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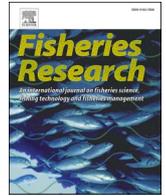
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Genetic-based evaluation of management units for sustainable vendace (*Coregonus albula*) fisheries in a large lake system

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ABSTRACT

The goal of the processing industry, trade and consumers is to get eco-labelled freshwater fish products from sustainable fisheries into the market as soon as possible. The fourth largest natural lake system in Europe, the Saimaa lake system supports a fishery for vendace (*Coregonus albula*). Certification of the fishery requires an understanding of population structure to help determine the number and spatial extent of management units. In this study, we analysed the genetic diversity of local vendace populations in the Saimaa lake system and aimed to identify the conservation and management units of vendace. Within the Saimaa, the genetic divergence between local populations of vendace was weak and their genetic divergence did not follow an isolation by geographic distance pattern. Vendace has potential to disperse effectively within and between local populations in different lake basins. Even if we observed subtle genetic divergence within our study systems, available information showed no significant evidence that the local populations had unique evolutionarily significant traits. The local populations of the Saimaa lake system seem to have similar life history and morphological traits as in the whole Central Finland lake district. The conservation of genetic diversity seemed not to require basin-specific actions and we conclude that management of local vendace populations of Saimaa as one management unit is advisable.

1. Introduction

Mandatory or voluntary eco-labelling of fish products is an increasing trend in seafood production and marketing (Wessells et al., 2001; Gutiérrez et al., 2012). The principal objective of eco-labels is to create a market-based incentive for better management of fisheries by directing consumer demand for seafood products to well-managed populations (Wessells et al., 2001). When quality controlled and sustainability certified fisheries were compared with those that had been declined to pursue full certification after pre-assessment, certified populations had much lower mean exploitation rates (67% of the rate producing maximum sustainable yield vs. 92% for those declined to pursue certification), allowing for more sustainable harvesting (Gutiérrez et al., 2012). The European commission report (EC, 2016EC) stated that EU is currently the largest market for eco-labelled fisheries and aquaculture products but the eco-labels concentrate on frozen or processed products. In many countries, where consumers mainly purchase fresh products, eco-labels and certifications play a marginal role. In inland fisheries,

certification is still rare and the proportion of the MSC (Marine Stewardship Council) certification units in inland fisheries in 2010–2020 ranged from 0.4% to 4.4% of all certified and in-assessment units in the MSC program globally (Koerner and Hair, 2021). A trend of MSC certificated inland populations is increasing but still the proportion is lower than the proportion of the inland commercial catch (12.4%) of the total global capture fisheries catch (FAO 2020).

In Finland, vendace (*Coregonus albula*) and pikeperch (*Sander lucioperca*) produced the most valuable inland catches in 2019 (5.7 vs. 5.8 million €, (Natural Resource Institute, 2020)). Both of them are marketed mainly fresh and neither vendace nor pikeperch fisheries are eco-labelled. Yet, the processing industry, trade, restaurants and consumers show growing interest in certificated freshwater fisheries products on the market. In the Saimaa lake system (Finland), the vendace fisheries have gone through the pre-assessment of MSC (Pawson and Pedersen, 2013; Karels and Posti, 2014). An essential task to accomplish before proceeding to final certification process was to define the management units of vendace in this fourth largest natural lake in Europe.

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Saimaa is a large, fragmented lake with islands and narrow straits connecting separate lake basins (Kuuisto, 1999) which have their own local vendace populations and fisheries. In Finnish lake systems, the existence of separate local populations of vendace in different basins with different growth rates and population densities has been recognized for a long time (Järvi, 1919; Marjomäki and Huolila, 2001) but whether the local populations are genetically and ecologically different enough to be defined as separate management units is unclear.

Vendace is a small-sized, short-lived schooling species, which belongs to Eurasian cisco (*Coregoninae*) complex consisting of two circumpolar species, vendace and least cisco (*C. sardinella*) (Vuorinen et al., 1981; Dellling et al., 2014; Sendek, 2021; Mehner et al., 2021). Vendace is typical in deep and oligotrophic lakes and lake systems in Western and Northern Europe (Vuorinen et al., 1981; Mehner et al., 2007). Morphological differences between vendace populations from different lakes are negligible in their boreal distribution range (Vuorinen and Lankinen, 1978; Sendek, 2021). During spawning, vendace population disperse their eggs widely across the lake basin (Karjalainen et al., 2021) and in spring after up to 6-month egg incubation, the newly hatched vendace larvae disperse efficiently with currents which can transport them several kilometres away from the original spawning places (Karjalainen et al., 2019). This dispersion potential of larval vendace suggests that the adjacent local populations may not be separate units (Karjalainen et al., 2019). Later in summer, young-of-the-year (YOY) vendace may move widely and mix within a basin (Valkeajärvi, 1983) but migration from one basin to another is also likely. Furthermore, transfers of vendace from one lake to another have been common in Finland (Lahti, 1987; Jurvelius et al., 1995; Huuskonen et al., 2004) and have occasionally diversified the genetic variation in the target population although often resulting in only minor changes in population structure (Huuskonen et al., 2004). On the other hand, Mehner et al. (2009) noted that enhancement stocking of vendace larvae caused significant genetic mixing in some German lakes.

Sustainable management of fish populations requires matching of biological processes and management actions, but mismatches between ecology or biology and the realized management actions occur frequently (Reiss et al., 2009). In marine fisheries, the management strategy needs to embrace a variety of conflicting factors such as biological, economic, social or political factors. Further, a major challenge in the determination of the genetic-based management units at the population level is mixing of distinct populations of migratory species at fishing grounds (Reiss et al., 2009). In Finnish lake fisheries, the challenges differ from management of marine populations: management units are normally small local systems, the decision-making practices are diverse and policies are local owner -driven, which has led to incoherence in management objectives and strategies even within a basin (Karjalainen and Marjomäki, 2005; Sipponen et al., 2006).

In this study, we aimed to clarify the genetic structure of local vendace populations inhabiting the Saimaa lake system, what extent they are genetically divergent and consequently, should they be managed as separate management units to preserve their possible unique traits resulting from local adaptation. The four criteria hierarchical approach for intraspecific conservation prioritization of the lake whitefish species complex (*Coregonus* spp.) introduced by Mee et al. (2015) was applied to define the management units for Saimaa vendace. Mee et al. (2015) determined the criteria for their designatable units (DU) as follows: Criterion 1 identifies subspecies as DUs and recognition of subspecies is typically assessed using morphology. Subspecies are a significant part of the evolutionary legacy of a species and are geographically disjunctive. In Criterion 2, the discreteness of phylogeographic lineages within the same species is recognized based on genetic evidence, statistical support for their discreteness (e.g. in a phylogenetic analysis) and evidence that the origin of such lineages is associated with different refugia that were occupied during the Pleistocene glaciation. Criterion 3 is based on the local adaptation, which is dependent on evidence that discreteness among potential DUs in adaptive traits is genetically controlled and

influenced by selection in a particular environment. Criterion 4 is based on the biogeography and Mee et al. (2015) used a priori identification of National Freshwater Biogeographic Zones (NFBZ) based on similarities of fish species communities across watershed boundaries to designate discrete groupings. Residence in different biogeographic zones may amount to significant discreteness between DUs due to their different biogeographic histories and geographic isolation (Mee et al., 2015). It is noteworthy that DUs generally aim to identify the conservation units of fish species but DUs are not necessarily useful operational management units to govern harvesting. Migration rates between adjacent local populations is a key criterion to determine demographic connectivity and operational management units while migrants per generation determines genetic connectivity and affects evolutionary processes within populations (Waples and Gaggiotti, 2006; Lowe and Allendorf, 2010). Lowe and Allendorf (2010) defined demographic connectivity as the degree to which population growth and vital rates are affected by dispersal.

We performed a literature review to evaluate the DU criteria for vendace in the Central Finland lake district. Furthermore, we analysed genetic structure of vendace populations in five separate lake basins in the Saimaa lake system (Vuoksi drainage system) and three lake basins in the separate Kymijoki drainage system. Migration of vendace between Vuoksi and Kymijoki systems is not possible. These analyses aimed to apply Mee's DU criteria 2 and 3 and test the specific hypotheses: 1) genetic divergence between the Kymijoki and Vuoksi drainage systems is significant due to the present geographical isolation, 2) genetic divergence between the separate basins of the Saimaa lake system are significant and 3) genetic divergence between the Saimaa local populations follows an isolation by geographic distance pattern. Finally, we formulated our recommendations for MSC management units in the Saimaa lake system from the genetic and demographic connectivity point of views.

2. Material and methods

2.1. Fishing areas and sample collection

Local commercial fishers collected vendace samples from 9 economically valuable fishing areas in central and southeast Finland in 2019–2020 (Fig. 1). Samples were taken from the commercial trawl, seine or gill net catches in autumn before spawning or in winter slightly after spawning except from Lake Puula where they were trawled in June, 2019. Six of the basins are located in the Saimaa lake system (Vs) in the Vuoksi drainage system (V) (surface area 427 946 ha). Sample sites 1Vs (Kaidonselkä) and 2Vs (Petraselkä) are located close to each other in the same lake basin, and between sites 3Vs and 5Vs there is only a short strait connecting adjacent basins (Haukivesi and Pihlajavesi). Lake Pielinen (7 V) is also situated in the Vuoksi drainage system. It is connected to the Saimaa Pyhäselkä basin (6Vs) via the 67 km long River Pielisjoki (mean discharge 228 m³/s) that has been dammed since 1870. Furthermore, samples from three lake basins from the adjacent large Kymijoki (K) drainage system (Puula 8 K, Southern Konnevesi 9 K, 10 K and Northern Konnevesi 11 K) were included in the study.

From these 9 sampling sites, 862 vendace individuals were sampled and genetic analyses were carried out on 812 fish (Table 1). In cases where some of the alleles were not successfully amplified or their fluorescent labels were not clear after several attempts, the fish were discarded from further analyses. This led us to abandon 50 vendace from the dataset. For analysing the temporal variation in the genetic diversity, stored vendace samples from Pyhäselkä (V) and Konnevesi (K) taken in 2004–2006 were also included in the microsatellite analysis. Samples from Pyhäselkä and S Konnevesi basins were stored at –20 °C and treated in the laboratory in the same way as the samples collected in 2019 and 2020. In S Konnevesi, samples from year 2004 to 2006 and 2019 are from the Häntiäisselkä spawning area (9 K). Additionally, another spawning area of S Konnevesi (10 K) Kotilahti was sampled in

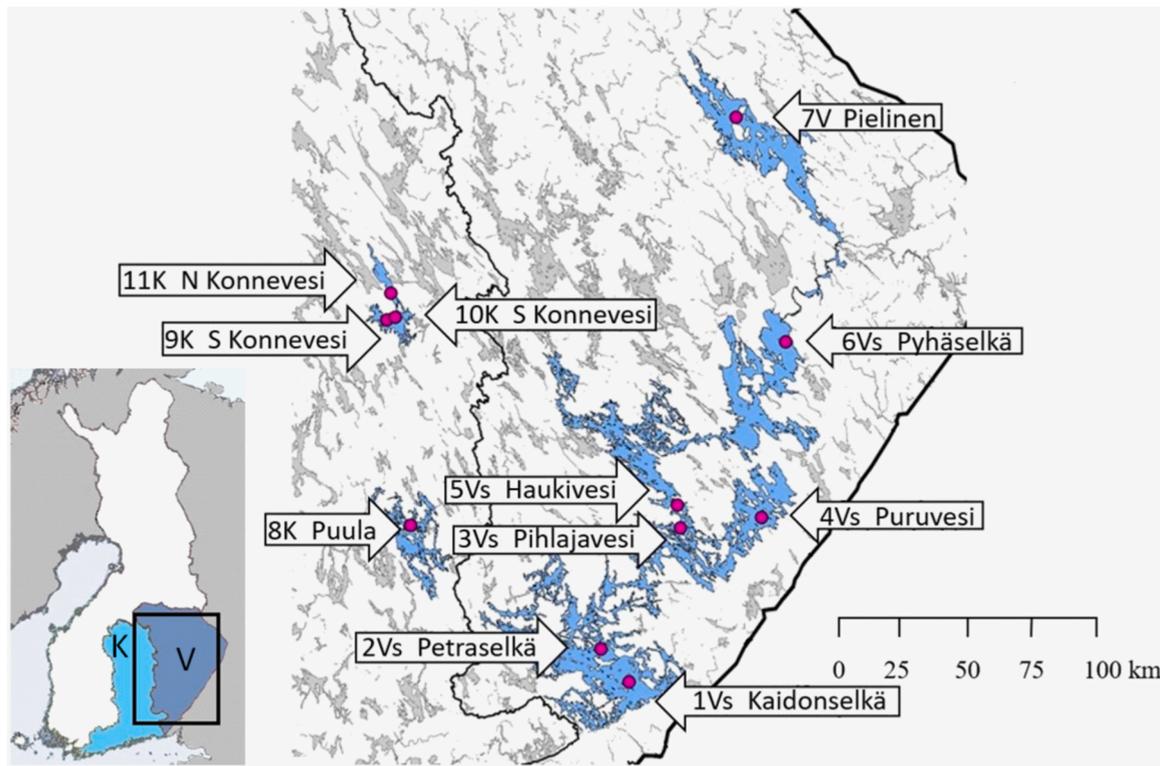


Fig. 1. The study lake basins in the Vuoksi (V, basin IDs 1–7) and Kymijoki (K, basin IDs 8–11) drainage system in Finland. The lake basins 1–6 belong to the Saimaa lake system (Vs).

Table 1

Sampling sites of vendace in the Vuoksi (V) and Kymijoki (K) drainage systems. ID is the location identification code used in all other figures and tables. Samples with ID Vs are from the Saimaa lake system (Vuoksi drainage). Site, sampling year, mean total length \pm SD (mm), mean wet weight \pm SD (g), number of samples (N), individuals per sex (female/male/immature) for the fish analysed in the analysis of genetic population structure.

ID	Lake basin	Year	Length mm	Weight g	N	Sex
1Vs	Kaidonselkä	2019	99 \pm 13	5.8 \pm 2.6	55	9/9/37
2Vs	Petraselkä	2019	90 \pm 21	4.3 \pm 2.9	57	8/13/36
3Vs	Pihlajavesi	2019	102 \pm 14	7.2 \pm 2.7	56	27/22/7
4Vs	Puruvesi	2020	141 \pm 20	17.5 \pm 7.2	58	28/30/0
5Vs	Haukivesi	2019	133 \pm 9	15.5 \pm 3.0	58	33/25/0
6Vs	Pyhäselkä	2004	170 \pm 12	32.5 \pm 8.0	33	7/26/0
		2005	151 \pm 13	21.9 \pm 5.5	34	9/25/0
		2006	151 \pm 5	23.1 \pm 3.2	34	8/26/0
7V	Pielinen	2019	134 \pm 24	18.2 \pm 9.4	57	17/40/0
		2019	104 \pm 11	8.1 \pm 2.6	59	37/22/0
8K	Puula	2019	115 \pm 12	10.7 \pm 3.5	57	31/25/1
9K	S Konnevesi	2004	129 \pm 14	12.3 \pm 4.6	31	7/24/0
		2005	115 \pm 13	8.4 \pm 2.9	33	9/24/0
		2006	119 \pm 13	9.4 \pm 3.7	33	8/25/0
		2019	110 \pm 13	9.0 \pm 2.9	58	21/29/8
10K	S Konnevesi	2019	142 \pm 14	17.9 \pm 4.5	57	30/27/0
11K	N Konnevesi	2020	123 \pm 17	11.6 \pm 4.7	42	27/15/0
Total					812	316/407/89

2019. The distance between these two spawning areas are ca. 6 km.

In the laboratory, total length (mm) and wet weight (g) of fish were measured (Table 1) and sex was determined. A piece of tissue from dorsal muscle was dissected for microsatellite analysis.

2.2. DNA extraction and amplification

Genomic DNA was extracted from frozen vendace muscle tissue

using PureLink™ Genomic DNA Mini Kit (Thermo Fisher Scientific) following the manufacturer’s protocol. Mean weight of a muscle sample was 24 mg. DNA yield was measured with Nanodrop™ One spectrophotometer (Thermo Fisher Scientific).

Vendace samples were genotyped at 13 microsatellite loci that Præbel et al. (2013a), (2013b) have found suitable for vendace in Norway and Finland (Table 2). DNA loci were amplified in three PCR multiplex assays using Qiagen Multiplex PCR mix using 20 ng template DNA. PCR amplification was done as follows: 15 min initial

Table 2

Details of the 13 microsatellite loci arranged in three PCR multiplex assays used in this study of vendace including the original publication references. Mlpx = PCR Multiplex group, Size range = expected marker size ranges in reference publications, T_a = PCR annealing temperature (°C), Dye = fluorescent label of the F primer.

Locus ID	Mlpx	Size range	T _a °C	Dye	Reference
<i>Bwf1</i>	1	195–225	57	pet	Patton et al. (1997)
<i>Bwf2</i>	3	160–232	61	pet	Patton et al. (1997)
<i>BFR0018</i>	2	191–219	60	pet	Susnik et al. (1999)
<i>ClaTet6</i>	3	181–205	61	6-fam	Winkler and Weiss (2008)
<i>ClaTet9</i>	3	174–326	61	vic	Winkler and Weiss (2008)
<i>ClaTet13</i>	1	218–290	57	6-fam	Winkler and Weiss (2008)
<i>Cocl-Lav4</i>	1	127–153	57	6-fam	Rogers et al. (2004)
<i>Cocl-Lav6</i>	1	124–190	57	ned	Rogers et al. (2004)
<i>Cocl-Lav10</i>	1	260–264	57	ned	Rogers et al. (2004)
<i>Cocl-Lav27</i>	1	181–187	57	vic	Rogers et al. (2004)
<i>Cocl-Lav49</i>	2	174–224	60	ned	Rogers et al. (2004)
<i>Cocl-Lav52</i>	2	94–130	60	6-fam	Rogers et al. (2004)
<i>C2-157/Cisco-157</i>	2	119–159	60	vic	Turgeon et al. (1999)

denaturation 95 °C, after which 25 cycles of 30 s at 95 °C, 90 s at 57 °C (Mlpx 1) / 60 °C (Mlpx 2) / 61 °C (Mlpx 3), 1 min at 72 °C, and 30 min at 60 °C. PCR products were run in ABI Prism 3130xl Genetic Analyzer (in POP-7™ polymer) with GeneScan™ 500 LIZ® Size Standard. Alleles were scored using Geneious Prime software version 2020.20.4 (Biomatters, LTD).

2.3. Genetic analysis

The genotype matrix consisted of 812 individuals, 13 microsatellite loci and 367 alleles (5–51 alleles per microsatellite; [Supplementary material Table S1](#)). All analyses were performed in R 3.6.1 (R Core Team, 2013). The packages Adegenet 2.1.3 (Jombart, 2008), graph4lg v. 1.0.1 and HierFstat v. 0.5.7 (Goudet, 2005) were used in data conversions and in the analyses. We used observed and expected heterozygosity to evaluate genetic diversity among loci and sampling site–year combinations using HierFstat (Table S1, Table 3). The significance of observed departures from Hardy–Weinberg equilibrium was assessed for each microsatellite locus within each sampling site by estimating the exact *P*-values using Markov chain method (Genepop v. 4.7.5, Rousset, 2008). We used 10000 dememorizations, 20 batches and 5000 iterations per batch, and corrected the *P*-values for multiple testing according to Bonferroni procedure with 143 comparisons (11 populations x 13 microsatellite loci). To compare the Hardy–Weinberg deviations among sampling sites, we also repeated the analysis using an entire lake as a sampling site (Saimaa, Puula, Konnevesi, Pielinen). Systematic deficiency of the observed proportion of heterozygotes from the expected values among microsatellites and sampling sites was verified using pairwise *t*-tests comparing the observed and expected heterozygosities among populations and among microsatellite loci. To further inspect differences in the heterozygosity estimates between microsatellite loci, we compared the observed levels of heterozygosities to the expected proportions of heterozygote genotypes, calculated using the observed allele frequencies and assuming Hardy–Weinberg equilibrium, and quantified the difference using the inbreeding coefficient Wright's F_{IS} for each microsatellite locus and sampling site, and averaging the values for each locus and sampling site.

We used principal component analysis (PCA, ade4 v. 1.7.15, Dray and Dufour, 2007) to visualize differences among sampling sites and years. Principal components (PCs) were calculated with mean-centered (mean allele frequency subtracted from all observations) allelic data

Table 3

Genetic variation in vendace samples in the studied lake basins for 13 microsatellite loci. *N* = sample size, H_O = observed heterozygosity, H_E = expected heterozygosity, N_A = number of alleles, N_{PA} = number of private alleles, P_{PA} = proportion of private alleles.

ID	Sampling site	Year	N	H_O	H_E	N_A	N_{PA}	P_{PA} (%)
1 Vs	Kaidonselkä	2019	55	0.61	0.69	208	3	1.4
2 Vs	Petraselkä	2019	57	0.65	0.71	206	2	1.0
3 Vs	Pihlajavesi	2019	56	0.63	0.68	169	1	0.6
4 Vs	Puruvesi	2020	58	0.62	0.73	200	4	2.0
5 Vs	Haukivesi	2019	58	0.63	0.71	205	3	1.5
6 Vs	Pyhäselkä	2004	33	0.67	0.71	160	1	0.6
		2005	34	0.64	0.69	165	3	1.8
		2006	34	0.62	0.71	165	2	1.2
		2019	57	0.61	0.70	209	1	0.5
		all	158	0.63	0.71	258	17	6.6
7 V	Pielinen	2019	59	0.65	0.71	198	2	1.0
8 K	Puulavesi	2019	57	0.66	0.70	186	3	1.6
9 K	S Konnevesi	2004	31	0.63	0.69	156	4	2.6
		2005	33	0.64	0.71	169	5	3.0
		2006	33	0.56	0.67	152	2	1.3
		2019	58	0.64	0.714	199	5	2.5
		all	155	0.62	0.72	260	53	20.4
10 K	S Konnevesi	2019	57	0.61	0.72	206	6	2.9
11 K	N Konnevesi	2020	42	0.60	0.72	177	3	1.7

(allele presence/absence matrix). Further, we estimated group means for PC1 eigenvalues within each sampling site and year, and the associated 95% confidence intervals for the means using 1000 bootstrap samples. Finally, we verified the difference between PC1 eigenvalues of individuals from different lake basins of Kymijoki and Vuoksi drain systems using a *t*-test.

Genetic divergence among sampling sites was estimated with pairwise Weir–Cockerham F_{ST} (Weir and Cockerham, 1984) using HierFstat. The significance levels of pairwise F_{ST} comparisons between sampling sites was evaluated using 95% confidence intervals obtained by bootstrapping the loci for 1000 times. Relationship between genetic (F_{ST}) and geographic distances (in a straight line between each two points) was calculated from distances (km) between sampling sites. To test whether genetic divergence is positively associated with geographic distance in the Saimaa lake system, we used a Spearman correlation coefficient and assessed the significance using Mantel test with 10 000 permutations (vegan v. 2.5.6, Dixon, 2003). To test whether null alleles affected the F_{ST} estimates, we compared our F_{ST} estimates to the F_{ST} estimates excluding null alleles, using a method described by Chapuis and Estoup (2007) and implemented in software FreeNA with 1000 bootstrap replicates (Chapuis and Estoup, 2007).

3. Results

In the studied vendace samples from the Vuoksi and Kymijoki drainage systems, the mean observed heterozygosities of the individual microsatellite loci ranged between 0.32 and 0.92 ([Supplementary material Table S1](#)). The observed heterozygosities for all samples over the 13 microsatellite loci (Table 3) averaged 0.63, ranging from 0.56 (S Konnevesi 10 K) to 0.67 (Pyhäselkä 6Vs). The vendace sample from S Konnevesi included private alleles unique for the lake basin (Table 3). In majority of the populations studied, significant departures from the Hardy–Weinberg equilibrium were detected at several loci ([Supplementary material Table S2](#)). Indeed, observed mean heterozygosity was consistently lower than expected among microsatellite DNA loci ($t_{12} = 3.4332$, $P = 0.005$, Table S1), sampling sites and years ($t_{16} = 12.036$, $P < 0.001$, Table 3) explaining the observed deviations from Hardy–Weinberg equilibrium. Consistently, inbreeding coefficients were positive at nearly every microsatellite locus ([Supplementary material Table S1, Table S3](#)). Among the individual sampling site × microsatellite –comparisons without deviations from Hardy–Weinberg allele proportions, the inbreeding coefficient estimates were negative (suggesting excess of heterozygotes) in 37 of the 109 estimates. In contrast, none of the 34 inbreeding coefficient estimates with deviations from Hardy–Weinberg detected had a positive inbreeding coefficient (suggesting deficiency of heterozygotes). This may suggest that deviations from Mendelian populations in some of the microsatellites were caused by null alleles. When we compared the fraction of outliers to all exact Hardy–Weinberg tests with sampling sites (24% of the 143 tests with adjusted $P < 0.05$) to the fraction of outlier tests using lakes as populations (33% of the 52 tests with adjusted $P < 0.05$), we found that pooling the sampling sites resulted in even higher frequency of deviations.

A principal component analysis of the allele presence data did not show distinct clusters between the lake basins. The first principal component (PC1) revealed no clear sample-based clustering (Fig. 2) and explained only 4.4% of the variation. However, the individuals from Kymijoki drainage system had consistently more positive eigenvalues along the first principal component than the individuals from the Vuoksi drainage system ($t_{530,52} = 11.914$, $P < 0.001$). Interestingly, PC1 values showed high between-year variation in the genetic structure in the vendace samples of S Konnevesi (9 K).

The pairwise F_{ST} -estimates indicated significant differences between several sampling sites (Table 4). Overall, the F_{ST} -values between the lake basins in the Vuoksi and Kymijoki drainage systems were generally higher than the F_{ST} -values within those systems, although the F_{ST} -values

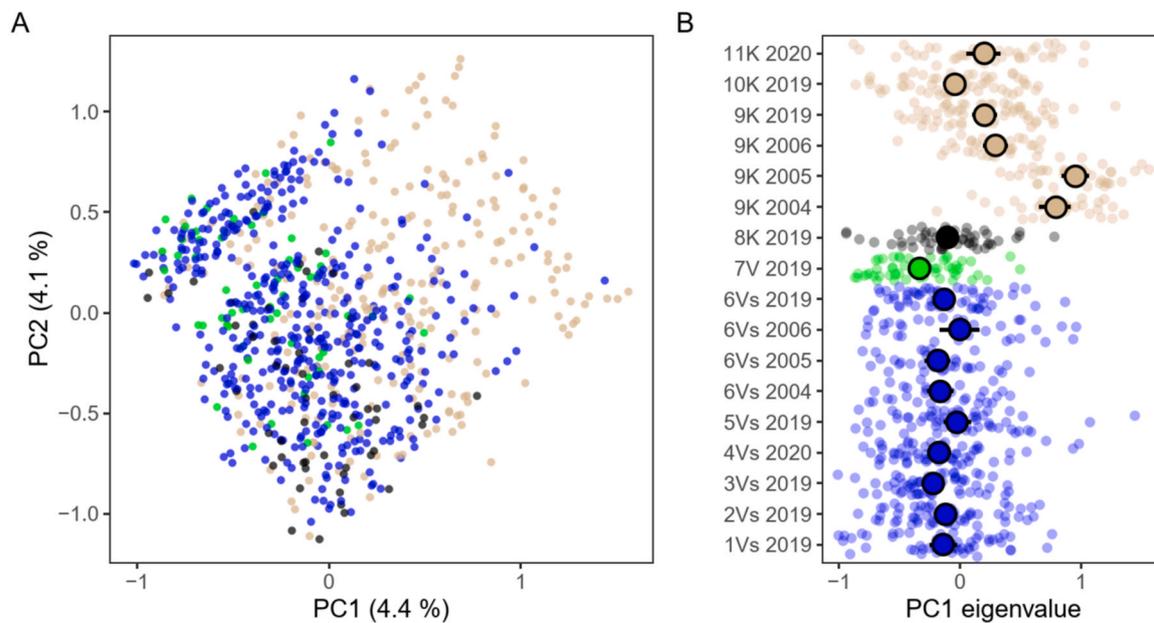


Fig. 2. Principal component analysis (PCA) plot of the genetic structure based on allelic data (allele presence/absence) among vendace individuals from the Vuoksi (V) and Kymijoki (K) drainage systems. Sampling sites with IDs are shown in Fig. 1. A) PC1 and PC2 explain 4.4% and 4.1% of the total variation, respectively. B) PC1 eigenvalues for each individual sample, grouped by sampling site and sampling year combinations and medians (large circles) and non-parametric 95% confidence intervals for each group mean indicated with bold horizontal lines. Blue = Saimaa (Vs), Green = Pielinen (V), Grey = Puula (K), Brown = Konnevesi (K).

Table 4

Genetic divergence between vendace samples among the sampling sites in 2019 and 2020. Pairwise Weir-Cockerham F_{ST} -estimates between the sites (different sampling years combined) over 13 microsatellite loci. F_{ST} -estimates are above diagonal and their lower 95% confidence intervals are below diagonal. Non-significant genetic distances (lower limit of confidence interval ≤ 0) are indicated in bold. IDs identify the Vuoksi (V) and Kymijoki (K) drainage systems and the Saimaa lake system (Vs): 1 Vs = Kaidonselkä, 2 Vs = Petraselkä, 3 Vs = Pihlajavesi, 4 Vs = Puruvesi, 5 Vs = Haukivesi, 6 Vs = Pyhäselkä, 7 V = Pielinen, 8 K = Puula, 9 K = Southern Konnevesi, Häntiäisselkä, 10 K = Southern Konnevesi, Kotilahti, 11 K = Northern Konnevesi.

Lake basin	1 Vs	2 Vs	3 Vs	4 Vs	5 Vs	6 Vs	7 V	8 K	9 K	10 K	11 K
1 Vs		0.002	0.004	0.010	0.004	0.001	0.024	0.015	0.029	0.009	0.025
2 Vs	-0.001		0.000	0.005	0.000	0.002	0.019	0.015	0.028	0.006	0.025
3 Vs	-0.001	-0.003		0.006	0.005	0.007	0.018	0.012	0.025	0.005	0.023
4 Vs	0.003	-0.001	-0.001		0.007	0.011	0.017	0.019	0.024	0.009	0.027
5 Vs	-0.001	-0.002	0.000	0.001		0.006	0.023	0.012	0.016	0.004	0.028
6 Vs	-0.001	0.000	0.000	0.001	-0.001		0.018	0.021	0.014	0.014	0.03
7 V	0.015	0.010	0.010	0.010	0.010	0.010		0.038	0.041	0.032	0.059
8 K	0.007	0.006	0.005	0.011	0.004	0.008	0.020		0.040	0.011	0.029
9 K	0.003	0.000	0.000	0.006	0.002	0.002	0.020	0.007		0.017	0.042
10 K	0.001	0.002	0.002	0.004	0.000	0.005	0.021	0.006	0.000		0.017
11 K	0.005	0.002	0.001	0.006	0.004	0.009	0.029	0.005	-0.002	-0.001	

between the sampling sites were low (Table 4, Fig. 3). The F_{ST} -estimates between sampling sites ranged from 0 to 0.059 and the highest F_{ST} was between two basins from the different drainage systems i.e. between N Konnevesi (11 K) and Pielinen (7 V). In the Vuoksi drainage system, the genetic distance between the lake basins within the Saimaa lake system (1Vs–6Vs) was low (median F_{ST} = 0.005) and only Puruvesi (4Vs) showed some divergence (median F_{ST} = 0.010) from three other basins (1Vs, 5Vs and 6Vs). The divergence between Pielinen (7 V) and the lake basins in the Saimaa lake system (1Vs–6Vs) was more pronounced (median F_{ST} = 0.019, Fig. 3). In Konnevesi, we did not find divergence between the sampling sites (9–11 K, Table 4). However, we found relatively high genetic differences between years particularly in S Konnevesi (median F_{ST} = 0.054), but also in Pyhäselkä (6Vs) (median F_{ST} = 0.014, Supplementary material Table S4). Mantel tests revealed no support for the hypothesis of positive association between genetic divergence and distance within the sampling sites in the Saimaa lake system (Mantel test, ρ = 0.257, P = 0.231, Fig. 4).

Although some null alleles were present (Supplementary material Table S5), correcting for null alleles had only a marginal effect on the

obtained F_{ST} values (null-corrected estimates differed from the raw values from -0.002 to 0.003). Thus, we concluded that the null-alleles were not biasing the estimates of sampling site divergence (Supplementary material Figure S1).

4. Discussion

In our genetic analysis based on 13 microsatellite loci, significant genetic divergence between the vendace populations of Kymijoki and Vuoksi drainage systems was observed. Within the Saimaa system, the genetic divergence among the sampling sites was weak and did not show any association with geographic distance among sites. The genetic divergence between the sampling sites in Saimaa was low: values of pairwise F_{ST} between sites were below 0.01 for all pairs. (Lowe and Allendorf, 2010) approximated that such drift connectivity that allows sufficient gene flow to maintain similar allele frequencies lead to F_{ST} < 0.02. In the microsatellite analysis of Delling et al. (2014), Swedish populations were grouped in two different assemblages and pairwise F_{ST} between lakes from the different assemblages were mostly over 0.15.

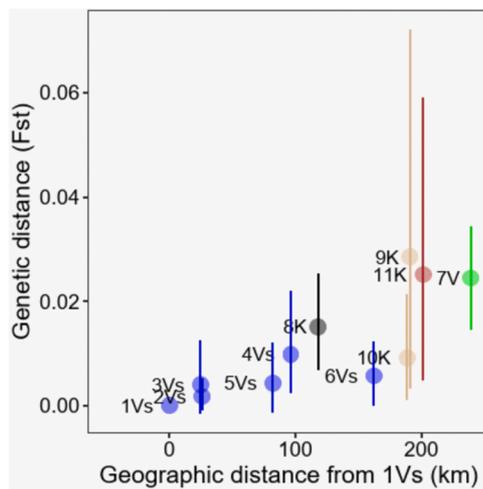


Fig. 3. Genetic divergence between Kaidonselkä (1 Vs) and other vendace sampling sites. The pairwise F_{ST} -values in 2019 and 2020 are represented as a function of geographic distance (km) from 1 Vs. Vertical lines represent 95% confidence limits of F_{ST} . IDs of sampling sites are given in the Fig. 1.

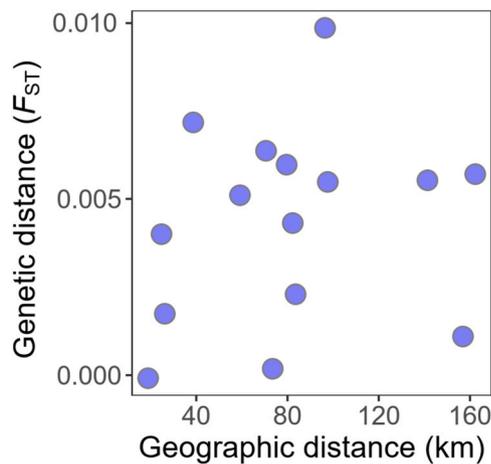


Fig. 4. Relationship between the pairwise genetic divergence (F_{ST}) and geographic distance within the Saimaa lake system (Vs).

These two assemblages had a different glacial history (Delling et al., 2014). In addition, Delling et al. (2014) did not find significant allele frequency differences between eastern and western sampling sites in large, fragmented Lake Mälaren ($F_{ST} = 0.002$) or twin lakes of Dellen ($F_{ST} = -0.001$) connected by a short channel. According to our genetic analysis, the local vendace populations of the Saimaa system could be considered one conservation unit, but the genetic analysis alone provides little information on demographic connectivity, which is of central importance to determine the harvest management units (Lowe and Allendorf, 2010).

Based on the literature review we evaluated the potential divergence of the local populations in Saimaa from a broader perspective. Regarding the Criterion 1 (reproductive isolation) by Mee et al. (2015) we must conclude that although the vendace populations within the whole Central Finland lake district have most likely a common phylogenetic origin and form a uniform species, the Kymijoki and Vuoksi drainage systems should be considered as separate conservation and management units, because of rather long-term geographical isolation of these two systems. In Finnish large lakes and lake systems, no morphologically distinct subspecies or documented observations of distinct morphological differences among vendace (Vuorinen and Laninen, 1978) or reproductive isolation are known, although the

fragmented nature of the Finnish lake systems have stirred speculations of genetic divergence between lakes and even lake basins. In these systems, vendace populations are autumn-spawning and we are not aware of any spring-spawning populations in the Saimaa system or the lakes in the Kymijoki system. It must be noted that all the lakes covered in this study are very young. By 9 500 yBP (year before present) they were all part of Ancylus Lake in the present Baltic Sea area (Saarnisto et al., 1999). As a result of the fall of the level of Ancylus Lake and Fennoscandia land uplift, the southernmost bays gradually began to shrink into separate basins, until about 8 500 yBP the entire area of present-day Saimaa and Kymijoki lakes (e.g. Päijänne, Puula, Konnevesi) separated from Ancylus Lake to form the Great Lake of Central Finland, whose waters flowed northwest (Saarnisto et al., 1999; Tikkanen, 2002). As the land uplifted rapidly in the northwestern part of Central Finland, the water rose rapidly and most of the basins of present-day Saimaa formed a large lake. Approximately 6 000 yBP most of the lakes in present-day Central and Eastern Finland were at the same water level. Gradually Lake Saimaa broke new outflows to the south. Approximately 5 400 yBP its water level began to decline and the connection to the north of Lake Konnevesi was cut off and the current Saimaa began to form.

Criterion 2 by Mee et al. (2015) recognizes the discreteness of phylogeographic lineages based on evidence for diagnostic alleles or haplotypes, the significance of these lineages depending on statistical support for their discreteness (e.g. in a phylogenetic analysis) and evidence that the origin of such lineages is associated with different refugia that were occupied during the Pleistocene glaciations. Delling et al. (2014) suggested that postglacial immigration of European vendace to Northern Europe occurred from at least two different glaciation refugia and the first immigration waves arrived along ice margin and reached German lakes ca. 12 000 yBP. Sendek (2021) proposed that already earlier, > 140 000 yBP, there have been separate freshwater refugia for Western European, Eastern European and Western Siberian cisco lineages and that European vendace are a result of introgressive hybridization of all these large lineages. In the mtDNA haplotype analysis of Delling et al. (2014), Finnish vendace populations grouped in clade II together with Siberian *C. sardinella*. During the Fennoscandian ice sheet about 60 000 yBP ago, the White Sea periglacial lake (location of present White Sea) was inhabited by the descendants of local European vendace and colonizers from the east (Sendek, 2021). These lineages could later spread to Europe (Sendek, 2021) and could form the genetic origin of Finnish and Russian vendace populations (i.e. clade II haplotypes in low-latitude lakes according to Delling et al., 2014). In all, the interaction of the various evolutionary lineages of cisco group upon the colonization of Europe is complex (Delling et al., 2014; Sendek, 2021) and the formation of modern cisco populations is based on the introgressive hybridization of several phylogenetic lineages and geographical isolations locally (Sendek, 2021).

Based on the literature review, no adaptive divergence and local adaptation in morphology or life cycle traits have been observed in Vuoksi and Kymijoki vendace (Mee's criterion 3, local adaptation and traits genetically controlled). We have no quantitative data to analyse this criterion. The only known differences in vendace between different Finnish lake basins are rather qualitative i.e. local people have stated that there are differences in their taste or tissue structure when cooked a meal. However, local populations of vendace in different neighbouring basins within the same drainage may have different growth rates and population densities (Järvi, 1919; Marjomäki and Huolila, 2001), which may indicate limited movement of older fish between the lake basins. The growth of vendace is strongly negatively dependent on population density (Helminen et al., 1993; Marjomäki and Kirjasniemi, 1995; Karjalainen et al., 2016) and for example, the wet mass of 0 + fish after the first growing season may have even a fourfold difference between successive years (Karjalainen et al., 2016). Thus, the growth of vendace will flexibly vary according to the basin-specific density and cannot be interpreted as a genetically controlled adaptive trait.

Mee's criterion 4 (significant biogeographic separation) is not exactly applicable to our rather small study area. We can inspect the river basin districts in the Finnish river basin management plans (EC, 2012) which determine the boundaries for the fisheries districts in the area of the Vuoksi and Kymijoki collaborative fisheries groups. The boundaries of the fishing districts are based on the river basin districts, the migration routes of migratory fish species and the management duties of the regional fisheries districts (Kalastuslaki, 2015). The boundaries of the river basin and fisheries districts in the Vuoksi and Kymijoki drainage systems, suggests separate management and conservation units for the Vuoksi and Kymijoki systems. This division is supported also by the indicative spatial genetic structure where Konnevesi and Puula populations had the highest genetic divergence from the populations of the Saimaa. Presence of genetic divergence between vendace from these neighbouring drainage systems recommend to conserve and protect their biodiversity and e.g. transfers of vendace between these drainages should be avoided.

Obviously, migration in the Saimaa lake system maintains low genetic divergence between local populations. Already low migration rate facilitates gene flow between adjacent populations and that can cause low F_{ST} values (Lowe and Allendorf, 2010). No quantitative estimates of migration rate between local populations in Saimaa are available. Higher rates of regular movement of individuals between adjacent populations are needed to cause demographic dependence between them. Waples and Gaggiotti (2006) have suggested that transition from demographic dependence to independence generally occurs when the fraction of immigrants in local populations falls below 10%, but this threshold is highly dependent on several other demographic parameters and must be interpreted cautiously in the context of all population parameters such as intrinsic population growth rates (Lowe and Allendorf, 2010). In the lake systems, migration rates of fish populations are very difficult to quantify and movement of individuals between local populations may vary temporally and be affected by population density and developmental stage of fish.

Within a lake basin, vendace disperse their reproductive output widely. Karjalainen and Marjomäki (2018) discovered that autumn-spawning vendace is a batch spawner which seems to have the bet-hedging reproductive strategy in space and time, where eggs and larvae are allocated widely to different habitats around the lake (Karjalainen et al., 2019, 2021). Valkeajärvi (1983) marked one-year-old vendace in N Konnevesi by adipose fin clipping and monitored recaptures of fish during a year after marking. One-year-old immature fish dispersed from two different marking places widely around the N Konnevesi basin but none of the fish were observed in the S Konnevesi (Valkeajärvi, 1983). However, in that study, the proportion of the population that was marked was low and the marking mortality high (30–35%) and expectedly, the proportion of recaptured fish of the total catch was low (0.2%, Valkeajärvi, 1983). Several observations by local fishers based on the changes in the size differences of fish between adjacent basins support the readiness to migration of young vendace. Based on distinctive differences in size-at-age, fish from S Konnevesi are thought to migrate to N Konnevesi in the years when the population density of vendace has been high in S Konnevesi (Marjomäki and Valkeajärvi, 2016). Similarly, in Saimaa, vendace have been observed to move from a lake basin to another via narrow straits (Airaksinen, 1967). Some direct observations of migration of young of the year (YOY) vendace are available. YOY vendace have moved in dense schools downstream from the Paasvesi basin to the Pyyvesi basin (both in Saimaa) via narrow straits in the end of June (Antti Pesonen, personal communication). Further, in the years of high YOY abundance in Southern Saimaa, dense schools of YOY vendace have been observed to end up in the River Vuoksi, which drains into Lake Ladoga (Aarno Karels, personal communication). In those years, fishing of YOY vendace in the River Vuoksi is popular. YOY fish have higher temperature tolerance (lethal temperature up to 27 °C and final temperature preferendum ca. 17 °C) than older fish (Tapaninen et al., 1996) and they move in their own YOY

schools separately from adults (Järvi, 1919; Airaksinen, 1967). YOY fish can then stay continually in the epilimnion until the middle of July, when they start to settle on the deep basins, mix partly with the adult population, stay under thermocline in low illumination in hypolimnion during daytime and in the evening, begin their daily vertical migration to epilimnion and back in the crepuscular light in the morning. Before the "settlement" to the deep areas of the basin, they seem to move widely and disperse. The movement is likely periodic and occurs most prominently in the years when in some basins the reproduction is very successful, YOY fish are starving and start to search for better feeding conditions.

In subarctic Pasvik system, invasive vendace population colonized the 120 km long water system during 6 years from 1989 to 1995 (Amundsen et al., 1999). The original introduction of vendace to Pasvik river system occurred already in the 1950's and 1960's in the tributaries of Lake Inari (Mutenia and Salonen, 1992) and fish colonised gradually the large Lake Inari and migrated finally to the outlet Pasvik river system of Lake Inari (Præbel et al. (2013a), (2013b)). Hence, the dispersion potential of vendace seem to be high, and the headwater populations of the central lakes such as Pielinen (V) and Puula (K) likely act as a source rather than a sink. However, we do not have data available for a rigorous analysis of possible demographic connectivity between the basins. Further combined genetic data, capture-mark-recapture studies, age distribution and growth analyses of resident and immigrants are needed (Kritzer and Sale, 2004; Lowe and Allendorf, 2010). The fluctuations in abundance of Finnish vendace populations have been observed to be spatially synchronized (Marjomäki et al., 2004). The scale of the anisotropic synchrony was typically 100–300 km and seemed to be induced by environmental factors (Marjomäki et al., 2004) but in the adjacent basins it can be strengthened by dispersion.

In our microsatellite analysis, the temporal variation in the genetic structure in S Konnevesi (9 K) was surprisingly high (Fig. 2, Supplementary material Table S4). Also in the 3-year data from Pyhäselkä (6Vs), the genetic difference between different years was relatively high (Supplementary material Table S4). The estimate of genetic distance is affected by the effective population size because the population size determines how much genetic variation can be maintained in populations and how quickly allele frequencies change with genetic drift (Kalinowski, 2002). The Weir–Cockerham F_{ST} when calculated between temporal samples from the same population tend to be small if the population size is high and high when the population size is low and thus, a change in the population size influences the estimation of the genetic distance (Kalinowski, 2002). In S Konnevesi from 1996 to 2011, the vendace population went through remarkable changes in the population density (Marjomäki et al., 2021). In late 1980's and 1990's the abundance of spawning population was very low but after the 13-year low-abundance period, spawning population increased multifold (ca. 60-fold) from 1996 to 2003. In 2000 and 2004, very abundant cohorts (over 750 million larvae) hatched to the lake. The spawning population in the Konnevesi and likely in most of the other lake basins in our study includes several million individuals. Interesting future research question is how these kind of extreme changes in population abundance shape the genetic population structure of vendace with short life cycle, early maturation and dominance of 1 + -2 + age groups in the spawning population. Our inter-annual comparisons are weakened by the fact that the number of fish in the samples in 2004–2006 from S Konnevesi and Pyhäselkä was lower ($N \leq 33$) than the number of fish sampled recently in 2019. Thus, those small sample sizes may have caused upwards ascertainment bias in the F_{ST} estimates involving S Konnevesi 2004–2006. Furthermore, annual sample size was lower than recommended sample size (50–100 individuals) for the studies of genetic structure by Ruzzante (1998). Low sample sizes can invalidate parameter estimates such as F_{ST} due to increased sampling variance (Ruzzante, 1998) and this is especially true during the years when the population size is high (Kalinowski, 2002). Although the samples from Konnevesi were taken in the same area every year it is also possible that rather

small sample size may have caused unidentified bias and considerable random variation in the F_{ST} estimates.

Null alleles and Wahlund effects have been commonly stated as the underlying reasons for observed heterozygote deficiency and, subsequently, deviations in Hardy–Weinberg equilibrium and in Wright's F_{IS} in microsatellite datasets (Waples, 2015). Null alleles are caused by non-amplified microsatellite alleles, whereas Wahlund effect is caused by sampling a mixture of true populations as a single unit. Indeed, we reported positive F_{IS} in all of the loci deviating from Hardy–Weinberg equilibrium. We also reported the presence of null alleles among most of the 13 microsatellite loci, suggesting that they are a potential cause for the observed allele frequency bias (Supplementary material Table S4). Wahlund effect seemed like a less probable source for bias, as the fraction of Hardy–Weinberg outlier tests increased when pooling sampling sites within lakes, potentially presenting populations. While we acknowledge the limitations of the current microsatellite data set, we anticipate that future research with next-generation sequencing methodologies, such as RAD sequencing, will provide more high-confidence data to explore the genetic makeup of the vendace populations in more detail.

In anadromous fishes, the genetic-based management units have been identified for river basins (Laikre et al., 2005; Wiens et al., 2021). In coastal fisheries management of Baltic Sea, Laikre et al. (2005) suggested the classification of genetic population structure of Baltic fish species into three types: distinct populations (anadromous salmon *Salmo salar* and brown trout *Salmo trutta*), continuous change (pike *Esox lucius*) and no differentiation in more or less panmictic populations (cod *Gadus morhua* and herring *Clupea harengus*). In freshwaters, (Taylor et al., 2013) determined 12 major conservation units for lake chub (*Couesius plumbeus*) and Mee et al. (2015) 36 designatable units (DU) for the management of the whitefish species complex (*Coregonus* spp.) in Canada. Some authors have requested to refine the management units among populations even within a large lake (Kocovsky et al., 2013) or marine areas (McKeown et al., 2020) based on their genetic analyses, but at the same time they highlighted the importance of using multidisciplinary approach for population identification purposes (McKeown et al., 2020). In all, it is worth to note the recommendation of Laikre et al. (2005): “In the context of genetic conservation it is typically harmless to “oversplit”, i.e. to manage a genetically homogeneous group of fish as if consisting of multiple divergent populations. In contrast, treating a series of genetically distinct populations as if constituting a single panmictic one may result in depletion of genetic variation. Thus, a manager should generally be more reluctant to adopt a suggestion for a model of no differentiation than one of distinct populations or continuous change.” However, in small-scale inland fisheries, it is not economically sustainable to use large number of small management units for certification and management purposes.

In all, the available information leaves open the question of what would be the ideal structure for the management units in the Saimaa lake system. The present administrative practice in Finland with fragmented units of fishing rights' ownership and management responsibilities based on the land ownership has resulted in hundreds of small units in Saimaa. Certification process documents (Marine Stewardship Council, 2020) suggest selection between minimal and moderate demographic connectivity in the case of fragmented local populations. Minimal connectivity (metapopulation type B, (Marine Stewardship Council, 2020)) leads to the separate local population units, which means tens of units for certification. Moderate connectivity (metapopulation type B, (Marine Stewardship Council, 2020) demands management of local units but their management reference points need to take into account also connections with adjacent local populations. Consequently, a large lake system such as Saimaa enables application of the interlocked management approach (Muje et al., 2004), which can be regarded as one form of portfolio management increasing both ecological and economic sustainability of fishing. In Saimaa, this would mean the integrated use and management of all local populations in different

basins and allocation of interlocked resource and effort of several fishers. The management of fisheries based on interlocked populations (i.e. basin-specific local populations) has potential to increase the minimum population abundance, reduce the inter-annual variation in yield and ensure fishers more stable income and more stable material flow to the market. The strategy requires population monitoring -based coordinated co-operation between fishers who may need to increase their mobility to achieve annually the desired allocation of fishing effort. The main objective is to allocate the total interlocked effort around the interlocked fishing district to the most abundant local populations to benefit from asynchronous fluctuations in abundance of vendace local populations between exploitable basins (Sipponen et al., 2006) and, importantly, leave the sparse local populations in peace to recover. Especially, the interlocked use of vendace populations requires collaborative research and fisheries management to co-create common knowledge bases for management (Davis, 2008; Holm et al., 2020). This means a new kind of shared information base of the basin-specific local populations, wider areas for fishing licenses for commercial fishers, regional management groups and institutions empowered to allocate fishing effort rapidly and flexibly according to the basin-specific information.

5. Conclusions

We observed slight genetic divergence within our study systems, but no available data show evidence of the populations having unique evolutionarily significant traits. Rather, the present knowledge supports the conclusion that local populations in the Saimaa system have similar life history and morphological traits. Such genetic diversity seemed not to demand basin-specific conservation actions. Contrary, we conclude that interlocked management of local vendace populations in the Saimaa lake system is advisable if the fishing effort can be annually flexibly allocated to the basins harbouring the strongest local populations for exploitation. The interlocked management of vendace in Saimaa demands institutionalised interlocked collaboration between commercial fishers, recreational fishers and fishing rights owners in the area and of course, regular and systematic basin-specific population assessment.

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CRediT authorship contribution statement

JK: Planning, supervision, data analysis, literature review, writing, editing; RS: sampling, laboratory work, genetic analysis, writing, reviewing; TV: genetic analysis, map constructions, writing, reviewing; TS: data analysis and statistics, writing, editing; LRS: Planning, supervision, genetic analysis, writing, reviewing; SUH: Planning, supervision, data analysis and statistics, writing, reviewing, editing; TJM: Planning, supervision, data analysis, writing, editing, reviewing.

Code availability

Not applicable.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Declaration of Competing Interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Data availability

Data available from the authors by inquiry.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2021.106173.

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