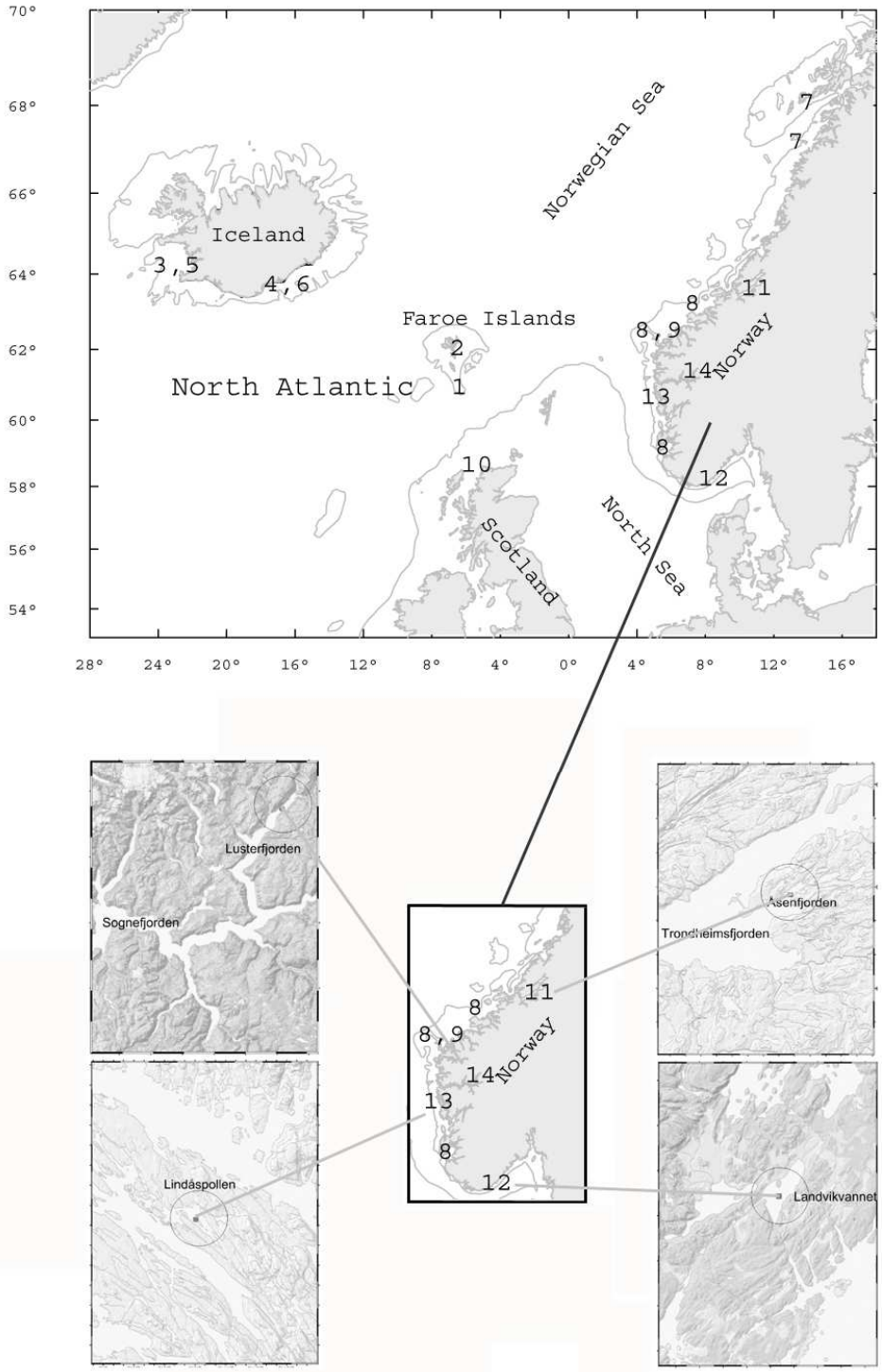
NASH
Spawning area
Feeding area
Ocean Data View

Fig. 1.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Åsenfjorden
Trondheimsfjorden
Landvikvannet

Fig. 2.

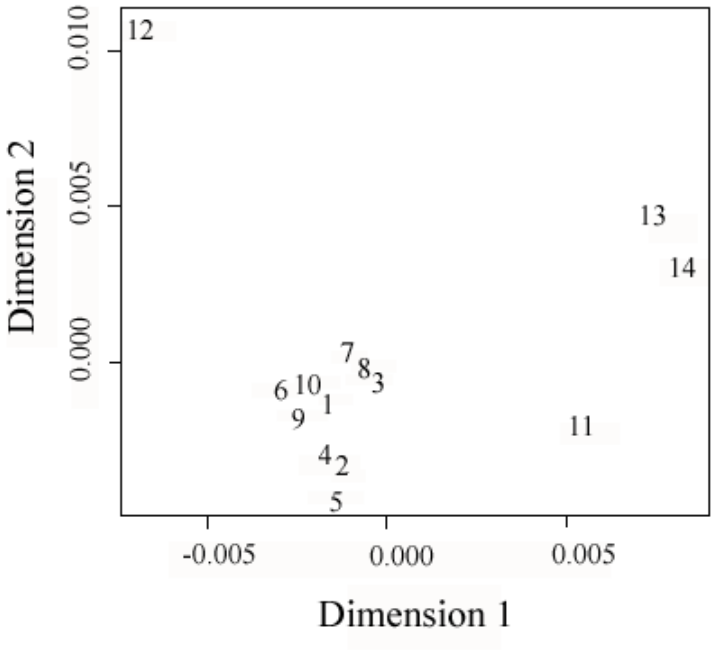
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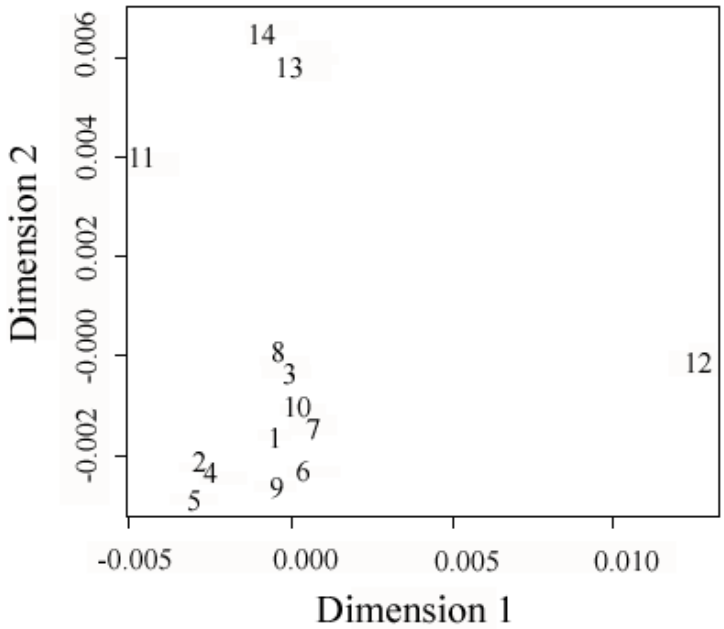
Fig. 3a.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Dimension 1

Fig. 3b.

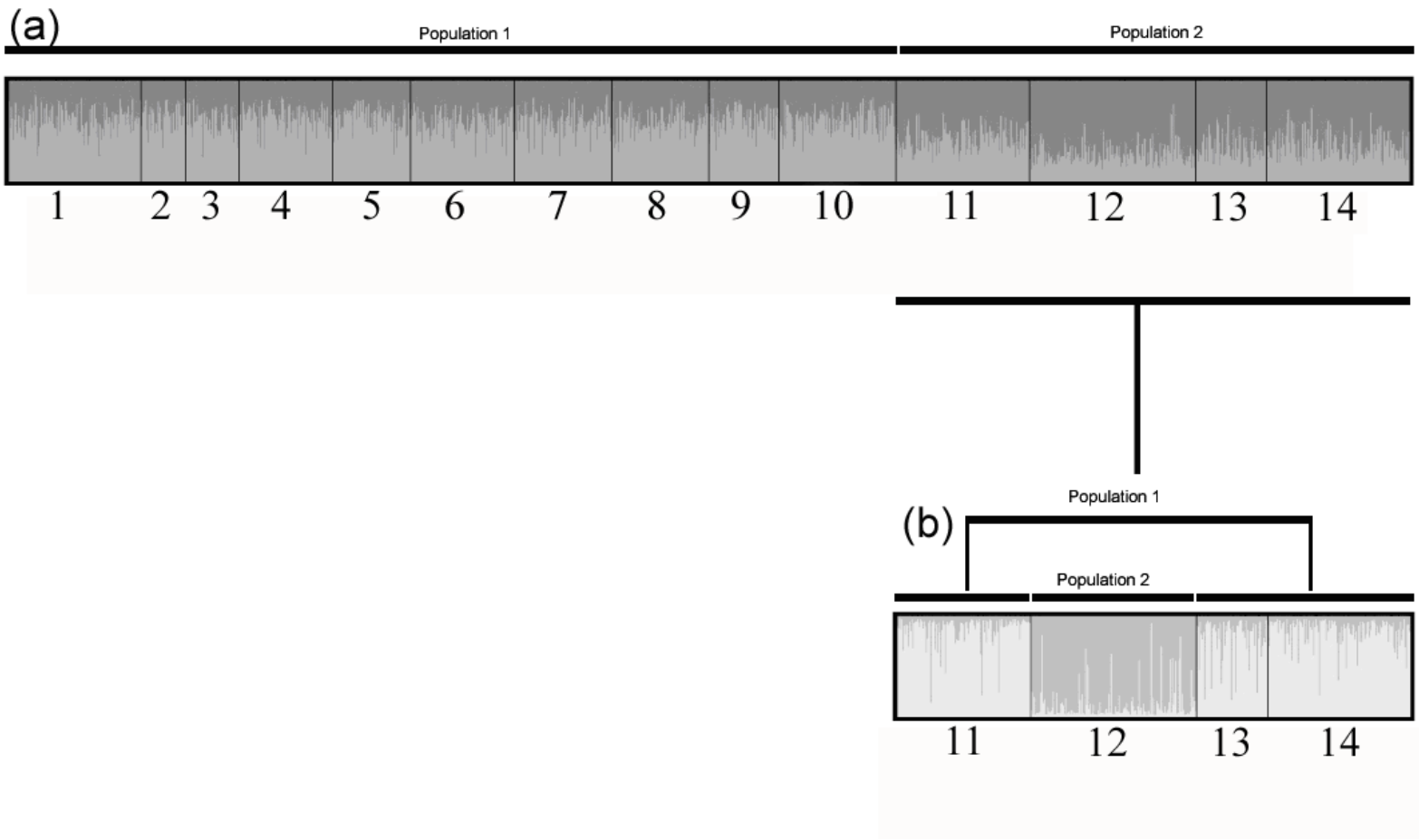

(a)
Population 1
Population 2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
(b)
Population 1
Population 2
11
12
13
14

Fig. 4.

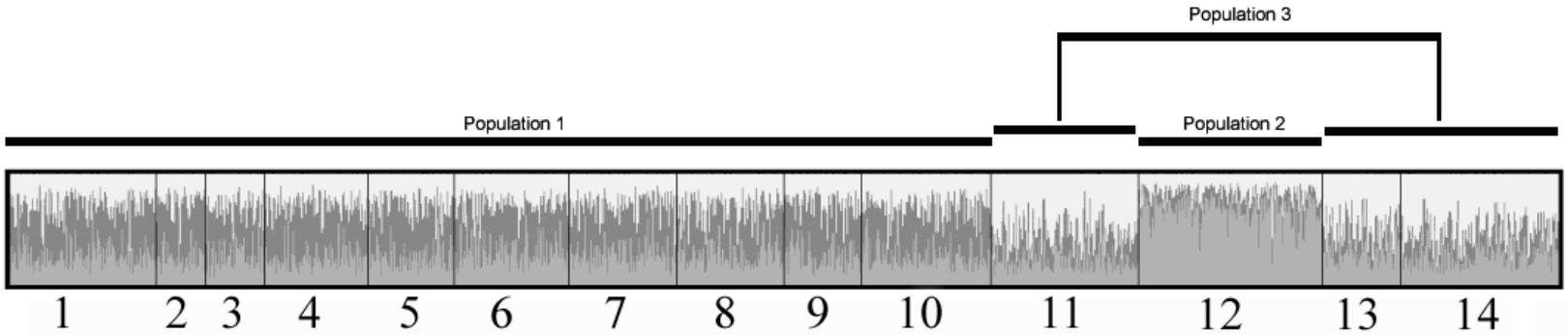
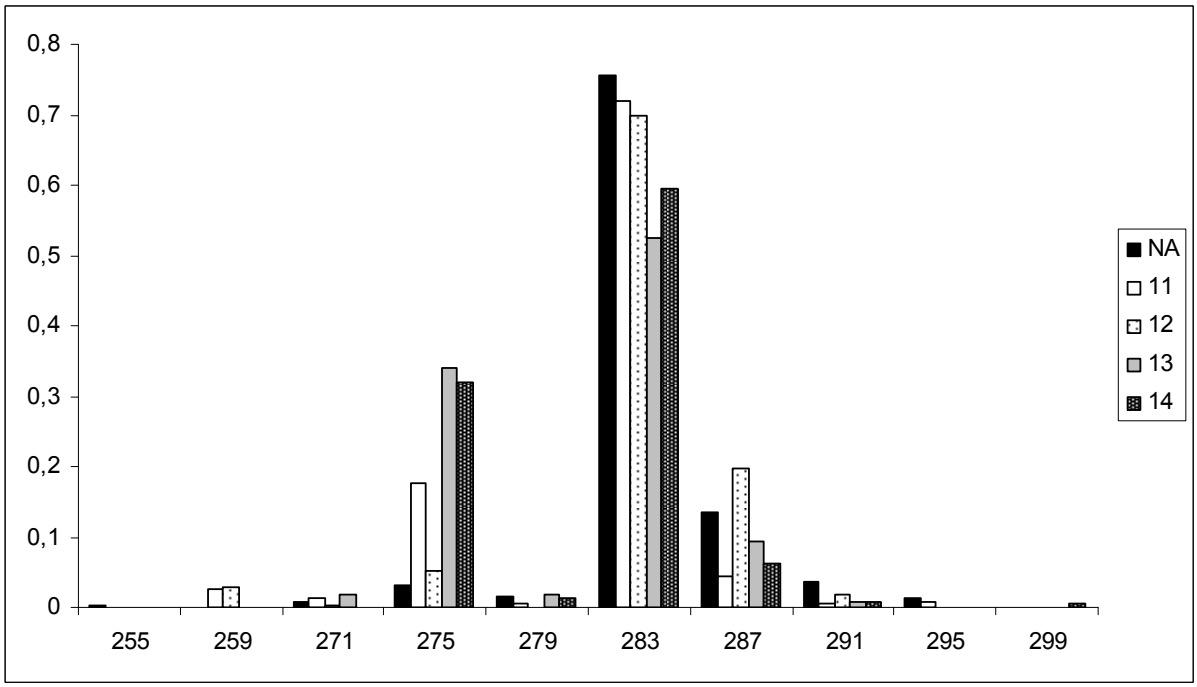

Population 3
Population 1
Population 2
1
2
3
4
5
6
7
8
9
10
11
12
13
14

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

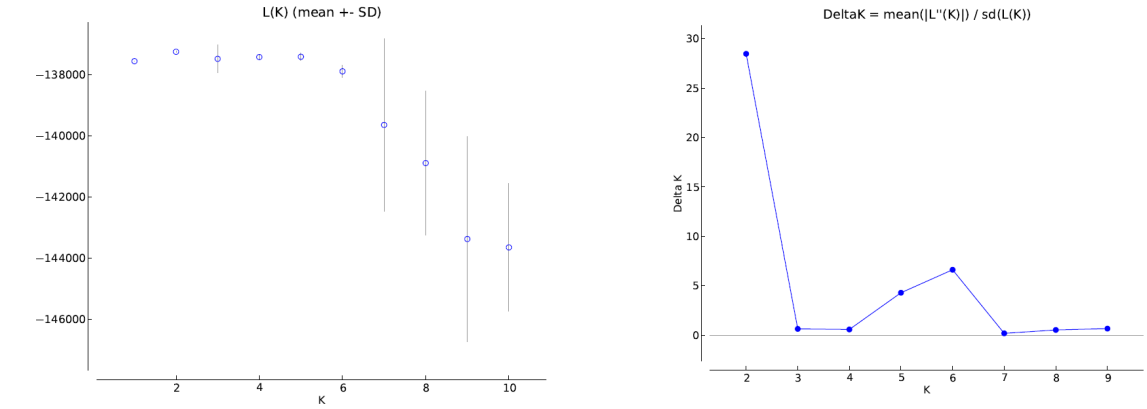
Emboldened values differ significantly from zero (Fisher's exact test. $p < 0.05$).
* Values remaining significant after Bonferroni correction ($\alpha = 0.05/91 = 0.0005$).

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.

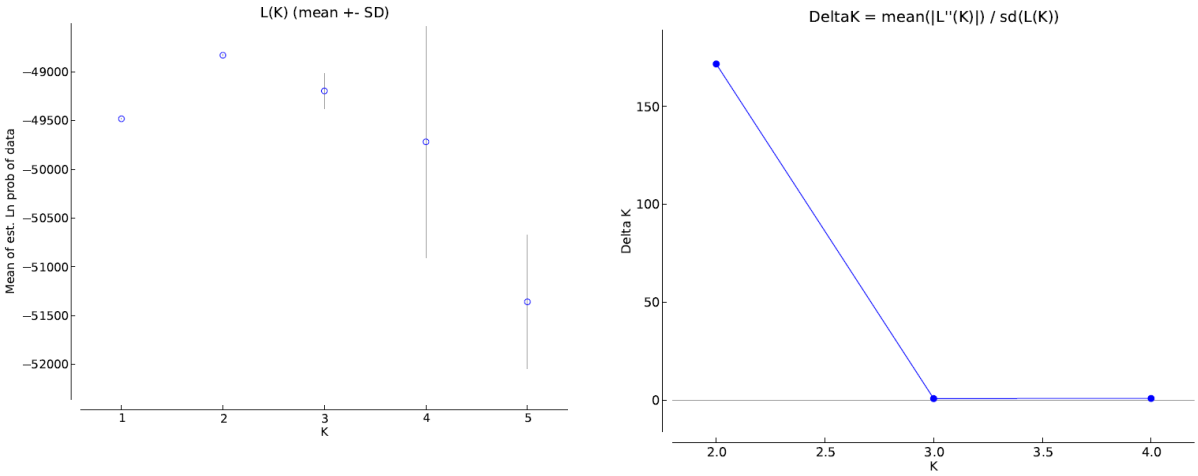
	K	Mean LnP(K)	StDev LnP(*K*)
North Atlantic	**1**	**-87102**	**0.2898**
	2	-87261	12.7600
	3	-87740	91.5819
	4	-88410	95.0116
	5	-89562	271.3621
	6	-91281	799.5722
	7	-93083	1390.0332
	8	-95410	1819.3528
	9	-95538	2152.4678
	10	-95920	1641.7548
Local fjords (all)	1	-49481	2.0991
	2	**-48829**	**5.9326**
	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.

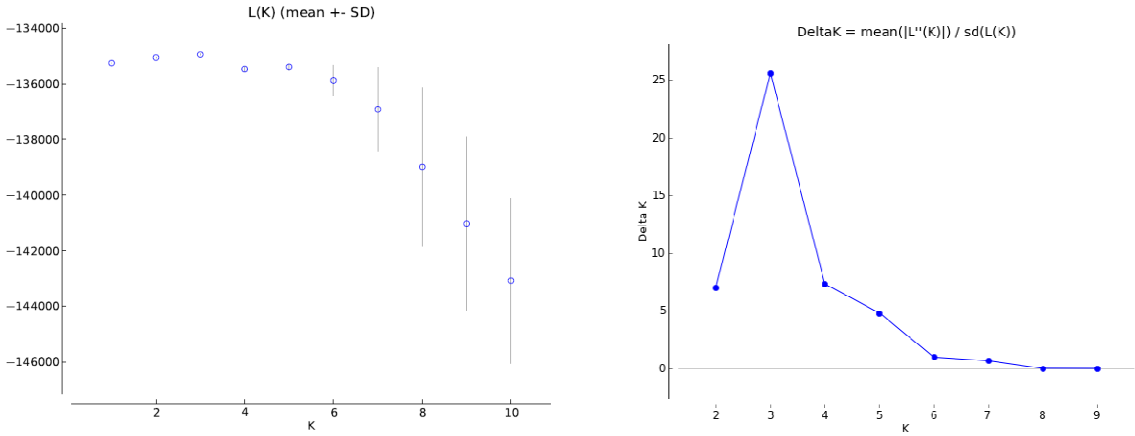
	K	Mean LnP(K)	StDev LnP(K)
North Atlantic	**1**	**-85817**	**0.1871**
	2	-85981	25.6621
	3	-86425	74.1802
	4	-87096	124.9924
	5	-88564	489.7930
	6	-90622	1073.9283
	7	-92667	2955.3703
	8	-94162	2935.9272
	9	-96560	3065.5698
	10	-97251	3204.5460
Local fjords	**1**	**-32919**	**0.6579**
	2	-32999	21.2130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