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Status Assessments for Two Endangered Populations of Vendace (*Coregonus albula*) and Evidence That Their Abundance Is Modulated by Percid Fishes

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ABSTRACT

The study of low-latitude populations can inform our understanding of how cold-adapted species might respond to environmental change. The vendace (*Coregonus albula*) is a lacustrine fish that is distributed across northern Europe. In the UK, there are two extant native vendace populations. These populations are at the south-western edge of the species' global distribution and both are exposed to a range of pressures including eutrophication, rising water temperatures and introduced fishes. These populations were assessed in 2024 using a combination of quantitative hydroacoustics and targeted gill netting. These data were then placed in the context of population assessments spanning the preceding three decades. Finally, the time series of population assessments was analysed to identify factors that were associated with low abundances of vendace. In both lakes, the abundance of post-juvenile vendace was higher in 2024 than expectations derived from a reference baseline. The balanced age structure of the vendace captured by gill net indicated regular recruitment to the post-juvenile age groups and there was no evidence that the lakes lacked the deep water refugia that vendace require to avoid thermal stress. High abundances of native perch (*Perca fluviatilis*) and introduced ruffe (*Gymnocephalus cernua*) in the natal years of the dominant post-juvenile vendace age groups were associated with markedly low vendace population sizes. As ruffe are not native to the studied lakes, this demonstrates one of the risks associated with the translocation of fish. However, despite the threats they face, the UK's two endangered populations of vendace appear to be persisting.

1 | Introduction

Peripheral populations, which are those located near the edge of the range of a species, are commonly of high conservation value (Lesica and Allendorf 1995). Peripheral populations can often be considered ecologically marginal in that the environmental conditions to which they are exposed are frequently towards the tolerance limits of the species (Scudder 1989). Such populations are often of conservation concern, and there are strong arguments for their conservation and monitoring (Nielsen et al. 2001). One of these arguments is that the study of peripheral populations can help predict how species might respond to environmental change (Abeli et al. 2018).

The vendace (*Coregonus albula*) is a small, planktivorous, salmonid fish that requires cold, well-oxygenated water (Winfield et al. 1994; Elliott and Bell 2011; Crête-Lafrenière et al. 2012). The overwhelming majority of vendace populations are found at high latitudes in lakes that drain to the Baltic Sea (Gjelland 2012). Vendace are common within this core native range, and lacustrine populations support recreational fisheries and long-standing, economically important commercial fisheries (Turunen et al. 1998; Marjomäki et al. 2014; Mustonen et al. 2023).

There are two remaining extant peripheral populations of vendace at the south-western fringe of the global distribution of the species (Gjelland 2012). These populations are found in the neighbouring UK lakes of Bassenthwaite Lake and Derwent Water. Both populations face a range of threats including eutrophication (Winfield et al. 2012), climate change–mediated compression of suitable oxy-thermal habitat (Elliott and Bell 2011), decreased rates of recruitment to the post-juvenile age groups due to the accumulation of silt on spawning grounds (Winfield et al. 2017), and competition and predation from introduced fishes (Winfield et al. 2004; Winfield et al. 2010). The only other two native vendace populations ever to have been recorded in the UK (Castle Loch and Mill Loch, both in south-west Scotland) were extirpated in the 20th century as a result of a similar range of stressors (Maitland and Lyle 2013). In Britain, because of the range of threats it faces and its geographically restricted distribution, the vendace is categorised as endangered (Nunn et al. 2023). Thus, there is a credible risk that the species, which is Britain's rarest freshwater fish (Winfield et al. 2012), could become extinct in the UK.

Assessments of the vendace populations of Bassenthwaite Lake and Derwent Water were conducted annually from the 1990s until 2018. Between 2001 and 2012, these assessments found no vendace in Bassenthwaite Lake, and at the time, the population was declared to have been extirpated (Winfield et al. 2012). However, in a possible sign of population recovery, a single juvenile vendace was captured in Bassenthwaite Lake in 2013 and following that a post-juvenile population was found in four of the five subsequent years of monitoring (Winfield and Gowans 2014; Winfield and James 2018). In contrast, the species was recorded consistently in Derwent Water between 1998 and 2018 (Winfield and James 2018).

Since the last vendace population assessment in 2018 there has been only one subsequent survey of the fish communities of these lakes. This was conducted using eDNA in the winter of 2018/2019 and indicated that vendace were present in both lakes (Di Muri 2020; Sellers et al. 2024). There have been no further records of native UK vendace since 2019. Therefore, the current status of the Derwent Water population is not known and it is unclear whether the Bassenthwaite Lake population has continued to recover.

The present study aims to (1) assess the current status of the UK's two peripheral, high conservation value vendace populations and (2) investigate what factors might be correlated with variation in the size of these populations. The first aim was addressed by placing contemporary population size estimates in the context of historical trends and by examining the age structure and spatial distribution of the populations. For the second aim, generalised linear modelling was used to determine which of a set of candidate explanatory variables were significantly associated with markedly low abundances of vendace.

2 | Methods

2.1 | Study Sites

Both Bassenthwaite Lake (54.65° N, 3.22° W) and Derwent Water (54.58° N, 3.15° W) are relatively small, adjacent lakes in north-west England. The two lakes are connected by 5.7 km of the River Derwent with Bassenthwaite Lake located downstream of Derwent Water (Figure 1a). Bassenthwaite Lake has a surface area of 5.2 km^2, a mean depth of 5.3 m, a maximum depth of 19.0 m and an elevation of 68 m (UK Centre for Ecology and Hydrology 2024a). The lake is largely mesotrophic in character and has a simple bathymetry with a deeper central basin flanked by shallower water to the north and south (Figure 1b; Mackay et al. 2023). Derwent Water has a surface area of 5.29 km^2, a mean depth of 5.5 m, a maximum depth of 22.0 m and an elevation of 76 m (UK Centre for Ecology and Hydrology 2024b). It is classed as oligotrophic on most characteristics and it has a more complex bathymetry than Bassenthwaite Lake including two deeper basins and a number of islands (Figure 1c; Mackay et al. 2023). Both Derwent Water and Bassenthwaite Lake are designated for conservation protection as sites of special scientific interest (SSSIs) with their vendace populations being conservation features of that designation. Both lakes are also protected as features of the River Derwent and Bassenthwaite Lake Special Area of Conservation under the EU Habitats Directive (Wood et al. 2024).

2.2 | Field Methods

Bassenthwaite Lake was surveyed from 24 to 25 September 2024 and Derwent Water between 25 and 26 September 2024. The field protocol and the order in which the fieldwork was executed were the same at both study sites. All fieldwork was conducted from a 5.95-m Orkney Pilothouse boat. To allow comparison with historical data, the overall study design followed that of Winfield and James (2018).

Gill nets were deployed in each lake at six predetermined, depth-stratified locations (Figure 1b, c; Supplementary Material A Table S1). Two types of multimesh Nordic pattern survey gill net (Appelberg et al. 1995; Appelberg 2000) were used; benthic nets were set on the lake bottom while pelagic nets were suspended in the water column approximately 5 m below the water surface. The benthic nets were 1.5 m deep and 30 m long, and they consisted of 12 panels with bar mesh sizes of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm arranged in a geometric series. The pelagic nets were 6 m deep, 27.5 m long and had 11 panels with bar mesh sizes of 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm. The gill nets were set overnight and then removed from the water the following morning (Supplementary Material A Table S1). The species and fork lengths of all captured fish were recorded. The sex of each vendace was identified by dissection and their ages were determined from the left opercular bone following the method of Mubamba (1989).

In each lake, a series of transects was surveyed by hydroacoustics at least 1.5 h after sunset. The transects formed a zig-zag pattern across areas where the water depth was at least 10 m (Figure 1b; Figure 1c). This deep water area was expected to be the primary

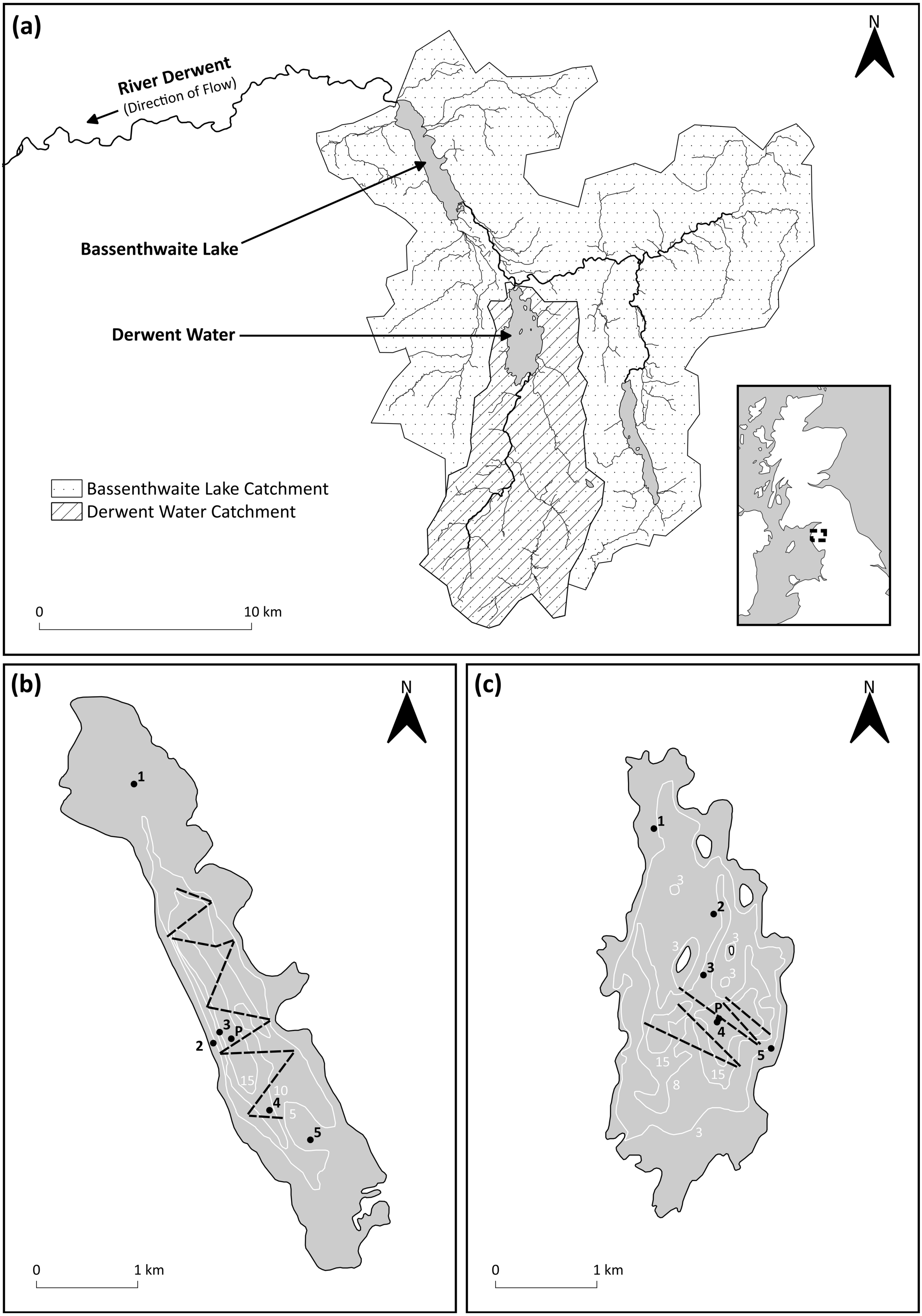

FIGURE 1 | Legend on next page.

FIGURE 1 | The location of the study area (a) and maps of the hydroacoustic transects (dashed lines) and gill net deployments (dots) for Bassenthwaite Lake (b) and Derwent Water (c). Benthic nets are numbered while pelagic nets are labelled 'P.' White lines and text represent depth contours in metres (bathymetry reproduced from Winfield and James 2018). Contains public sector information licensed under the Open Government Licence v3.0.

habitat of post-juvenile vendace (Winfield and James 2018). Nine hydroacoustic transects were surveyed in Bassenthwaite Lake and five transects were surveyed in Derwent Water. The number of transects and their locations broadly followed that of previous hydroacoustic surveys (Winfield and James 2018). The echosounder used was a Simrad WBT Mini with Simrad EK80 controlling software. The transducer was an ES120-7C 120 kHz split beam unit with a circular 3 dB beam angle of 7°. The pulse rate was set to 5 pings.s^{-1}, the pulse width was 0.256 ms and the transmit power was 250 W. Spatial data were recorded and transferred to the echosounder system by a Garmin GPSMAP 79s handheld GPS. A bracket was used to attach the transducer to the port side of the survey boat at a depth of 1.2 m below the water surface. The boat was driven at approximately 1.5 m.s^{-1} during the surveys. The echosounder was calibrated in the afternoon before each survey using a tungsten carbide sphere with a target strength of −39.5 dB. During the surveys, the surface water temperature was approximately 14°C, and the speed of sound in fresh water was assumed to be 1462 m.s^{-1}.

2.3 | Hydroacoustic Data Analysis

In order to accurately estimate fish density in vendace-suitable habitat, only the sections of the hydroacoustic transects where the water column depth was at least 10 m were analysed. In Bassenthwaite Lake the total length of the analysed portions of the hydroacoustic transects was 3.63 km, while in Derwent Water, the total analysed transect length was 2.63 km. The surface areas of Bassenthwaite Lake and Derwent Water where the depth was at least 10 m were 85.2 and 65 ha respectively (Winfield and James 2018). The coverage ratios (hydroacoustic transect length: square root of the research area) were 3.93 in Bassenthwaite Lake and 3.27 in Derwent Water. This exceeded the minimum recommended target for hydroacoustic monitoring of fish populations of 3:1 (Bean et al. 2015).

A fish track counting approach was used to estimate fish density per hectare of lake surface area. This is an identical approach to that used in previous surveys of vendace in these lakes (Winfield and James 2018). Single targets were extracted from the target strength echograms using the Echoview 'single target detection (split beam method 2)' algorithm with the parameters specified in Table S2 of Supplementary Material A. Fish tracks were then delineated using the Echoview fish track detection algorithm (Table S2) followed by manual editing to validate all identified tracks. Mean fish track target strengths were converted to estimated total fish lengths (TL) in centimetres using the equation of Love (1971):

$$\mathrm{TL} = 10^{\left(\frac{(\mathrm{TSM}+0.9\log(f)+62)}{19.1}\right)}$$

where TSM is the mean fish track target strength and f is the operating frequency of the echosounder in kilohertz. Each detected fish track was assigned to a size category. Fish from 40 to 100 mm were assigned to the small size category, fish from 100 to 250 mm to the medium category and fish from 250 mm upwards to the large category. The surface area of sampled water for each transect was calculated for each 1-m depth layer from 2 m below the transducer to the lake bottom using the wedge method in Sonar5-Pro. The first 2 m of water was not included in the analysis to avoid the near field (Simmonds and MacLennan 2005). Fish density was estimated for each depth layer by dividing the number of detected fish tracks by the area of sampled water. Then, density estimates were calculated for each transect as the sum of the fish densities across all of the depth layers. The overall fish density (all three size classes combined), and fish density per size class, was determined as the geometric mean of the transect-specific density estimates. The precision of the geometric mean density estimates may have been influenced by the varied lengths and zig-zag patterns of the transects, but the use of this estimator ensured that the resulting data were comparable with previous years of monitoring.

2.4 | Vendace Status Assessment

The density of post-juvenile vendace on each hydroacoustic transect was determined as the density of fish of 100–250 mm in length, which is the typical size range of age 1+ or older vendace in these lakes as defined by Winfield and James (2018), multiplied by the proportion of 100- to 250-mm long fish captured at deep water sites during gill netting that were vendace. In Bassenthwaite Lake, the deep water nets comprised benthic net number three and the single pelagic net, while in Derwent Water they were benthic net number four and the single pelagic net (Supplementary Material A Table S1). Estimated post-juvenile vendace densities were converted to whole lake post-juvenile vendace abundances according to the surface area of each lake where the depth of the water column was at least 10 m (see Section 2.3). The density and abundance of post-juvenile vendace in each lake were calculated as the geometric means of the sets of estimates from the hydroacoustic transects. One-sample t tests of natural logarithm transformed data were used to compare the estimated 2024 abundances with reference baselines for abundance determined from previous monitoring (Winfield and James 2018). In Bassenthwaite Lake, the baseline was calculated as the geometric mean of the annual post-juvenile vendace abundance estimates recorded between 1995 and 2000 prior to the population collapse of 2001 (Winfield et al. 2017). In Derwent Water, the baseline was the geometric mean of the whole time series (1998–2018).

To establish if vendace were found throughout their expected preferred habitat, the locations where the species was captured were recorded. Given that the surveys were conducted overnight, vendace were expected to occupy the whole water column, above and below any thermocline present, in the deeper basins of each lake

(Winfield and James 2018). Therefore, vendace were expected to be caught by both the pelagic nets and the deepest benthic nets (Supplementary Material A Table S1). Finally, to investigate evidence of a failure to recruit to the post-juvenile age groups, the age structure of the vendace captured by gill net was examined to determine if there were missing age groups.

2.5 | Correlates of Variation in Post-Juvenile Vendace Abundance

Two generalised linear models were used to explore factors that may explain variation in post-juvenile vendace abundance. The aim of the first model was to identify which of a set of plausible candidates were the best predictors of vendace abundance while the second model was used to examine any significant effects identified in the first model in more detail. This two-stage modelling process was used because the sample size limited the number of explanatory terms that could be included in each model. The response variable of both models was binary and represented whether or not post-juvenile vendace abundance was markedly low in a particular year (0 = not low, 1 = low). Years with markedly low abundance were defined as those in which the upper limit of the 95% confidence interval of the post-juvenile vendace population size estimate for that year was lower than the lake-specific baseline abundance. This simplification was motivated by the broad confidence intervals around some of the abundance estimates.

For the first of the two models, the literature was consulted to assemble a set of candidate explanatory variables that were expected to affect the abundance of vendace in Bassenthwaite Lake and Derwent Water. Each explanatory variable was categorised according to whether it was expected to affect post-juvenile vendace abundance directly via impacts on post-juvenile mortality or indirectly via impacts on recruitment to the post-juvenile age groups. The direct effects were time matched while the values of the indirect effects were taken from the third and fourth lagged years. This choice of lag was in accordance with the expected dominance of the 2+ and 3+ age groups (Winfield and James 2018). The structure of the initial complex model was as follows:

$$\ln\left(\frac{p_i}{1-p_i}\right) = c + \alpha_l + \beta_v + m_F x_{F,i} + m_T x_{T,i} + m_C x_{C,i} + m_E x_{E,i} + m_H x_{H,i} + m_{T:C} x_{T,i} x_{C,i} + m_{E:H} x_{E,i} x_{H,i}$$

Where p_i ($i = 1 \ldots 36$) is the estimated probability of a low vendace abundance year, c is the intercept and α_l is the coefficient for lake (l = Bassenthwaite Lake, Derwent Water). β_v is the coefficient for the occurrence of low vendace abundance in both the 3rd and 4th lagged years (v = not low or low). This was included as a proxy for the size of the parental cohort. m_F is the slope coefficient for the mean combined gill net catch per unit effort (CPUE) of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and ruffe (*Gymnocephalus cernua*) across the 3rd and 4th lagged years. These were the three species that were most frequently captured by gill net in both of the study lakes, and they were expected to potentially compromise the recruitment of vendace to the post-juvenile age groups via competitive and predatory interactions (Valkeajärvi and Marjomäki 2004; Winfield and Durie 2004; Winfield et al. 2010). CPUE was expressed as the number of individuals captured per 100 m^2 of gill net mesh per hour of gill net deployment. Catch data were pooled across all deployed gill nets to provide one whole-lake CPUE estimate per year. Details of the 2024 gill net deployments are given in Section 2.2 while the historical sampling methodologies are available in Winfield and James (2018) and references therein. The annual maximum surface water temperature and annual mean chlorophyll-*a* concentration were also included as explanatory variables to represent the availability of oxythermal habitat that is suitable for vendace (Elliott and Bell 2011). These continuous variables, and their interactions, were included in time matched (m_T = temperature, m_C = chlorophyll-*a*) and time lagged (m_E = temperature, m_H = chlorophyll-*a*) formats. Each annual maximum surface water temperature was calculated from 20 to 27 samples collected each year at roughly biweekly intervals. Annual mean chlorophyll-*a* concentrations were calculated from between 21 and 29 samples also collected at roughly biweekly intervals in each year. All samples were collected from the surface of the lakes and the data were supplied by UK Centre for Ecology & Hydrology (Maberly et al. 2017a; Maberly et al. 2017b; Feuchtmayr, Beith, et al. 2021; Feuchtmayr, Clarke, et al. 2021). The data from 2001 were excluded from the model because they were incomplete. The lagged CPUE variables could not be calculated for 2024 nor the first 4 years of monitoring in each lake. Hence, these years were also not included in the models.

The structure of the second initial complex model, which was designed to explore the effects of individual fish species on vendace abundance, was as follows:

$$\ln\left(\frac{p_i}{1-p_i}\right) = c + \alpha_l + m_P x_{P,i} + m_R x_{R,i} + m_U x_{U,i} + (m_R + \gamma_l) x_{R,i} + (m_U + \delta_l) x_{U,i}$$

Where m_P, m_R and m_U are the respective slope coefficients for the mean whole lake CPUE values across the third and fourth lagged years for perch, roach and ruffe. γ_l is the interaction between lake and lagged roach CPUE and δ_l is the interaction between lake and lagged ruffe CPUE. Lake interactions were included for roach and ruffe because an initial inspection of the raw data suggested that the effects of these variables may have differed between the two studied lakes.

The most parsimonious models were determined by stepwise backwards model selection. All explanatory terms included in the initial complex model were tested with likelihood ratio tests in increasing order of their effect on residual deviance. Interactions were tested before main effects that were not involved in significant interactions. The significance of the terms included in the final model was assessed with further likelihood ratio tests. Plots of the candidate explanatory variables are presented in Figure 2.

2.6 | Software

Echoview Version 15.0.246 (Echoview Software Pty Ltd. 2024) was used for the initial post processing of the hydroacoustic data. The area of water that was sampled on each hydroacoustic

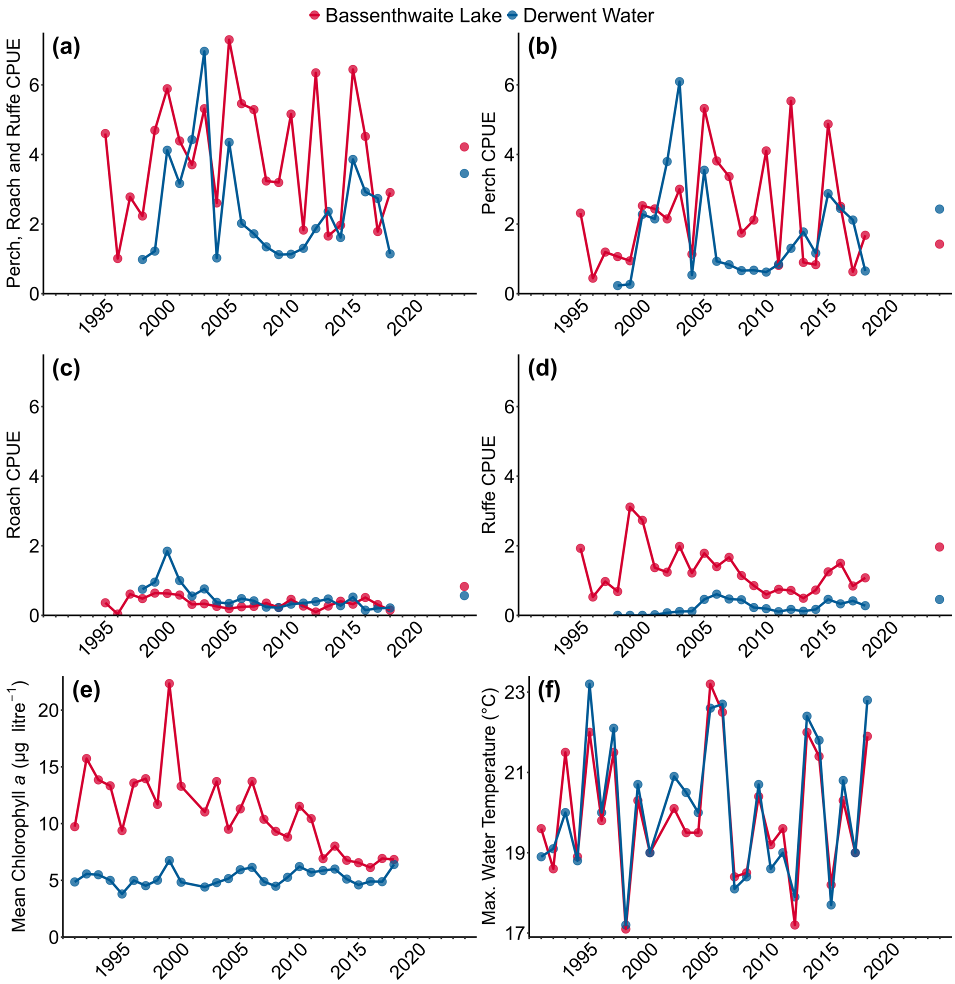

FIGURE 2 | Temporal variation in selected biological and physical characteristics of Bassenthwaite Lake and Derwent Water. Catch per unit wffort (CPUE) of (a) perch, roach and ruffe combined, (b) perch, (c) roach and (d) ruffe is expressed as the number of individuals captured per 100 m^2 of gill net mesh per hour of gill net deployment. (e) Annual mean chlorophyll-*a* concentrations were calculated from between 21 and 29 samples. (f) Annual maximum surface water temperatures were calculated from between 20 and 27 samples. All chlorophyll-*a* and temperature samples were collected from the lake surface at roughly biweekly intervals. Contains data supplied by UK Centre for Ecology & Hydrology (Maberly et al. 2017a; Maberly et al. 2017b; Feuchtmayr, Beith, et al. 2021; Feuchtmayr, Clarke, et al. 2021).

transect was estimated with Sonar5-Pro Version 608.53 (Balk and Lindem 2024). All subsequent data analysis was completed in R Version 4.4.2 (R Core Team 2024). Graphs were made with the package 'ggplot2' (Wickham 2016). Model assumptions were checked using the DHARMa package (Hartig 2024). Odds ratios were calculated for 0.1 unit increments using the or_glm function of the oddsratio R package (Schratz 2017). Maps were produced with QGIS Version 3.34.12 (QGIS Development Team 2024).

3 | Results

3.1 | The Status of Vendace in Bassenthwaite Lake

The estimated density of post-juvenile vendace (fish of 100- to 250-mm fork length) in Bassenthwaite Lake in 2024 was 91.2 individuals.ha^{-1} (95% CI: 55.5, 149.9). This translated to a total post-juvenile vendace population size of 7771 individuals (95% CI: 4729, 12,769) in Bassenthwaite Lake; an estimate higher than in all but one of the previous 24 years of population assessment (Figure 3a; Supplementary Material A). However, the 95% confidence interval overlapped with those from the years of 1995, 1997, 1998, 1999, 2000, 2014 and 2017. The 2024 abundance estimate was significantly higher than the reference population baseline of 4406 individuals ($t = 2.64$, $df = 8$, $p = 0.030$).

The gill net survey of Bassenthwaite Lake in 2024 captured four species of fish (Table S3). No vendace were caught in benthic nets set in deeper water (≥ 10 m); four were caught by the pelagic net at a depth of ca. 5 m and one was caught by the nearby benthic net two, at a depth of approximately 4.5 m. Given that only five vendace were captured in total in 2024, their absence in the deeper benthic nets may not be evidence of a restricted spatial distribution. The deepest benthic net (benthic net three), which was set at a depth of 17.9 m, yielded five perch and four ruffe, which indicates that the deepest part of the lake was habitable by these fish species. Roach, the fourth species of fish that was captured, were found in all gill nets apart from the pelagic net and benthic net three. The captured vendace ranged in age from 2+ to 5+ years (Figure 4a). The age

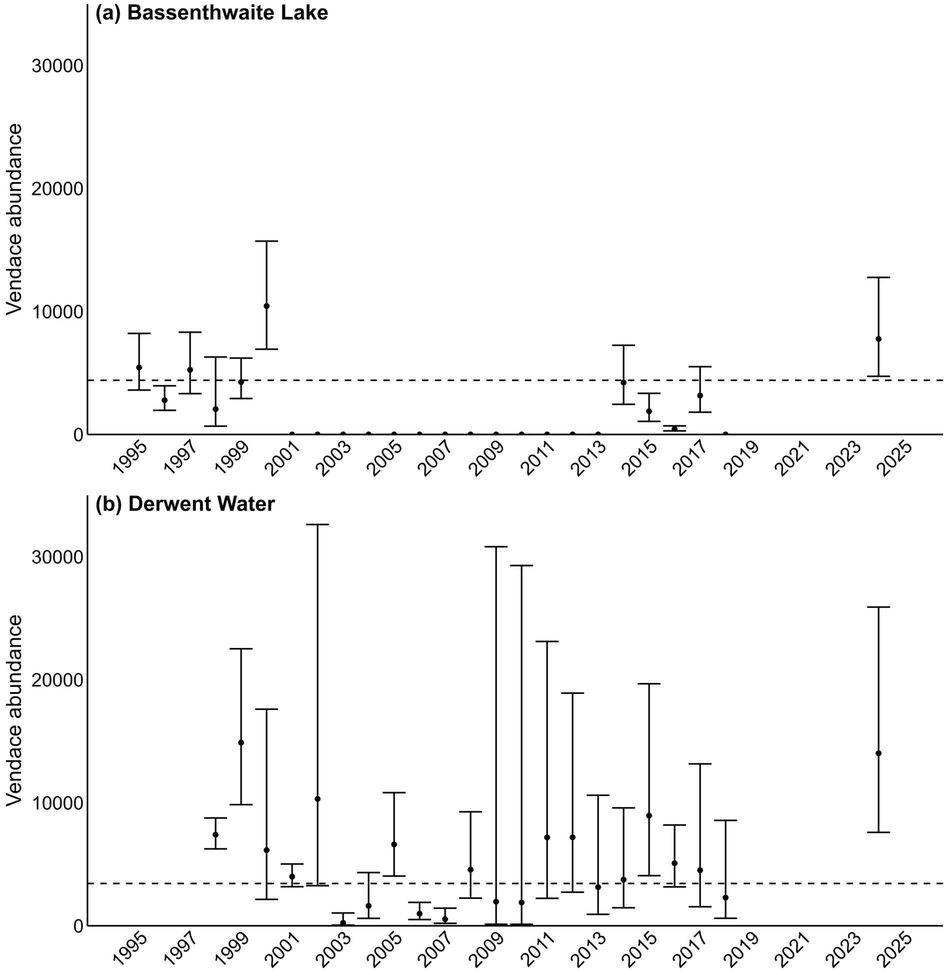

FIGURE 3 | Temporal variation in the estimated population size of post-juvenile vendace in (a) Bassenthwaite Lake and (b) Derwent Water. Abundance is expressed as the number of individual vendace of 100–250 mm in length. This size class is assumed to be exclusively composed of post-juvenile individuals (Winfield and James 2018). Points and brackets respectively represent the geometric mean and the 95% confidence interval. The dashed horizontal line represents the baseline vendace abundance which was calculated from the estimates for the years of 1995–2000 in Bassenthwaite Lake and for all years from the 1998–2018 time series in Derwent Water. The post-juvenile vendace abundances and densities are available in a tabular format in Supplementary Material A.

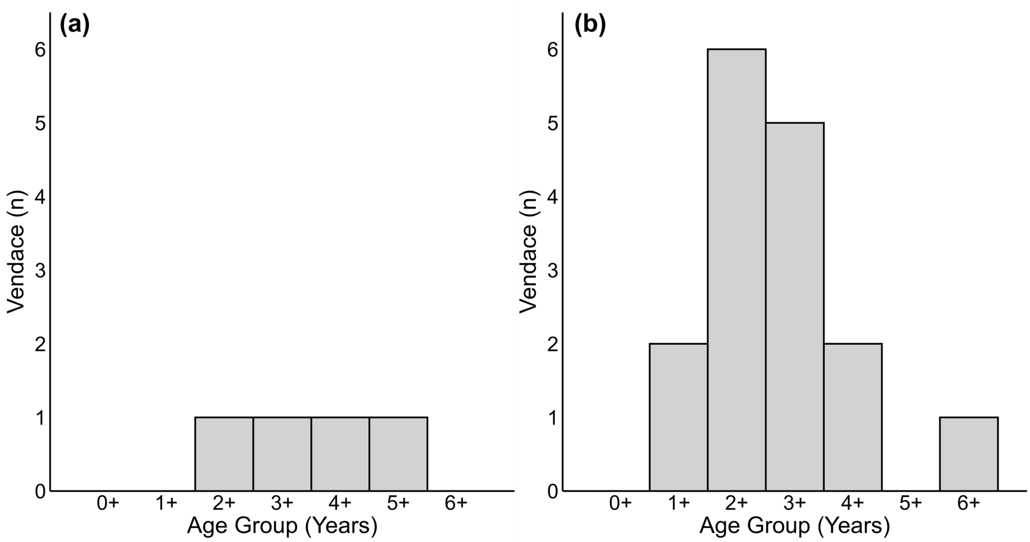

FIGURE 4 | Age distributions of the vendace captured by gill net in (a) Bassenthwaite Lake and (b) Derwent Water in 2024. A fish belonging to the 1+ years age group would have been in its second year of growth at the time of capture, a 2+ years fish in its third year of growth and so on.

of one captured vendace could not be determined because the fish was damaged.

3.2 | The Status of Vendace in Derwent Water

In Derwent Water, the estimated density of post-juvenile vendace in 2024 was 215.8 individuals.ha^{-1} (95% CI: 116.9, 398.6). The estimate of post-juvenile vendace abundance in this lake of 14,029 individuals (95% CI: 7596, 25,911) was the second highest on record but the 95% confidence interval overlapped with those from every previous year of monitoring apart from 2001, 2003, 2004, 2006 and 2007 (Figure 3b; Supplementary Material A). The 2024 abundance estimate was significantly higher than the reference baseline of 3442 individuals ($t=6.36$, df = 4, $p=0.003$).

A total of seven species of fish were captured during the gill net survey of Derwent Water (Table S4). Of the 17 vendace captured, most ($n=13$) were caught by the pelagic net, which captured fish at a depth of 5–11 m, while one was caught by the nearby benthic net four, which was deployed at a depth of 14.8 m. The remaining three vendace were captured in benthic net two ($n=1$) and benthic net three ($n=2$), which were both set in shallower water to the north of the deepest basin (Figure 1c). Therefore, vendace were found throughout their expected deep water habitat and also in shallower areas of the lake. The ages of the captured vendace ranged from one to 6 years, with most fish belonging to the 2+ and 3+ year age groups (Figure 4b). The age of one vendace could not be determined because both opercula were missing.

3.3 | Correlates of Variation in Post-Juvenile Vendace Abundance

Only one of the candidate explanatory variables was found to significantly affect the probability that vendace abundance would be markedly low in a particular year. That variable was the mean combined CPUE of perch, roach and ruffe across the third and fourth lagged years ($\chi^2=31.43$, df = 1, $p<0.001$). The direction of the effect was positive (Figure 5; odds ratio = 1.33, 95% CI = 1.15–1.72). As such, increases in the abundance of these non-salmonid fishes in the years when the dominant 2+ and 3+ vendace age groups would have hatched were associated with below baseline post-juvenile vendace population sizes. The McFadden's pseudo R^2 of the model was 0.63.

Further modelling indicated that the three component species of the composite lagged CPUE variable did not contribute equally to its effect. Instead, their significance differed substantially. The lagged CPUE values of both perch (Figure 6a; $\chi^2=15.57$, df = 1, $p<0.001$; odds ratio = 1.32, 95% CI = 1.11–1.90) and ruffe (Figure 6c; $\chi^2=17.56$, df = 1, $p<0.001$; odds ratio = 1.80, 95% CI = 1.24–4.32) had positive and highly significant effects on the probability that vendace abundance would be lower than the reference baseline. Conversely, the effect of lagged roach CPUE was also positive but only marginally significant (Figure 6b; $\chi^2=4.02$, df = 1, $p=0.045$; odds ratio = 1.65, 95% CI = 1.01–4.01). The McFadden's pseudo R^2 of the final model of species-specific effects was 0.70 indicating that the abundances of these three fish species accounted for 70% of the variation in the probability that vendace population size would exceed (or not) the baseline population size.

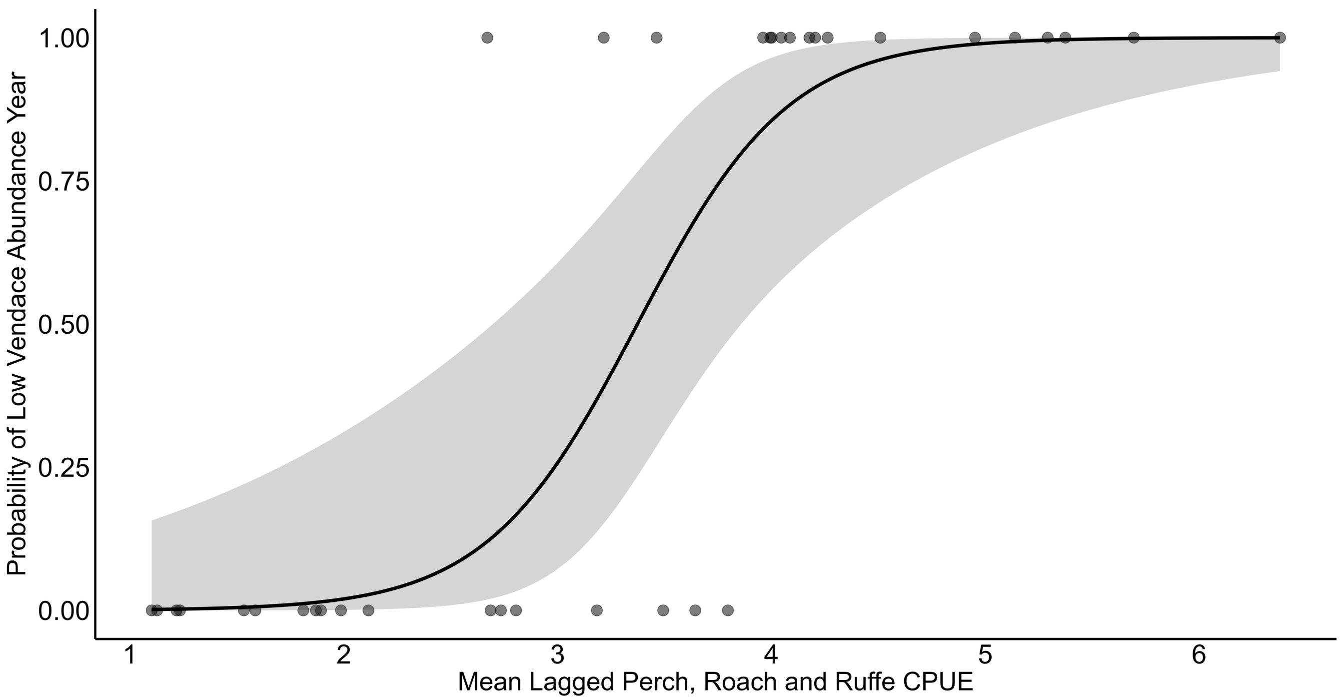

FIGURE 5 | The effect of lagged perch, roach and ruffe catch per unit effort (CPUE) on the probability of a low vendace abundance year. The line represents model fitted values and the grey area the 95% confidence interval of these predictions. The points represent observations ($n=36$). Low vendace abundance years were defined as those where upper limit of the 95% confidence interval of the post-juvenile population size estimate was below the lake-specific reference baseline abundance. CPUE is expressed as the number of individuals captured per 100m^2 of gill net per hour. All CPUE values were calculated as means of the third and fourth lagged years.

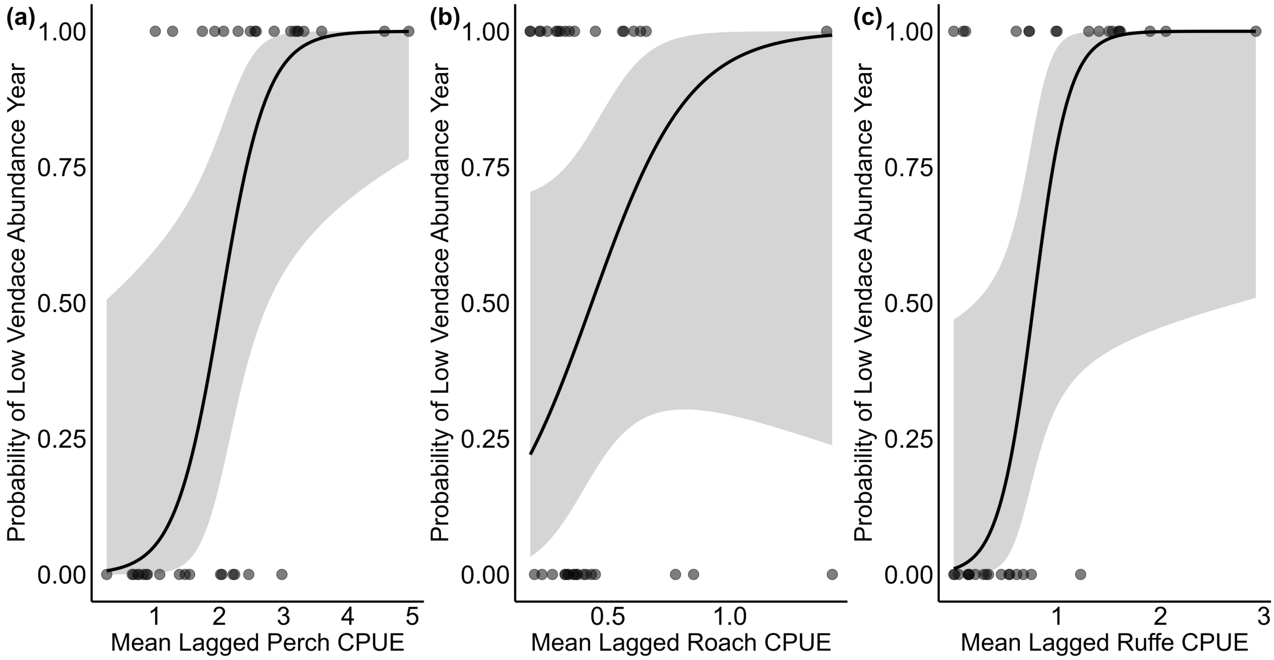

FIGURE 6 | The effects of the lagged catch per unit effort (CPUE) of (a) perch, (b) roach and (c) ruffe on the probability of a low vendace abundance year. The lines represent model fitted values while the grey area represents the 95% confidence interval of those predictions. The points represent observations (n = 36). CPUE is expressed as the number of individuals captured per 100m^2 of gill net per hour. All CPUE values were calculated as means of the third and fourth lagged years.

4 | Discussion

The UK's two peripheral populations of vendace were found to be abundant in 2024. Although gill net captures were limited, there was no evidence to suggest that their age structures were skewed nor that their spatial distributions were restricted with respect to their required habitat. As such, both populations were determined to be in good condition in 2024. However, high abundances of non-salmonid fishes were associated with markedly low post-juvenile vendace population sizes 3–4 years later. This relationship was predominantly driven by the effects of perch and ruffe, with the time lag suggesting compromised recruitment to the post-juvenile age groups.

In Bassenthwaite Lake, the 2024 post-juvenile vendace population size estimate was significantly greater than that from 17 of the previous 24 monitoring years and for Derwent Water in 5 of the previous 21 monitoring years. The estimated abundances in 2024 were also significantly greater than each of the lake-specific reference baselines. In Derwent Water, vendace were captured outside the area of the lake that was sampled by hydroacoustics, which suggests that the true abundance of post-juvenile vendace was likely higher than the estimate reported here. The size of vendace populations can fluctuate dramatically (Marjomäki et al. 2021; Mehner et al. 2023), so it is possible that the estimates from this single year (2024) were exceptional and may not represent a consistent deviation from the longer term average. However, the balanced age structure of the population, which was inferred from the small sample of fish captured by gill net, may grant some stability to the abundance of post-juvenile vendace in the coming years.

Although efforts were made to ensure the comparability of the vendace abundance estimates across the whole time series, the design of the 2024 study differed from that of previous surveys in two notable ways. Firstly, in Bassenthwaite Lake, fewer hydroacoustic transects were surveyed in 2024 ($n = 9$) than in each previous year of monitoring ($n = 10$). This slight reduction in hydroacoustic sampling effort is unlikely to have had a strong effect on the estimate of vendace abundance because the region of the lake that was sampled did not change and the coverage ratio continued to exceed the target of 3:1 (Bean et al. 2015). Secondly, the Simrad EK80 120-kHz echosounder used in 2024 differed from the Biosonics 200 kHz (or cross-calibrated Simrad 200 kHz) system used in all previous years of monitoring. Fish density estimates from these two types of echosounder are comparable, so it is unlikely that the large vendace population sizes observed in 2024 were an artefact of this equipment change (Wanzenböck et al. 2003; Draštík et al. 2017).

The hydroacoustic estimates of fish density were apportioned to vendace based on the composition of the gill net catch. This process will have contributed a degree of uncertainty to the accuracy of the vendace abundance estimates. It was necessary to limit gill netting effort to minimise any potential impact on the sensitive populations of fish that were being studied. However, it is possible that random variability affected the composition of the resulting small samples. The representativeness of the gill net catch may also have been affected by differential capture probabilities among species (Carol and García-Berthou 2007; Hamley 1975). As such, considering these limitations, the vendace population sizes reported in this study should be interpreted as tentative estimates.

The evidence of unrestricted habitat use and successful recruitment to the post-juvenile age groups provides further support to the argument that the Bassenthwaite Lake and Derwent Water vendace populations were in a favourable state in 2024. A low concentration of oxygen in the hypolimnion has, in the past, prevented vendace from accessing their preferred deep water habitat in both Bassenthwaite Lake and Derwent Water (Winfield et al. 2012; Winfield et al. 2017). However, in 2024 there was no strong evidence in either lake that the spatial distribution of vendace was restricted. There was also no evidence that the recruitment of vendace to the post-juvenile age groups had failed in recent years. This indicates that the populations remain viable because, given that vendace have a typical maximum lifespan of approximately 6 years (Maitland and Lyle 1991), a population can be extirpated by only a small number of consecutive years of unsuccessful recruitment.

Modelling indicated that the occurrence of markedly low post-juvenile vendace population sizes did not vary as a function of chlorophyll-*a* concentration or maximum surface water temperature. This was despite expectations that oxythermal stress may be an important factor controlling vendace habitat quality in the studied lakes (Elliott and Bell 2011; Winfield et al. 2017). Instead, the probability of a below-baseline post-juvenile vendace population size increased with the mean combined CPUE of perch, roach and ruffe across the third and fourth lagged years. Further modelling indicated that this effect was clearer for perch and ruffe than it was for roach. These results are consistent with a substantial body of research reporting negative effects of the abundances of perch (Auvinen 1994; Valkeajärvi and Marjomäki 2004; but see Beier 2001), ruffe (Pokrovskii 1961) and non-salmonid fishes (smelt (*Osmerus eperlanus*), perch, roach and bleak (*Alburnus alburnus*); Helminen and Sarvala 2021) on the size of vendace populations. The results also complement observations of an inverse relationship between the size of vendace year classes and a temperature-based proxy for perch abundance (Helminen and Sarvala 1994). However, the data presented in this study are correlative and as such there is some uncertainty about what mechanisms are driving the observed relationships. The lagged nature of the significant CPUE variables used in this study strongly suggests that the impact of these species is on the recruitment of vendace to the post-juvenile age groups rather than on the survival of mature vendace. However, while perch do consume age 0+ vendace, the intensity of this predation may not be sufficient to affect the overall size of the vendace population (Huusko et al. 1996; Haakana et al. 2007). It is also plausible that perch could compete with vendace because small perch are planktivorous (Helminen and Sarvala 2021). Ruffe predate the eggs of *Coregonus* fishes (Adams and Tippett 1991; Winfield et al. 2004) and, unlike perch, are a relatively recently introduced species in Bassenthwaite Lake (first recorded 1991) and Derwent Water (first recorded 2001; Winfield et al. 2007). A study of the rate of ruffe predation on vendace eggs in these lakes would help determine if this might be driving their negative effect on vendace population size.

In the present study, evidence for an effect of roach on vendace abundance was less pronounced. This is also consistent with the literature. There have been concerns that roach, which is also an introduced species in Bassenthwaite Lake (first recorded in 1986) and Derwent Water (first recorded in 1991; Winfield et al. 2010), could compete with vendace for zooplankton (Winfield et al. 2004). However, elsewhere, vendace population sizes have been found to remain stable despite substantial increases in roach abundance (Linløkken et al. 2025), perhaps because vendace can outcompete roach for pelagic zooplankton (Beier 2001).

The results of this study have clear management implications. The negative impact of the introduced ruffe on the abundance of the two remaining native UK populations of vendace demonstrates one of the risks associated with the artificial redistribution of fish species. This underlines the importance of the regulation of fish translocations. However, recent improvements in water quality in Bassenthwaite Lake (Figure 2e) may have mitigated the impacts of ruffe because less eutrophic waters are thought to favour vendace over percids (Helminen and Sarvala 2021). Water quality improvement efforts should be continued to buffer these vulnerable populations of vendace against the potentially deleterious effects of habitat compression (Elliott and Bell 2011) and increased percid abundance (Linløkken 2023; Marjomäki et al. 2024) that are predicted to develop with climate change.

Author Contributions

Ruaidhri Forrester: conceptualization, writing – original draft, investigation, methodology, visualization, writing – review and editing, formal analysis. **Jim Lyons:** investigation, writing – review and editing, methodology. **Ian J. Winfield:** investigation, writing – review and editing, methodology. **Colin W. Bean:** writing – review and editing, supervision, conceptualization, methodology. **Melanie Fletcher:** conceptualization, funding acquisition, writing – review and editing, investigation. **Chris Harrod:** supervision, writing – review and editing, conceptualization. **Hannele M. Honkanen:** conceptualization, writing – review and editing, funding acquisition, supervision. **Dave Ottewell:** conceptualization, funding acquisition, writing – review and editing, investigation. **Philip Ramsden:** conceptualization, investigation, writing – review and editing. **Colin E. Adams:** conceptualization, investigation, funding acquisition, writing – review and editing, supervision, methodology.

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Ethics Statement

All gill netting was conducted under licence granted by the Environment Agency and Natural England.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The time series of gill netting data and vendace abundances are respectively available as Supplementary Material B and Supplementary Material C. The chlorophyll-*a* and water temperature data, which were supplied by UK Centre for Ecology & Hydrology, are available at 10.5285/FE579FBF-E371-4320-8875-A8AF8736F3E5, 10.5285/7E7D7

22C-BDD7-4900-A443-E26370D72438, 10.5285/91D763F2-978D-4891-B3C6-F41D29B45D55 and 10.5285/106844FF-7B4C-45C3-8B4C-7CFB4A4B953B.

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The chlorophyll-*a* and water temperature data were supplied by UK Centre for Ecology & Hydrology (Maberly et al. 2017a; Maberly et al. 2017b; Feuchtmayr, Beith, et al. 2021; Feuchtmayr, Clarke, et al. 2021).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supplementary Information. **Data S2:** Supplementary Information. **Data S3:** Supplementary Information.