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Original Article

Scrutinizing the current management units of the greater argentine in the light of genetic structure

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Abstract

The greater argentine is a benthopelagic fish with a northern amphi-Atlantic and southern Arctic distribution. Landings of this species have been steadily increasing since the early 2000s, mainly for ultra-processed fish food. The rising economic importance of this species begs for an accurate delineation of the management units needed to ensure the sustainability of the fishery. The alignment between management and biological units was investigated on three of the ICES stocks in the NE Atlantic (123a4, 5a14, and 5b6a) by genotyping 88 *ad hoc*-developed SNPs on 1299 individuals sampled along the Norwegian coast, north of Shetland, around the Faroe Islands, and in the Denmark Strait within Icelandic waters. Candidate loci to positive selection were particularly crucial for units' delineation and supported the current ICES 5b6a and 5a14 stocks around the Faroe Islands and Iceland, respectively. However, within the third stock investigated, 123a4, which corresponded mainly to the Norwegian coast, the sample from area 3a (Skagerrak) was significantly different from all the remaining in the same stock. This differentiation advocates for reconsideration of the present policy and suggests considering ICES Area 3a (Skagerrak) as an independent management unit. The environmental conditions in the Skagerrak area have left a genetic print on other marine taxa, which could putatively be the case in the greater argentine.

Keywords: Argentina silus; greater argentine; benthopelagic; northeastern Atlantic; population structure; fisheries; SNPs; management units

Introduction

Fisheries are considered sustainable when they do not compromise the persistence of viable wild populations; however, major global threats such as illegal, unreported, and unregulated fishing, overfishing, pollution, climate change, and often complex bureaucracy hinder this goal (Worm et al. 2009, Hilborn and Stokes 2010, Osio et al. 2015, Spies et al. 2015, Pauly and Zeller 2016). A reliable management is one of the requirements of sustainability and needs to be based, among other pillars, on biologically valid management units (also called stocks) (Kerr et al. 2017). Stock delineation based upon political and administrative considerations (Stephenson 2002) has often led to misalignment with biological units (Frank and Brickman 2000, Reiss et al. 2009, Kerr et al. 2017), whereas methods of stock definition based on biology (see Cadrin et al. 2014 for revision) have in recent decades been complemented by genetic- and genomic-based approaches (Reiss et al. 2009, Funk et al. 2012, Ovenden et al. 2015, Casey et al. 2016, Bernatchez et al. 2017) to increase accuracy and prevent the overexploitation of unique spawning components (Allendorf et al. 2008, Kerr et al. 2017). Sampling adults during spawning periods, particularly in migratory species, is the best approach to identify population structure and to accurately outline management units (Nesbø et al. 2000, Hutchinson et al. 2001).

The greater argentine, also known as Atlantic argentine, greater silver smelt, or herring smelt (*Argentina silus* Ascanius 1775), is a benthopelagic fish found along the continental shelves on both sides of the northern Atlantic and southern Arctic oceans (Emery and McCracken 1966, Bergstad 1993, Magnússon 1996) within a bathymetric distribution ranging from 140 to 1440 m depth (Cohen 1984). In Norwegian waters, spawning takes place from April through October (Bergstad 1993) although the locations of the spawning grounds are not known. However, Magnússon (1996) reported that, in Icelandic waters, spawning individuals were found in all months except January. Males in spawning condition were most abundant in March, April, and July, whereas females were most abundant in February, July, and December, indicating that although the species spawns year-round in Icelandic waters, intensive spawning seems to take place between April and July, and in December.

Greater argentine is a long-lived, slow-growing species that can reach 30 years of age (Bergstad 1993) and matures at the age range of 4–12 years, mean age for females being 6 years and 7 for males (Johannessen and Monstad 2003). Growth is slightly faster in females, and, at 1 year of age, fish measure ∼12–22 cm, reaching 30 cm at the age of 5 (Bergstad 1993). Unlike most of the Argentinidae, which rarely >25 cm

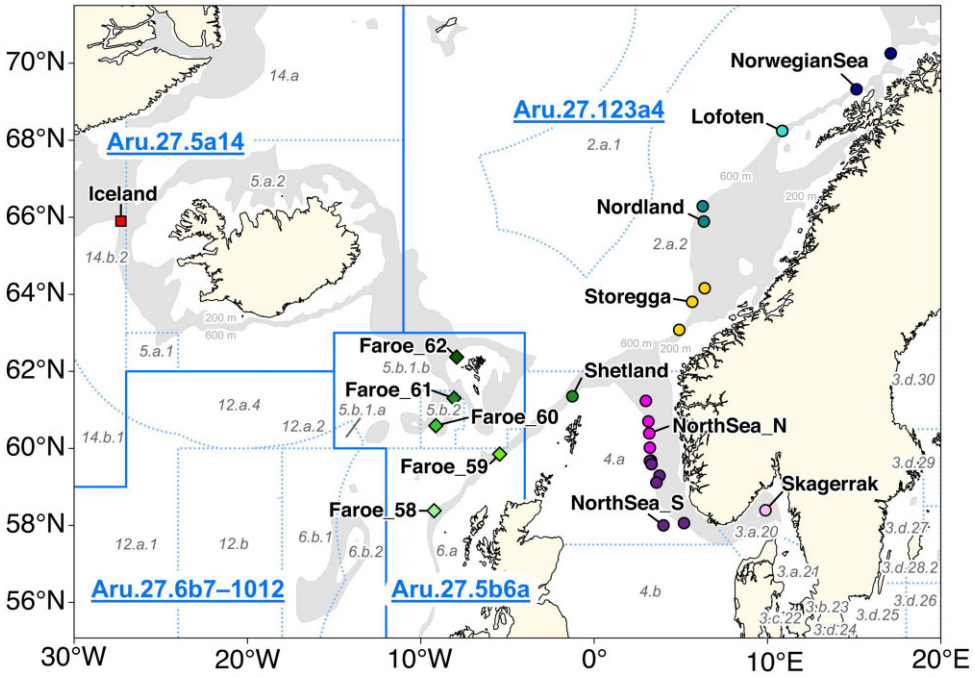

Figure 1. Map displaying the sampling locations of *Argentina silus* along with the current stock codes and management units. Stations marked with symbols of identical colours represent samples that were merged for analyses. Symbol shapes indicate the current ICES fishing stocks, delineated with thick lines and labelled with big fonts. Dotted lines demarcate ICES statistical areas, identified by small numerals. The 200–600 m depth interval, the core depth range for *A. silus*, is shaded. Note: ICES areas 1a and 1b, situated in the Barents Sea, are not depicted in this map.

in length, greater argentine can grow up to 40–50 cm after 20 years. The 50% maturity point is reached by males at a length of 36–37 cm and at an age of ∼8 years, and by females at a length of 37–38 cm and ∼9 years (Magnússon 1996). In the Rockall area (Fig. 1, see Faroe_58), greater argentines feed on salps, ctenophores, and other prey in the benthopelagic environment (Mauchline and Gordon 1983), whereas in the western Atlantic they have been found with 'shrimp-like crustaceans' in their stomachs (Cohen 1958, Cohen 1964). A diet analysis conducted by Borodulina (1964) showed that European and American Atlantic greater argentines foraged on chaetognaths, euphausiids, hyperiid amphipods, shrimp, squid, and ctenophores, as well as fish (by large individuals of 48–49 cm).

Landing records of greater argentine depict the rising economic importance of this species since the early 2000s (Supplementary Fig. S1) as well as bycatch landings, which have increased from 350 t in 2012 to 7786 t in 2018 (ICES 2021). Historically, the harvest was the result of by-catches in the mixed industrial trawl fisheries, mainly in the North Sea, and was either discarded or processed for reduction. However, from the mid-1970s, a directed fishery intended for human consumption started in Skagerrak and mid-Norway (Johannessen and Monstad 2003), in Icelandic and Faroese waters in the mid-1990s, and in West Scotland–Northern Ireland in early 2000s (ICES 2021). Greater argentine meat is primarily used in ultra-processed fish food, due to its softness, binding capacity, and high fat content (Østebrød 2020).

Greater argentine inhabits 2 of FAO major fishing areas: 21 and 27 in the NW and NE Atlantic, respectively. The management of the latter is subdivided by the International Council for the Exploration of the Sea (ICES) into four stock units (ICES 2021): (i) ICES areas 1, 2, 3a, and 4 (Aru.27.123a4); (ii) ICES areas 5a and 14 (Aru.27.5a14); (iii) ICES areas 5b and 6a (Aru.27.5b6a); and (iv) ICES areas 6b, 7–10, and 12 (Aru.27.6b7–1012), with most of the fisheries concentrated in deeper waters and on shelf edges within the three first mentioned stock units. Until 2015, only greater argentine around Iceland was treated as a separate assessment unit, as Icelandic life-history studies suggested that a separate stock might exist in Subarea 5a (ICES 1998). During the ICES benchmark meeting in 2010 (ICES 2010), the outline of stock structure was put forward, and hence, data and analyses were presented on growth curves (age and length data), maturity ogives (age at first maturity and gonad stage), and distribution and timing of spawning (Hallfredsson 2010). These analyses generally grouped data into the three main fisheries areas: Iceland, Faroe Islands, and Norway. In 2015, the remaining ICES areas were allocated into current advisory units, as fishing grounds were considered sufficiently isolated (ICES 2014). This delineation regarded the stock units as populations, but without an underlying genetic basis. Therefore, assessing genetic structure would provide important information to better manage the species, be it as independent populations requiring local management, or as transboundary stocks requiring close international cooperation.

The objective of this study is to assess the genetic structure of greater argentine in the north-east Atlantic and use this information to investigate whether the current management units of ICES stock delineation align with biological units.

Material and methods

Sampling

A total of 1299 individuals were sampled at multiple locations in the NE Atlantic Ocean (Fig. 1), covering 3 of the 4 stocks outlined by ICES hereafter referred to as: 'Norwegian',

Aru.27.123a4 ($N = 762$); 'Icelandic', Aru.27.5a14 ($N = 95$); and 'Faroese', Aru.27.5b6a ($N = 235$). Within those stocks, individuals were distributed into 14 samples ranging from $N = 40$ to $N = 201$ (see Table 1). Most of the fish were collected in seven sampling areas along the Norwegian coast, from the Norwegian Sea in the north to the North Sea and Skagerrak in the south. In addition, fish were collected north of Shetland, around the Faroe Islands (including in the Faroe Trench), and in the Denmark Strait in Icelandic waters. Some areas, such as northern and western Norway and the Faroe Islands, were sampled several years. Sampling was conducted during scientific trawl surveys (2016–2019), and fish were caught in bottom trawls near the seafloor, handled and sampled by trained personnel in accordance with national legislation. Geographically close sampling stations showing no genetic differentiation across years were merged in one sample to increase sampling size and statistical power. More than 300 individuals were collected around Faroe Islands; they were therefore distributed in samples according to their geographic positions within 1° latitude from 58° to 62°. Fin clips were preserved in 96% ethanol prior to DNA extraction.

Finally, in spite that ideally only breeding adults should be used for genetic stock assessment, the wide breeding time window of this species led to have mixed samples of adults and juveniles in some of the locations (Supplementary Table S1). The discrimination between both age groups was based upon maturity, with juveniles belonging to stage 1 and adults belonging to stage 2 and upwards. However, sample NorthSea_S contained representative numbers of both groups to assess genetic divergence in connection to age.

Development of SNP markers and genotyping

To capture as much genetic differentiation as possible, high-quality DNA (high molecular weight fragments with an $A_{260}/_{280}$ absorbance ratio between 1.8 and 2.0) from 16 individuals collected in geographically distant areas, i.e. Bear Island (Barents Sea; $N = 8$) and Faroe Islands ($N = 8$), was used for the initial SNP detection. DNA was isolated using a Qiagen blood and tissue kit following the manufacturer's recommendations. A double-digest RAD (ddRAD) library was constructed for SNP mining following Manousaki et al. (2015) using a SbfI–SphI restriction enzyme combination and sequenced on the Illumina MiSeq platform. Sequence reads were demultiplexed, and SNPs were identified/scored using STACKS 1.47 (Catchen et al. 2013) parameters (de novo assembly; parameters $m = 6$, $M = 2$, and $n = 1$) before SNP locus primer design for the MassARRAY iPLEX Platform (Agena Bioscience). A panel of 100 SNPs was thus developed and genotyped in-house in an attempt to balance genotyping costs and statistical power based upon former successful experiences (e.g. Quintela et al. 2020, 2021b, Seljestad et al. 2020). For genotyping the complete set of samples, total genomic DNA was extracted from fin clips using the Qiagen DNeasy 96 Blood and Tissue Kit following the manufacturer's instructions. Individuals were genotyped for an array of 100 SNPs on a MassARRAY platform using an iPLEX reaction (Agena Bioscience) (Gabriel et al. 2009). Genotypes were called with TyperAnalyzer 4.1.83 (Agena Bioscience), and all genotypes with a mass height <0.4 were removed. Both the markers developed for this study and the resulting genotypes can be publicly accessed from the HI repository (https://hdl.handle.net/11250/3122412).

Table 1. Sample summary statistics for the set of 88 SNP loci.

Stock	Sample	Month	Year	N	H_o	uH_e	F_{IS}	Dev HWE (FDR)	Dev LD (FDR)
Aru.27.123a4	Norwegian Sea	3, 4	2016, 2018	113	0.321 ± 0.015	0.336 ± 0.015	0.033 ± 0.019	7 (5)	213 (0)
	Lofoten	3, 4	2016, 2018	78	0.324 ± 0.016	0.343 ± 0.014	0.060 ± 0.024	12 (8)	180 (1)
	Nordland	3, 4	2016	40	0.309 ± 0.016	0.331 ± 0.015	0.055 ± 0.022	9 (3)	192 (0)
	Storegga	3, 4	2018	62	0.338 ± 0.014	0.344 ± 0.014	0.009 ± 0.015	9 (0)	200 (1)
	Shetland	9	2019	42	0.331 ± 0.016	0.345 ± 0.014	0.038 ± 0.026	9 (4)	177 (1)
	NorthSea_N	6, 7, 9, 10	2018, 2019	201	0.322 ± 0.014	0.337 ± 0.013	0.045 ± 0.016	15 (6)	204 (2)
	NorthSea_S	1, 6, 7	2018	179	0.325 ± 0.014	0.338 ± 0.013	0.037 ± 0.015	18 (9)	189 (2)
	Skagerrak	1	2018	47	0.333 ± 0.014	0.346 ± 0.014	0.021 ± 0.016	7 (1)	196 (1)
Aru.27.5a14	Iceland		2017	95	0.317 ± 0.017	0.326 ± 0.015	0.028 ± 0.021	18 (8)	284 (0)
Aru.27.5b6a	Faroe_62	3, 9, 10	2016, 2018	45	0.334 ± 0.017	0.338 ± 0.014	0.024 ± 0.024	10 (5)	178 (1)
	Faroe_61	3, 9, 10	2016, 2018	61	0.313 ± 0.015	0.335 ± 0.014	0.058 ± 0.022	11 (5)	166 (1)
	Faroe_60	3, 9, 10	2016, 2018	68	0.317 ± 0.016	0.327 ± 0.015	0.029 ± 0.021	16 (9)	179 (1)
	Faroe_59	3, 9, 10	2016, 2018	61	0.329 ± 0.017	0.336 ± 0.014	0.034 ± 0.026	9 (6)	170 (0)
	Faroe_58	3, 9, 10	2016, 2018	74	0.323 ± 0.014	0.333 ± 0.014	0.016 ± 0.014	4 (1)	163 (1)

Sampling sites within fishery stocks, number of individuals (N); observed heterozygosity, H_O (mean ± SE); unbiased expected heterozygosity, uH_E (mean ± SE); inbreeding coefficient, F_{IS} (mean ± SE); number of deviations from Hardy-Weinberg expectations (HWE) at $\alpha = 0.05$; number of deviations from linkage disequilibrium (LD) at $\alpha = 0.05$ both before and after (FDR) false discovery rate correction.

Data handling and analysis

SNP loci and individuals missing >20% data were discarded, resulting in the removal of 8 loci and 133 individuals. Likewise, 4 monomorphic markers were also discarded, leaving a dataset of 1166 individuals genotyped at 88 polymorphic SNP loci. To assess whether the SNP array would accurately discriminate between individuals in a population, a genotype accumulation curve was built using the function *genotype curve* in the R (Team 2020) package *poppr* (Kamvar et al. 2014) by randomly sampling × loci without replacement and counting the number of observed multilocus genotypes (MLGs). This was repeated *r* times for 1 locus up to *n*-1 loci, creating *n*-1 distributions of observed MLGs.

Observed (H_O) and unbiased expected heterozygosity (uH_E), as well as the inbreeding coefficient (F_{IS}), were estimated for each sample with GenAlEx (Peakall and Smouse 2006). The genotype frequencies of each locus and heterozygote deficit or excess were compared with Hardy-Weinberg expectations (HWE) using the programme GENEPOP 7 (Rousset 2008), as was linkage disequilibrium (LD) between pairs of loci. HWE and LD were examined with the following Markov chain parameters: 10 000 steps of dememorization, 1000 batches, and 10 000 iterations per batch. The False Discovery Rate (FDR) correction (Benjamini and Hochberg 1995) was applied to *P*-values to control for Type I errors. Data were plotted via a principal component analysis (PCA), which was conducted using the function *dudi.pca* in *ade4* (Dray and Dufour 2007).

Loci carrying signatures of locally divergent selection can be powerful markers to assess spatially explicit genetic structure, and to define stocks for fisheries management (Russello et al. 2012, Schulze et al. 2020). Thus, three approaches were combined to identify loci possibly departing from neutrality: BayeScan 2.1 (Foll and Gaggiotti 2008), LOSITAN (Antao et al. 2008), and Arlequin 3.5.1.2 (Excoffier et al. 2005). In BayeScan, sample size was set to 10 000 and thinning interval to 50. Loci with a posterior probability >0.99, corresponding to a Bayes factor >2 'decisive selection' (Foll and Gaggiotti 2006), were retained as candidate outliers. In LOSITAN, a neutral distribution of F_{ST} with 1 000 000 iterations was simulated, with forced mean F_{ST} at a significance level of 0.05 under an infinite allele model. In Arlequin, analysis was simulated based on 1000 demes with 50 000 simulations under a hierarchal island model. Loci flagged as deviating from neutral expectations by the three methods simultaneously were handled as candidate outliers and kept separate when appropriate.

Genetic structure was assessed using AMOVA and pairwise F_{ST} (Weir and Cockerham 1984) estimated with Arlequin 3.5.1.2 (Excoffier et al. 2005) using 10 000 permutations. The Bayesian clustering approach implemented in STRUCTURE 2.3.4 (Pritchard et al. 2000), and conducted with ParallelStructure (Besnier and Glover 2013), was used to identify genetic groups under a model assuming admixture and correlated allele frequencies, both with and without LOCPRIORS to assist the clustering. Ten runs with a burn-in period of 100 000 replications and a run length of 1 000 000 MCMC iterations were performed for $K = 1$–$K = 10$ clusters. STRUCTURE output was then analysed using two approaches to assess the number of clusters: (i) the *ad hoc* summary statistic ΔK of Evanno et al. (2005) and (ii) the four statistics Puechmaille (2016) (MedMedK, MedMeanK, MaxMedK, and MaxMeanK), both implemented in StructureSelector (Li and Liu 2018). Finally, the 10 runs for the selected *K*s were averaged with CLUMPP 1.1.1 (Jakobsson and Rosenberg 2007) using the FullSearch algorithm and the G' pairwise matrix similarity statistic, and graphically displayed using barplots. Furthermore, the relationships among samples were also examined using the discriminant analysis of principal components (DAPC; Jombart et al. 2010) implemented in *adegenet* (Jombart 2008), in which groups were defined using (i) geographically explicit samples and (ii) current ICES stocks. To avoid overfitting, both the optimal number of principal components and discriminant functions to be retained were determined using the *xvalDapc* cross-validation function, also in *adegenet* (Jombart and Collins 2015, Miller et al. 2020).

The relationship between genetic (F_{ST}) and geographic distance (*Km*) was examined to test for isolation by distance (IBD) (Wright 1943, Slatkin 1993, Rousset 1997). A two-tailed Mantel (1967) test was conducted using PASSaGE 2 (Rosenberg and Anderson 2011) and significance was assessed via 10 000 permutations. The matrix of pairwise shortest distance by water was calculated with the R (Team 2020) package *marmap* (Pante and Simon-Bouhet 2013).

Results

The genotype accumulation curve showed that as few as 15–20 loci carried enough power to discriminate between unique individuals, thus confirming the resolution capacity of the SNP array used (Supplementary Fig. S1). Observed (H_O) and unbiased expected heterozygosity (uH_E) were similar across samples (~0.3) (Table 1). Some 154 SNP locus-population combinations (12.5% of the total 1232) deviated from HWE, which dropped to 70 (5.7%) after FDR correction. A total of 2691 of the 53 592 pairwise tests for LD (5%) showed significant associations, which dropped to 12 (0.02%) after FDR correction. Heterozygote deficits were significant in all samples but Storegga. Loci Asi_112 and Asi_127 displayed strong and significant linkage in all samples.

The first axis of the PCA biplot, built upon 88 loci, drove a striation pattern lacking a geographic basis (Fig. 2a). The loadings on the first axis of the PCA revealed that the two abovementioned loci in LD were responsible for such clustering. The topological distribution of the individuals into three groups (Supplementary Fig. S2) resulted in a frequency of 1–0.5–0 per group for loci Asi_112 and Asi_127, which could putatively be regarded as AA–AB–BB karyotypes. Collectively, 87.5% of the fish carried karyotype AA, whereas BB was the minority (3.5%). Karyotype AA showed a decreasing frequency trend southward (Supplementary Table S2), broken by Faroe samples. Skagerrak not only showed the smallest proportion of AA (63.8%) but singled out for displaying the largest frequency of AB (29.8%). Dataset was LD-pruned by removing locus Asi_112, as it contained a slightly larger percentage of missing data than Asi_127. The PCA resulting from the 87 LD-pruned loci lacked the striped pattern, yet remained unable to show geographic discrimination among individuals (Fig. 2b).

The three outlier procedures conducted on the LD-pruned dataset consistently flagged five loci as candidates to positive selection: Asi_052, Asi_073, Asi_088, Asi_103, and Asi_127 (Supplementary Table S3). All of them were retained as putative outliers; however, none of their flanking regions could be

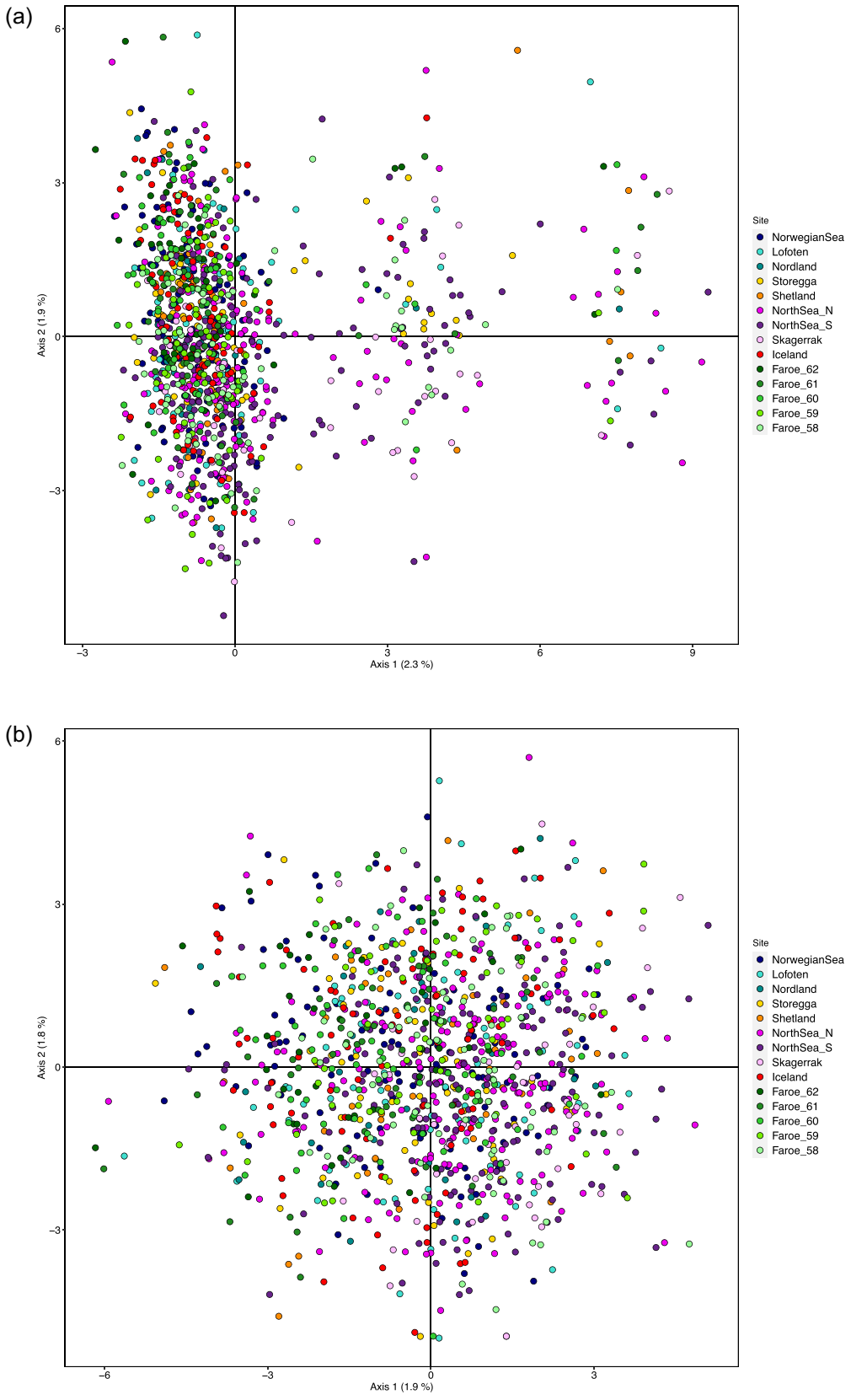

Figure 2. Principal Component Analysis (PCA) of greater argentine (*Argentina silus*) from NE Atlantic with individuals coloured according to samples based upon: (a) 88 polymorphic SNPs and (b) 87 polymorphic SNPs after removing one of the two linked loci.

Table 2. Genetic differentiation between geographically explicit samples: heatmap of pairwise F_{ST} assessed using the LD-pruned 87 SNPs (lower diagonal) with *P*-values computed after 10 000 permutations (upper diagonal).

	Norwegian								Icelandic	Faroese				
	NorwegianSea	Lofoten	Nordland	Storegga	Shetland	NorthSea_N	NorthSea_S	Skagerrak	Iceland	Faroe_62	Faroe_61	Faroe_60	Faroe_59	Faroe_58
NorwegianSea	*	0.261	0.949	0.089	**0.014**	**0.002**	**0.001**	**0.000**	0.116	**0.006**	0.081	**0.001**	0.908	0.390
Lofoten	0.001	*	0.654	0.366	**0.004**	0.051	0.030	**0.000**	0.123	**0.012**	0.287	**0.001**	0.465	0.528
Nordland	0.000	0.000	*	0.989	0.147	0.669	0.443	**0.009**	0.312	0.034	0.641	0.137	0.998	0.904
Storegga	0.002	0.001	0.000	*	0.033	0.057	0.067	**0.001**	0.764	0.035	0.423	**0.000**	0.414	0.412
Shetland	0.004	0.005	0.003	0.004	*	0.044	**0.002**	**0.000**	0.167	**0.000**	0.053	**0.001**	0.050	0.067
NorthSea_N	0.002	0.002	0.000	0.002	0.003	*	0.089	**0.000**	**0.000**	**0.000**	**0.003**	**0.000**	0.056	0.763
NorthSea_S	0.002	0.002	0.000	0.002	0.005	0.001	*	**0.003**	**0.000**	**0.000**	**0.000**	**0.000**	0.114	0.382
Skagerrak	0.011	0.009	0.006	0.006	0.011	0.006	0.004	*	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Iceland	0.001	0.001	0.001	0.000	0.002	0.004	0.006	0.019	*	0.577	0.744	0.953	0.421	0.052
Faroe_62	0.004	0.004	0.005	0.003	0.010	0.010	0.008	0.024	0.000	*	0.307	0.077	0.018	**0.000**
Faroe_61	0.002	0.001	0.000	0.000	0.004	0.003	0.004	0.018	0.000	0.001	*	0.217	0.767	0.020
Faroe_60	0.004	0.005	0.002	0.006	0.008	0.007	0.007	0.023	0.000	0.003	0.001	*	0.195	**0.002**
Faroe_59	0.000	0.000	0.000	0.000	0.003	0.002	0.001	0.011	0.000	0.004	0.000	0.001	*	0.158
Faroe_58	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.007	0.002	0.007	0.003	0.005	0.001	*

Increasing genetic differentiation is coded by colours moving from green towards red. Boldface type depicts statistically significant F_{ST} values after FDR correction at $\alpha = 0.05$.

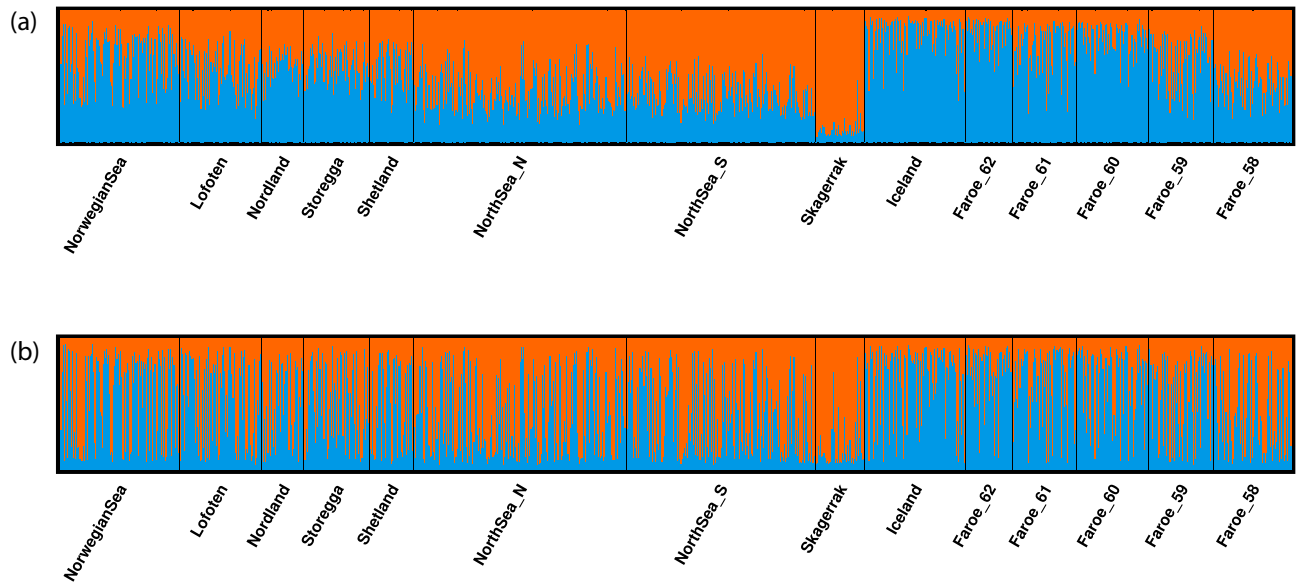

Figure 3. Barplot representing the proportion of individuals' ancestry to cluster as inferred from Bayesian clustering in STRUCTURE using LD-pruned set of 87 SNPs at $K = 2$ (a) with LOCPRIORS to assist the clustering, and without LOCPRIORS at $K = 2$ (b) and $K = 4$ (c), respectively. Samples were organized following the division of ICES stocks.

annotated using BLAST. Major allele frequencies per sample for the outliers can be found in Supplementary Table S4. Allele Asi_052_A showed the greatest divergence between samples, ranging from a frequency of 91.1% in Faroe_62% to 26% in Skagerrak.

Hierarchical AMOVA based on 87 LD pruned loci revealed no significant differentiation among current ICES stocks ($F_{CT} = 0.0008$, $P = .098$), whereas significant differentiation was detected among samples within ICES stocks ($F_{SC} = 0.0024$, $P < .0001$), as well as within samples ($F_{ST} = 0.0035$, $P < .0001$). After FDR correction, pairwise F_{ST} revealed that Skagerrak significantly differed from all samples (Table 2), whereas in the rest of the samples within the Norwegian stock, F_{ST} ranged between 0 and 0.005. Only five pairwise comparisons were significant. Iceland only differed from the southernmost Norwegian samples (NorthSea_N/S and Skagerrak). Within the Faroese stock, the southernmost sample (Faroe_58) showed weak ($F_{ST} = 0.005$–0.007) but significant differentiation from Faroe_62 and Faroe_60, respectively. The southernmost samples of the Faroese stock (Faroe_58 and Faroe_59) did not differ from the samples in the Norwegian stock with the exception of Skagerrak.

Hierarchical AMOVA based upon the 82 neutral loci revealed no significant differentiation among current ICES stocks ($F_{CT} = 0.000$, $P = .696$), but weak significant differentiation among samples within stocks ($F_{SC} = 0.001$, $P = .004$), and within samples ($F_{ST} = 0.001$, $P = .003$). The pairwise F_{ST} matrix revealed that few pairwise comparisons retained statistical significance; however, Faroe_62 and Faroe_60 remained significantly different from the Norwegian samples south of Storegga, and Skagerrak still differed from the northernmost Faroese samples (Supplementary Table S6). The five candidate outliers to positive selection revealed significant differentiation among ICES stocks ($F_{CT} = 0.039$, $P = .021$) within stocks ($F_{SC} = 0.039$, $P < .001$), and within samples ($F_{ST} = 0.076$, $P < .0001$). In the F_{ST} pairwise comparisons, Skagerrak differed from all samples and showed large F_{ST} values when compared to the Icelandic and Faroese samples. All samples in the Norwegian stock differed from Iceland as well as from Faroe_60 to Faroe_62 (Supplementary Table S6). Deficits of heterozygotes in the set of neutral loci, were detected in only four samples (NorthSea_N and S, Lofoten, and Nordland).

STRUCTURE analysis was conducted on the LD-pruned dataset of 87 loci. A posteriori analysis of STRUCTURE outcomes using LOCPRIORS selected $K = 2$ as the most likely number of clusters, both following Puechmaille and Evanno's methods (Supplementary Fig. S3a). The corresponding barplot (Fig. 3a) confirmed the distinctiveness of Skagerrak and suggested subtle latitudinal trends both in the Norwegian and Faroese stocks. The outcome of STRUCTURE without priors yielded $K = 2$ and $K = 4$ for Puechmaille and Evanno's methods, respectively (Supplementary Fig. S3b). Despite the lack of geographic information to interpret the clustering, at $K = 2$, Skagerrak retained its uniqueness (Fig. 3b), but no patterns appeared among the remaining samples. The clustering at $K = 4$ did not provide further clarity (Fig. 4c). STRUCTURE conducted using LOCPRIORS on the set of 82 neutral loci revealed differentiation between the Norwegian and Iceland–Faroese stocks but little differentiation within stocks (Supplementary Fig. S4a). Lacking priors to assist the clustering revealed the inability of the set of neutral markers to show differentiation among samples (Supplementary Fig. S4b). Likewise, no divergence related to maturity stage was detected in the sample from NorthSea_S (Supplementary Fig. S7a–b).

The cross-validation function for DAPC analysis on the geographically explicit samples at 87 LD-pruned SNPs selected 30 principal components (PCs) and 3 discriminant functions. The first axis of differentiation, accounting for 40.7% of the variation, showed that the centroid for Skagerrak individuals slightly deviated from the remaining individuals (Fig. 4a), despite the general overlap of samples. DAPC was also conducted on the three ICES stocks plus Skagerrak considered as an extra one. The first axis of variation of the DAPC built upon 80 PCs and 3 discriminant functions explained 63% of the variation and revealed no overlapping among centroids

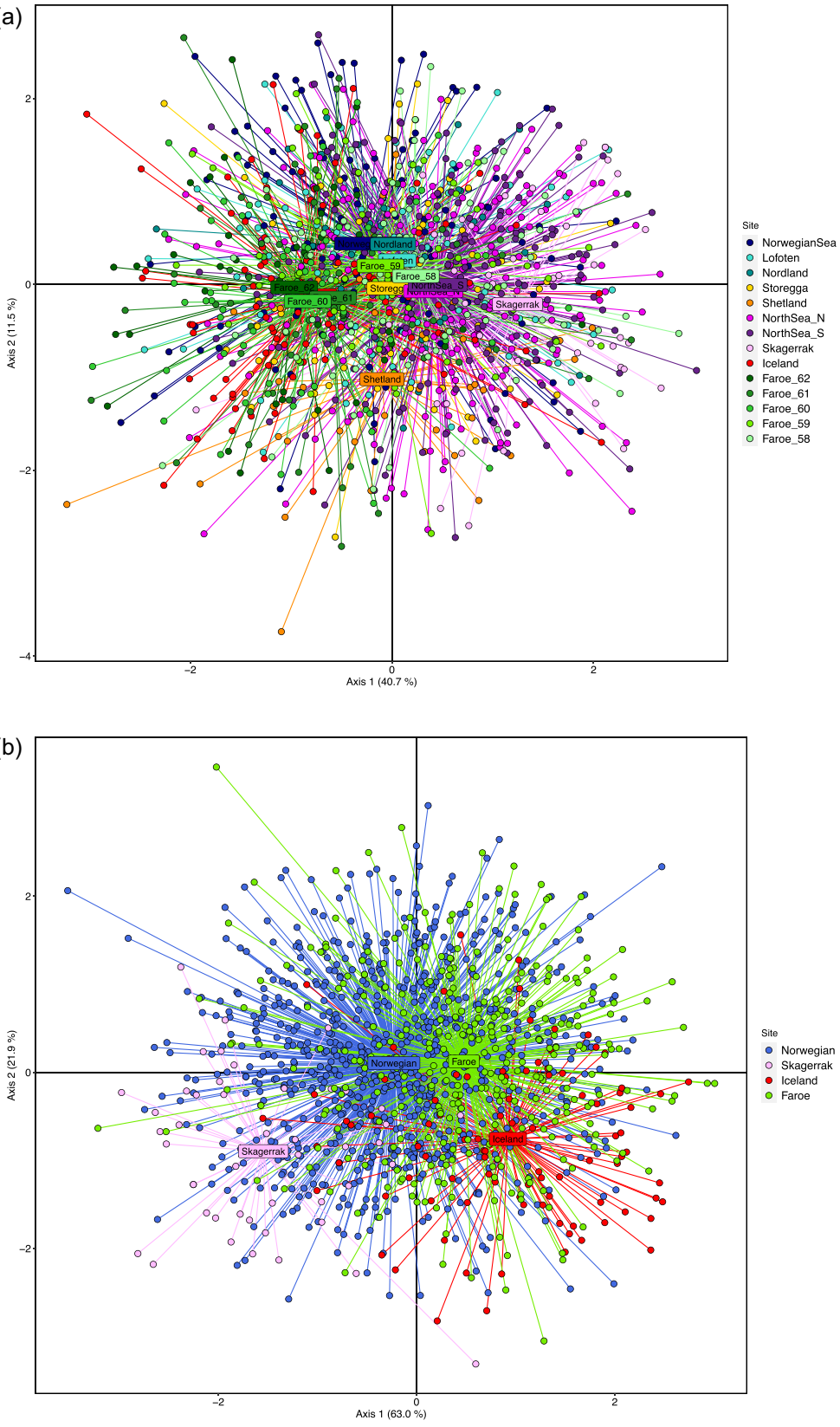

Figure 4. DAPC based upon 87 polymorphic SNPs of greater argentine (*Argentina silus*) from NE Atlantic. Individuals were grouped according to: (a) geographically explicit samples and (b) current ICES stocks plus Skagerrak.

of the 4 putative units, which would further support the distinctiveness of Skagerrak (Fig. 4b). The loadings on the first axis revealed that four loci (Asi_052, Asi_088, Asi_120, and Asi_127) were the main drivers of the genetic differentiation among stocks. Major allele frequency per locus and stock (Supplementary Table S7) further singled Skagerrak out.

No significant correlation between genetic distance (F_{ST}) and shortest water distance (km) was detected for any of the sets of SNPs, including the total dataset of 88 loci ($r_{xy} = 0.185$, $P = .157$), the 87 LD-pruned SNPs ($r_{xy} = 0.182$, $P = .159$), the putatively neutral 82 ones ($r_{xy} = 0.000$, $P = .441$), or the 5 candidate outliers to directional selection ($r_{xy} = 0.299$, $P = .097$).

Discussion

The need to harmonize biological and management units has been repeatedly put forward when contrasting population genetics information and stock delineation of commercial species (Leone et al. 2019, Rodríguez-Ezpeleta et al. 2019, Quintela et al. 2020, Aguirre-Sarabia et al. 2021). In particular, genotyping spawning adult individuals improves the accuracy of the delineation of genetic stocks (Nesbø et al. 2000, Hutchinson et al. 2001).

This study scrutinizes the delineation of ICES current stocks for *Argentina silus* by analysing 88 SNP loci genotyped on 1166 fish. The neutral fraction of those markers revealed extremely low overall differentiation, close to a panmictic single stock. However, adaptive divergence sometimes appears in fish populations despite neutral markers suggesting panmixia (Hemmer-Hansen et al. 2007, Freamo et al. 2011). The importance of outliers for management delineation, highlighted by Russello et al. (2012), has been illustrated in the literature using various molecular tools. Allozyme locus *SOD∗* suggested two stocks of sardine along the Moroccan coast (Chlaida et al. 2008). Locus *PanI* not only discriminated between northeast Arctic and Norwegian coastal cod stocks but also allowed real-time management of the fishery (Johansen et al. 2018). Outlier candidates at microsatellites and SNPs also differentiated spring- and autumn-spawning herring in the Baltic Sea (Bekkevold et al. 2016), and diagnostic SNPs differentiated four herring management units in the Faroese and surrounding waters (Kongsstovu et al. 2022). Likewise, outlier SNPs were proposed to outline stocks of kingklip (*Genypterus capensis)* in Namibia, South Africa (Schulze et al. 2020).

In the current study, the contribution of the five candidate outliers to positive selection depicted a non-panmictic scenario and suggested that the ICES current Faroese stock (Aru.27.5b6a) aligned with biological units and differed from the remaining stocks. The Icelandic stock (Aru.27.5a14) should be taken with caution because, although the only sample available (collected far west in the Danmark Strait) was significantly different from all the remaining at the five putative outliers, the species is also distributed both south and east of Iceland, and therefore some mixing may occur in the Iceland–Faroe Ridge.

In contrast, a revision of the stock boundaries could be suggested for the so-called Norwegian stock (Aru.27.123a4: ICES areas 1, 2, 3a, and 4), as the clear genetic differentiation detected between Skagerrak and the rest of the Norwegian coastal samples (F_{ST} computed at 87 loci ranging from 0.004 to 0.011) would support establishing the ICES 3a area as an independent management unit. Even though divergence was weak, small F_{ST} values can be biologically meaningful in marine fish; e.g. in coastal Atlantic cod, F_{ST} values as low as 0.0037 correspond to separate temporally persistent local populations (Knutsen et al. 2011). The differentiation between Skagerrak and the remaining samples of the Norwegian stock is virtually absent at the subset of putatively neutral markers in an analogous manner to what occurs among European hake populations, where no differentiation between North Sea and Skagerrak–Kattegat was detected at neutral loci but revealed with loci under positive selection (Westgaard et al. 2017). However, the differentiation computed using the set of candidate outliers (F_{ST} ranging from 0.087 to 0.203) further corroborates the importance of markers under positive selection for management outline.

The Baltic Sea is a young and evolving environment that turned from fresh to brackish water ∼6500–9800 year BP (Zillén et al. 2008) and is connected to the North Sea via the narrow channels of the Kattegat, Skagerrak, and Belt Sea. This marine region is characterized by both restricted water movement and strong environmental gradients in an area that transitions from the marine waters of the North Sea to the west-to-east gradient of low salinity of the Baltic. Johannesson et al. (2020) provide a comprehensive review on the North Sea–Baltic Sea multispecies contact zone. Marine organisms colonized the Baltic from the North Sea over the course of the past 8000 years (Johannesson et al. 2020), or from recently derived Pacific lineages (Nikula et al. 2007). Others seem to have gradually evolved by local adaptation in the contact zone despite experiencing gene flow from ancestral marine populations (Martínez Barrio et al. 2016, Jiménez-Mena et al. 2020). Adaptation to salinity has been invoked as the driving force of speciation of at least two species that evolved in the Baltic (Pereyra et al. 2009, Momigliano et al. 2017). As a transition zone, Skagerrak is inhabited by several taxa that show adaptations to salinity, including fish (Nielsen et al. 2003, Gaggiotti et al. 2009, Berg et al. 2015, Guo et al. 2016, Quintela et al. 2020, Jansson et al. 2023), molluscs (Väinölä and Hvilsom 2008, Luttikhuizen et al. 2012), jellyfish (Lucas 2001), and diatoms (Sjöqvist et al. 2015). Genome sequencing studies on Atlantic herring and Atlantic cod have suggested the existence of standing genetic variation available for adaption to a changing environment, which allowed both species to successfully adapt to the brackish waters of the Baltic (Andersson et al. 2023).

Differentiation between Skagerrak and the rest of the samples (in particular those within the same stock) occurred mostly at loci putatively under directional selection and suggests that differentiation may be connected to adaptive processes. However, the reduced representation of the molecular markers used in this study does not allow further inferences, including the association between genetics and environmental factors.

Finally, the three-stripped pattern in the PCA biplot was driven by two loci in strong linkage disequilibrium. Again, the sample from Skagerrak singled out with a percentage of heterozygotes for those loci that was much larger than the remaining samples. Striations in PCA can potentially unravel chromosomal inversions using high-density SNPs (Ma and Amos 2012); this approach has been validated using large SNP arrays (Jiménez-Mena et al. 2020, Nowling et al. 2020, Hale et al. 2021, Mérot et al. 2021) and has been suggested using reduced-SNP representation (Quintela et al. 2021a). Large-scale chromosome inversions involved in ecological adapta-

tion have been identified in Atlantic herring in connection with temperature at spawning (Pettersson et al. 2019) and allegedly linked to migratory lifestyle and salinity tolerance in Atlantic cod (Matschiner et al. 2022). We cannot exclude the possibility of chromosome inversions occurring in the greater argentine genome, but more powerful genomic tools would be needed to clarify this issue.

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Author contributions

J.I.W. conceived and led the study; G.W.S. and G.D. conducted the laboratory work; M.Q. and G.W.S. analysed the data; M.Q., G.W.S., E.H.H., K.E., T.J.L., E.J., and K.A.G. interpreted the data; M.Q. and G.W.S. wrote a first draft with contributions from E.H.H., K.E., T.J.L., E.J., J.I.W., and K.A.G. All authors contributed critically to the drafts and gave final approval for publication.

Supplementary data

Supplementary material is available at *ICES Journal of Marine Science* online.

Conflict of interest: None declared.

Data availability

The SNP loci developed for this study as well as the resulting genotype raw data can be publicly accessed from the electronic archive of the Institute of Marine Research at: https://hdl.handle.net/11250/3122412.

References

Aguirre-Sarabia I, Díaz-Arce N, Pereda-Agirre I *et al.* Evidence of stock connectivity, hybridization, and misidentification in white anglerfish supports the need of a genetics-informed fisheries management framework. *Evol Appl* 2021;**14**:2221–30. https://doi.org/10.1111/eva.13278

Allendorf FW, England PR, Luikart G *et al.* Genetic effects of harvest on wild animal populations. *Trends Ecol Evol* 2008;**23**:327–37.

Andersson L, André C, Johannesson K *et al.* Ecological adaptation in cod and herring and possible consequences of future climate change in the Baltic Sea. *Front Mar Sci* 2023;**10**:1101855. https://doi.org/10.3389/fmars.2023.1101855

Antao T, Lopes A, Lopes R *et al.* LOSITAN: a workbench to detect molecular adaptation based on a F_{ST}-outlier method. *BMC Bioinf* 2008;**9**:323. https://doi.org/10.1186/1471-2105-9-323

Bekkevold D, Gross R, Arula T *et al.* Outlier loci detect intraspecific biodiversity amongst spring and autumn spawning herring across local scales. *PLoS One* 2016;**11**:e0148499. https://doi.org/10.1371/journal.pone.0148499

Benjamini Y, Hochberg Y. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc Series B Stat Methodol* 1995;**57**:289–300.

Berg PR, Jentoft S, Star B *et al.* Adaptation to low salinity promotes genomic divergence in Atlantic cod (*Gadus morhua* L.). *Genome Biol Evolut* 2015;**7**:1644–63. https://doi.org/10.1093/gbe/evv093

Bergstad OA. Distribution, population structure, growth, and reproduction of the greater silver smelt, *Argentina silus* (Pisces, Argentinidae), of the Skagerrak and the north-eastern North Sea. *ICES J Mar Sci* 1993;**50**:129–43. https://doi.org/10.1006/jmsc.1993.1015

Bernatchez L, Wellenreuther M, Araneda C *et al.* Harnessing the power of genomics to secure the future of seafood. *Trends Ecol Evol* 2017;**32**:665–80.

Besnier F, Glover K A. ParallelStructure: a R package to distribute parallel runs of the population genetics program STRUCTURE on multi-core computers. *PLoS ONE* 2013;**8**:e70651.

Borodulina OD. Some data on argentine biology. *Voprosy Ichthyologii (in Russian)* 1964;**4**:30.

Cadrin SX, Kerr LA, Mariani S. *Stock Identification Methods: Applications in Fishery Science*. San Diego, CA: Academic Press, 2014, 566pp.

Casey J, Jardim E, Martinsohn JT. The role of genetics in fisheries management under the E.U. common fisheries policy. *J Fish Biol* 2016;**89**:2755–67. https://doi.org/10.1111/jfb.13151

Catchen J, Hohenlohe P A, Bassham S *et al.* Stacks: An analysis tool set for population genomics. *Mol Ecol* 2013;**22**:3124–40.

Chlaida M, Laurent V, Kifani S *et al.* Evidence of a genetic cline for *Sardina pilchardus* along the northwest African coast. *ICES J Mar Sci* 2008;**66**:264–71. https://doi.org/10.1093/icesjms/fsn206

Cohen DM. A revision of the fishes of the subfamily Argentininae. *Bull Florida State Mus* 1958;**3**:93–172.

Cohen DM. Argentinidae (including *Microstomatidae*). In: P. J. P. Whitehead, M. L. Bauchot, J. C. Hureau, J. Nielsen, E Tortonese (eds), *Fishes of the North-Eastern Atlantic and Mediterranean*. Vol. **1**. Paris: UNESCO, 1984, 386–91pp.

Cohen DM. Suborder Argentinoidea. In: *Fishes of the Western North Atlantic*. New Haven, CT: Sears Foundation for Marine Research, 1964, 599pp. 1–70

Dray S, Dufour A-B. The ade4 package: implementing the duality diagram for ecologists. *J Stat Softw* 2007;**22**:1–20. https://doi.org/10.18637/jss.v022.i04

Emery AR, McCracken FD. Biology of the Atlantic argentine (*Argentina silus* Ascanius) on the Scotian Shelf. *J Fish Res Board Can* 1966;**23**:1145–60. https://doi.org/10.1139/f66-107

Evanno G, Regnaut S, Goudet J. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Mol Ecol* 2005;**14**:2611–20.

Excoffier L, Laval G, Schneider S. Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evol Bioinform Online* 2005;**1**:47–50.

Foll M, Gaggiotti O. A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics* 2008;**180**:977–93. https://doi.org/10.1534/genetics.108.092221

Foll M, Gaggiotti O. Identifying the environmental factors that determine the genetic structure of populations. *Genetics* 2006;**174**:875–91. https://doi.org/10.1534/genetics.106.059451

Frank KT, Brickman D. Allee effects and compensatory population dynamics within a stock complex. *Can J Fish Aquat Sci* 2000;**57**:513–7. https://doi.org/10.1139/f00-024

Freamo H, O'Reilly P, Berg PR *et al.* Outlier SNPs show more genetic structure between two Bay of Fundy metapopulations of Atlantic salmon than do neutral SNPs. *Mol Ecol Res* 2011;**11**:254–67.

Funk WC, McKay JK, Hohenlohe PA *et al.* Harnessing genomics for delineating conservation units. *Trends Ecol Evol* 2012;**27**:489–96.

Gabriel S, Ziaugra L, Tabbaa D. SNP genotyping using the sequenom MassARRAY iPLEX platform. *Curr Protoc Hum Genet* 2009;**60**:hg0212s60. https://doi.org/10.1002/0471142905.hg0212s60

Gaggiotti OE, Bekkevold D, Jørgensen HBH *et al.* Disentangling the effects of evolutionary, demographic, and environmental factors influencing genetic structure of natural populations: Atlantic herring as a case study. *Evolution* 2009;**63**:2939–51. https://doi.org/10.1111/j.1558-5646.2009.00779.x

Guo B, Li Z, Merilä J. Population genomic evidence for adaptive differentiation in the Baltic Sea herring. *Mol Ecol* 2016;**25**:2833–52. https://doi.org/10.1111/mec.13657

Hale M, Campbell M, McKinney G. A candidate chromosome inversion in Arctic charr (*Salvelinus alpinus*) identified by population genetic analysis techniques. *G3* 2021;**11**:jkab267. https://doi.org/10.1093/g3journal/jkab267

Hallfredsson EH. Greater silver smelt assessment units in the northeast Atlantic. *ICES Document CM* 2010;**38**:11pp. /ACOM

Hemmer-Hansen J, Nielsen EE, Frydenberg J *et al.* Adaptive divergence in a high gene flow environment: Hsc70 variation in the European flounder (Platichthys flesus L.). *Heredity* 2007;**99**:592–600.

Hilborn R, Stokes K. Defining overfished stocks: have we lost the plot? *Fisheries* 2010;**35**:113–20. https://doi.org/10.1577/1548-8446-35.3.113

Hutchinson WF, Carvalho GR, Rogers SI. Marked genetic structuring in localised spawning populations of cod *Gadus morhua* in the North Sea and adjoining waters, as revealed by microsatellites. *Mar Ecol Progr Ser* 2001;**223**:251–60. https://doi.org/10.3354/meps223251

ICES. Benchmark workshop of greater silver smelt (WKGSS; outputs from 2020 meeting). *ICES Scientific Reports* 2021;**3**:485pp.

ICES. Report of the benchmark workshop on deep-water species (WKDEEP). *ICES Document CM* 2010:**38**:247pp. /ACOM

ICES. Report of the study group on the biology and assessment for deep-sea fisheries resources. *ICES Document CM* 1998:**12**:55pp. /ACFM

ICES. Revision of ICES assessment units for greater silver smelt based on the distribution of fishing grounds. *ICES Document CM* 2014:**17**:862pp. /ACOM

Jakobsson M, Rosenberg NA. CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics* 2007;**23**:1801–6. https://doi.org/10.1093/bioinformatics/btm233

Jansson E, Faust E, Bekkevold D *et al.* Global, regional, and cryptic population structure in a high gene-flow transatlantic fish. *PLoS One* 2023;**18**:e0283351. https://doi.org/10.1371/journal.pone.0283351

Jiménez-Mena B, Le Moan A, Christensen A *et al.* Weak genetic structure despite strong genomic signal in lesser sandeel in the North Sea. *Evol Appl* 2020;**13**:376–87. https://doi.org/10.1111/eva.12875

Johannessen A, Monstad T. Distribution, growth and exploitation of greater silver smelt (*Argentina silus*) in Norwegian waters 1980–1983. *J Northwest Atlantic Fish Sci* 2003;**31**:319–32. https://doi.org/10.2960/J.v31.a24

Johannesson K, Le Moan A, Perini S *et al.* A Darwinian laboratory of multiple contact zones. *Trends Ecol Evol* 2020;**35**:1021–36.

Johansen T, Westgaard J-I, Seliussen BB *et al.* "Real-time" genetic monitoring of a commercial fishery on the doorstep of an MPA reveals unique insights into the interaction between coastal and migratory forms of the Atlantic cod. *ICES J Mar Sci* 2018;**75**:1093–104. https://doi.org/10.1093/icesjms/fsx224

Jombart T, Collins C. A tutorial for discriminant analysis of principal components (DAPC) using adegenet 2.0.0. 2015. https://adegenet.r-forge.r-project.org/files/tutorial-dapc.pdf (24 April 2004, date last accessed).

Jombart T, Devillard S, Balloux F. Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genet* 2010;**11**:94. https://doi.org/10.1186/1471-2156-11-94

Jombart T. *Adegenet*: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 2008;**24**:1403–5. https://doi.org/10.1093/bioinformatics/btn129

Kamvar ZN, Tabima JF, Grünwald NJ. Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. *PeerJ* 2014;**2**:e281. https://doi.org/10.7717/peerj.281

Kerr LA, Hintzen NT, Cadrin SX *et al.* Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES J Mar Sci* 2017;**74**:1708–22. https://doi.org/10.1093/icesjms/fsw188

Knutsen H, Olsen EM, Jorde PE *et al.* Are low but statistically significant levels of genetic differentiation in marine fishes 'biologically meaningful'? A case study of coastal Atlantic cod. *Mol Ecol* 2011;**20**:768–83. https://doi.org/10.1111/j.1365-294X.2010.04979.x

Kongsstovu Sí, Mikalsen S-O, Homrum Eí *et al.* Atlantic herring (*Clupea harengus*) population structure in the northeast Atlantic Ocean. *Fish Res* 2022;**249**:106231. https://doi.org/10.1016/j.fishres.2022.106231

Leone A, Álvarez P, García D *et al.* Genome-wide SNP based population structure in European hake reveals the need for harmonizing biological and management units. *ICES J Mar Sci* 2019;**76**:2260–6. https://doi.org/10.1093/icesjms/fsz161

Li Y-L, Liu J-X. StructureSelector: a web-based software to select and visualize the optimal number of clusters using multiple methods. *Mol Ecol Resour* 2018;**18**:176–7. https://doi.org/10.1111/1755-0998.12719

Lucas CH. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* 2001;**451**:229–46. https://doi.org/10.1023/A:1011836326717

Luttikhuizen P, Drent J, Peijnenburg KTCA *et al.* Genetic architecture in a marine hybrid zone: comparing outlier detection and genomic clines analysis in the bivalve *Macoma balthica*. *Mol Ecol* 2012;**21**:3048–61. https://doi.org/10.1111/j.1365-294X.2012.05586.x

Ma J, Amos CI. Investigation of inversion polymorphisms in the human genome using principal components analysis. *PLoS One* 2012;**7**:e40224. https://doi.org/10.1371/journal.pone.0040224

Magnússon JV. Greater silver smelt, *Argentina silus* in Icelandic waters. *J Fish Biol* 1996;**49**:259–75. https://doi.org/10.1111/j.1095-8649.1996.tb06080.x

Manousaki T, Tsakogiannis A, Taggart JB *et al.* Exploring a nonmodel teleost genome through RAD sequencing-linkage mapping in common pandora, *Pagellus erythrinus* and comparative genomic analysis. *G3* 2015;**6**:509–19.

Mantel N. The detection of disease of clustering and a generalized regression approach. *Cancer Res* 1967;**27**:209–20.

Martínez Barrio A, Lamichhaney S, Fan G *et al.* The genetic basis for ecological adaptation of the Atlantic herring revealed by genome sequencing. *eLife* 2016;**5**:e12081. https://doi.org/10.7554/eLife.12081

Matschiner M, Barth JMI, Tørresen OK *et al.* Origin and fate of supergenes in Atlantic cod. *Nat Ecol Evol* 2022;**6**:469–84.

Mauchline J, Gordon JDM. Diets of clupeoid, stomiatoid and salmonoid fish of the Rockall Trough, northeastern Atlantic Ocean. *Mar Biol* 1983;**77**:67–78. https://doi.org/10.1007/BF00393211

Mérot C, Berdan EL, Cayuela H *et al.* Locally adaptive inversions modulate genetic variation at different geographic scales in a seaweed fly. *Mol Biol Evol* 2021;**38**:3953–71. https://doi.org/10.1093/molbev/msab143

Miller JM, Cullingham CI, Peery RM. The influence of a priori grouping on inference of genetic clusters: simulation study and literature review of the DAPC method. *Heredity* 2020;**125**:269–80. https://doi.org/10.1038/s41437-020-0348-2

Momigliano P, Jokinen H, Fraimout A *et al.* Extraordinarily rapid speciation in a marine fish. *Proc Natl Acad Sci* 2017;**114**:6074–9. https://doi.org/10.1073/pnas.1615109114

Nesbø CL, Rueness EK, Iversen SA *et al.* Phylogeography and population history of Atlantic mackerel (*Scomber scombrus* L.): a genealogical approach reveals genetic structuring among the eastern Atlantic stocks. *Proc Biol Sci* 2000;**267**:281–92. https://doi.org/10.1098/rspb.2000.0998

Nielsen EE, Hansen MM, Ruzzante DE *et al.* Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Mol Ecol* 2003;**12**:1497–508. https://doi.org/10.1046/j.1365-294X.2003.01819.x

Nikula R, Strelkov P, Väinölä R. Diversity and trans-arctic invasion history of mitochondrial lineages in the North Atlantic *Macoma balthica* complex (Bivalvia: tellinidae). *Evolution* 2007;**61**:928–41. https://doi.org/10.1111/j.1558-5646.2007.00066.x

Nowling RJ, Manke KR, Emrich SJ. Detecting inversions with PCA in the presence of population structure. *PLoS One* 2020;**15**:e0240429. https://doi.org/10.1371/journal.pone.0240429

Osio GC, Orio A, Millar CP. Assessing the vulnerability of Mediterranean demersal stocks and predicting exploitation status of unassessed stocks. *Fish Res*2015;**171**:110–21. https://doi.org/10.1016/j.fishres.2015.02.005

Østebrød TN. Effects of protein enrichment in texture modified and minced fish products. In: *Faculty of Science and Technology*. Stavanger: University of Stavanger, 2020, 120p.

Ovenden JR, Berry O, Welch DJ *et al.* Ocean's eleven: a critical evaluation of the role of population, evolutionary and molecular genetics in the management of wild fisheries. *Fish Fish* 2015;**16**:125–59. https://doi.org/10.1111/faf.12052

Pante E, Simon-Bouhet B. marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. *PLoS One* 2013;**8**:e73051. https://doi.org/10.1371/journal.pone.0073051

Pauly D, Zeller D. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat Commun* 2016;7:10244. https://doi.org/10.1038/ncomms10244

Peakall R, Smouse PE.GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. *Mol Ecol Notes* 2006;**6**:288–95. https://doi.org/10.1111/j.1471-8286.2005.01155.x

Pereyra RT, Bergström L, Kautsky L *et al.* Rapid speciation in a newly opened postglacial marine environment, the Baltic Sea. *BMC Evol Biol* 2009;**9**:70. https://doi.org/10.1186/1471-2148-9-70

Pettersson ME, Rochus CM, Han F *et al.* A chromosome-level assembly of the Atlantic herring genome-detection of a supergene and other signals of selection. *Genome Res* 2019;**29**:1919–28. https://doi.org/10.1101/gr.253435.119

Pritchard JK, Stephens M, Donnelly P. Inference of population structure using multilocus genotype data. *Genetics* 2000;**155**:945–59. https://doi.org/10.1093/genetics/155.2.945

Puechmaille SJ. The program structure does not reliably recover the correct population structure when sampling is uneven: subsampling and new estimators alleviate the problem. *Mol Ecol Resour* 2016;**16**:608–27. https://doi.org/10.1111/1755-0998.12512

Quintela M, Bhat S, Præbel K *et al.* Distinct genetic clustering in the weakly differentiated polar cod, *Boreogadus saida* Lepechin, 1774 from East Siberian Sea to Svalbard. *Polar Biology* 2021a;**44**:1711–24. https://doi.org/10.1007/s00300-021-02911-7

Quintela M, Kvamme C, Bekkevold D *et al.* Genetic analysis redraws the management boundaries for the European sprat. *Evol Appl* 2020;**13**:1906–22. https://doi.org/10.1111/eva.12942

Quintela M, Richter-Boix À, Bekkevold D *et al.* Genetic response to human-induced habitat changes in the marine environment: a century of evolution of European sprat in Landvikvannet, Norway. *Ecol Evol* 2021b;**11**:1691–718. https://doi.org/10.1002/ece3.7160

Reiss H, Hoarau G, Dickey-Collas M *et al.* Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish Fish* 2009;**10**:361–95. https://doi.org/10.1111/j.1467-2979.2008.00324.x

Rodríguez-Ezpeleta N, Díaz-Arce N, Walter Iii JF *et al.* Determining natal origin for improved management of Atlantic bluefin tuna. *Front Ecol Environ* 2019;**17**:439–44. https://doi.org/10.1002/fee.2090

Rosenberg MS, Anderson CD. PASSaGE: pattern analysis, spatial statistics and geographic exegesis. Version 2. *Methods Ecol Evol* 2011;**2**:229–32. https://doi.org/10.1111/j.2041-210X.2010.00081.x

Rousset F. GENEPOP'007: a complete re-implementation of the genepop software for Windows and Linux. *Mol Ecol Resour* 2008;**8**:103–6. https://doi.org/10.1111/j.1471-8286.2007.01931.x

Rousset F. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 1997;**145**:1219–28. https://doi.org/10.1093/genetics/145.4.1219

Russello MA, Kirk SL, Frazer KK *et al.* Detection of outlier loci and their utility for fisheries management. *Evol Appl* 2012;**5**:39–52. https://doi.org/10.1111/j.1752-4571.2011.00206.x

Schulze MJ, von der Heyden S, Japp D *et al.* Supporting fisheries management with genomic tools: a case study of kingklip (*Genypterus capensis)* off southern Africa. *Front Mar Sci* 2020;**7**:557146. https://doi.org/10.3389/fmars.2020.557146

Seljestad GW, Quintela M, Faust E *et al.* "A cleaner break": genetic divergence between geographic groups and sympatric phenotypes revealed in ballan wrasse (*Labrus bergylta*). *Ecol Evol* 2020;**10**:6120–35. https://doi.org/10.1002/ece3.6404

Sjöqvist C, Godhe A, Jonsson PR *et al.* Local adaptation and oceanographic connectivity patterns explain genetic differentiation of a marine diatom across the North Sea–Baltic Sea salinity gradient. *Mol Ecol* 2015;**24**:2871–85. https://doi.org/10.1111/mec.13208

Slatkin M. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* 1993;**47**:264–79. https://doi.org/10.2307/2410134

Spies I, Spencer PD, Punt AE. Where do we draw the line? A simulation approach for evaluating management of marine fish stocks with isolation-by-distance stock structure. *Can J Fish Aquat Sci* 2015;**72**:968–82. https://doi.org/10.1139/cjfas-2014-0366

Stephenson RL. Stock structure and management structure: an ongoing challenge for ICES. *ICES Mar Sci Symp* 2002;**215**:305–14.

Team RC. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing, 2020.

Väinölä R, Hvilsom MM. Genetic divergence and a hybrid zone between Baltic and North Sea *Mytilus* populations (Mytilidae: mollusca). *Biol J Linn Soc* 2008;**43**:127–48. https://doi.org/10.1111/j.1095-8312.1991.tb00589.x

Weir BS, Cockerham C. Estimating F-statistics for the analysis of population structure. *Evolution* 1984;**38**:1358–70.

Westgaard J-I, Staby A, Aanestad Godiksen J *et al.* Large and fine scale population structure in European hake (*Merluccius merluccius*) in the northeast Atlantic. *ICES J Mar Sci* 2017;**74**:1300–10. https://doi.org/10.1093/icesjms/fsw249

Worm B, Hilborn R, Baum JK *et al.* Rebuilding global fisheries. *Science* 2009;**325**:578–85.

Wright S. Isolation by distance. *Genetics* 1943;**28**:114–38. https://doi.org/10.1093/genetics/28.2.114

Zillén L, Conley DJ, Andrén T *et al.* Past occurrences of hypoxia in the Baltic Sea and the role of climate variability, environmental change and human impact. *Earth Sci Rev* 2008;**91**:77–92. https://doi.org/10.1016/j.earscirev.2008.10.001

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