

Degree project



Where can the Vendace (*Coregonus albula*) live during the least favourable period of the summer stratification in Lake Mälaren?

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Abstract

Temporal stratification in lakes due to high air temperatures and dynamic wind conditions changes the environment for organisms in the depth gradient. For fish that have narrow requirements for temperature and oxygen conditions, stratification can lead to a significant reduction in habitat volume during the summer when surface temperatures are high. In Sweden, temporal stratification occurs between July and October. The vendace (*Coregonus albula*) is a cold-water fish that is found in several waters around Sweden. In Lake Mälaren, there is targeted commercial fishing for the species, but the total annual catch has drastically decreased in recent decades. Shrinking habitats and longer periods of temporal stratification during the summer could be a partial explanation. Understanding and predicting changes of the vendace population in Lake Mälaren requires mapping of available habitat during the summer temporal stratification. This study has investigated the worst habitat conditions in terms of habitat thickness for vendace during the years 2017-2022 in Lake Mälaren based on the habitat requirements temperature ≤ 18 °C and DO concentration ≥ 2 mg/L. The spatial distribution in two basins were analysed. The results showed that the vendace had limited available habitat in three of seven water bodies investigated (habitat thickness ≤ 2.5 m). The spatial analysis of the two basins showed that habitat volume represented 41 % and 11 % of the total volume of water in each basin. The available habitat of the vendace during the summer temporal stratification in Lake Mälaren is thus limited in parts of the lake.

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Introduction

The global minimum and average temperatures have increased in recent decades due to ongoing climate change (Kraaijenbrink et al., 2017). The IPCC has stated that the global average temperature should not increase by more than 1.5 °C to prevent major impacts on ecosystems and biodiversity (Shukla et al., 2019). However, the increase in temperature has already been shown to have direct effects on nature and its biodiversity (Vittoz et al., 2013). Prolonged periods of heat lead to plant desiccation and death, threatening plant species in many parts of the world (Walther, 2003). Altered reproductive patterns have been observed in ectothermic organisms (Forster et al., 2012). Resource competition that changes animal behaviour and creates aggressive interactions within and between species has become more common (Fattorini et al., 2023). The temperature of the atmosphere and waters is increasing while sea levels are rising as a result of melting glaciers (Bergström et al., 2020). Sea level rise wipes out isolated habitats as islands are flooded, threatening the extinction of several hundred endemic species (Bellard et al., 2013). The loss of ice also results in the loss of migration routes for some species and limits foraging opportunities (Marander, 2022; Stirling & Derocher, 1993). Thus, the direct impacts on biodiversity due to increased global temperature are extensive (Lin et al., 2017; Wetzel et al., 2013). Indirect effects of climate change have also been documented, although these are often complex and difficult to identify. For example, changes in species interactions have been observed in both aquatic and terrestrial ecosystems (Jamieson et al., 2012; Thomas, 2010). This is because the rate of change between phenology occurs at different speeds and can thus drift apart so interactions between species dependent on these phenology alternate (Durant et al., 2007). Such trophic mismatches have been seen in aquatic predator-prey relationships where species that were previously part of predator-prey cycles are no longer involved as a result of warmer winters (Jonsson & Setzer, 2015).

The indirect effects of climate change are often driven by direct effects on abiotic processes due to change in the annual process dynamics (Wright & Trippel, 2009). An example of such an abiotic process is the stratification that occurs in lakes. This stratification is a result of density differences between colder deeper water (higher density) and warmer surface water (lower density) (Boehrer & Schultze, 2008). The warmer upper layer of the water body is called the epilimnion and the colder lower layer of the water body is called the hypolimnion (Mortimer, 1952). Between these layers there is a drastic temperature change in the form of a gradient zone from warm at the top of the zone to cold at the bottom. This gradient zone is called the metalimnion or thermocline (Irmasyithah et al., 2019). Not all lakes experience temporal stratification during the summer, only those lakes that are deep enough to have sufficiently large density differences between the surface and the bottom (Boehrer & Schultze, 2008). The position of the thermocline in lakes

undergoing stratification varies in depth and volume depending on the depth of the lake, surface temperature and wind conditions (Benoit et al., 2022; Bengtsson, 1978; Mortimer, 1952; Flood et al., 2021). During temperature stratification in summer, when the surface temperature is highest, the volume of water in the hypolimnion is lowest (Reavie et al., 2017). Warm air temperature combined with increased wind speeds are the main factors that push the thermocline into deeper water. This is due to warm surface water mixing with deeper cold water, raising the temperature further down the water body (Mortimer, 1952). Although stratification dynamics differ between lakes, one similarity is that the summer period of temperature stratification becomes longer with a warmer climate (Benoit et al., 2021).

In mesotrophic and eutrophic lakes, algal blooms and other high primary production can occur and cause organic matter to sink to the bottom of the lake during the summer months (McDonald et al., 2022; Wurtsbaugh et al., 2019). Due to the decomposition of this organic matter by bacteria on the bottom, which is an oxygen demanding process, the concentration of dissolved oxygen (DO) is decreased in the hypolimnion during summer (Delfino & Lee., 1971) if not resupplied from elsewhere. In eutrophic lakes exposed to high nutrient emissions from, for example, agriculture and sewage treatment plants, algal blooms can be severe which means more organic matter at the bottom than normal and thus a greater oxygen loss (Wurtsbaugh et al., 2019). Since algal blooms and high primary production make the water turbid, sunlight is prevented from reaching photosynthesising organisms in deeper waters and oxygen production therefore decreases at higher depths (Wurtsbaugh et al., 2019). Since vertical mixing of water in a lake is the process in such a scenario that adds oxygen to the hypolimnion, the DO concentration becomes limited in this part of the water body when vertical mixing is hindered by temperature stratification (Ito & Momii., 2015). In general, DO concentration is lower deeper in the water column, with a sharp decrease below the thermocline (Rowe & Chisnall, 1995). In eutrophic lakes with high nutrient inputs, this limitation of oxygen concentration can lead to severe effects on bottom life in extreme scenarios with large bottom areas where all flora and fauna disappears (Andersson et al., 2013). In parts of the world with seasonal temperature stratification, DO concentration is lowest at the end of the stratification period and as temperature stratification dissolves, oxygenation increases in deeper waters (Benoit et al., 2021).

The gradual decrease in DO concentration from the thermocline to the bottom of the lake during summer, together with the increasing temperatures at deeper depths due to high surface temperatures and wind patterns, poses a significant challenge for organisms that depend on cold water and high DO concentrations (Rowe & Chisnall, 1995). The available habitat is then determined by the physical requirements and preferences of different organisms for temperature and oxygen concentration (Magnuson, 1990). Fish that are sensitive to high water temperatures

and low DO concentrations are pressed between these parameters in a so-called 'habitat squeeze' (Kraus et al., 2015; Kangur et al., 2020; Magnuson, 1990; Flood et al., 2021; Tapaninen et al., 1998). As habitat volume decreases, competition between organisms and individuals coexisting in the same temporal zone increases. The lack of resources during competition in the habitat zone means that individuals are forced to visit other temperature zones outside their preferred one for extended periods of time to counteract nutrient deficiencies (Benoit et al., 2022). Foraging then typically occurs through diel vertical migration (DVM) for organisms that have narrow habitat requirements in terms of temperature. Cold water fishes are defined as fish species that are adapted to water temperatures below 18 degrees. These fishes stay below this temperature limit during summer and only visit surface waters when it is favourable from a foraging point of view (Lilja et al., 2013). However, DVMs expose the individual to an unfavourable environment that can lead to increased predation or other negative physical effects (Benoit et al., 2022). Zooplankton perform DVM at night to reach food in surface waters (Wilson et al., 1993). Night-time migration is believed to be beneficial since darkness prevents visually hunting predators from foraging, thus reducing the risk to zooplankton (Bandara et al., 2021; Hays, 2003). However, an adaptation can be seen in fish that feed on zooplankton. These fish follow the same vertical migration pattern as zooplankton and forage in surface waters at night (Hays, 2003; Wilson et al., 1993). The darkness that protects these fish during their foraging is controversial but is not excluded as a potential partial explanation for DVM along with the food that concentrates in the surface water during summer nights (Hays, 2003; Mehner, 2012). A further explanation for DVM in fish is the fish's search for an optimal temperature that favours their metabolism (Mehner, 2012). A study conducted in 2020 in eleven different lakes in China shows that the rate of change of surface water temperature per decade is +0.43 °C during the day but only +0.19 °C at night (Yang et al., 2020). The nocturnal vertical migration may therefore help to reduce the negative effects that vertical migration would otherwise have on fish in terms of exposure to unfavourable temporal zones (Wilson et al., 1993). However, although cold-water fishes adapt their foraging behaviour through DVM during habitat squeeze, these fishes will eventually have to return to their temporal zone in order not to be negatively affected when surface water temperatures increase during the day (Flood et al., 2021; Lehtonen, 1996; Tapaninen et al., 1998).

The vendace (*Coregonus albula* Linnaeus, 1758) is a characteristic cold-water fish that avoids epilimnion during the summer when surface temperatures are high. Instead, the thermocline is the upper limit of the vendace's preferred residence area and large schools have been found just below the thermocline, in the hypolimnion, where the water temperature is lower (Hamrin, 1986; Tapaninen et al., 1998). Adult vendace are elaborate zoo-planktivorous and perform DVM for foraging but avoid water temperatures above 18 degrees and have a metabolic optimum in temperatures between 7 and 9 degrees (Elliott & Bell, 2011; Kangur et al., 2020; Hamrin, 1986;

Lilja et al., 2013; Sarkar & Tiwari., 2006; Parkinson et al., 2016; Wehrly et al., 2003; Marszelewski & Solarczyk, 2011). However, vendace is sensitive to poor oxygen conditions and cannot survive unless oxygen levels are sufficiently high. Previous studies have indicated 2 mg/L as a lower limit for oxygen concentration in the available habitat of the vendace (Elliott & Bell, 2011; Fiszler et al., 2012; Marszelewski & Solarczyk, 2011). Therefore, this species is sensitive to habitat squeeze during the summer when the thermocline is at its deepest and the oxygen concentration in the hypolimnion is at its lowest. Vendace is an important prey for predators in lakes where vendace is present and play a key role in predator-prey relationships and the prevailing functioning of aquatic ecosystems (Kangur et al., 2020).

Functioning aquatic ecosystems also provide several ecosystem services to humans, one of which is food in the form of fish. Vendace in Lake Mälaren, Sweden, have historically been an important resource for humans with catch levels of 150 tonnes per year between 1964-1989 (Sonesten et al., 2013). Today, catch levels are at historically low and have fluctuated between 1 and 15 tonnes since the beginning of the year 2000 (Sonesten et al., 2013). Studies that have demonstrated a reduction of the stock suggest that a partial explanation for the sharp decline of the vendace in Lake Mälaren may be higher temperatures and its consequent effects on the aquatic ecosystem (Nyberg et al., 2001). Strong links between reduced abundance of vendace populations and increased temperatures have also been demonstrated in other lakes in northern Europe (Kangur et al., 2020). However, there is great uncertainty in how the dynamics of summer temperature as well as water oxygen levels affect the available habitat of vendace from lake to lake due to the lakes' individual changes in these parameters (Benoit et al., 2022). Estimating the amount of available habitat in a lake provides data that can be used to analyse and predict effects of environmental change (e.g. climate warming) on the dynamics of cold- water fish (Rowe & Chisnall, 1995). Since vendace prefer a certain temperature in the habitat and rarely move outside the zone that fulfils the preferred temperature and physical oxygenation requirements (Magnuson, 1990), it is possible to measure and calculate the volume of water that the fish depend on during habitat squeeze. Estimates of vendace habitat volume during temporal stratification have been carried out in Lake Mälaren with depth data, hydroacoustic and trawl data by Axenrot et al. (2023). Trawl data and hydroacoustic gave a detailed picture of the vendace habitat in the depth gradient and the importance of implementing temporal stratification in the estimation of vendace population size in Lake Mälaren is emphasised. However, due to poorly resolved depth data over the lake, a less detailed spatial distribution of vendace habitat was provided. Available habitat is in this case a limited resource and analysing the limiting resources of fish will help to predict future species shifts in the ecosystem and increase the understanding of how climate change affects aquatic ecosystems (Angeler et al., 2014).

The purpose of this study was to analyse the habitat requirements of vendace in Lake Mälaren by creating data similar to that requested by Angler et al. (2014) to increase understanding of how climate change affects vendace specifically as well as Lake Mälaren from an ecosystem perspective. This was carried out by matching both metabolic optimum temperature and habitat requirements for the vendace with depth profiles from eleven measuring stations during the stratification period for the years 2017-2022. The date in the five-year period for each station that showed the worst habitat conditions was taken forward for comparison. This was considered relevant as the habitat limitation described in the literature only occurs during the summer temporal stratification and it is thus a limited period that the vendace must survive poor habitat conditions because the temporal stratification is dissolved during the rest of the year. A more in-depth spatial analysis was conducted for two of the eleven stations that showed the greatest difference in habitat conditions between them. This was carried out to create a basis for a more detailed estimation of the vendace's habitat and thus complement the data provided by Axenrot et al. (2023). The potential for migration of vendace from poor habitat conditions to better habitat conditions was also mapped for both basins to provide a basis for discussion on whether vendace can escape from basins with limited habitat and thus nuance the discussion on vendace utilisation of available habitat. The aim of conducting the above analyses was to answer the question: Where can the vendace (*Coregonus albula*) live in Lake Mälaren during the least favourable period of the summer temporal stratification? Data from the study can be used as a basis for discussion as well as data for future tests concerning the distribution of vendace in Lake Mälaren. For example, the results can be used to study climate-driven habitat changes for vendace in Lake Mälaren or the role of vendace as prey from a predator perspective.

Materials and methods

Data collected by SLU (Swedish University of Agricultural Sciences) from 11 stations in Lake Mälaren between 2017 and 2022 was used. The data included temperature and oxygen measurements from different depths at each station and date. These data were used to identify the depth of the temperature limit and DO limit that define the habitat requirements of the vendace. Based on Elliott & Bell (2011), Fiszler et al (2012), Kangur et al (2020), Hamrin (1986), Lilja et al (2013), Marszelewski & Solarczyk (2011), Sarkar & Tiwari (2006), Parkinson et al (2016) and Wehrly et al (2003), the habitat requirements for vendace were concluded to be ≤ 18 °C for temperature and ≥ 2 mg/L for DO concentration. The depth interval for the vendace habitat was then used as the habitat interval in the entire basin where the station was located with delimitation of basins according to the county administration (VISS 2023a & b). Available habitat (Z) was then calculated according to the following formula:

$$Z_i = ((DO_{lim} - T_{lim}) \times Area) - BS$$

Where:

- Z_i = Volume (m^3) of available habitat around a measuring station
- DO_{lim} = The depth (m) of the corresponding DO concentration 2mg/L
- T_{lim} = The depth (m) of the corresponding temperature level 18 °C
- $Area$ = Total area (m^2) around the station
- BS = Bottom structures (m^3) interfering on the habitat volume

The maximum potential habitat is described by $Z_{i,max} = (DO_{lim} - T_{lim}) * Area$. However, because lake depth is not constant throughout the estimated area around a station, BS will interfere on potential habitat and reduce the total volume for Z_i . By matching the lakes depth data in a 3D model with the spatial position of Z_i , BS interfering on Z_i can be identified and subtracted from the total volume and a more accurate result of the vendace available habitat can be determined. The available habitat is then calculated as $Z_{i,real} = Z_{i,max} - BS$. Since a negative difference between DO_{lim} and T_{lim} indicates that there is no available habitat, only basins with positive differences could be used to calculate $Z_{i,real}$. The calculation of $(DO_{lim} - T_{lim})$ was executed with the programming language R (Version 4.2.2). Calculation of $Area$ and subtraction of BS was executed with geographical information systems (GIS). A complete list of hardware and software used during this project can be found in table 1.

Figure 1 presents an overview of the workflow to facilitate the understanding of the different steps of the method used in this study. Table 1 presents the hardware and software used during the method. All code and detailed workflow for conducting the analysis in this study are available on Github (https://github.com/Lozon95/BSc_project-.git).

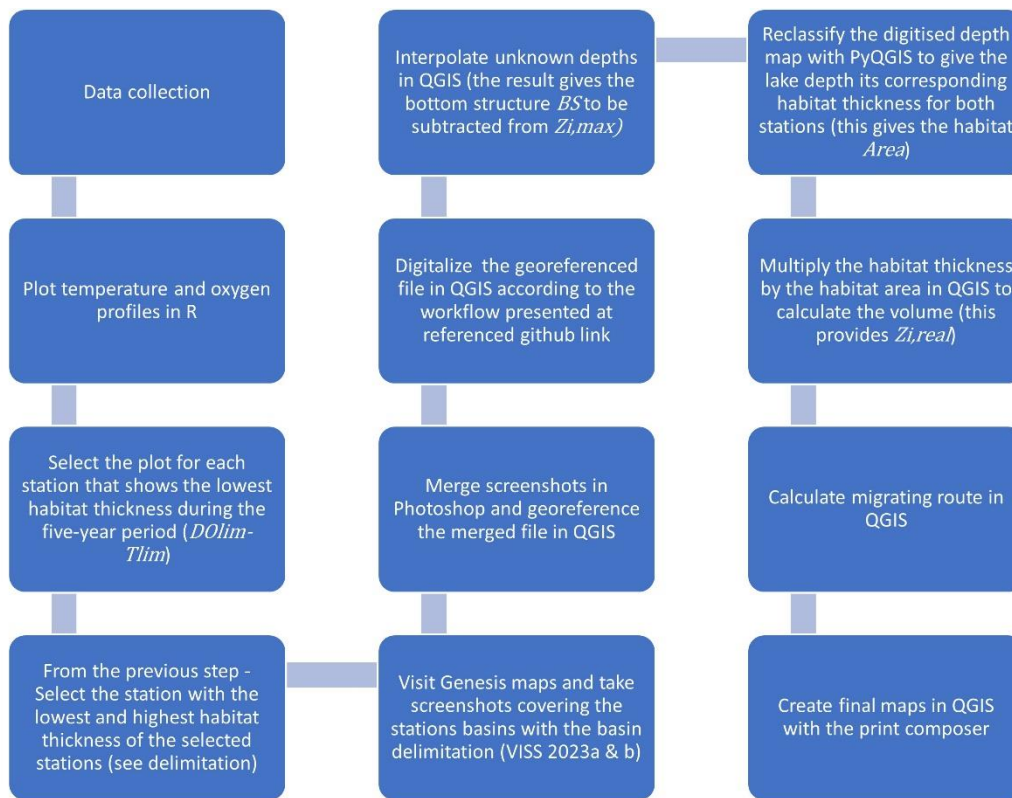


Figure 1: Workflow of the methodology used in this study.

Table 1: Hardware and software used during the methodology part of this report. Lower specs for the hardware are not recommended as the output would be slow.

Hardware	Software
Intel core i7, 8- core, 3.20GHz	Adobe Photoshop (2022)
16Gb RAM	FWTools (Version 2.4.7)
IntelR irisR Xe Graphics, 1Gb, 32bit	GDAL (2022)
	GRASS (2022)
	NumPy (2023)
	Python (Version 3.11.2)
	R (Version 4.2.2)
	RStudio (Version 2022.12.0)
	R package tidyverse (Version 2.0.0)
	Value Tool (Version 3.0.15)
	QGIS (Version 3.26.3)

Data Collection

Data on temperature and oxygen for the measuring stations were retrieved from SLU Environmental Data MVM (accessed 2023-02-02). Selections are presented in Figure 2 with associated figure text.

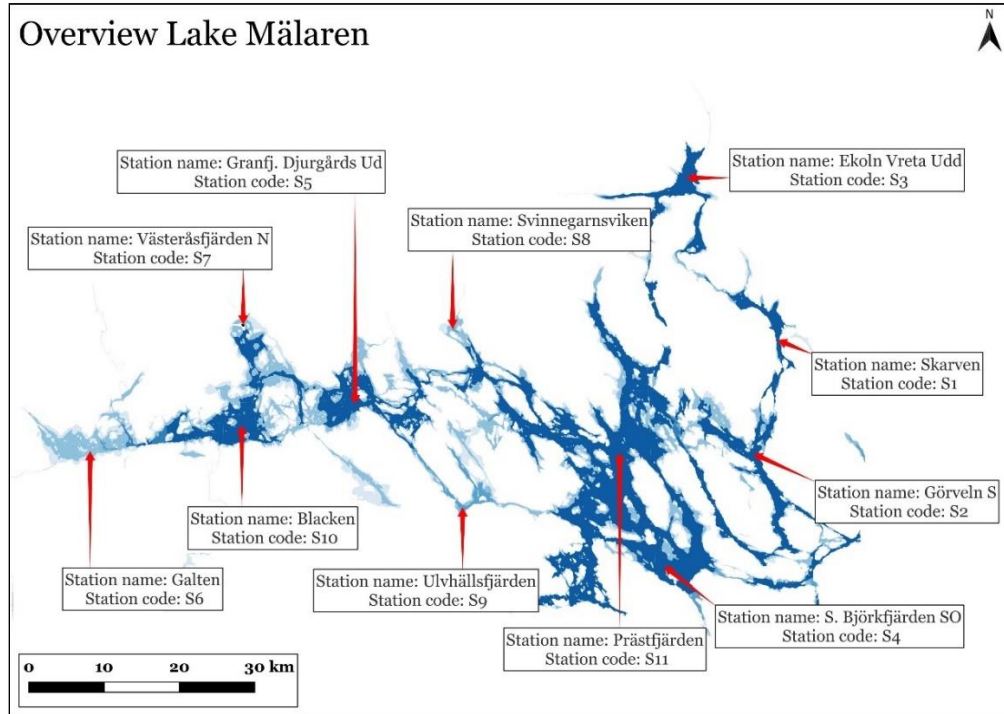


Figure 2: Overview map of Lake Mälaren, Sweden. Highlighted are the measuring stations from which data were used in the analysis. Data was retrieved from SLU environmental data MVM (2023) in .xlsx format and the selection in the database was made on 'Lake', 'Water chemistry', 'Oxygen and Temperature' and the dates "2017-07-18 to 2022-10-01". Each station has been assigned a station code to facilitate the reading of the report. Lake map: Swedish Maritime Administration (S57 data).

Nautical charts for Lake Mälaren were retrieved from SLU's Geodata extraction tool (accessed 2023-02-14) where 'Maritime Administration: Nautical latest (S-57) Nautical Chart' was ordered. Since files in S-57 format cannot be used in QGIS, the files were converted to .shp format with the function 'ogr2ogr' (GDAL, 2023). The function was run in FWTools Shell version 2.4.7 with the syntax 'ogr2ogr -skipfailures output input' where 'output' was set to the path of an empty folder on the computer's hard drive and 'input' to the path of the S-57 file. The procedure was repeated for all S-57 files that came with the order from the Geodata extraction tool (2023). Since the Swedish Maritime Administration's chart only covers depths down to 30m at 5m and 10m intervals and then 20 m intervals down to 50 m, the chart was supplemented with depth data from Genesis Maps (accessed 2023-02-28). 85 screenshots were taken with the highest level of detail of the lake where the stations S1 and S2 are located according to VISS (2023) and saved in .jpeg format. The files were then imported into Adobe Photoshop (2022) where all files were merged into a .png file (https://github.com/Lozon95/BSc_project-git).

R analysis

Data were cleaned from NA values and sorted into a list of data frames where each data frame contained temperature and oxygen data from one station and date. A function was then created using ggplot (Tidyverse, version 2.0.0). The function took the arguments: List of data frames, temperature limit, oxygen limit, metabolic optimum and station. The function interpolated the depth value for the specified temperature limit, oxygen limit and metabolic optimum. Then the difference between the depths of oxygen limit and temperature limit was calculated. The delta value represented the habitat thickness at the given station for a given date. The function visualised the delta value on a plot with the depth values on the x-axis and the temperature and oxygen measurements on a dual y-axis. Three vertical lines were added to the x-axis for the specified y-values (temperature limit, oxygen limit and metabolic optimum). The vertical line for temperature limit indicates the depth of the habitat ceiling, the vertical line for oxygen limit indicates the depth of the habitat floor and the vertical line for metabolic optimum indicates the depth of where the metabolic optimum temperature occurs (https://github.com/Lozon95/BSc_project-.git). The plots were studied visually and the extreme values for S1 and S2 were used for further analysis in QGIS (Figure 1).

Delimitations

Due to the lack of detailed depth data for Lake Mälaren in a format that could be processed in QGIS version 3.26.3, extensive digitisation of nautical charts in .jpeg format was required. The digitisation limited the possibilities for the spatial analysis due to the time required for the digitisation. It was therefore decided to limit the analysis in QGIS to only 2 out of the 11 basins. The basin showing the lowest difference between habitat boundaries and the station showing the highest difference between habitat boundaries was taken forward to the spatial analysis in QGIS.

GIS analysis

Import and prepare data

The National Land Survey's terrain map (Lantmäteriet, 2020) and the converted S-57 files (the nautical chart) were imported as vector layers into QGIS. The Swedish Maritime Administration's nautical chart is delivered in the reference coordinate system 'EPSG:4326 - WGS 84'. Since the National Land Survey's terrain map is projected with 'EPSG:3006 - SWEREF99 TM', the merged chart was re-projected to the same reference coordinate system. The merged .png file with screenshots from Genesis Maps was georeferenced using the terrain map as a template for the

georeferencing. Since the screenshots covered land structure and the file was large and heavy to work with for the computer's RAM, the raster was cropped according to the extent of the nautical chart.

Digitalize georeferenced .png

In order to perform analyses on the data from Genesis Maps, the georeferenced .png- file needed to be assigned depth values. Several steps had to be performed before this was possible. By obtaining the cell values that corresponded to the colour of the depth lines on the georeferenced .png- file, a reclassification of the grid could be made. All cells corresponding to the colour of the depth lines were assigned the value 1 and all other cells the value 0. The result was a white grid with black lines. During reclassification, the new layer was saved by default in the data type 'int32'. As the new file only contains values 0 and 1, the file can be converted to the data type 'int16' without losing data as 'int16' can hold values up to up to 32767 (2 bytes). This change makes the file smaller and thus less demanding for the computer hardware to work with. By setting all cells with value 0 to 'NULL' the file could be made even smaller without losing the relevant data to be vectorised. This was done with the function 'r.null' (GRASS, 2022). The bottom structure in Lake Mälaren is in several places strongly varied where shallow areas quickly become deep. This means that the depth lines from Genesis Maps are so densely drawn that a separation between the polygons cannot be discerned. When vectorising, the result is therefore a large clump of polygons rather than an elongated linear polygon. To get a vectorised result that would require as little manual post-processing as possible, the function 'r.thin' (GRASS, 2022) was used, which reads contiguous non-NULL cells and converts them to a centred pixel. The new layer had thin depth lines even where the depth lines are densely drawn. The vectorisation was then performed using the 'r.to.vect' function (GRASS, 2022). Despite the modification of the width of the depth lines, there were some depth lines that were so densely drawn that the result was a single large polygon. These polygons were removed, and new depth lines were drawn manually against the depth lines that could be distinguished on the data from Genesis Maps. Several depth lines at deep slopes along the littoral zone could not be discerned even by eye. This was solved by merging the data from Genesis Maps with the Swedish Maritime Administration's S-57 data. The polygon layer was then converted to a line layer. With the attribute table, one line at a time was lit and assigned the depth that corresponded to the depth lines from the georeferenced .png- file.

Interpolation of unknown depths

Since the extreme values from the analysis in R were produced with an accuracy of 0.1m, the level of detail from the Swedish Maritime Administration's nautical charts and the vectorised images from Genesis Maps was not sufficient as the accuracy of the vectorised result varied between

different parts of the lake due to the difference in density between the depth lines. To create depth data with similar accuracy as the analysis in R over the entire depth data, values were interpolated between known depth values in the vectorised result. This was done by converting the line layer to a temporary point layer with 0.1 m distance between each point. There were then two possible interpolation methods to apply to the data. IDW and TIN interpolation. Since the distance between the depth lines differs depending on how the depth changes over a given area, TIN interpolation was used as it is the most suitable method for data with uneven spatial variance (QGIS, 2023). The interpolation was carried out with 0.1m accuracy.

Three dimensional analyse and visualisation of habitat spread

To be able to run analysis tools on each basin separately, the interpolated result was split in two. The boundary between the two basins was drawn according to the water body for each basin (VISS, 2023a & b) with the coordinates lat/long: 6595932 N°, 658113 E°.

QGIS does not offer a predefined function that calculates the volume between two depths in a depth gradient. Although other functions offered by QGIS could have been used in several steps to calculate the habitat volume, another method was chosen for two reasons: i). the chosen method was considered to require fewer steps and thus result in fewer possible miscalculations and ii). the chosen method was considered to facilitate the visualisation of the habitat thickness and could thus save time in a later part of the analysis. Since the pixel size during the digitisation was set to '1' and the unit of the grid was in 'metres', the depth value of each pixel was equivalent to the volume value of each pixel because $(\text{depth(m)} * 1(\text{m}) * 1(\text{m}) = \text{depth}(\text{m}^3))$. This meant that if all cells with a value <0 in the grid were summed and multiplied by -1 (the depth of the lake in QGIS was given as meters below ground level and thus in negative numbers), it resulted in the total volume of the basin. By reclassifying the grid and assigning each pixel depth its corresponding habitat thickness, the habitat volume could be summarised in the same way. QGIS offers a function for reclassifying raster with a table, but since the result from the analysis in R showed habitat thickness between 0-28.5 m and the raster have an accuracy of 0.1 m, this would mean >285 rows in the reclassification table and a human factor that could result in wrongly entered values. Due to this uncertainty, a reclassification method was chosen that automated the process in the QGIS Python console (Python, Version 3.11.2). By opening the raster file with GDAL (2022) and reading the raster file as an array with NumPy (2023), all the features NumPy offers for arrays are made available. A copy of the read array can then be overwritten with a custom function. The copy of the loaded array is then added to QGIS for further analysis (https://github.com/Lozon95/BSc_project-.git). The process was repeated for both raster layers. The new raster layers show the thickness of the habitat in different cells instead of the depth of

the water body. Since the raster layers have NVD (no data values) that all have the value -9999, a mask layer is needed to separate the data to be analysed from values that should not be included in the analysis. The mask layer for each raster layer was used in the 'Zone statistics' function together with the raster layer as input. The function summarised the value from all cells in a contiguous habitat patch in the raster layers and collected it in an attribute table. The volume of all habitat patches in the same basin was then added together.

Analysing migrating route

There is no data or studies on vendace habitat migrating behaviour or what a possible escape from a shrinking habitat would look like. The study therefore did not model further deterioration of habitat conditions but carried out the analysis on the worst conditions measured. The distance between the basin with the least habitat volume to the basin with the greatest habitat volume was analysed with the criterion that the distance between each habitat patch should be measured at the distance following the highest possible depth of the route. The 'shortest line between objects' function was used. Next, lines intersecting land structure were moved by adding vertices. New vertices were placed in the centre of the maximum depth of the route. The distance was then calculated with the 'Field Calculator'.

Results

Of the eleven different stations studied, only seven had temporal stratification during the dates when $DO_{lim} - T_{lim}$ was at its lowest (Figure 3). The other four lacked temporal stratification because the maximum depth in these basins was not sufficient (S6: 10 m, S7: 8 m, S8: 9 m, S9: 8 m) and therefore lacked available habitat for the vendace. Of the seven stations that offered available habitat during the dates that $DO_{lim} - T_{lim}$ was lowest for each station in the period between 2017 and 2022, S5 had the lowest value of 2.1 m closely followed by S10 which had 2.4 m. The highest value was measured at S2 at 28.5 m closely followed by S11 at 28 m. The seven stations in figure 3 all have surface water with temperature $>18^{\circ}\text{C}$. The depth where the temperature is equal to 18°C varies from station to station. In S5 the 18-degree limit occurs at its deepest at 15.2 metres. S1 has the shallowest 18-degree limit at 9.4 m.

S2, S11 and S4 had a DO concentration $>2\text{ mg/L}$ throughout the oxygen profile. However, S2 lacks measurements deeper than 40 m even though the basin has a maximum depth of 61 m (Figure 4). S3 had a DO concentration $<2\text{ mg/L}$ at the last measurement point closest to the bottom in the oxygen profile. S5, S10 and S1 have a DO concentration $<2\text{ mg/L}$ from 17.2 m, 16.5 m and 11.9 m down to the bottom respectively. Five of seven stations (71.5 %) show the lowest measured DO_{lim}

- T_{lim} value during the last ten days of August 2018. S1 and S11 show the lowest measured $DO_{lim} - T_{lim}$ value in August 2017. However, no measurements were made in August 2018 for any of these stations. Seven of seven stations (100 %) show the lowest measured $DO_{lim} - T_{lim}$ value during the last half of August regardless of the year (Figure 3).

Epilimnion can be discerned by studying the curvature of the dot plots. The surface water maintains a steady temperature curve relative to the rest of the plot without increasing or decreasing. Where the temperature begins to drop, the thermocline (metalimnion) begins. S4, S3, S2, S11 and S1 have a depth of epilimnion of between 9.4 m and 12.1 m. S10 and S5 have a greater depth of the epilimnion of 14.1 m and 15.2 m respectively. Exactly where the thermocline ends and the hypolimnion begins is more difficult to determine by studying the plots, although for some of the plots it is possible to distinguish a definite threshold for when the temperature stops falling.

Of the seven stations showing temporal stratification, three stations have temperatures $<9^{\circ}\text{C}$ (where 9°C is the upper metabolic optimum temperature for vendace) within the defined habitat boundaries (S4, S3 and S2). At the other stations, no temperatures $<9^{\circ}\text{C}$ were detected within the defined habitat boundaries (Figure 3).

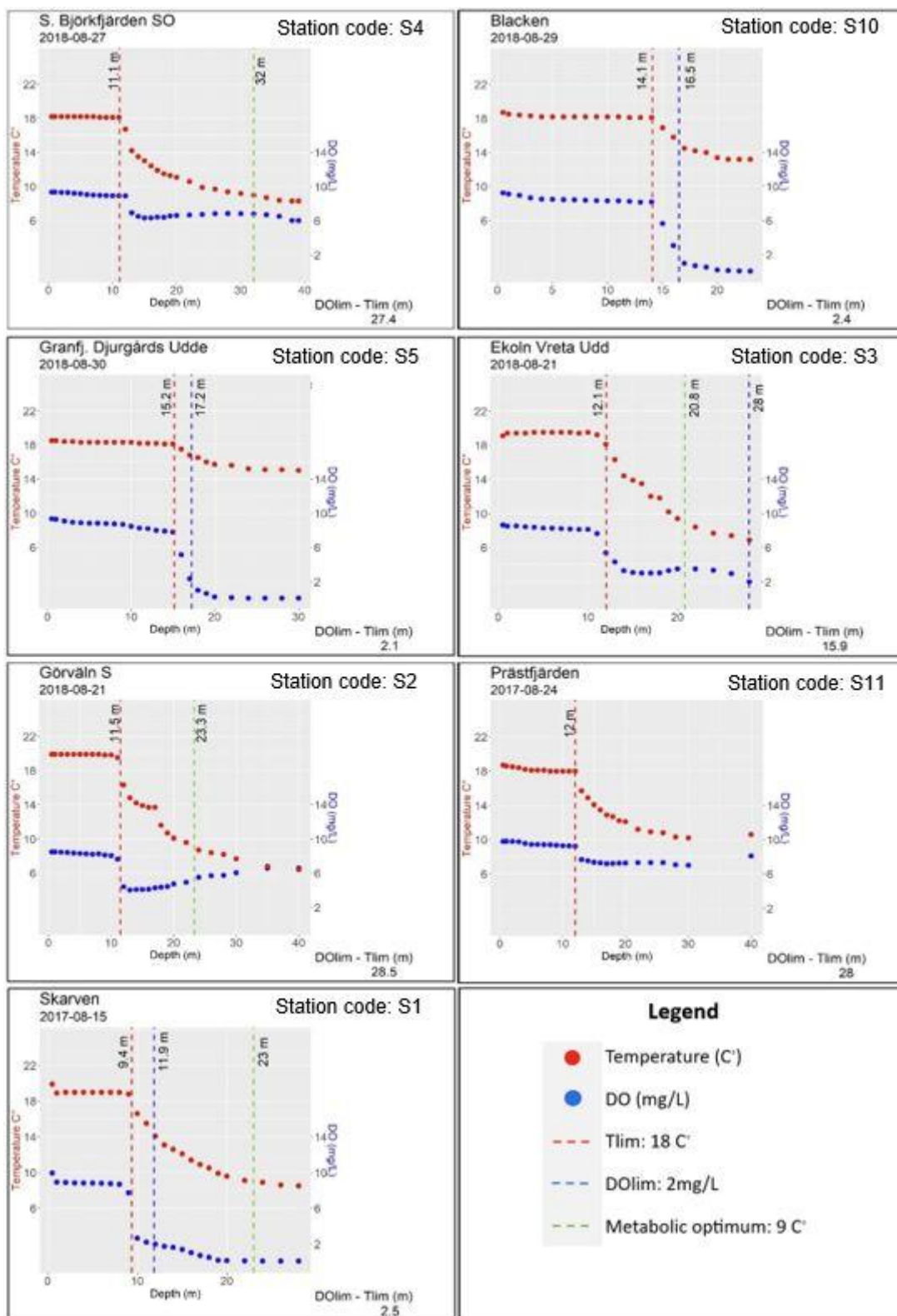


Figure 3: Oxygen and temperature profiles over seven different water bodies in Lake Mälaren, Sweden. Each plot shows temperature profiles and oxygen profiles for the date that showed the worst conditions for meeting the habitat requirements of the vendace over a five-year period. The red dashed line shows the depth of the upper temperature requirement of the vendace (18 °C), i.e., the temperature that must not be exceeded to meet the habitat requirements of the vendace. The blue dashed line shows the depth of the

lower oxygen requirement of the vendace (2 mg/L), i.e., the lower limit for the concentration of dissolved oxygen (DO) to meet the habitat requirements of the vendace. The green dashed line shows the depth of the vendace metabolic optimum temperature (9 °C), which is the temperature that enables the vendace optimal metabolism. In the plots that lack dashed lines in blue, the DO concentration does not fall below 2 mg/L anywhere in the oxygen profile.

S5 and S10 fulfilled the criteria for the delimitation of the study to make a three-dimensional analysis on the station that had the lowest $DO_{lim} - T_{lim}$ value of the stations that had a temporal stratification (Figure 3). However, there was no depth data available for these two stations and therefore S1 was taken forward for analysis in QGIS as it was the station with the lowest value for $DO_{lim} - T_{lim}$ after S5 and S10 and that had depth data available. S2 met the criteria for the study's delimitation of the largest $DO_{lim} - T_{lim}$ value (Figure 3) and for that station there was also depth data available. Figure 4 shows the different layers of the water body for S2 and S1 based on the habitat criteria temperature ≤ 18 °C and DO concentration ≥ 2 mg/L. The first map for each station (1.1 and 2.1) shows the study area with water surfaces. All blue water within the study area has a temperature > 18 °C. Second map for each station (1.2 and 2.2) shows where water temperature ≤ 18 °C and DO concentration ≥ 2 mg/L in green (habitat zone). The third map (1.3) for S2 shows water where measurement data is missing, while the third map for S1 (2.3) shows water where the DO concentration is < 2 mg/L. The volume for all water with missing measurement data in map 1.3 amounts to 0,043 km³ or 4 % of the total basin volume. The volume for all water showing a DO concentration < 2 mg/L in map 2.3 amounts to 0,079 km³ or 28 % of the total basin volume.

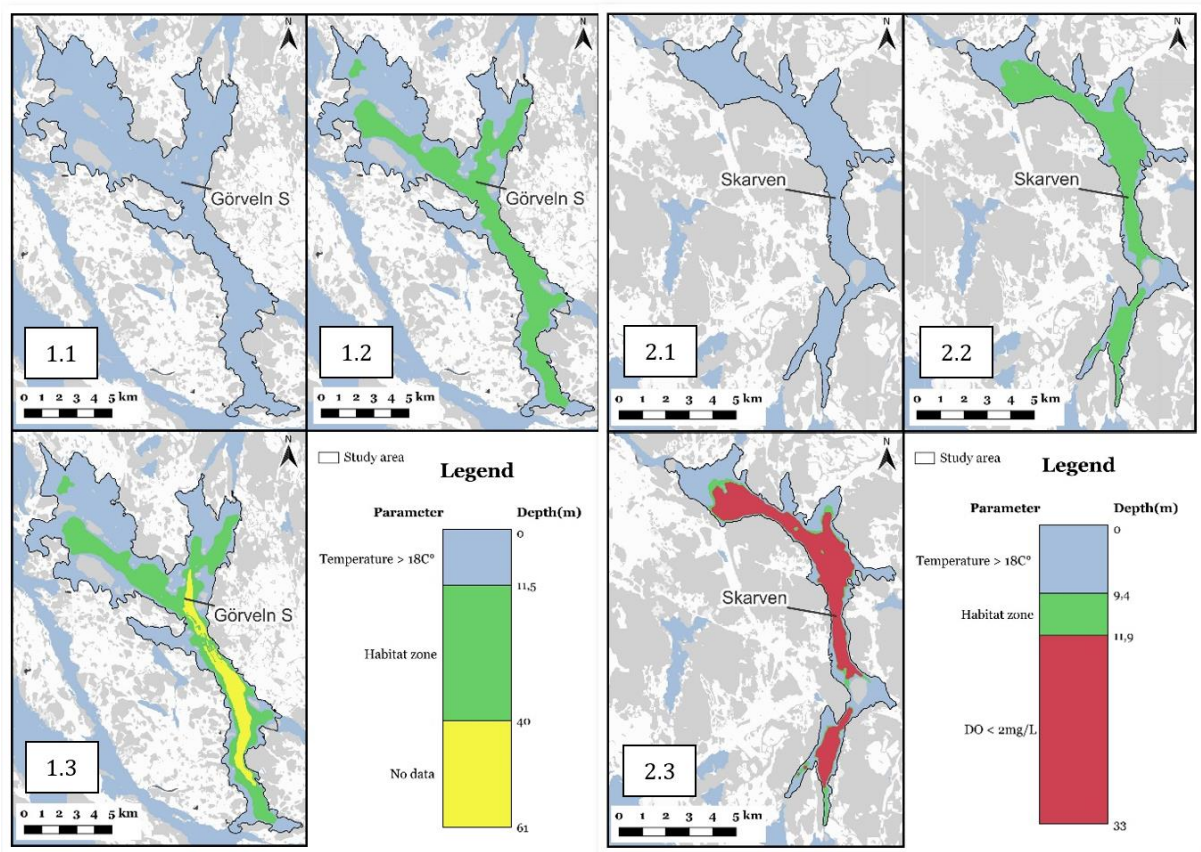


Figure 4: Maps of vendace habitat in two water bodies in Lake Mälaren, Sweden. Image series 1 on the left of the figure shows the basin S2 and image series 2 on the right shows the basin S1. Blue colour shows areas where the temperature in the upper water column is greater than 18 °C. Green colour shows areas that meet the habitat requirements for vendace (temperature ≤ 18 °C and concentration of dissolved oxygen (DO) ≥ 2 mg/L in some part of the water column, see legend). Yellow colour shows areas with depths with missing data and red colour shows area where DO concentration < 2 mg/L in some part of the water column, see legend. When studying the maps, the understanding of a 3D thinking is facilitated. The legend shows the thickness of each parameter in units of metres and shows that the layers are superimposed on top of each other. For example, this means that the habitat zone in S1 (image series 2) that is visualised in green will not extend all the way down to the bottom over the entire surface visualised in map 2.2, but only in the green edge seen between blue and red in image 2.3. In deeper water, the oxygen content is too low for the habitat zone to extend all the way down to the bottom, but in shallower water the habitat zone overlaps DO concentrations < 2 mg/L up to the limit where the temperature exceeds 18 °C. Background map: Terrain map ©Lantmäteriet (2020).

Figure 5 visualises the distribution and thickness of the habitat in the study area for S2 and S1 in green. The green colour gradient has the same scale for both basins and the habitat thickness can thus be compared between the basins. The total volume of water in S2 and S1 amounted to 1.03 km³ and 0.277 km³ respectively. The total volume of habitat in S2 constituted 41 % of the total volume of water and amounted to 0.426 km³. The total volume of habitat in S1 constituted 11 %

of the total volume of water and amounted to 0.0303 km^3 . As illustrated in Figure 2, the habitat zone starts at 11.5 m depth in S2 and at 9.4 m depth in S1. The habitat zone then extends down to 40 m depth in S2 and 11.9 m depth in S1.

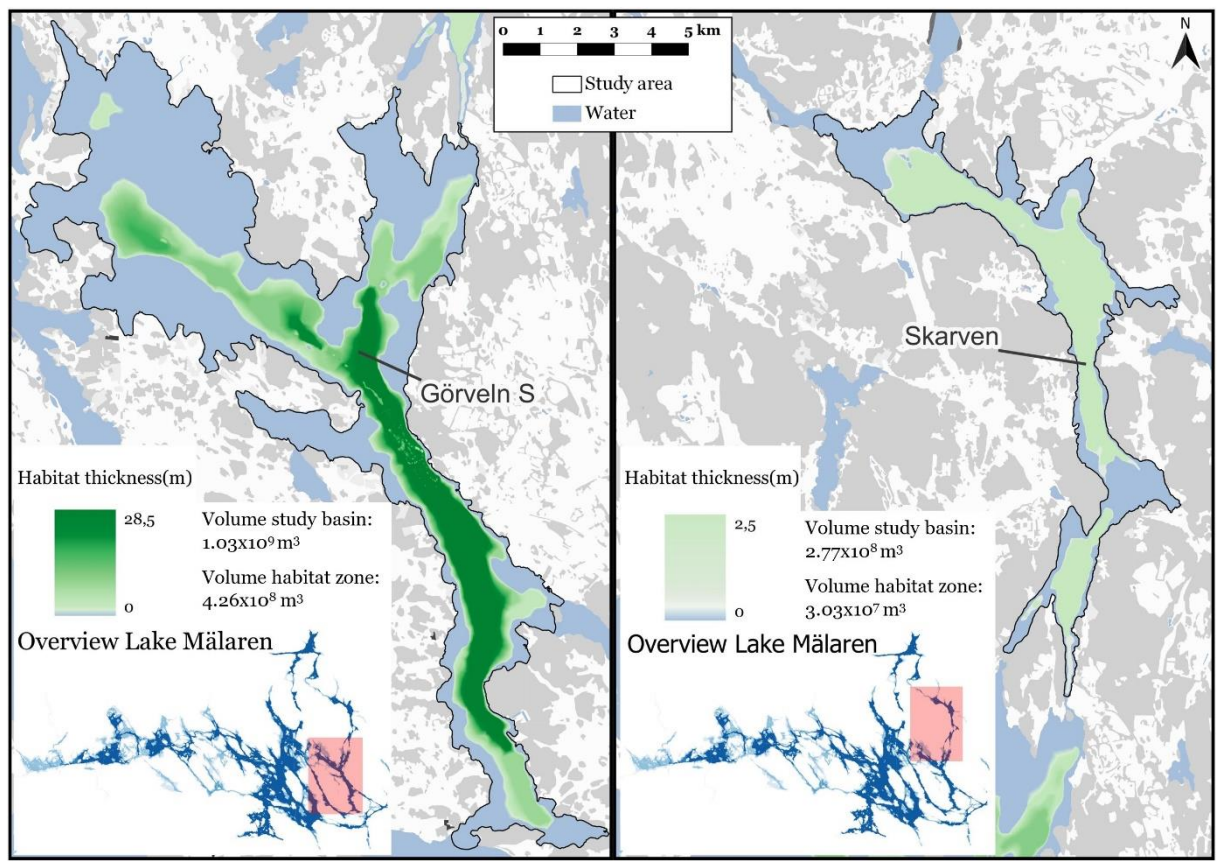


Figure 5: Maps of estimated habitat thickness for vendace in two water bodies in Lake Mälaren, Sweden. The map on the left shows the basin S2 and the map on the right shows the basin S1. The green colour gradient follows the same gradient scale for both maps and shows the habitat thickness of vendace in different parts of the two basins. The habitat thickness is derived from the habitat requirements of the vendace, which are temperatures $\leq 18^\circ \text{C}$ and concentration of dissolved oxygen (DO) $\geq 2 \text{ mg/L}$. Background map: Terrain map ©Lantmäteriet (2020).

Figure 6 illustrates the route the vendace must swim to get from S1 to S2. The red arrows follow the maximum depth of the water, and the distance is calculated for each stage. The first stage has a distance of 694 m. The second stage has a distance of 1455 m.

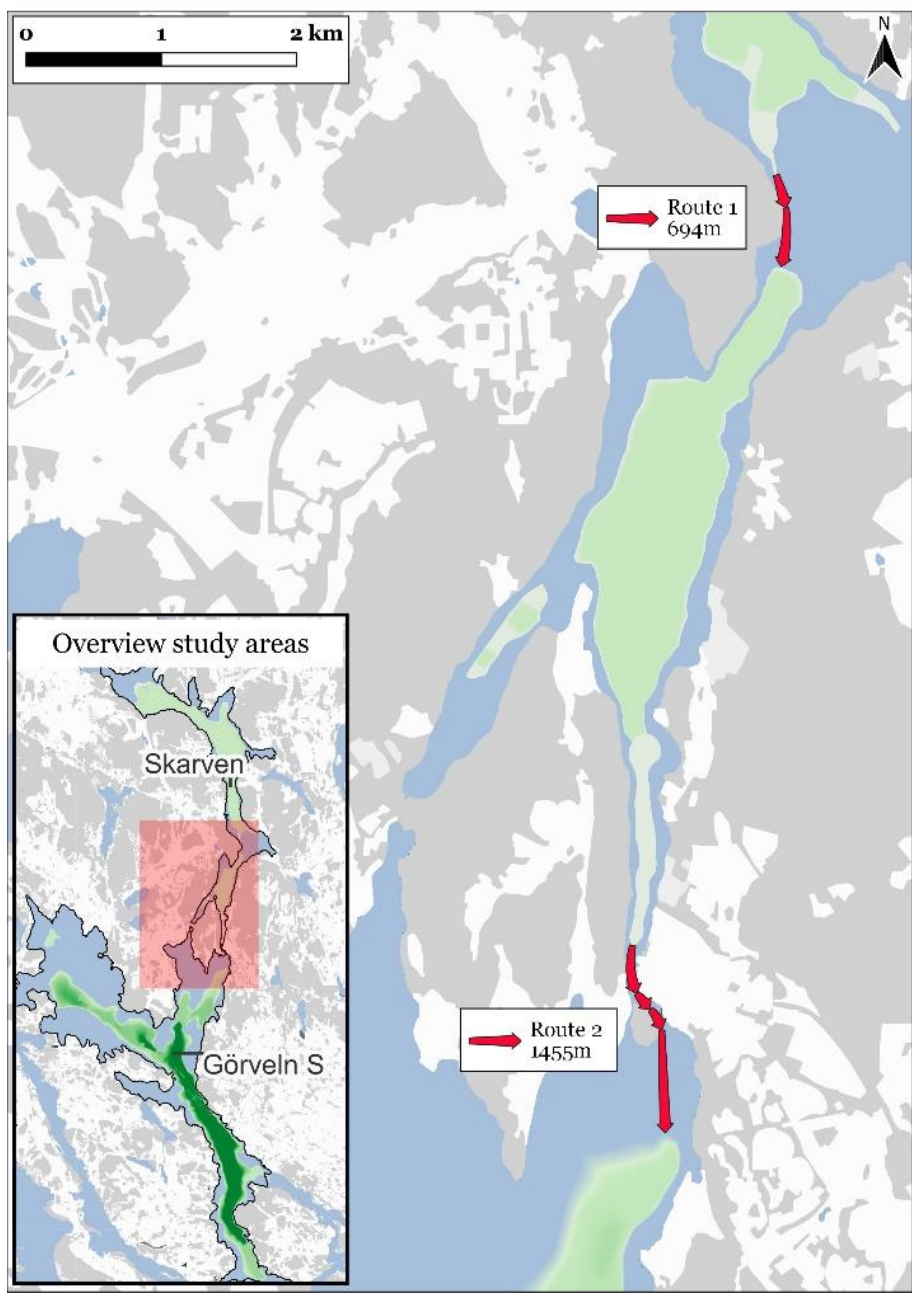


Figure 6: The map shows the passage between two water bodies in Lake Mälaren, Sweden. In the northern basin S1 and the southern basin S2, the vendace habitat is shown in green based on the vendace habitat requirements (temperatures $\leq 18^{\circ}\text{C}$ and concentrations of dissolved oxygen (DO) $\geq 2\text{ mg/L}$). The red arrows (Route 1 and 2) show the path the vendace would have to swim in unfavourable conditions to get from S1 to S2. Background map: Terrain map ©Lantmäteriet (2020).

Discussion

Temperature and DO concentration

The analysis of the eleven stations showed that in four stations there was a complete lack of available habitat for the vendace during the five year period most strained habitat conditions because of the shallow depth not allowing stratification. Therefore, the water temperature exceeds the vendace habitat requirements throughout the depth gradient. Data from the seven stations showing temporal stratification shows that at three stations there has been limited available habitat for vendace (≤ 2.5 m). Both low DO concentration (< 2 mg/L) and high temperature (> 18 °C) have contributed to the compression and reduction of habitat thickness (Figure 3). These results are in line with previous studies demonstrating deteriorating habitat conditions during the summer temperature stratification for cold-water fishes (Kraus et al., 2015; Kangur et al., 2020; Magnuson, 1990; Flood et al., 2021; Tapaninen et al., 1998). The seven stations with available habitat show a water temperature of 18 °C at the beginning of the thermocline and the temperature is decreasing with increasing depth (Figure 3). The upper temperature habitat limit (18 °C) in this study was determined based on Elliott & Bell, (2011), Kangur et al., (2020), Hamrin, (1986), Lilja et al., (2013), Sarkar & Tiwari, (2006), Parkinson et al., (2016), Wehrly et al., (2003) and Marszelewski & Solarczyk, (2011). These articles also state that vendace avoid staying in the epilimnion during temporal stratification. Since the boundary between the epilimnion and the thermocline is only a boundary at which surface water circulation with deeper water ceases, no temperatures are given in the articles covering the temporal layers. Regarding this, an observation was made during the analysis for two stations whose worst habitat conditions occurred on the same date (S2 and S3). The thickness of the epilimnion was 11.5 m and 12.1 m for S2 and S3, respectively, and the pools are separated from each other. The upper temperature habitat limit of 18 °C also occurs at different depths and seems to follow the change between epilimnion and thermocline in the depth gradient (Figure 3). This observation is also seen at other stations from the analysis even if the measurements at them are made on different dates (Figure 3). Thus, when vendace habitat is referred to water temperatures < 18 °C, it coincides with water below the epilimnion in this study and supports that vendace avoid staying in the epilimnion during summer temporal stratification. The difference in the depth of the thermocline in S2 and S3 also supports Benoit et al. (2022), Flood et al. (2021) and Mortimer (1952) who describe that the position of the thermocline in the water body differs depending on the structure of the water body and what external factors the surface water is exposed to, such as wind dynamics.

Although the habitat requirements of vendace are met at temperatures < 18 °C, the habitat requirement is not necessarily the optimal temperature for vendace. According to Kangur et al.

(2020), the vendace has a metabolic optimum of 7-9 °C. When the vendace performs DVM for foraging, it seems that the hypolimnion is the layer that the vendace uses to digest the food where the temperature in the water body is at its lowest (Flood et al., 2021; Hamrin, 1986; Tapaninen et al., 1998). This report has also investigated whether the metabolic optimum of the vendace can be met within the habitat zone (temperature <18 °C and DO concentration >2 mg/L) which could affect the preference of the vendace for different basins. The results show that three of the seven stations showing temporal stratification have temperatures <9 °C within the habitat zone (Figure 3). As expected, most of the stations that lack temperatures <9 °C within the habitat zone are the stations that have the worst conditions to meet the habitat requirements of the vendace. However, an interesting observation is S11 which in Figure 3 shows good conditions for the vendace based on the habitat requirements, but which completely lacks temperatures <9 °C in the depth gradient. If the vendace strives to meet its metabolic optimum temperature, which DVM behaviour may indicate (Mehner, 2012) and as suggested by Hamrin (1986) and Tapaninen et al (1998), S11 could then be a less preferred basin for the vendace to stay in during the temporal stratification even though it is a basin that has good conditions to meet the habitat requirements of the vendace.

S5, S10 and S1 are the three stations with temporal stratification that exhibit the most restricted habitat with the DO concentration being lower than the habitat requirement already in the boundary between the thermocline and hypolimnion (Figure 3). This observation supports the statements of previous studies that oxygen levels are lowest below the thermocline when the water is stratified (Rowe & Chisnall, 1995). The three deepest basins (S4, S2 and S11) also showed the lowest oxygen levels below the thermocline, but in these stations no limited DO concentration (<2 mg/L) was observed in the oxygen profile. S3 stands out from the other seven stations by offering a medium-sized habitat zone relative to the other stations and has a DO concentration <2 mg/L only at the last measurement point. Even there, a decreasing oxygen level is observed below the thermocline. Low DO concentration has a direct impact on habitat thickness and this study shows that the lowest habitat thickness is measured during the last half of August regardless of the year (Figure 3). Since the summer temporal stratification in Sweden takes place between July and October (Axenrot et al., 2023), the results of this study contradict Benoit et al. (2021) who reported that the DO concentration is lowest during the end of the season of the temporal stratification. In the basin S1, the low DO concentration is evident, and it is the most limiting parameter that allows the vendace to have only a narrow strip that meets its habitat requirements. This habitat strip is not constant throughout the basin but varies in thickness depending on the depth of the water body and has a maximum thickness of 2.5 metres (Figure 4 and 5). The DO concentration in S2 is above the determined habitat limit (2 mg/L) in the entire water body for the depth at which measurements were made. In Figure 3, the last measuring point at 40m shows

a DO concentration >6 mg/L. Since the DO concentration was 4 mg/L above the determined limit for the vendace habitat (2 mg/L), it can be imagined that the vendace's habitat requirements were also met in deeper water >40 m. However, when the temperature and oxygen profiles were plotted, a strongly deteriorated oxygen level was observed during short depth changes at several measuring stations, thus the DO concentration could not be determined with certainty in the entire depth gradient for S2 and therefore the depth of 40 m was used as the habitat floor for the vendace in the analysis. The good oxygen supply in S2 means that the vendace has plenty of habitat relative to other stations, even though the temperature limit occurs at a depth of 11.5 metres, which is 1.9 metres deeper than in S1. However, S2 has a higher maximum depth in the basin than S1 has. As mentioned in the introduction, lakes with excessive nutrient inputs can have problems with algal blooms and turbid water resulting in low oxygen levels in hypolimnion. Lake Mälaren has suffered from eutrophication over the years due to the water catchment area carrying nutrients from agriculture and sewage treatment plants into the lake (Sonesten et al., 2013). The vendace temperature requirements throughout the depth gradient are difficult to influence. However, emissions from agriculture and sewage treatment plants can be reduced (Johansson et al., 2021). Reduced emissions would make Lake Mälaren less eutrophic over time resulting in higher oxygen concentrations in hypolimnion, thus increasing the available habitat for the vendace. Since the proportion of water that does not meet the vendace oxygen concentration requirements is 28 % in the basin S1, the available habitat could amount to 39 % (11 % + 28 %) of the total water volume if this basin had the conditions for sufficient oxygen supply down to the bottom. If the oxygen level is below the habitat requirements of vendace at depths below 40m in the basin S2, the same improvement potential is 4 % which would result in 45 % (41 % + 4 %) available habitat of the total water volume of the basin. Improvement measures against eutrophication in Lake Mälaren are implemented throughout the water catchment area and agricultural nutrient emissions are described as the source that requires the greatest action (Havs & vattenmyndigheten, 2019). However, reversing eutrophication is a slow process (Havs & vattenmyndigheten, 2019) and the improvement potential for vendace habitat described in this study could only occur gradually over time.

The habitats in basin S1 and S2 are not entirely contiguous but are divided into larger and smaller habitat patches. This is because within each basin, separate habitat zones are formed by deeper areas surrounded by shallower areas (Figure 5). The shallower areas lack temporal stratification and thus have a water temperature that exceeds the habitat requirements of vendace throughout the depth gradient. S2 has two habitat patches, one of which constitutes most of the total habitat. North-west of the large habitat patch there is a small, isolated habitat patch where it is conceivable that the vendace can get 'stuck' when the habitat shrinks during the summer. Even in the basin S1,

the habitat is divided into patches that can potentially isolate vendace that get stuck there. South of the large habitat patch in S1 there are two isolated habitat patches, one larger and one smaller. It could be imagined that vendace need to escape habitat patches that offer poor habitat conditions. Such a scenario could also apply between basins as, for example, S1, despite its basin size, only offers about 1/10 of the total volume to the vendace habitat in the worst measured scenario during the years 2017-2022. It has been seen that the stock of vendace has increased in recent years because of successful reproduction with high survival (Havs och vatten myndigheten, 2022). However, this increase has only been demonstrated in the deeper basins of Lake Mälaren. It is not entirely unreasonable to imagine that vendace migrate from basins with poor conditions and gather in basins with good conditions during habitat squeeze. If so, this could mean that the increase reported in Havs och vatten myndigheten (2022) can be explained by the fact that the basin studied has held an abnormally large amount of vendace relative to the rest of the year. Havs och vatten myndigheten (2022) also mentions in the report that the increase should be seen in the light of the accumulation of individuals in the places that meet the habitat requirements during the temporal stratification. This study has analysed how an escape from S1 which exhibits poor habitat conditions during the temporal stratification, to S2 which has significantly better conditions for the vendace could look like (Figure 6). Before the analysis, no assumptions were made about further deteriorating conditions, but the analysis was carried out on the known habitat areas that were produced in the spatial analysis. Since the bottom structure in the two basins varies across the lake, habitat patches are formed within each basin as previously mentioned. This means that the vendace will encounter several obstacles along a possible escape route in the form of zones with conditions that do not meet the vendace's habitat requirements. These obstacles can also mean an increased risk of predation from both terrestrial and aquatic predators (Benoit et al., 2022). In the analysis, two non-suitable zones could be found if the vendace starts from the large habitat patch in S1 (Figure 6). The length of the first non-suitable zone was measured at 694 m and goes from the large habitat patch in S1 to a smaller habitat patch further south. The second non-suitable zone was measured at 1455 m and goes from the smaller habitat patch in S1 to the large habitat patch in S2. In relation to the distances that vendace can swim during their spawning migration (Sandlund et al., 1991), the distances analysed are not in any way impossible for vendace to cross. However, the spawning migration takes place during autumn/winter when the temporal stratification is dissolved and thus not under unfavourable conditions. The total distance of 2149m will be completed in temperatures between 18 °C and 21 °C, which is higher than the habitat requirements of the vendace (≤ 18 °C) and only a few degrees colder than 22 °C, which is considered lethal for the vendace (Axenrot et al., 2023). The smaller habitat patch south of the large habitat patch in S1 could serve as a recovery site in case of a possible escape where the vendace can fulfil its habitat requirements to regain strength for the

longer route down to S2. However, if the escape were to occur in shoals, the smaller habitat patch could potentially offer limited opportunities for recovery due to the competition for resources within the boundaries of the habitat. It is also difficult to say how DO concentration would evolve in such an isolated and limited habitat patch. Data from one measuring station is the basis for the habitat calculation in the entire water body for S1, which gives a certain margin of error as DO concentrations with high probability vary in these delimited habitat patches from the large contiguous habitat patches. Both S2 and S1 are large basins with varying structure and surrounding topography that probably create a stratification dynamic within the basin when two habitat patches are cut off from each other in the same way as two separate lakes (Bengtsson, 1978; Flood et al., 2021). Whether the vendace can carry out a similar escape to that presented in this study is difficult to answer and requires further investigation.

The year of 2018 and the heatwave

Five of seven basins show the smallest habitat zone during the last ten days of August 2018. S11 and S1 show the smallest habitat zone in August 2017, but at the same time lack measurement values for August 2018. During the analysis it was also observed that the stratification period was extended in 2018 with a stratification period reaching from May to October. In Sweden, the summer of 2018 was abnormally hot compared to what was previously measured and modelled future scenarios indicate that these types of extreme weather will occur more frequently, last longer and show higher maximum temperatures (Sjökvist et al., 2019). If the thermocline is pushed down to deeper water and reduces the volume of cold water ($\leq 18^{\circ}\text{C}$) during longer and warmer summers, which seems to be the case (Reavie et al., 2017; Mortimer, 1952; Benoit et al., 2021), then the available habitat for vendace in Lake Mälaren will further decrease in the future. It is not completely unreasonable to think that the basins that show the lowest volume of habitat during the summer temporal stratification will be the basins where the habitats first disappear when the temperatures and the time interval for the summer temporal stratification increases.

In Axenrot et al. (2023), the reduction of habitat is described as a potentially population-regulating factor. In their study, data between the years 2011-2014 show that only 10 % of Lake Mälaren fulfils the habitat requirements during the temporal stratification according to the ceiling and floor values for temperature and oxygen that the study used (upper limit: thermocline, lower limit: DO concentration ≥ 3 mg/L). When the study was conducted, only the Swedish Maritime Administration's S-57 data on the depth of Lake Mälaren was available, which results in a less accurate result than by the method described in this report for the depth data. However, it should be mentioned that complete depth data for the entire Lake Mälaren is inadequate in some basins even on Genesis Maps. The digitization of the charts from Genesis Maps also requires interpolation

between known depth values which means that the result may lack bottom structure between them. Supplementing the Swedish Maritime Administration's S-57 data with the depth charts from Genesis Maps would thus increase the depth accuracy but not make it complete. Axenrot et al. (2023) used hydroacoustic and trawl data to obtain actual distribution during the temporal stratification and not just a theoretical distribution as presented in this study. Data on the actual distribution of vendace confirms the theoretical one produced by Axenrot et al. (2023) (<thermocline and DO concentration >3 mg/L) which reinforces the theoretical results presented in terms of spatial habitat distribution. This does not exclude that the temperature limit used in this study (18 °C) is the habitat ceiling of the vendace but at the same time strengthens the hypothesis that the vendace seeks temperatures that meet its metabolic optimum (Kangur et al., 2020). Axenrot et al. (2023) conclude that limited habitat during the summer temporal stratification increases the risk of overfishing on vendace and reduces the vendace's resistance to climate change. Similar to what Jonsson & Setzer (2015) describes in their article on Arctic charr (*Salvelinus umbla*) in Lake Vättern, the impact of climate change on the vendace could also lead to indirect effects, such as trophic mismatch. Jonsson & Setzer (2015) shows that the reproduction process of the Arctic charr can be negatively affected by the development of the fry under resource shortage due to trophic mismatch between the fry and zooplankton. If the vendace chooses to flee basins with poorer conditions to basins with better conditions during the summer, trophic mismatch could occur by the vendace adapting an annual migration behaviour that its predators do not adapt if the predator is not affected in the same way by warmer water. In Lake Mälaren, these warm water predators could be pike (*Esox lucius*), perch (*Perca fluviatilis*) and zander (*Sander lucioperca*) (Granit, 2018). Predators that stay in the basin will have to change prey and hunting behaviour when the vendace escapes the pelagic and the cold free water mass. This would then affect both the predator through a forced change in foraging behaviours and other prey species through higher predator pressure. If the temporal stratification also takes place over a longer period of time, it is not unreasonable to think that a regime shift similar to that described in Angeler et al. (2014) will first occur locally in basins where the habitat is first lost. Such a regime shift would further reduce human utilisation of vendace as a resource and in the long term, directed fishing for vendace would probably cease due to poor profitability. The impact on the ecosystem is difficult to assess in a regime shift, but the change may entail a loss of both biodiversity and ecosystem services (Angeler et al., 2014; Kangur et al., 2020). Such a scenario may therefore require that the ecosystem service provided by the vendace today may have to be taken from another ecosystem, potentially putting another ecosystem under pressure. Knowledge, such as the results produced by this study, can help to anticipate regime shifts and present an opportunity to prevent excessive damage and loss of ecosystem services.

This study and the study conducted by Axenrot et al. (2023) highlight the temporal stratification of Lake Mälaren as a limiting abiotic process for vendace, which is advantageously considered when estimating vendace population size. Using GIS such as QGIS to map the spatial distribution of available habitat as this study has done can be used as a complement to trawl data and hydroacoustic. Although studies on vendace habitat can facilitate the understanding of vendace population dynamics, the results cannot be taken as absolute truth for where vendace will be located in the lake under different conditions. The results from this study only show where the vendace habitat requirements were met on the dates from which the analysis was carried out. Not where the vendace has actually been located. Future studies would benefit from combining theoretical spatial habitat distribution with the actual distribution of the population as carried out by Axenrot et al. (2023). The production of more detailed depth data covering the whole lake would then be beneficial. With such data, highly accurate results of the available habitat of vendace could be produced and any theoretical uncertainties can be confirmed with actual distribution through trawl data and hydroacoustic. To study and understand the temporal stratification dynamics in each basin could also be combined with GIS studies to model future extreme scenarios and thus predict changes in vendace habitat that have not yet occurred and thus deepen the understanding of future vendace population dynamics.

In summary, the results from this study show that the vendace currently has available habitat in parts of Lake Mälaren during the summer temporal stratification, although in some basins it is highly deficient (Figure 3). The future available habitat during the summer temporal stratification in Lake Mälaren can be assumed to decrease with the increased global temperatures and extreme weather situations expected. However, as oxygen levels have been shown to be a limiting factor for vendace habitat, there are measures to be taken to prevent further reduction of available habitat that increases the volume of sufficiently oxygenated water in the depth gradient.

Ethical considerations

No ethical aspects had to be taken into consideration regarding vendace as the study did not conduct any field-based data collection or direct studies on vendace. However, depth data is sensitive to national interests and dissemination authorisation is required when using detailed data from the Swedish Maritime Administration or when collecting detailed data in the field. This study has used the Swedish Maritime Administration S-57 data and open-source data from Genesis Maps which is not subject to dissemination authorisation requirements (SFS 2016:319).

Appendix and Supplementary data

Complete data and appendices such as Photoshop and QGIS workflows, PyQGIS code and R code can be found online at the following link: (https://github.com/Lozon95/BSc_project-git)

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