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The population structure in the Baltic herring reflects natural selection and local adaptation

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How species time reproduction and adapt to environmental conditions are key topics in ecology and evolutionary biology. Here, we conducted a high-resolution population genetic analysis of Baltic herring, a subspecies of Atlantic herring (*Clupea harengus*). Genotypes at >4,500 SNPs were generated from >4,500 spawning individuals, sampled from 150 locations spanning Swedish's eastern coast. Abiotic factors—week of spawning, latitude, temperature, salinity—were used to assess how genetic variation is shaped by temporal, spatial, and environmental gradients. Our results reaffirm strong genetic differentiation between spring- and autumn-spawning ecotypes, despite hybridization suggesting ongoing gene flow between the two ecotypes. We document significant substructuring within the spring-spawning ecotype, delineating three main, previously unidentified, genetic clusters underpinned by adaptative genetic variation associated with latitude, salinity, temperature, and spawning time. Complementary linkage disequilibrium (LD) partitioning showed that adaptive loci—especially those in inversion regions—exhibit strong elevated among-population LD, consistent with divergence maintained by local selection despite ongoing gene flow. Clinal variation in allele frequencies indicated regionally distinct selection pressures, including shifts in allele frequencies at two major supergenes (inversions) and at a suite of genes correlated with abiotic factors. Importantly, rare genetic outlier populations are identified within each geographic region which further illustrates the unexpected fine-grained population structure of Baltic herring and implies a strong homing behavior in this abundant marine fish. Overall, this study demonstrates the capacity for targeted population genetic studies to detect adaptive variation in natural populations, the outcomes of which have direct implications for sustainable fisheries and biodiversity management.

natural selection | biodiversity | population structure | ecological genetics | fisheries biology

Significance

Atlantic herring are subdivided into genetically differentiated subpopulations, despite being broadcast spawners that migrate between spawning and feeding grounds, providing opportunities for substantial gene flow. Using large-scale genotyping of >4,500 spawning herring from 150 Baltic Sea localities, we provide a high-resolution population study of marine fish. We reveal fine-scale genetic structure, with strong differentiation between spring- and autumn-spawning populations, evidence of hybridization between spawning ecotypes, parallel genetic clines across adaptive loci, and several populations showing signatures of ecological adaptation. Linkage disequilibrium analyses support that local selection maintains adaptive loci despite gene flow. These findings offer unique insight into how natural selection shapes allele frequencies and local adaptation in marine fish, with direct implications for fishery management and biodiversity conservation.

The development of high-throughput sequencing has revolutionized our ability to reveal the structure of natural populations and identify the genetic basis for adaptation and evolutionary change (1), which is essential for monitoring biodiversity as well as for management of species subjected to commercial exploitation such as marine fisheries (2). However, comprehensive analysis of the population structure and how natural selection shapes the genetic constitution requires large-scale studies (3). The aim of the present study was to perform a high-resolution analysis of population genetic structure in a species that is particularly well suited for studies of ecological adaptation, the Atlantic herring (*Clupea harengus*). Additionally, the Atlantic herring is one of the world's most heavily exploited marine fishes (2), and there are multiple examples where important stocks of Atlantic herring have collapsed due to overfishing (4, 5). Within the Baltic Sea, particularly, Atlantic herring represents a keystone species in rapid decline; therefore, knowledge of its genetic structure is essential to alleviate the threat of overfishing.

Previous analyses of whole genome sequencing data have revealed at least seven major genetic groups of Atlantic herring, well separated by a PCA (6). These include i) and ii) spring- and autumn-spawners in the Atlantic Ocean, iii) North-Sea and the waters surrounding Ireland and Great Britain, iv) Norwegian fjords, v) the transition zone between Atlantic Ocean and Baltic Sea, and vi) and vii) spring- and autumn-spawners in the Baltic Sea. Furthermore, there is evidence for subpopulations within these seven major groups; for example, recently the evolution of a distinct piscivorous Baltic herring was documented (7). In 1925, Hessle (8) proposed that multiple Baltic herring races exist based on ecology and morphology, but noted characterizing the genetic basis for such classifications "will certainly be a matter of great difficulty." A full century later, genetic studies have shown that the seven main genetic groups in Atlantic herring show strong genetic differentiation

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related to environmental variation between geographic regions, including dramatic shifts in salinity between the Atlantic Ocean and the brackish Baltic Sea, and differences in climate (northern vs. southern parts of the species distribution) (6). Strong genetic differentiation also correlates with timing of reproduction [primarily spring vs. autumn (6)] and feeding behavior [planktivorous vs. piscivorous (7)]. Importantly, this strong genetic differentiation occurs in the absence of genetic differentiation at selectively neutral loci (6, 7). Thus, this low level of noise due to genetic drift allows detection of even small differences in allele frequencies related to ecological adaptation with strong statistical support.

Here, we present a high-resolution analysis of the population structure of Atlantic herring in one geographic region, the brackish Baltic Sea. The study involves >4,500 fish, all in spawning condition, from 150 locations along the Swedish east coast. The sample locations encompass gradients for several key environmental variables, e.g. latitude, temperature, and salinity, as well as a temporal variation in spawning from early spring to autumn. Genotyping was performed using a SNP-chip comprising >4,500 SNPs carefully selected to include SNPs representing the great majority of loci showing genetic differentiation among herring populations, as established in earlier works (2, 7). In addition, the chip contains a set of neutral markers spread over all chromosomes; these were selected based on having a high (>0.3) minor allele frequency, while also having low variance across all sampled populations.

This unique dataset allows us to study the degree of local adaptation at a high resolution, in particular for a marine fish that migrates between spawning and feeding grounds, providing plenty of opportunities for gene flow between populations. Another aim was to document gene flow between spring- and autumn-spawning herring which can explain the lack of genetic differentiation at neutral loci despite the separation in spawning time (6). We reveal a complex population structure in the Baltic Sea with two major ecotypes (spring- and autumn-spawners), considerable genetic differentiation within the spring-spawning ecotype as well as several outlier populations with more extreme local adaptation.

Results

Strong Genetic Differentiation Between Spring- and Autumn-Spawning Ecotypes Despite Gene Flow. Survey and capture efforts in collaboration with local fishermen and the Swedish Agency for Marine and Water Management resulted in a dataset of 4,678 spawning fish, representing 150 locations sampled with 7-50 individuals per location, henceforth referred to as the Swedish East Coast Dataset (SECD) (Datasets S1 and S2). SNP-chip genotyping yielded data for a total of 4,773 SNPs across all individuals (Dataset S3).

The most divergent ecotypes represented in this material constituted the spring- and autumn-spawning Baltic herring. Discrimination of individual-level spawning-ecotype using discriminant analysis of principal components (DAPC) yielded high confidence assignments for both spring- and autumn-spawners (averaging 99% confidence for both) (Fig. 1*A* and Dataset S1). In total, 4,345 and 333 individuals were designated as spring- or autumn-spawners, respectively. The distribution of both spring- and autumn-spawners on discrimination axis 1 included a skewed tail of individuals with a more intermediate classification (Fig. 1*A*). When assessing the deviation of individuals within ecotype assignments, most individuals within the spring- or autumn-spawning distribution tails had absolute z-scores >3 relative to the group median, and were assigned as outliers. In total, 15 individuals were designated as autumn outliers, while 40 individuals were classified as spring outliers. When considering spring- and autumn-spawners as the parent 1 and 2 respectively, outlier individuals were assigned a hybrid index (*h*) score consistent with hybrid individuals. Autumn outliers were primarily composed of F1 hybrids (average $h = 0.43 \pm 0.09$), while spring-spawners composed of spring backcrosses (average $h = 0.69 \pm 0.12$). When separated by time of spawning (week number) both spring- and autumn-outliers had intermediate spawn timings (weeks 25.9 ± 4.1 and 27.4 ± 4.24 respectively), indicating the timing of reproduction may be offset in outlier individuals relative to typical spring (week 22.9 ± 2.3) and autumn (week 36.8 ± 2.43) spawners (spawn timing did not differ between spring- and autumn outliers ($P > 0.05$) (*SI Appendix*, Fig. S1).

Mixed spring- and autumn-spawning ecotypes were observed at 16 of the 150 sampled locations (Fig. 1*B* and Dataset S2). When both ecotypes were observed, the less frequent spawning ecotype was typically an extreme minority, potentially constituting a single individual. However, the occurrence of spawning-ecotype mixing is notable as all samples sequenced were from individuals in spawning condition, suggesting potential for hybridization and gene flow between spawning ecotypes. The occurrence of population samples with mixed ecotype was more common in the northern Baltic Sea, particularly within the Gulf of Bothnia (latitude > 60°N).

A SNP-by-SNP analysis revealed striking allele frequency differences between spring- and autumn-spawning populations with Bonferroni-corrected *P*-values approaching $10^{-1,000}$ using this extensive dataset (Fig. 1*C*). This included the loci that have previously been consistently associated with spawning type both in Atlantic and Baltic herring (6), such as the genomic regions harboring a cluster of *myosin heavy chain* genes (*MYH,* chr 12: 15,540,272 to 16,261,070), *thyroid stimulating hormone receptor* (*TSHR*, chr 15: 8,873,382 to 8,908,516), *SRY-box transcription factor 11B* (*SOX11B*, chr 15: 7,717,899 to 7,721,161), *estrogen receptor 2A* (*ESR2A*, chr 15: 10,897,683 to 10,910,686), and *HERPUD2* (chr 19: 20,605,934 to 20,613,811). Peaks of significance were concordant with increased Δ allele frequency, with *MYH, SOX11B, CEP128,* and *TSHR* regions in particular approaching fixation between spring- and autumn-spawners.

Allele frequency differences between outlier individuals (either spring or autumn) and typical spring- and autumn-spawners yielded a high degree of concordance between the two contrasts (Fig. 1 *D* and *E*). The majority of significant peaks associated with spawn timing (Fig. 1*C*) were replicated across Fig. 1 *D* and *E*, albeit with reduced significance (*P*) and intermediate Δ allele frequencies. Heat maps of allele frequency variation for all significant SNPs detected across outlier contrasts, confirmed that both spring and autumn outlier groups have intermediate allele frequencies at these loci, compared with typical spring and autumn spawners and also have high heterozygosity, particularly for loci on chromosomes 10, 12, and 15 (Fig. 1 *F* and *G*), the chromosomes harboring loci showing very strong genetic differentiation between spring- and autumn-spawning Baltic herring (Fig. 1*C*). These results further support that outlier individuals are likely hybrids or have spring/autumn hybrids among their close ancestors, providing evidence for some gene flow between groups.

Substantial Local Adaptation Within Ecotypes. Pooled per-location allele frequencies were used to profile the population structure of spring- and autumn spawners independently. However, the number of population samples of autumn-spawning Baltic herring, as well as their geographic distribution, were limited, and a principal component (PC) analysis of allele frequencies assigned the majority to a single cluster (*SI Appendix*, Fig. S2). In contrast, the corresponding analysis of the 144 population samples of spring-spawning herring, revealed three population clusters

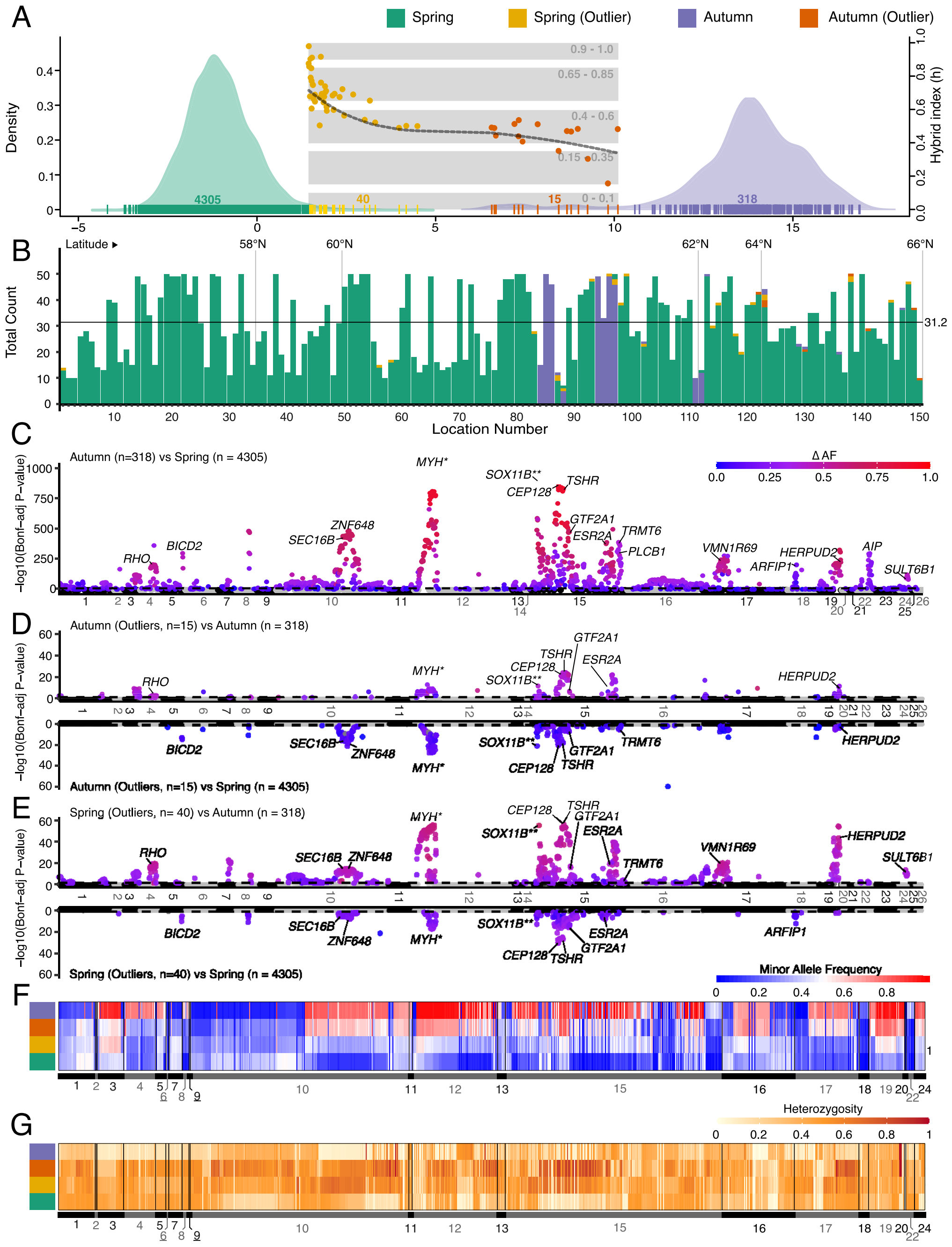

Fig. 1. Summary of individual assignments (n = 4,677) to either spring- or autumn-spawning ecotypes. (*A*) Individual assignments to either spring (green) or autumn (purple) spawning ecotypes inferred from discriminant analysis of principal components (DAPC). A z-score-based approach was utilized to detect outliers within spring- and autumn-spawning cohorts, where samples with absolute z-scores >3 relative to the group median (of discriminant axis 1) were classified as spring (outlier, visually represented in gold) or autumn (outlier, visually represented in orange) respectively. The inset dotplot visualizes the hybrid index (h) scores of all spring and autumn outlier samples, with the gray background used to define breakpoints for the following designations: Pure spring (h-score = 1.0 to 0.9), back cross (to spring, h-score = 0.85 to 0.65; to autumn, h-score = 0.15 to 0.35), F1 (h-score = 0.4 to 0.6), pure autumn (h-score = 0.1 to 0.0). (*B*) Per location histogram showing total number of individuals sampled (per location) and the proportional allocation to spawning ecotype and outlier groups. Sampling locations are ordered from *Left* (south) to *Right* (north) by latitude (exact location data available in Dataset S2). (*C*) Summary of pairwise, SNP-by-SNP chi-squared test contrast [SNP(n) = 4,669; both adaptive and neutral SNPs included] between genetically autumn (n = 318) and spring (n = 4,305) spawning Baltic herring (outliers were excluded). Nonsignificant SNPs ($P > 0.05$) are colored in an alternating fashion between gray and black to differentiate consecutive chromosomes, while SNPs with a Bonferroni-corrected $P < 0.05$ colored using a gradient (blue to red) to indicating the absolute delta allele frequency difference for the given SNP. (*D*) Summary of pairwise, SNP-by-SNP chi-squared test contrast between autumn (outlier) (n = 15) and autumn (n = 318, *Upper* panel) or spring-spawners (n = 4,305, *Lower* panel). Both significant and nonsignificant SNPs are colored as in Fig. 1*C*. (*E*) Summary of pairwise, SNP-by-SNP chi-squared test contrast between spring (outlier) (n = 40) and autumn (n = 318, *Upper* panel) or spring-spawners (n = 4,305, *Lower* panel). Both significant and nonsignificant SNPs are colored as in Fig. 1*C*. Significant SNPs that are common to all contrasts in Fig. 1 *C*–*E* were annotated using positional coordinates referenced against the Atlantic herring (*Clupea harengus*) reference annotation file (Clupea_harengus.Ch_v2.0.2.108.gtf). Note that SNPs annotated as *MYH** indicate a 0.72 Mb region of chromosome 12 (chr12: 15,540,272 to 16,261,070 bp) containing *MYH* genes, while SNPs annotated *SOX11B*** indicate significant SNPs 85 kb upstream of the *SOX11B* coding region (chr15: 7,717,899 to 7,806,161). All other annotations represent SNPs within coding regions. (*F* and *G*) Heatmaps showing allele frequencies (*F*) and heterozygosity (*G*) in all spring-, spring (outlier), autumn (outlier), and autumn individuals for all significant SNPs (Bonferroni-corrected $P < 0.05$, n = 956) present in at least one pairwise, SNP-by-SNP chi-squared contrast (Fig. 1 *D*–*E*). Note that while spring(outlier), autumn(outlier) groups are represented in full, spring-, and autumn-spawning cohorts represent the n = 10 individuals closest to the group median (of discriminant axis 1) for their respective spawn-cohort.

(Fig. 2 *A* and *B*). The first principal component correlates with latitude, therefore the three clusters were labeled as "southern," "central," and "northern," based on their geographic occurrence (Fig. 2*B*). The majority of population samples clustered according to their geographic location but some notable exceptions indicating local differentiation were identified (see below).

Genetic differentiation underlying the three clusters were investigated using pairwise SNP-by-SNP contrasts, with differences in

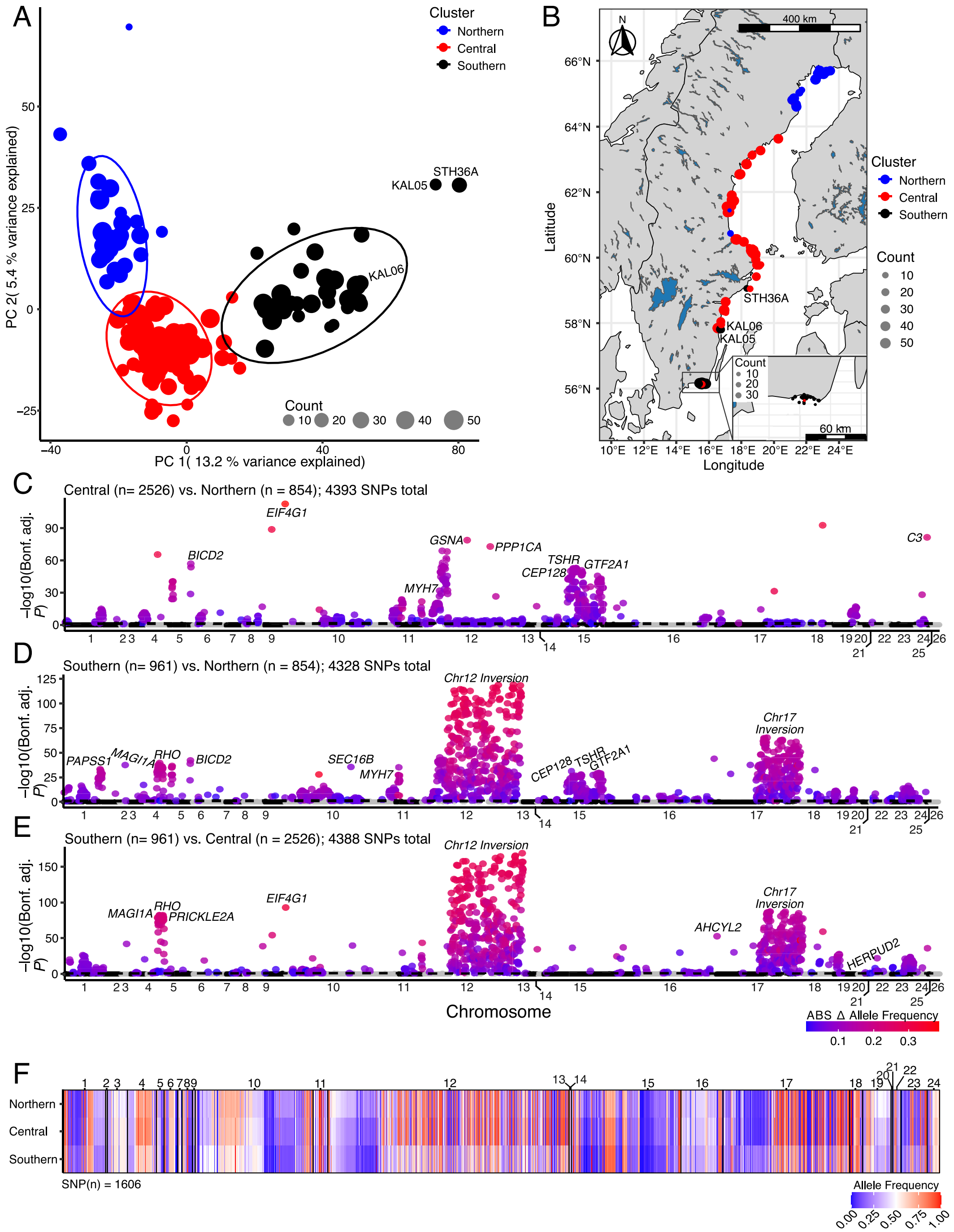

Fig. 2. Summary of population structure and cluster assignment for spring spawning individuals (n = 4,345 fish). (*A*) Principal component analysis (PCA) of per-location pooled allele frequencies. Note that locations must contain at least three individuals to be visualized in PCA. All locations are colored relative to K-Means assigned clustering groups, which are summarized using a 95% confidence ellipse, while point size is scaled relative to sample numbers per location. (*B*) Map showing sampling locations for all spring-spawning herring, colored by K-Means cluster assignment. Sample locations with fewer than three individuals were excluded, while point size is scaled relative to sample numbers per location. Location annotations highlight locations where pooled samples are geographically displaced from their assigned cluster (i.e., outlier populations). The zoom-in shows sample coverage for the southern population cluster. The underlying map was sourced from the public domain maps hosted by rnaturalearth (https://github.com/ropensci/rnaturalearth). (*C*) Summary of pairwise, SNP-by-SNP (n = 4,393) chi-squared test contrasts between central and northern clusters. Nonsignificant SNPs (Bonferroni-corrected $P > 0.05$) are colored in an alternating fashion between gray and black to differentiate consecutive chromosomes, while SNPs with a Bonferroni-corrected $P < 0.05$ are colored using a gradient (blue to red) to indicating the absolute delta allele frequency difference (between clusters) for the given SNP. (*D*) Summary of pairwise, SNP-by-SNP (n = 4,328) chi-squared test contrasts between southern and northern clusters, with all SNPs colored as in Fig. 2*C*. (*E*) Summary of pairwise, SNP-by-SNP (n = 4,388) chi-squared test contrasts between southern and central clusters, with all SNPs colored as in Fig. 2*C*. (*F*) Heatmap showing allele frequency differences between all clusters, for all significant SNPs (Bonferroni-corrected $P < 0.05$, n = 1,606) present in at least one pairwise, SNP-by-SNP chi-squared contrast (Fig. 2 *C*–*E*).

allele frequencies evaluated using chi-square tests (Fig. 2 *C–E*). In total, 1,568 SNPs were identified as statistically significant in at least one pairwise contrast between the population clusters. When compared against known SNPs associated with difference in salinity and spawning time (6), a total of 704 (44%) SNPs had previously been associated with salinity, while 311 (20%) had been associated with spawning (n. b. salinity and spawning SNPs are not mutually exclusive). Notably, the set of diagnostic SNPs were composed of 136 SNPs that were globally differentiated in each pairwise comparison of the three clusters, 794 that differentiate the southern cluster (Dataset S4), 161 SNPs that differentiate the central cluster (Dataset S5), and 558 SNPs that differentiate the northern cluster (Dataset S6) from all other population clusters. The composition of diagnostic SNP specific to southern and central clusters was heavily skewed toward known salinity-associated SNPs (ranging from 35% in central, and 37% in southern clusters) relative to known spawning-associated SNPs which represented <1% of each. However, SNPs diagnostic for the northern cluster contained 41% and 47% SNPs previously associated with salinity and spawning, respectively.

Strong peaks of genetic differentiation between the southern cluster and the two other clusters occurred over large regions on chromosome 12 and 17 (supported by increased Δ allele frequency), and to a lesser extent on chromosome 23 (Fig. 2 *C–E*); these blocks all correspond to previously characterized inversions (9). Using allele frequencies polarized to the major Baltic allele (i.e., the Northern allele as per Han *et al.* 2020), heatmaps demonstrate that the minor (i.e., Southern) alleles had comparatively high frequencies in populations from the southern cluster while populations from the central and northern clusters were close to fixation for the Northern allele at all three inversions (Fig. 2*F*). Similarly, contrasts involving the northern cluster showed clear peaks of differentiation across a 0.72 Mb region of chromosome 12 (chr12: 15,540,272 to 16,261,070 bp) containing *MYH* genes, but more prominently across a 0.5 Mb region on chromosome 15 (chr15: 8,813,384 to 9,323,382) containing the *TSHR*, *CEP128*, and *GTF2A1* genes showing strong association with spawning type (6). The central cluster had the fewest cluster-specific SNPs, reflecting its status as an intermediate along a north–south cline.

When considering population clusters in isolation, none showed clear evidence of within-population structure, with the majority of sample locations occurring in a single cluster nested within the 95% confidence range (with the exception of a few outliers) (*SI Appendix*, Fig. S3). Overall, within-population structuring was most correlated with week number (R^2 = 0.24) for the south population, while central (R^2 = 0.39) and north (R^2 = 0.24) by latitude; although the trends in said correlations were marginal.

Adaptive Loci Show Clinal Allele Frequency Variation in Spring-Spawning Baltic Herring. To investigate potential clinal variation in allele frequencies, a correlation analysis between allele frequencies per population sample and the abiotic factors latitude, week of spawning (referred to as week number), bottom temperature, and salinity was undertaken. Due to available sample size, this analysis was restricted to spring-spawning herring. Following filtering (minimum $R^2 \geq 0.2$; $P \leq 0.05$), significant correlations between SNPs and all abiotic factors were observed, albeit to varying degrees (*SI Appendix*, Fig. S4). Latitude was the most represented factor, with 791 SNPs showing significant correlation, although only 76 were uniquely correlated with latitude (*SI Appendix*, Fig. S4*A* and Dataset S7). Sea bottom temperature was the next most represented factor (737 SNPs, out of which 29 unique) (*SI Appendix*, Fig. S4*A* and Dataset S8), followed by sea bottom salinity (*SI Appendix*, Fig. S4*A* and Dataset S9); both of which shared considerable overlap with SNPs correlated with latitude. Week number was the most independent abiotic factor, consisting of 112 SNPs in total, of which 46 were unique (*SI Appendix*, Fig. S4*A* and Dataset S10).

The relative contribution of each abiotic factor to the ordination of the per-location allele frequency PCA was examined (*SI Appendix*, Fig. S4*C*). Abiotic factor fitting indicates that latitude (R^2 = 0.80), bottom sea temperature (R^2 = 0.69), and bottom salinity (R^2 = 0.32) are the main predictors of variation along PC1; reflecting the major north–south gradient and strong correlation among these factors in the Baltic Sea. PC2 is primarily associated with week number (R^2 = 0.37), indicating temporal differences in spawning among population clusters, with the northern cluster spawning later than the southern and central clusters. Overall, the biplot shows the southern cluster spawns earlier in higher temperatures and higher salinity, the northern cluster spawns later under lower temperatures and lower salinity, while the central cluster occupies intermediate conditions. This relationship is illustrated by a correlation plot showing that some of the most important loci controlling spawning also show genetic differentiation between the northern and southern cluster of spring-spawning herring most likely reflecting a late-shift in spawning time at high latitude (*SI Appendix*, Fig. S5).

When visualized per-chromosome, correlations between allele frequency and latitude (minimum cutoff $-\log10(P) > 15$) were dominated by the inversion regions on chromosome 12, 17, and 23, reflecting the extensive linkage disequilibrium (LD) within these regions, alongside a number of isolated peaks across various chromosomes (Fig. 3 *A* and *B* and *SI Appendix*, Fig. S4*B*); the most extreme of which consistently show multitest support (*SI Appendix*, Fig. S6). The frequency of the southern haplotype (the minor allele in the Baltic Sea) for the chr12 and chr17 inversions decreased by latitude (Fig. 3*C*), consistent with the cline observed in the Atlantic Ocean (6, 9). Outside of the inversion regions, the frequency of the major Baltic allele in correlated genes [minimum cutoff $-\log10(P) > 15$] decreased with increasing latitude. When considering a cutoff for genetic differentiation supported by $-\log10(P) > 15$, chromosome 1 was the most overrepresented noninversion chromosome, with multiple peaks of significance across the genes *PLPPR2A*, *NPNTA*, *PAPSS1*, *AATKA*, *BOKB1*, *SPET2*, and *GSTCD*. Genetic differentiation was also observed for loci on chromosome 4 (*RHO* and *MAGI1A*), 5 (*BICD2*), 12 (*MYH*), 15 (*TSHR*, *CEP128*, *GTF2A1*), and 16 (*PLEKHA5*). Significant interchromosomal correlations were observed for all inversions and highly differentiated peaks reflecting selection driven LD (10–13).

Unlike the above, correlations between week of spawning and allele frequencies were not dominated by the inversion regions (*SI Appendix*, Figs. S4*B* and S7 *A* and *B*). Instead, the most prominent peaks were observed across the *MYH* locus on chr12, chr15 (including *RAD51B*, *TSHR*, *CEP128*, and *GTF2A1*), and chromosome 19 (*HERPUD2*). These are all loci that show strong genetic differentiation between spring- and autumn-spawning herring (Fig. 1*C*); with the majority of associated SNPs supported by multiple tests (*SI Appendix*, Fig. S8). Additionally, a highly correlated peak was observed across a narrow region of chr5, containing the *BICD2* gene. Again, significant interchromosomal correlations were observed for all differentiated peaks. When plotted against week number, all genes [minimum $-\log10(P) > 10$] showed a consistent decrease in allele frequency of the major allele in spring-spawning Baltic herring with increasing week number (*SI Appendix*, Figs. S7*C* and S9). Thus, the minor allele—present

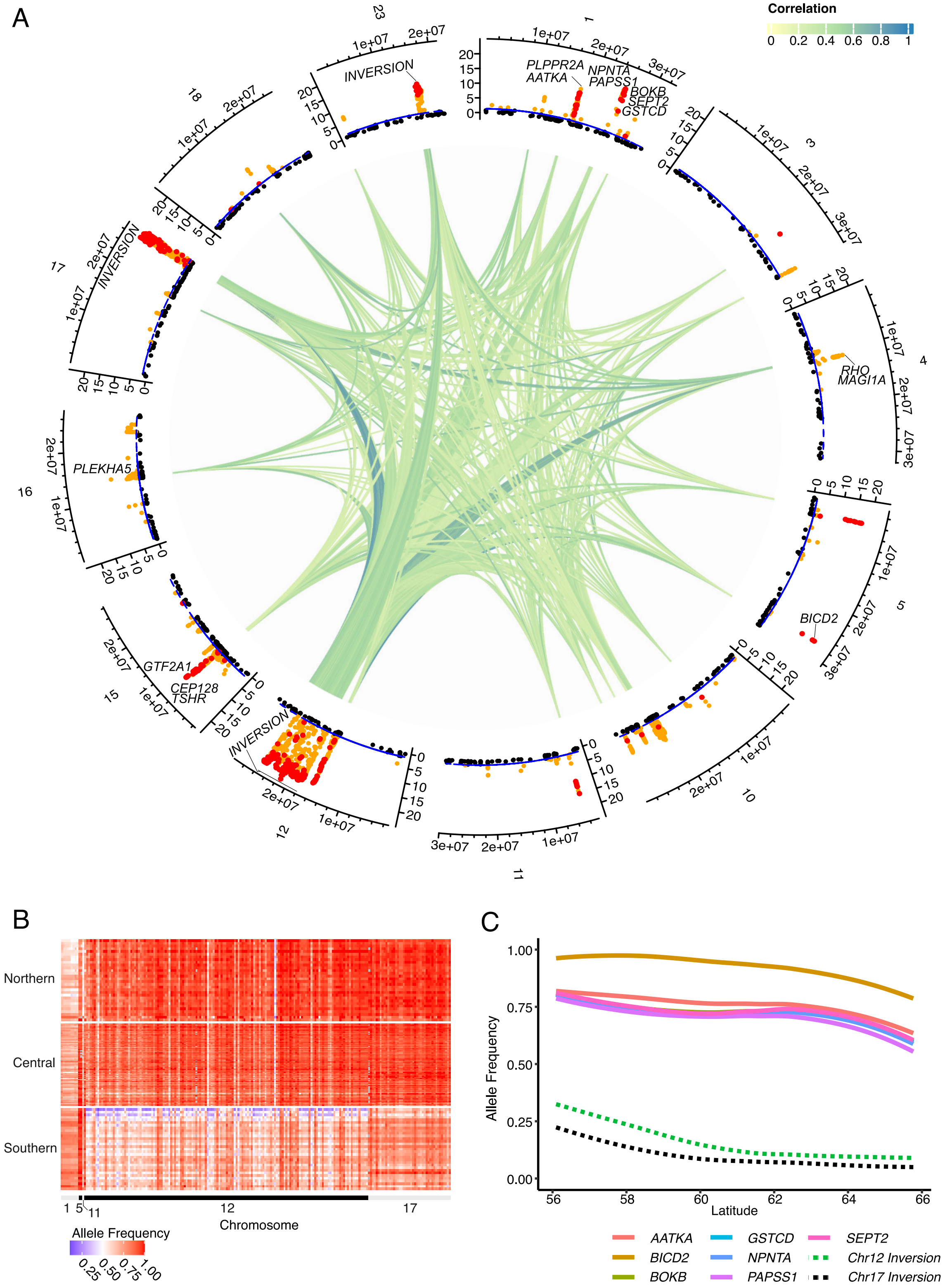

Fig. 3. Summary of clinal variation in Baltic spring-spawning herring relative to latitude. (*A*) Circos plot representing SNP showing significant correlation with latitude ($R^2 > 0.2$ and Bonferroni corrected $P < 0.05$). Labels on the outer ring indicate the chromosome that SNP are located, with the position of SNPs indicated by the axes in parallel. For all chromosomal plots, the y-axis represents the log10 *P*-value, where all points above the blue line (set at $P = 0.05$) are significantly correlated with latitude (appearing in orange), or if additionally significant in at least two of the correlation, LFMM, or RDA tests in red. SNPs with peaks that exceed log10(*P*) = 10 were annotated with their respective gene names or as inversion regions (i.e., chromosome 12 and 17). The inner ring represents pairwise SNP-by-SNP correlations between all SNPs significantly correlated with latitude. Only pairwise correlations between SNP with an $R^2 > 0.2$ and Bonferroni corrected $P < 0.05$ are visualized, with the strength of the correlation indicated by the color gradient. (*B*) Heatmap showing all SNPs significantly correlated with latitude, for all locations assigned to the northern, central, and southern Baltic Sea clusters (see Fig. 2 for cluster definitions). Labels below each box represent the chromosome that SNPs are located. (*C*) Plot showing averaged allele frequency clines per gene, or genes within inversions with significance peaks exceeding log10(*P*) = 15. Colored lines represent averaged allele frequency change across latitude per gene/inversion region.

at high frequency among autumn-spawners—increased in spring-spawners the later they spawned.

When considering clinal variation individually within the three clusters of spring-spawning herring (Fig. 2*A*), considerably fewer correlations to abiotic factors were observed (*SI Appendix*, Fig. S3). For the southern cluster, significant correlations were observed for week number (n = 56 SNPs) and sea bottom temperature (n = 55 SNPs) only, with n = 27 SNPs overlapping. The significant correlation of week number and a suite of loci in the southern cluster is noteworthy, as it implies a degree of genetic differentiation between (and potentially underlying) early versus late spawning in the region. For the central cluster, significant correlation was only observed for the latitude factor (n = 25 SNPs). No significant correlations were observed for the northern cluster for either of the four abiotic factors surveyed. Thus, the observed clinal variation largely reflects variation between the three clusters defined by the PC analysis (Fig. 2*A*).

Outlier Populations Show Distinct Local Adaptation. All three spring-spawning population clusters contained locations that were considered outliers based on discordance between their cluster assignment and geographical location. The southern cluster is primarily composed of locations from Blekinge County (Bornholm Basin region), with the exceptions of two locations, from the central Baltic, sampled from the Gamlebyviken region (KAL05 and KAL06) and one location in the southern part of Stockholm archipelago (STH36A) (Fig. 2*B*). The central cluster extends from Kalmar County up till the northern boundary of the Bothnian Sea, with the exception of a single sample intermixed with the southern cluster in Blekinge (BLE07). The northern cluster is restricted to locations sampled in Bothnian Bay, with the exception of two locations (GAV17 and UPP06) located in the Bothnian sea. Genetic contrasts were performed for all outlier populations, but clear differentiation was detected only in KAL05, KAL06, and STH36A (see below); BLE07, GAV17, and UPP06 were therefore excluded from further analysis.

STH36A was one of the most striking outlier populations, with a geographic location in the central region but with a genetic profile more extreme, in terms of the allele frequencies at loci showing a latitudinal cline, than the southern populations. Interestingly, STH36A is in fact a summer spawner; these fish were in spawning condition when sampling occurred July 6, 2021. STH36A was compared with both the southern cluster (to which it was assigned) and the central cluster (the geographically proximate cluster) using a SNP-by-SNP contrast (Fig. 4). Clear peaks of differentiation and increased Δ allele frequency was observed between STH36A and both the southern and central clusters, in particular for the inversions on chromosomes 12 and 17, as well as the region on chromosome 19 (19: 20,476,429 to 20,622,999 bp) containing *HERPUD2* and two long noncoding RNAs. Similar, but less extreme patterns, were observed for the two other outliers in the southern cluster KAL06 and KAL05. The allele frequencies of the Southern haplotype for both the chromosome 12 and 17 inversions in these three outlier populations were as high or even higher than the average frequencies in the populations assigned to the southern cluster. For the *HERPUD2* region, STH36A, KAL05 and KAL06 had a higher allele frequency of the haplotype associated with autumn-spawning than other spring-spawning populations. Notably, STH36A, KAL05, and KAL06 all score in the upper quartile for both weight and length across all locations sampled in this study, with STH36A in particular, having the largest population average for both weight and length (*SI Appendix*, Fig. S10 and Dataset S11).

Indicator Metrics and Population Statistics are Consistent With Large Short-Term Effective Population Size and Genetic Differentiation Driven by Natural Selection. To establish baselines for ongoing monitoring of genetic diversity (national program run by the Swedish Agency for Marine and Water Management in collaboration with L.L.), currently adopted population genetic and indicator metrics were calculated using neutral loci (n =438), with the exception of F_{ST} which used neutral (n =438) and adaptive (n = 4,231) loci separately, note SNPs located on unplaced scaffolds (n = 104) were excluded. Across both seasonal (spring- and autumn-spawning) and within spring population clusters (southern, central, and northern) group comparisons, levels of observed (H_o) and expected (H_e) heterozygosity, nucleotide diversity (π), and proportion of polymorphic loci (PL) were almost identical (SD <1% for aforementioned metrics), indicating that for neutral loci genetic diversity was consistent across all surveyed groups (*SI Appendix*, Table S1).

Estimates of recent effective population size (N_e), inferred from LD patterns using GONE (14), were generally high (4.2 to 5.0 million) when surveying neutral SNPs, but varied depending on group comparison. Regarding seasonal comparisons, the spring-spawning stock (4.7 million) were estimated to have a higher N_e relative to autumn-spawners (4.2 million); while comparison within the spring population clusters indicate N_e was similar in the southern (4.8 million) and northern clusters (5.0 million), with the central cluster estimated to have the lowest overall N_e at 4.2 million. Across all contrasts (*SI Appendix*, Table S1), F_{ST} estimates based on adaptive loci were approximately an order of magnitude or greater than those based on neutral loci (range 9.1 to 50.0×), providing evidence that differentiation is largely driven by selection.

We partitioned LD among the three spring-spawning populations (south, central, north) using Ohta's D-statistics (*SI Appendix*, Table S2), which partitions LD into a total component (D^2_{IT}) and two sources: within-population LD (D^2_{IS}) and among-population LD (D^2_{ST}). The latter reflects covariance introduced by differences in allele frequencies across populations (Wahlund effect), while the former captures LD generated within populations, such as through physical linkage, epistasis, or drift. We also calculated canonical Ohta ratios: D^2_{IS}/D^2_{IT} (within population proportion) and D^2_{ST}/D^2_{IT} (among population proportion). This partitioning allowed us to distinguish LD attributable to within-population processes from LD arising via population subdivision.

Neutral SNP pairs showed very low total LD, with a median D^2_{IT} of 9.2×10^{-4}. The within-population proportion ($D^2_{IS}/D^2_{IT} = 0.18$) and among-population component ($D^2_{ST}/D^2_{IT} = 0.20$) were similar, indicating weak LD distributed between within- and among-population processes. Overall, neutral loci reflect weak LD shaped by modest drift and low subdivision, with no strong signature of population differentiation.

The strongest LD signals were observed for adaptive SNPs located inside chromosomal inversions. Here, the median D^2_{IT} reached 7.5×10^{-2}, which is more than an order of magnitude higher than adaptive SNPs outside inversions and approximately 80 times higher than neutral SNPs. Raw LD proportions indicate that among-population differentiation dominated ($D^2_{ST}/D^2_{IT} = 0.25$, while $D^2_{IS}/D^2_{IT} = 5.8 \times 10^{-3}$) and thus, raw LD captures strong differentiation among populations. Adaptive SNPs outside inversions were less extreme ($D^2_{IT} = 5.2 \times 10^{-3}$), but still remained an order of magnitude higher than the neutral set. Raw LD ratios were again dominated by among-population contributions ($D^2_{ST}/D^2_{IT} = 0.24$) relative to within-population ($D^2_{IS}/D^2_{IT} = 0.02$) contributions.

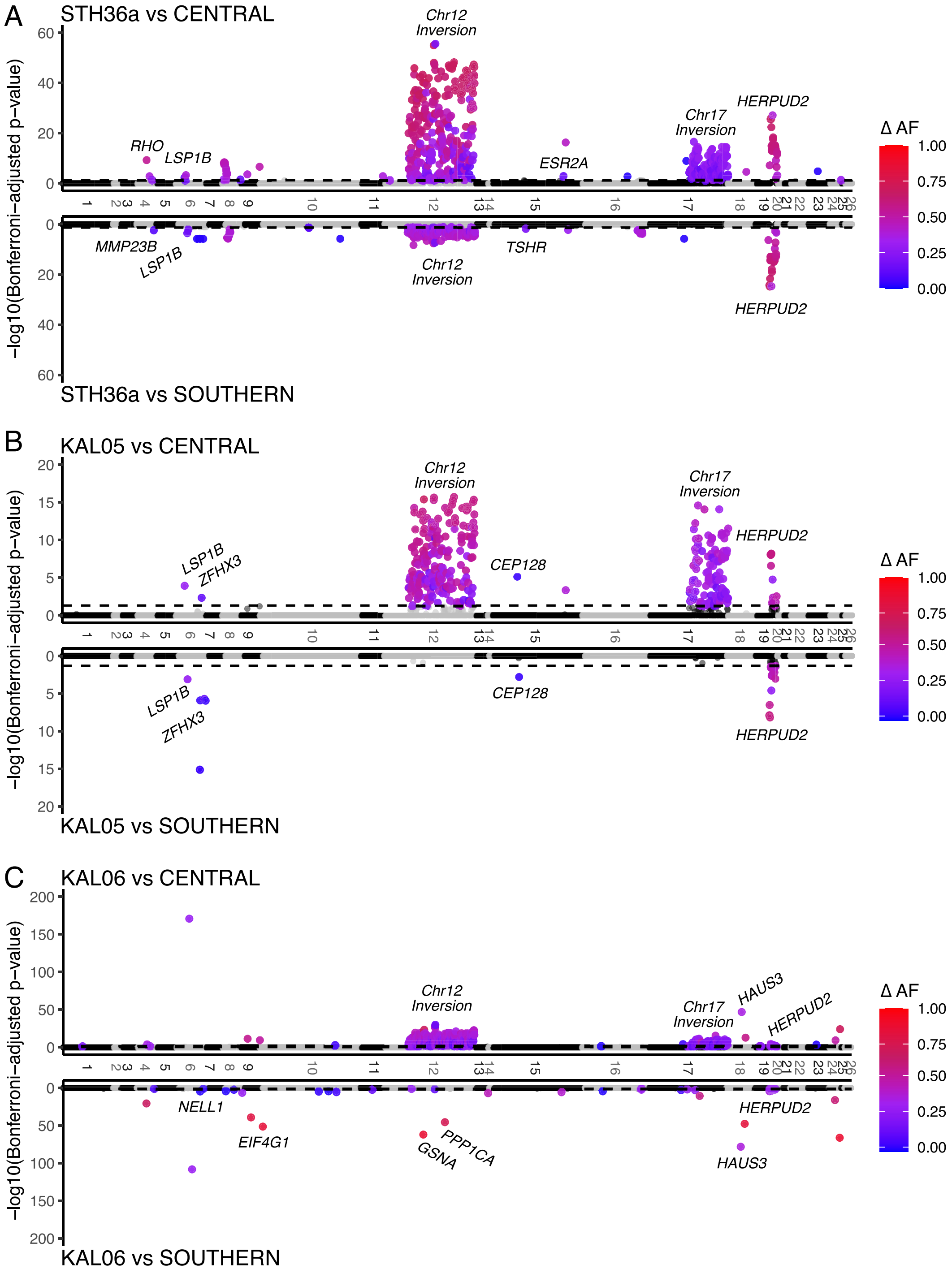

Fig. 4. Summary and annotation of pairwise, SNP-by-SNP chi-squared contrasts between outlier populations STH36a (*A*), KAL06 (*B*), and KAL05 (*C*), and the spring-spawning cluster averages for the southern (*Lower* panel, representing the cluster to which each outlier was assigned) or central populations (*Upper* panel, representing the cluster where each outlier is geographically located). Nonsignificant SNPs (Bonferroni-corrected $P > 0.05$) are shown in alternating gray and black to distinguish consecutive chromosomes, while significant SNPs (Bonferroni-corrected $P < 0.05$) are colored using a gradient (blue to red) to indicate the absolute delta allele frequency difference for the given SNP.

Across all comparisons, the ratio of among-population to within-population LD was greatest for adaptive SNPs inside inversions, high for adaptive SNPs outside inversions, and smallest for neutral SNPs. Taken together, these results indicate that population subdivision and local adaptation—reinforced by structural variation—are the dominant forces shaping LD in this dataset, whereas processes such as epistatic selection within populations appear to play a minor role. For neutral loci, low overall LD and balanced raw within- and among population contributions reflect weak drift-dominated structure and limited differentiation between the southern, central, and northern clusters. In summary, the results support a scenario in which strong local selection maintains adaptive differentiation despite homogenizing gene flow.

Discussion

Here we have presented a comprehensive genetic analysis of the Baltic herring, which was classified as a subspecies of the Atlantic herring by Linneaus (15). The analysis of 150 population samples from the Swedish Baltic Sea coast, involving only herring in spawning condition, has provided a high-resolution view of the population structure of this abundant, broadcast-spawning fish. The results reveal a fine-grained population structure in the Baltic Sea. The result is unexpected for this abundant, migratory marine fish, in particular since the first population genetic studies, based on a dozen neutral allozyme markers, could not exclude the possibility that all Atlantic and Baltic herring constitutes a single panmictic population (16). Broadly, we reaffirm the previously reported (6, 17) strong genetic differentiation between spring- and autumn-spawning herring. Additionally, principal component analysis (PCA) revealed three genetically distinct clusters within the spring-spawning ecotype (Fig. 2*A*). While these clusters (southern, central, and northern) were clearly differentiated, we also detected fine-scaled differentiation within clusters, suggesting potential for further local adaptation within the major clusters. Supporting this, we identified several outlier populations with distinct genetic profiles (i.e., STH36A, KAL05, and KAL06), further illustrating the potential for local adaptation and maintenance of genetic variation. Interestingly, we also detected genetic differentiation between early versus late spring-spawners within geographic regions. Previous studies have described how waves of herring arrive at spawning grounds (18, 19), now we show that these waves of spawning fish are often associated with genetic differentiation.

The strong genetic differentiation between spring- and autumn-spawning herring involves loci that are consistently associated with spawning type in populations from the Baltic Sea, eastern Atlantic Ocean, and western Atlantic Ocean (6, 17). These include three distinct regions on chromosome 15, harboring the *SOX11B*, *TSHR,* and *ESR2A* genes and several other genes, and on chromosome 19 harboring *HERPUD2* and some lncRNA genes. These genomic regions are expected to be directly involved in the genetic basis for photoperiodic regulation of reproduction in herring (6). The consistency across geographic regions involves not just the same genomic region, but it is shared haplotypes associated with spring- vs. autumn-spawning (17). In addition to these regions, several loci in this study (Fig. 2 *C–E*) were not reported in previous global analyses (including *BICD2*, *VMN1R69*, *ARFIP1*, and *AIP*). Their absence from earlier works likely reflects two factors: first, the current study's large sample size (>4,500 individuals) and individual-level genotyping provided greater resolution to detect fine-scale variation; and second, these loci may reflect adaptive signals specific to fitness in the Baltic Sea. These loci are therefore unlikely to be directly involved in photoperiodic regulation of reproduction but may influence fitness in spring- and/or autumn-spawning Baltic herring. The most important finding regarding spawning ecotypes constitutes clear evidence for gene flow between spring- and autumn-spawning herring as documented by the presence of hybrid individuals (consisting primarily of F1 and spring backcross individuals) with offset spawn timings, intermediate allele frequencies, and high heterozygosity at loci associated with spawning ecotype (Fig. 1*G*). The results suggest that in the absence of strong natural selection there would be no genetic differentiation between spring-and autumn-spawning herring, because the amount of gene flow is well above the minimum amount required to eliminate genetic differentiation at neutral loci (20). This finding, together with the observed minimal differentiation between seasonal ecotypes at neutral loci, is consistent with previous data suggesting the presence of gene flow (17). The fitness of these hybrid individuals is unknown, but natural selection at loci showing genetic differentiation is sufficiently strong to maintain differentiation regardless. However, the observed gene flow provides an explanation for low genetic differentiation at neutral loci even between spring- and autumn-spawning populations (*SI Appendix*, Table S1).

As many as 16 population samples (which consisted of spawning capable fish) contained at least one individual with a mismatched genotype at loci associated with spawning type, with these occurrences being more frequently observed at northern latitudes, particularly within the Bothnian Bay. How a minority of, for example, autumn-spawners are able to synchronize their reproductive cycle with a school of spring-spawners poses questions around the mechanisms underlying initiation of spawning in herring; whether timing of reproduction as a trait shows plasticity in the presence of specific behavioral or chemical cues (potentially dictated by the school's majority spawning component). The degree of mixing between herring ecotypes at offshore feeding grounds in the Baltic Sea is not known, but our result suggests that mixing, or, more specifically, incomplete sorting of schools based on spawning ecotype regularly occurs in the Baltic.

Previous work on Atlantic herring has characterized the evolutionary history of four megabase-scale inversions on chromosomes 6, 12, 17, and 23, and all show strong latitudinal clines in the Atlantic Ocean (6, 9); at each locus the Northern and Southern haplotypes are dominating in the northern and southern parts of the species distribution, respectively. The latter three inversions are segregating in Baltic herring and show similar north–south clines in allele frequencies among populations of spring-spawning Baltic herring (Fig. 2). In particular, the inversions on chromosomes 12 and 17 play a prominent role in the genetic differentiation within the Baltic Sea. Interestingly, the Northern haplotype does not show complete fixation even in the Bothnian Bay (Fig. 3*C*). A possible explanation is some degree of heterozygote advantage, which could occur if the Northern haplotype has accumulated genetic load due to suppressed recombination (21). Another interesting finding was the relatively high-frequency of the autumn allele at loci strongly associated with spawning type on chromosomes 12 (*MYH*), 15 (*TSHR*), and 19 (*HERPUD2*) among spring-spawning populations in the northerly Bothnian Bay, which are spawning much later than spring-spawning populations from the south due to the colder climate in the north.

Partitioning LD with Ohta's statistics (12, 22, 23) revealed that adaptive loci exhibit much stronger LD than neutral loci, with the among-population component (D^2_{ST}) exceeding the within-population component ($\mathrm{D}^2_{\mathrm{IS}}$) by ~13-fold outside of inversions and by ~74-fold inside inversions. Total LD ($\mathrm{D}^2_{\mathrm{IT}}$) was approximately 10 times higher for adaptive loci and nearly eighty times higher inside inversions compared to neutral pairs. This partitioning is informative because it distinguishes whether LD reflects direct selection within populations, indirect selection via population subdivision, or drift. Our observed pattern is the expected signature of a Wahlund effect created by local adaptation and differences in spawning time and location, rather than pervasive epistatic selection (which would yield $D^2_{IS} \gg D^2_{ST}$). Inversions magnify this signal through recombination suppression and divergent inversion haplotype frequencies along the north–south cline, consistent with a high frequency of Southern haplotypes in warm, shallow systems such as Gamlebyviken and in summer-spawning populations such as STH36A. The consistently small $\mathrm{D}^2_{\mathrm{IS}}$ across the various SNP partitions is consistent with low gene flow and approximately random mating within the three spring clusters (south, central, north), even though neutral differentiation remains minimal (as indicated by low F_{ST}). This pattern reflects migration–selection balance, where strong local selection maintains adaptive differentiation despite homogenizing gene flow. While our SNP-chip design limits inference on genome-wide LD and epistasis, future studies using whole-genome data could test whether selection induces subtle nonrandom mating or epistatic interactions beyond the loci examined here.

In a recent study, we reported the finding of a piscivorous ecotype of Baltic herring that is much larger than the planktivorous herring dominating in the Baltic Sea (7). The piscivorous herring present in the Bothnian Sea were well known among local fishermen and had a local name, Slåttersill (meaning big herring spawning at hay-harvesting time). Similarly, here we identified outlier population samples, in particular STH36A from the archipelago of Stockholm as well as KAL05 and KAL06 from a geographic region close to Gamlebyviken (Fig. 2*B*). These two groups show striking genetic differentiation from other population samples from the same geographic regions (Fig. 4). They were also outliers regarding length and weight (*SI Appendix*, Fig. S10 and Dataset S11), but to a lesser degree than the piscivorous Baltic herring. STH36A herring are in fact summer spawners that were sampled in spawning condition in July and carries the local name "wild-rose herring" (translated from Swedish), since it spawns when the wild roses are flowering in mid-July. Thus, it makes perfect sense that this summer-spawning population is characterized by high frequencies of the Southern haplotypes at the chromosome 12 and 17 inversions, since it is spawning when the water is much warmer than in the spring (April–May). Already in the 1920s, Hessle (8) described the presence of a distinct ecotype present in Gamlebyviken, in the near vicinity where the KAL05 and KAL06 samples were collected. Baltic herring from Gamlebyviken was included in the first population genetic study of Baltic herring, but no genetic differentiation was noted in comparison with other populations of Baltic and Atlantic herring, based on a dozen neutral allozyme loci (16). However, 35 years later exactly the same samples from Gamlebyviken were used for whole genome sequencing, which revealed clear genetic differentiation from other populations of Atlantic and Baltic herring (6). The most striking difference was an exceptionally high frequency of the Southern haplotype of the chromosome 12 inversion. This result is now replicated in the two population samples (KAL05 and KAL06) from the same geographic region and the pattern involves both the chromosome 12 and 17 inversions (Fig. 4). Gamlebyviken is a narrow and shallow bay on the Swedish east coast where the water warms up faster than in offshore areas, which may explain the unexpectedly high frequency of the Southern haplotypes at these inversions. Subpopulations adapted to spawning in relatively warm water are expected to harbor gene variants that can be of critical importance for future adaptation to the expected increasing water temperatures. The relatively small water body in the Baltic Sea makes it particularly affected by global warming (24) implying that it is important to protect the outlier populations detected here.

The complex population structure now documented in this highly abundant, migratory marine fish was unexpected. The observed pattern of genetic differentiation can only be explained if this species has a sophisticated homing behavior, where fish have a high probability to return to the spawning grounds where they were born, and at the same time of the year, when ready to reproduce. As a consequence, the allele frequencies at loci contributing to ecological adaptation are to a large extent determined by when and where the population is spawning. Atlantic and Baltic herring are demersal spawners, they deposit sticky eggs on the sea floor or on vegetation. Thus, development takes place under the abiotic conditions at the spawning ground and during this period geographic imprinting can take place, which likely is required for the homing behavior. The molecular mechanisms contributing to homing behavior in herring is not known, but it has been proposed that herring may use cryptochrome 4 as a magnetoreceptor during migration (25). However, the homing behavior, as well as timing of spawning, is not 100% accurate, allowing for gene flow between subpopulations as well as between spawning ecotypes. This, together with large population size and high fecundity, which leave plenty of room for natural selection to operate, provide a reasonable explanation for the unique feature of the Atlantic herring; strong genetic differentiation at loci contributing to ecological adaptation but minute genetic differentiation at neutral loci (*SI Appendix*, Table S1) (6). It is likely that a similar comprehensive genetic analysis across the species distribution in the Atlantic Ocean will reveal a large number of subpopulations with local ecological adaptation, although it is plausible that the population structure is more fine-grained in the Baltic Sea, due to the presence of a salinity gradient and the much larger amplitude of temperature variation over the year.

The present study has important implications for fishery management and maintenance of genetic diversity in this keystone species in the Baltic Sea. Our data show that the herring in the Baltic Sea includes a number of subpopulations with variable degrees of genetic differentiation between them. This is not taken into account in current fishery management programs. At present the absolute majority of all landings of Baltic herring are made by large-scale trawling at feeding and wintering areas for the production of fish meal (26, 27). It is unknown how much this practice affects the mortality of different subpopulations of Baltic herring, the monitoring of which can be improved using the tools provided here., i.e. by using mixed fishery analyses and assignment of captured fish to genetic population. Further, the results implies that traditional coastal fishery targeting spawning fish is a more sustainable alternative for commercial fishing, since it has the potential to target individual spawning groups in relation to their abundance.

Methods

Herring were sampled from 150 timepoint/locality combinations along Sweden's east coast, and 4,678 reproductively mature [stage 6 (28)] individuals genotyped using the MultiFishSNPChip_1.0 array (2, 7) (n = 4,773 loci, see *SI Appendix*, Fig. S11). Filtered SNP datasets were used to assign spawning ecotypes, identify outliers, and assess hybridization. Population structure, allele-frequency contrasts, genotype–environment associations, and outlier populations were assessed using PCA, K-means, chi-square tests, LFMM (29), and RDA (30). Genetic diversity, F_{ST}, effective population size, and LD statistics were estimated from various combinations of neutral and adaptive SNP datasets. Complete methodological procedures and analysis parameter settings are detailed in the *SI Appendix*.

Data, Materials, and Software Availability. All code used to analyze genotype data are available at https://github.com/LeifAnderssonLab/Baltic_herring_pop_structure (31). Tissues from all herring individuals analyzed in this study are stored in a biobank kept at the Department of Zoology, Stockholm University by L.L. and N.R. All genotype data are available from the European Variant Archive (EVA) under accession PRJEB96176 (32).

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