

Genetic population structure of vendace (*Coregonus albula*) in the Gulf of Finland and in adjacent watercourses

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Vendace (*Coregonus albula*) is a freshwater species found in brackish water in the northern Baltic Sea. It has been most abundant in the northernmost part of the Gulf of Bothnia and in the easternmost parts of the Gulf of Finland (GoF), where the stocks have been declining. We assessed the level of genetic diversity and differentiation among the vendace populations in the GoF and adjacent areas. We analysed a total of 385 vendace samples from eight sampling sites. All the samples were genotyped at 17 microsatellite loci. Levels of genetic diversity were generally high within the sampled vendace populations, but the genetic differentiation between the populations was relatively low. The vendace population in the easternmost GoF is genetically close to the freshwater vendace of Lake Ladoga, flowing into the GoF via the Neva River. A previously known local vendace population in Virolahti Bay, on the Finnish coast 150 km west of the mouth of the Neva River, appears to have become extinct during the last 30–40 years. In the Pyhtää archipelago, close to the mouth of the Kymijoki River, there is still a small local vendace population, which is genetically close to the sea-spawning vendace population in the Bothnian Bay. This still genetically viable Pyhtää population evidently carries the genes of a sea- or estuarine-spawning vendace that, based on observations from the previous century, sporadically occurred along the entire Finnish coast. This population is an important part of the local fish biodiversity.

Introduction

Vendace (*Coregonus albula*) is a freshwater fish commonly found in lakes in Northern Europe. In Russia, the continuous distribution area of the species extends to the Urals (Sendek 2021). Vendace is also found in brackish water in the northern Baltic Sea but prefers low salinities up to 2–3 ppm (Lehtonen 1981). It has been most abundant in the northernmost part of the

Gulf of Bothnia, i.e., in the Bothnian Bay, and in the easternmost part of the Gulf of Finland (hereafter GoF) (Lehtonen 1981). Surface water salinity in the Bothnian Bay is generally between 2 and 3.5 ppm. In the GoF, up to 67% of the total annual river runoff flows via the Neva River into the eastern end of the gulf (Alenius *et al.* 1998). Because of the high freshwater input in the east, the salinity of surface waters in the GoF displays a clear gradient, from > 6 ppm in the west to

< 1 ppm in the east. Vendace also sporadically occurs in many other areas along the Finnish and Swedish coast, usually near river mouths and in some archipelago areas with lower salinity (Lehtonen 1981). Spawning of vendace takes place in late autumn, commonly during October and November.

The Baltic Sea vendace has been a target species for both commercial and recreational fisheries. In the Bothnian Bay, annual commercial catches (Sweden and Finland) during 1970–1972 were between 1000 and 2000 tonnes (Lehtonen 1981), with most of it taken by trawlers. The stock in the Bothnian Bay is still viable and the catches remained at the same level between 2010–2020 (OSF 2023a). In the Finnish waters of the Baltic Sea, the fishing effort for vendace is not regulated, while in Sweden, there are annual quotas and temporal restrictions (Lopez *et al.* 2022, Lehtonen *et al.* 2023). The main reproduction areas of this sea-spawning stock are located in the northernmost and less saline areas of the Bothnian Bay (Veneranta *et al.* 2013).

In the eastern GoF, the sea area outside of the Neva River has traditionally been important for vendace, and at least some of the vendace there are anadromous, spawning in the Neva River (Bogdanov *et al.* 2021). The fishery has also been most intense in the Russian area of the GoF. Between 1946 and 1960, the average annual catch in the Russian area was 80 tonnes. The catches decreased after the early 1970s, and between 2006 and 2016, the average annual catch was around 11 tonnes, most of this taken using trap nets (Bogdanov *et al.* 2021). According to Bogdanov *et al.* (2021), the decline in vendace stocks and the fishery in the easternmost GoF is unlikely to be due to overfishing but is more likely associated with changes in abiotic factors, such as salinity or temperature in the nursery areas. The negative impact of increasing eutrophication and pollution in the Neva River and adjacent parts of the GoF on the vendace population cannot be ruled out (Bogdanov *et al.* 2021).

On the Finnish coast of the GoF, the commercial vendace catch was 2.6 tonnes in 1979 (Lehtonen 1981), only 1 tonne in 1980, and since then has annually been less than 500 kg (OSF 2023b). Unfortunately, no catch statistics from

earlier periods are available from the Finnish coast. Nevertheless, in the 1980s, there used to be a targeted gill-net fishery at the spawning sites on the Finnish coast, at least in the Inkoo archipelago in the west and in Virolahti Bay in the easternmost Finland. However, according to the retired local fishermen, fishing at these sites gradually became unprofitable as the stocks decreased in the 1980s (Jarmo Holmström, Jaakko Koskela, pers. comm.). There is still a small-scale gill-net fishery for vendace on the eastern Finnish coast in the Pyhtää archipelago, close to the estuary of the Kymijoki River. The annual catches of this fishery are closer to tens than hundreds of kilograms.

The distribution pattern of genetic variation within and between populations is referred to as the genetic population structure of the species. Microsatellite DNA-based analysis has widely been used to investigate the genetic population structure of fish in lakes, as well as in coastal and marine environments, where strict dispersal barriers are lacking. Several studies have also been conducted on the Baltic Sea coast (e.g., Florin and Höglund 2008, Säisä *et al.* 2010, Olsson *et al.* 2011). In the freshwater drainage areas of the Baltic Sea, genetic structuring among vendace populations has been detected with enzyme loci (Sendek 2021) and microsatellites (Karjalainen *et al.* 2022). Weak structuring of vendace populations of the northern Baltic coasts of Finland and Sweden has also been observed using a genome-wide approach based on RAD sequencing (Lopez *et al.* 2022).

Our aims were to study the genetic population structure of the vendace "stocks" in the GoF and to assess the level of genetic diversity and differentiation between the populations in the GoF and adjacent areas. Our main hypothesis was that the remaining vendace stocks in the GoF are not satellite populations of adjacent lakes flowing to the coast, but remnants of earlier, more widely spread sea-spawning populations. According to this hypothesis, the GoF stocks should be genetically closer to the still viable sea-spawning stock of the Bothnian Bay than to lake populations. In conservation biology, this type of knowledge of the genetic structure of natural populations underlies the correct identification of conservation units. Neglecting

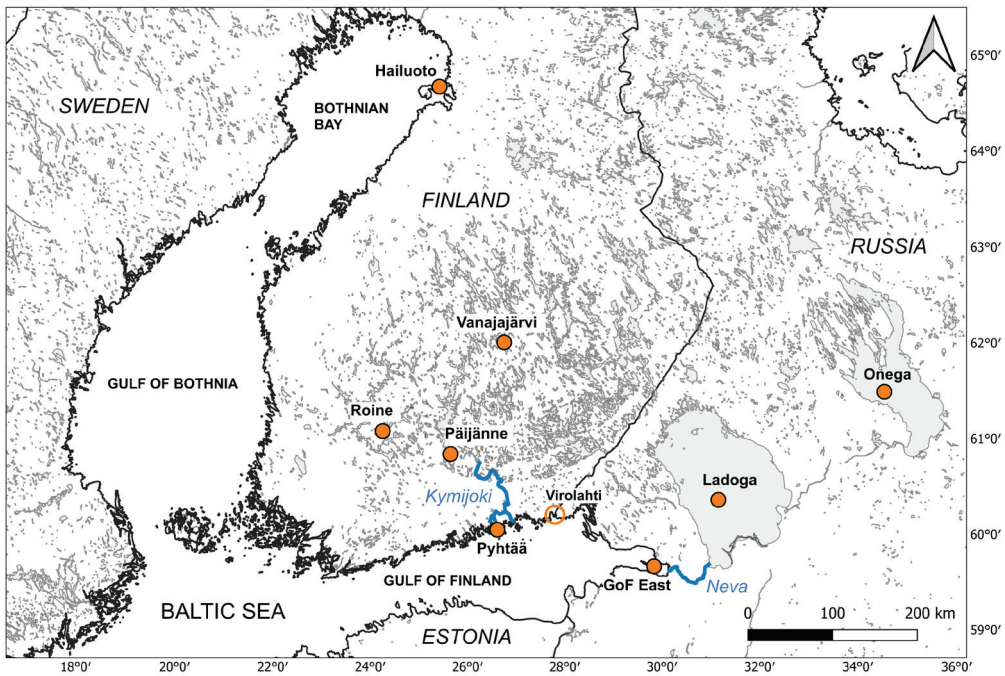


Fig. 1. Eight sampling sites of vendace marked in orange dots. In Virolahti (orange circle) samples were not obtained

such information can potentially lead to the depletion of genetic resources and the reduction of population and ecosystem viability (Laikre *et al.* 2005, Klütsch and Laikre 2021). In addition, we were interested in the genetic variability and, thus, the viability of the assumed original sea-spawning vendace stocks of the GoF. Overall, our aim was to shed light on the potential conservation value of the local vendace stocks in the GoF and briefly discuss the main threats to these local stocks.

Material and methods

We analysed a total of 385 vendace samples from eight sampling sites (Table 1, Fig. 1). All or almost all of them were adult (mature) individuals. Samples from the GoF (Pyhtää on the Finnish side and Sestroretsk on the Russian side, hereafter GoF East) and from the Bay of Bothnia (Hailuoto) were taken from commercial catches. Lake Päijänne flows close to Pyhtää via the Kymijoki River, and reference samples were thus taken from this lake. Similarly, Lake Onega flows

into Lake Ladoga, which in turn flows into the easternmost part of the GoF via the Neva River. The reference samples from lakes Ladoga and Onega included two vendace morphotypes, large and small, which were analysed separately. These samples were taken from the catches of commercial fishermen in the southern parts of both lakes. The division of vendace (all mature individuals) into small and large forms was carried out in the field. The weight of fish in the latter group in Lake Onega varied between 170 and 640 g and in Lake Ladoga between 130 and 160 g. For reference, 140 vendace samples from Lakes Roine and Vanajärvi, analysed earlier in collaboration between the University of Helsinki and the Natural Resources Institute Finland (Luke), were added to our data in order to gain a better understanding of the variation between populations in the region.

In addition, an old known spawning area on the Finnish coast of the GoF (Virolahti Bay, Fig. 1) was test fished with bottom gillnets during the spawning season in order to obtain vendace samples. The mesh sizes used (22, 25 and 27 mm, from knot to knot) were similar to those employed

there by commercial fishermen during the 1980s. Virolahti Bay was visited during 29–30 October 2020 and 27–28 October 2021, and the total effort was nine gill-net nights. Only one vendace was caught. This mature female was not included in the analysis. Instead of vendace, a lot of roach (*Rutilus rutilus*) and other cyprinids were caught.

All the samples were genotyped at 17 microsatellite loci. Deviations from the Hardy-Weinberg equilibrium (HWE) for each sampling site and each locus were tested with the *pegas* package for R ver. 1.3 (Paradis 2010) using an exact test based on 1000 Monte Carlo permutations of alleles (Guo and Thompson 1992), adjusted for multiple testing with the false discovery rate. Linkage disequilibrium among the microsatellite markers was tested with the *poppr* package for R (Kamvar et al. 2015) using the *rbarD* measure of correlation (Agapow and Burt 2001). Indices of genetic diversity within and between the vendace populations were calculated with the *diveRsity* package for R (Keenan et al. 2013). Genetic distances (D_A) (Nei et al. 1983) were calculated with *populations* software (version 1.2.32) (Langella 2000). The presence of null alleles was tested and discriminant analysis of principal components (DAPC) was conducted with the *adegenet* package for R (Jombart 2008). The most probable number of genetic clusters was determined with the k-means clustering algorithm as implemented in *adegenet* (Jombart et al. 2010). Relatedness estimates for each population were obtained using the *demeRelate* package for R (Kraemer and Gerlach 2017). Effective population sizes (N_e) were estimated

with the full likelihood method as implemented in *COLONY* software (Jones and Wang 2010).

Results

There were no significant deviations from HWE across markers or populations at the global level, except in the Lake Roine population, where 17.6% of the loci were out of HWE. There was also no significant effect of linkage disequilibrium (mean correlation between loci: 0.002, highest: 0.061). Three of the 17 microsatellite loci had null allele frequencies of > 8% (null allele test in *adegenet*) (Brookfield 1996). Therefore, all the analyses were performed with both a full set of microsatellites and a reduced set of 14 microsatellites from which the loci with possible null alleles had been removed. Most of the population genetic results were qualitatively similar with both data sets. As we found no marked differences between the results from full and reduced datasets, the results from the analysis of genetic differentiation with the full dataset are presented here (see supplemental material for results without the loci with possible null alleles).

Genetic variation within populations

Levels of genetic diversity were generally high within the sampled vendace populations. The total number of alleles and allelic richness varied between 109–245 and 5.93–9.16, respectively

Table 1. Vendace samples, their original habitat, sampling year and sample sizes (*n*).

| Population | Habitat | Sampling year | <i>n</i> |
|------------------------------|---------|---------------|----------|
| Onega, RUS (small) | Lake | 2020 | 19 |
| Onega, RUS (large) | Lake | 2020 | 20 |
| Ladoga, RUS (large) | Lake | 2020 | 15 |
| Ladoga, RUS (small) | Lake | 2020 | 25 |
| Päijänne, FIN | Lake | 2020 | 37 |
| Pyhtää (GoF), FIN, | Sea | 2020 | 41 |
| Roine, FIN | Lake | 2015 | 81 |
| GoF East, (Sestroretsk), RUS | Sea | 2020 | 47 |
| Hailuoto, FIN | Sea | 2020 | 40 |
| Vanajajärvi, FIN | Lake | 2015 | 59 |
| Total | | | 384 |

(Table 2). Based on the allelic richness, genetic diversity was highest in the sample from GoF East, as well as in the samples from Lakes Roine and Päijänne. Genetic diversity was lowest in the Lake Vanajärvi sample, which is likely to be due to the higher relatedness compared to the other samples (Fig. 2). The mean relatedness in the Lake Vanajärvi sample ($r_{\text{wang}} = 0.12$) was practically same as the relatedness level of first cousins ($r = 0.125$). There were no marked differences in the expected (H_e) or observed (H_o) levels of heterozygosity in any of the samples (Table 2). Differences between observed and expected heterozygosity would indicate inbreeding ($H_o < H_e$) or heterozygote excess caused, for example, by mixing of previously isolated populations or a recent bottleneck ($H_o > H_e$). Consequently, significant deviations from random mating ($F_{\text{IS}} > 0$) were not observed in any of the samples. The effective population sizes (N_e) were between 125 and 228, except in Lake Vanajärvi, where N_e was 68 (Table 2). The number of large morphotype samples from Lake Ladoga was too low for reliable estimation of N_e (Table 1).

Genetic variation between populations

Genetic differentiation between the populations was generally relatively low (global

$F_{\text{ST}} = 0.04$), although most of the F_{ST} values, measuring genetic differentiation between populations, were statistically significant (Table 3). Lake Vanajärvi samples differed most from the other samples. Genetic differentiation was also low between the large and small morphotypes in the Russian Lake Onega and slightly higher in Lake Ladoga (Table 3). Discriminant analysis of principal components (DAPC) revealed that the optimal number of genetic clusters with the present set of samples was five. Apart from Lake Vanajärvi, none of the populations formed a clearly distinct genetic cluster (Fig. 3).

The clustering analysis (DAPC) also revealed that Lake Vanajärvi clearly differed from the other populations (Fig. 4). The samples from Lake Onega additionally formed a clear cluster, while the rest of the populations were somewhat mixed (Fig. 3). Because of the large sample size of the Lake Vanajärvi population and clear differentiation from all the other populations, DAPC was also conducted without Lake Vanajärvi to improve the interpretation of the results (Fig. 4). Without the Lake Vanajärvi samples, the rest of the populations formed four clusters with some overlap. The most distinct cluster was formed by the Lake Onega samples. Samples from GoF East (Sestroretsk) and Lake Ladoga clustered together and closer to Lake Päijänne samples than to the rest of the Baltic Sea sam-

Table 2. Genetic diversity within populations of vendace, means across the 14 microsatellite loci. Number of individuals typed per locus per population sample (n), percentage of the total number of alleles across loci per population sample (%), number of alleles observed (A), allelic richness (A_r ; 1000 resamples, $n =$ smallest sample, 15), observed and expected heterozygosity (H_o and H_e), inbreeding coefficient (F_{IS}) with its associated 95% confidence limits, and the effective population size N_e ; estimated with full likelihood method) with the associated 95% confidence limits.

| Population | n | % | A | A_r | H_o | H_e | F_{IS} (95%CL) | N_e (95%CL) |
|----------------|------|------|-----|-------|-------|-------|-------------------------|-----------------|
| Onega (small) | 18.1 | 42.2 | 129 | 7.02 | 0.65 | 0.67 | 0.032 (-0.038–0.094) | 152 (74–5534) |
| Onega (large) | 20.0 | 47.5 | 143 | 7.67 | 0.70 | 0.68 | -0.020 (-0.080–0.029) | 228 (95–∞) |
| Ladoga (large) | 15.0 | 42.3 | 127 | 7.23 | 0.64 | 0.67 | 0.046 (-0.033–0.118) | NA ¹ |
| Ladoga (small) | 24.9 | 55.5 | 167 | 8.17 | 0.65 | 0.68 | 0.035 (-0.009–0.074) | 133 (73–491) |
| Päijänne | 37.0 | 60.2 | 197 | 8.63 | 0.66 | 0.69 | 0.035 (-0.004–0.078) | 167 (106–324) |
| Pyhtää | 40.9 | 50.5 | 160 | 7.57 | 0.63 | 0.66 | 0.034 (-0.005–0.079) | 143 (93–255) |
| Roine | 80.9 | 70.1 | 245 | 8.96 | 0.65 | 0.68 | 0.029 (0.002–0.060) | 171 (126–236) |
| GoF East | 48.0 | 68.4 | 237 | 9.16 | 0.62 | 0.63 | 0.003 (-0.017–0.061) | 146 (101–227) |
| Hailuoto | 40.0 | 56.5 | 192 | 8.53 | 0.66 | 0.65 | 0.013 (-0.021–0.050) | 125 (82–219) |
| Vanajärvi | 58.9 | 36.8 | 109 | 5.93 | 0.62 | 0.64 | 0.030 (-0.015–0.072) | 68 (48–100) |

¹ Sample size too low for an estimate

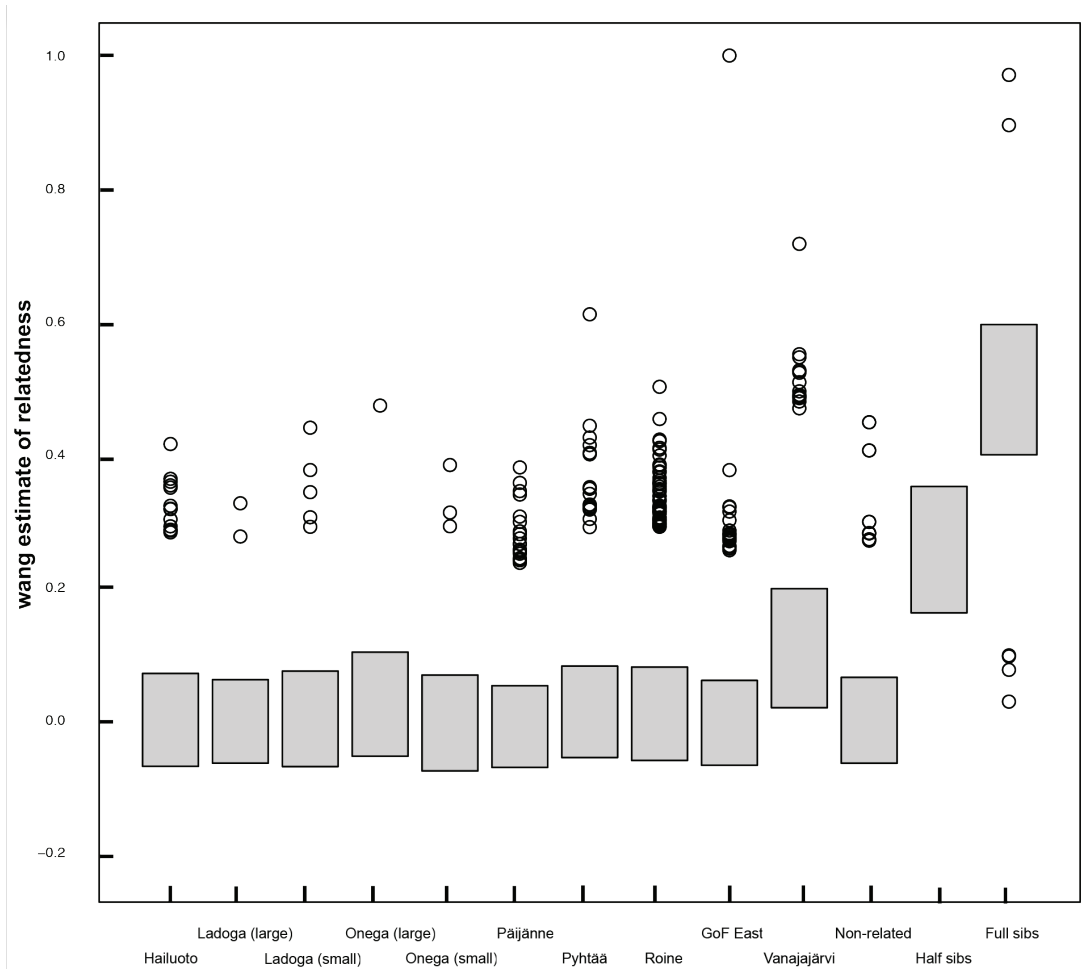


Fig. 2. Mean relatedness (r_{wang}) in the vendace populations. The last three columns on the right show the simulated relatedness estimates for non-related individuals, half siblings and full siblings, and provide a scale for the empirical relatedness estimates.

ples. The samples from Hailuoto clustered close to the Lake Roine samples, while the samples from Pyhtää clearly clustered separately (Fig. 4).

The dendrogram with genetic distances (D_A) displayed similar patterns. The positions of the large morphotype samples from Lake Ladoga and the samples from Lake Päijänne were uncertain, as the statistical support (bootstrap value) for their position in the dendrogram was low (Fig. 5). In the remaining three clusters, Lake Ladoga samples grouped together with the GoF East samples, the samples from Pyhtää clustered together with the Hailuoto and Lake Roine samples, and the Lake Onega samples clustered together and close to the Lake Vanajajärvi samples (Fig. 5).

Discussion

Levels of genetic diversity were generally high in the sampled vendace populations. The total number of alleles and allelic richness in our data were similar to those reported by Karjalainen *et al.* (2022) from vendace populations in large lakes in central Finland. The effective population size (N_e) gives an indication of genetic variability and, thus, the viability of the population. According to a rule-of-thumb, for a population to be viable in the short term, N_e should exceed 100 (Frankham 2014). The genetic estimates of N_e in all our populations, except for the reference population of Lake Vanajajärvi, exceeded the rule-of-thumb threshold value, indicating that

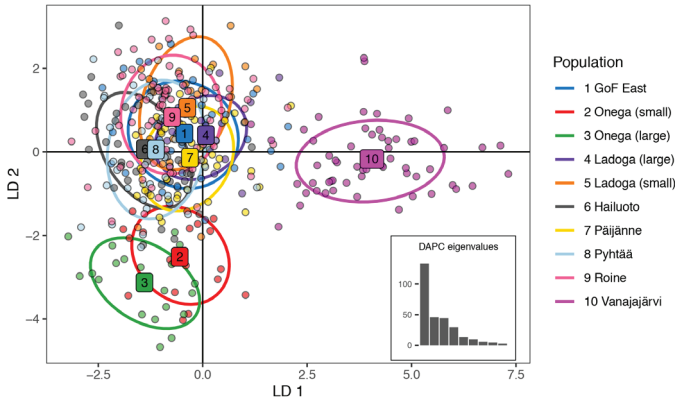


Fig. 3. The first two axes of the discriminant analysis of principal components (LD 1 and LD 2). Each dot represents an individual sample, and each population is represented by different colours and inertia ellipses.

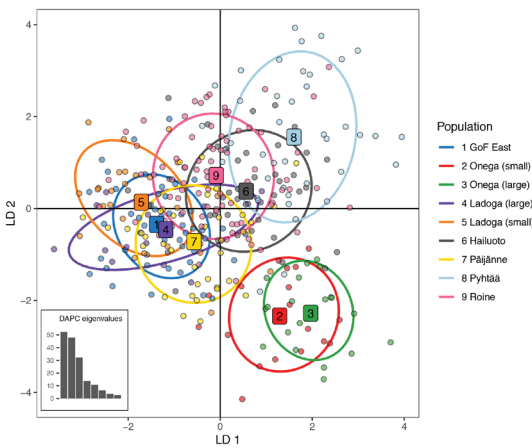


Fig. 4. The first two axes of the DAPC (LD 1 and LD 2) without Lake Vanajärvi samples. Each dot represents an individual sample, and each population is represented by different colours and inertia ellipses.

Table 3. Genetic differentiation (F_{ST} with 95% CI) among populations. F_{ST} values with 95% confidence intervals overlapping zero are highlighted in grey.

| | Onega (small) | Onega (large) | Ladoga (small) | Ladoga (large) | Päijänne |
|----------------|------------------|------------------|-------------------|--------------------|-------------------|
| Onega (large) | 0.03 (0.01–0.06) | | | | |
| Ladoga (large) | 0.05 (0.02–0.09) | 0.05 (0.03–0.09) | | | |
| Ladoga (small) | 0.05 (0.03–0.08) | 0.08 (0.06–0.11) | 0.03 (0.004–0.06) | | |
| Päijänne | 0.03 (0.01–0.05) | 0.05 (0.04–0.07) | 0.04 (0.01–0.07) | 0.01 (0.003–0.03) | |
| Pyhtää | 0.05 (0.03–0.07) | 0.07 (0.05–0.10) | 0.06 (0.03–0.09) | 0.04 (0.02–0.05) | 0.03 (0.02–0.04) |
| Roine | 0.05 (0.03–0.06) | 0.07 (0.06–0.09) | 0.04 (0.02–0.07) | 0.03 (0.02–0.04) | 0.01 (0.007–0.02) |
| GoF East | 0.05 (0.03–0.08) | 0.07 (0.05–0.09) | 0.02 (0.004–0.05) | 0.01 (-0.003–0.02) | 0.03 (0.02–0.04) |
| Hailuoto | 0.04 (0.02–0.07) | 0.05 (0.04–0.08) | 0.03 (0.01–0.06) | 0.03 (0.01–0.04) | 0.03 (0.01–0.04) |
| Vanajärvi | 0.05 (0.04–0.07) | 0.08 (0.07–0.10) | 0.06 (0.04–0.09) | 0.07 (0.05–0.09) | 0.05 (0.04–0.06) |

| | Pyhtää | Roine | GoF East | Hailuoto |
|-----------|------------------|-------------------|------------------|------------------|
| Roine | 0.03 (0.02–0.05) | | | |
| GoF East | 0.05 (0.03–0.06) | 0.03 (0.02–0.04) | | |
| Hailuoto | 0.03 (0.02–0.05) | 0.01 (0.005–0.02) | 0.03 (0.02–0.04) | |
| Vanajärvi | 0.07 (0.06–0.09) | 0.06 (0.05–0.07) | 0.07 (0.06–0.08) | 0.07 (0.06–0.08) |

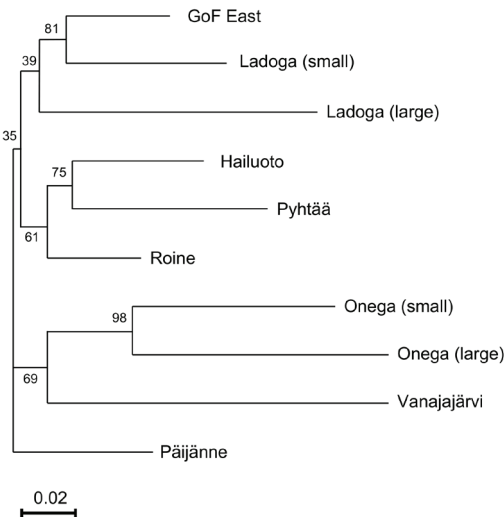


Fig. 5. Genetic distances (D_A ; Nei 1984) among the vendace samples. The bootstrap values (%) are based on 1000 replicates. Bootstrap values are only shown for the branches that were in a similar position in at least half of the bootstrap replicates (bootstrap values > 50).

the populations are genetically viable in the short term. The lowest N_e estimate was in Lake Vanajajärvi, which is a small (7 km²) headwater lake with limited possibilities for vendace to migrate there from other lakes.

Genetic differentiation among the populations was generally relatively low. The level of genetic differentiation was lower than, for example, among salmon (*Salmo salar*) populations in the Baltic Sea ($F_{ST} = 0.11$, Säisä *et al.* 2005), but similar to other Baltic Sea salmonids with weaker homing behaviour compared to salmon, e.g., sea trout (*Salmo trutta*) ($F_{ST} = 0.06$, Nilsson *et al.* 2008) and whitefish (*Coregonus lavaretus*) (sea-spawning $F_{ST} = 0.02$; anadromous $F_{ST} = 0.012$, Ozerov *et al.* 2015). Compared to genetic differentiation among vendace populations from large lake basins in central and eastern Finland, estimated using 13 microsatellite loci (Karjalainen *et al.* 2022), the levels of genetic differentiation among the Baltic Sea populations here were slightly higher ($F_{ST} = 0.034$ without the lake populations), and differentiation between the samples from the GoF (Pyhtää and GoF East) was similar ($F_{ST} = 0.01$), suggesting no restrictions of gene flow between the GoF sampling sites. Similar patterns of weak structur-

ing among the northern Baltic Sea have also been found using a genome-wide approach (Lopez *et al.* 2022). However, differences in the patterns of neutral genetic differentiation between closely related fish species have also been found in the Baltic Sea, suggesting a fundamental role of life-history traits in neutral genetic differentiation (e.g., DeFaveri *et al.* 2012). This is reflected in the patterns of genetic differentiation of vendace from the Baltic Sea and northern European freshwaters, where neutral genetic differentiation among populations is generally low, with larger differences only occurring between different ecotypes: the autumn and spring spawning vendace (Vuorinen and Lankinen 1978, Vuorinen *et al.* 1981, Mehner *et al.* 2009, Delling *et al.* 2014, Mehner *et al.* 2021). Genetic distances (D_A ; Nei *et al.* 1983), which also measure distances between populations, were higher (up to 0.04) here than reported from ten Russian lakes ($D_A < 0.01$) in the drainage area of the Baltic Sea (Sendek 2021). The low F_{ST} values recorded here reflect gene flow (historic or current) among the studied vendace populations, although even low migration rates between populations are sufficient to maintain gene flow that results in low F_{ST} values (Wright 1949, Lowe and Allendorf 2010). On the other hand, a low F_{ST} value does not mean that there cannot be a considerable amount of differentiation among subpopulations (Wright 1969), especially in adaptive traits. Even with negligible F_{ST} values, there can be significant differentiation in genes that underlie quantitative traits — the genes that are under selection (e.g., Leinonen *et al.* 2013).

Although F_{ST} values were generally low among all the vendace populations in the present study, they revealed some structuring, especially among the GoF populations (the main target of interest in the present study). Contrary to our hypothesis, the results suggest that vendace in the easternmost GoF (Sestroretsk) form a common population with vendace of Lake Ladoga. This was not a surprise, as it has been reported, for example, by Bogdanov *et al.* (2021) that at least some of the vendace in the easternmost GoF undergo spawning migrations to the 60-km-long Neva River, connecting the GoF and Lake Ladoga without any dams or hydroelectric power plants. Unfortunately, there are no quan-

titative estimates of how common this anadromous behaviour is in the easternmost GoF.

As stated by Bogdanov *et al.* (2021), the decline in vendace stocks and the fishery in the easternmost GoF is hardly due to overfishing, but more likely associated with changes in abiotic factors. The decline in catches began in the 1970s, and before this, vendace was common in several areas in the eastern GoF over 80 km from the mouth of the Neva River (see Bogdanov *et al.* 2021). The largest share of nutrient (P and N) input to the GoF still comes from Russia to the easternmost part of the gulf (Räike *et al.* 2016). Prior to 1978, the year when the central wastewater treatment plant became operational, the purification of wastewaters in St. Petersburg, the largest city in the region, was almost non-existent, and practically all waste waters were discharged directly into the GoF or the Neva River. This means that the lower parts of the river and the bay outside of it received enormous amounts of nutrients. The effects must have been drastic in the relatively shallow areas, although systematic data on the effects on water quality and benthic habitats from that time are lacking. Most vendace populations are autumn spawners, and cumulative eutrophication increases the risk that eggs laid on the bottom will suffocate due to increased siltation or even a temporary lack of oxygen. The risk of harmful effects from deteriorated water quality is highest in the sea area (Neva Bay). The situation became worse after 1979 due to the construction of a flood control dam 20 km outside of the city of St. Petersburg. Thereafter, water exchange between the inner parts of the Neva Bay and the open sea decreased, and sedimentation, as well as the general trophic level, increased (Sendek and Korolev, 2010). Unfortunately, no data on the possible old spawning areas are available to support this hypothesis. It is, however, likely that the present vendace stock in the easternmost GoF is largely dependent on reproduction areas in the upper reaches of the Neva River or even in Lake Ladoga. However, it cannot be ruled out that small numbers of spawning vendace could have been preserved in the easternmost part of the bay: this is indirectly indicated by the increased levels of genetic diversity in the sample of feeding vendace from the Sestroretsk area.

The dispersion potential of vendace to downstream areas appears to be high, even in rivers dammed by hydroelectric power plants. Vendace introduced into Lake Inari, northern Finland, colonized downstream along the 120-km-long subarctic Pasvik river system during six years from 1989 to 1995 (Amundsen *et al.* 1999), despite the presence of several power plants. In the Kymijoki River, flowing from Lake Päijänne to the GoF, there are also several hydroelectric power plants preventing upstream migration, but it is possible, at least in theory, that fish can survive downstream. However, the vendace from Pyhtää, close to the mouth of the Kymijoki River, were more closely related to the sea-spawning vendace from the Bothnian Bay than to the vendace of Lake Päijänne or to any other sampled areas. This supports our hypothesis and suggests that the vendace population in Pyhtää is merely a remnant of a common sea-spawning vendace population that earlier inhabited the Finnish coast between the two main distribution areas, the Bothnian Bay and the easternmost GoF. This is supported by observations that vendace have earlier sporadically occurred along the entire Finnish coast (Lehtonen 1981 and references therein). Unfortunately, the vendace population in the GoF (Virolahti Bay), which was still the target of a small-scale fishery in the 1980s, appears to have been virtually lost, as only one individual was caught in our test fishing. Adequate samples from this population would have been valuable to understand the connections and history of the coastal vendace populations.

The earlier spawning area, Virolahti Bay, is a shallow (< 10 m) semi-enclosed bay area, into which the relatively small River Virojoki flows. Nowadays, Virolahti Bay is highly eutrophic. According to a recent classification of Finnish coastal waters, based on the EU Water Framework Directive (Aroviita *et al.* 2019), it was in a "poor" ecological state. This is mostly due to diffuse loading via the River Virojoki and due to loading from the local fish farming industry since the beginning of the 1980s and municipal waste waters until 2002. The deterioration of water quality and increased siltation of spawning grounds poses risks to vendace (e.g., Winfield *et al.* 2004), and the poor state of Virolahti Bay is likely to be at least one factor behind the col-

lapse of the local vendace stock during the previous 40 years. The Pyhtää area, where vendace still exists, is located a little further out in the archipelago zone, where the ecological state was classified as "satisfactory" (Aroviita et al. 2019). It is still in the range of the Kymijoki River, the largest river flowing to the Finnish coast of the GoF.

To conclude, the still existing but evidently decreased vendace population in the easternmost GoF is genetically close to the freshwater vendace of Lake Ladoga, flowing into the GoF via the Neva River. The previously known local population in the Virolahti Bay appears to have become extinct during the last 30–40 years, possibly due to strong eutrophication. In the Pyhtää archipelago, there is still a small local vendace population, which is genetically close to the sea-spawning vendace population of the Bothnian Bay. This genetically viable population evidently carries the genes of a sea- or estuarine-spawning vendace which, based on observations from the previous century, sporadically occurred along the entire Finnish coast. This population is an important part of the local biodiversity. According to the goals of the EU Marine Strategy Framework Directive, as well as the Water Framework Directive, coastal areas, including coastal bays, should reach at least a "good" status. The goal is ambitious, but if the state of the coastal waters of the GoF recovers in the future and if the possible restricting effect of salinity diminishes, due to climate change, it is possible that this freshwater population might act as a source of vendace to re-inhabit other areas in the GoF.

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