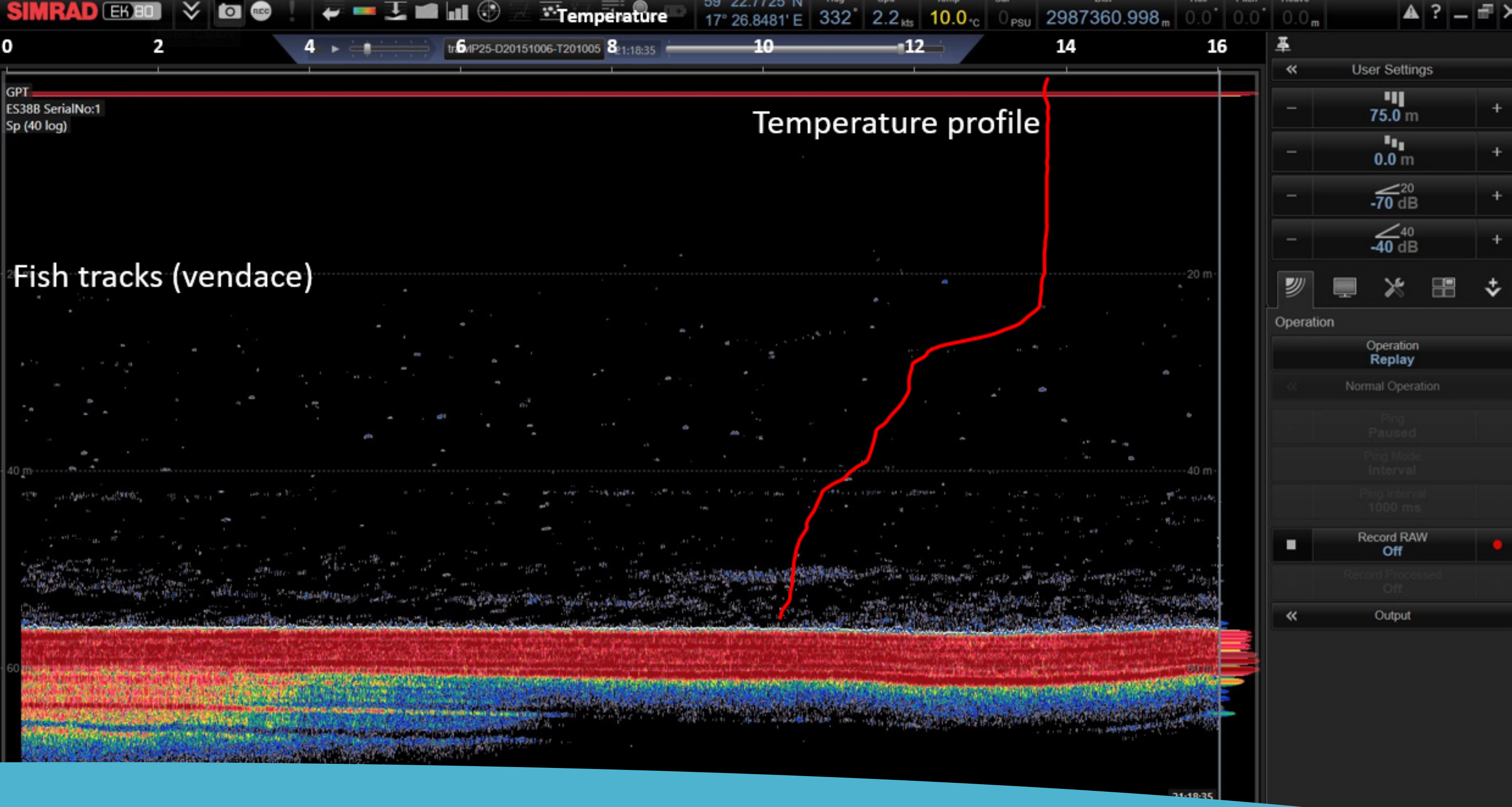

Aqua reports 2023:7

Seasonal variation in thermal habitat volume for cold-water fish populations

– implications for hydroacoustic survey design and stock assessment

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Seasonal variation in thermal habitat volume for cold-water fish populations - implications for hydroacoustic survey design and stock assessment

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Funding: Swedish Agency for Marine and Water Management, 1:11 (SLU.aqua.2022.5.1-256)

The report has been produced on behalf of the Swedish Agency for Marine and Water Management. The authors of the report are responsible for the content and conclusion of the report. The content of the report does not imply any position on the part of the Swedish Agency for Marine and Water Management.

Responsible for publication series:	Noél Holmgren, Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources
Editor:	Stefan Larsson, Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources
Publisher:	Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources
Year of publication:	2023
Place of publication:	Uppsala
Illustration cover:	Echogram from Simrads EK80. Collage by Thomas Axenrot.
Copyright:	All images are used with the permission of the author.
Title of series:	Aqua reports
Part number:	2023:7
ISBN:	978-91-8046-847-3
DOI:	https://doi.org/10.54612/a.5i05rb1iu1
Nyckelord:	Habitat volume, thermal stratification, survey design, stock assessment, vendace, *Coregonus albula*
Rekommenderad citering:	Axenrot T, Degerman E, Asp A (2023) Seasonal variation in thermal habitat volume for cold-water fish populations; implications for hydroacoustic survey design and stock assessment. Aqua reports 2023:7. Uppsala: Institutionen för akvatiska resurser, 27 pp. https://doi.org/10.54612/a.5i05rb1iu1

Abstract

For accurate stock assessment, survey design must consider fish behavior and ecology. Yearlings and older individuals of the commercially exploited cold-water species vendace (*Coregonus albula*) are found below the metalimnion through periods of thermal stratification. These stratification periods generally last for 3-4 months, from the middle of summer to early autumn. In lakes with heterogeneous distribution of depths, the habitat volume for vendace vary drastically within and across years, which affects the distribution and population densities. Variable thermal habitat volumes, with food and oxygen depletion in the hypolimnion through the period of stratification, may act as a population size-regulating factor.

Using hydroacoustics in combination with trawl data and temperature profiles, we examined the distribution of vendace through annual periods of thermal stratification. We found that yearling and older vendace these periods were confined to cold-water habitat volumes representing less than 10 % of the total water volume of Lake Mälaren, the third largest lake in Sweden. By introducing stratification to the design of hydroacoustic surveys supported by midwater trawling, seasonal aggregations of fish in temporally restricted thermal habitat volumes can be used to lower survey effort and improve the precision in estimates of population size. Temporally restricted habitat volumes may induce risks for the populations to over-fishing and sensitivity to environmental changes that potentially may call for directed management.

Sammanfattning

Vid skattning av beståndsstorlek måste undersökningen utformas med hänsyn till fiskarnas beteende och ekologi. Ettåriga och äldre individer av den kommersiellt utnyttjade kallvattenarten siklöja (*Coregonus albula*) återfinns under språngskiktet under perioder av temperaturskiktning. I siklöjans utbredningsområde varar dessa perioder i allmänhet i 3-4 månader, från mitten av sommaren till tidig höst. I sjöar med heterogen fördelning av djup kan habitatvolymen för siklöja variera drastiskt under ett år såväl som mellan år. Detta påverkar siklöjepopulationers utbredning och täthet. Habitat med varierande temperatur, med brist på föda och syre i hypolimnion under den temperaturskiktade perioden, kan fungera som en populationsstorleksreglerande faktor. Vi använde hydroakustik med tråldata och temperaturprofiler för att undersöka utbredningen av siklöja vid årligen återkommande perioder av temperaturstratifiering. Resultaten visade att utbredningen av ett-åriga och äldre siklöjor under dessa perioder var begränsad till habitat med kallvatten som utgör mindre än 10 % av Mälarens totala volym. Genom att införa stratifiering vid utformningen av hydroakustiska undersökningar som stöds av pelagisk trålning, kan ansamlingar av fisk i säsongsvis temperaturbegränsade habitat användas för att minska ansträngningen och förbättra precisionen vid uppskattning av populationsstorlek. Tillfälligt begränsade habitatvolymer kan medföra risker för populationer med avseende på överfiske och känslighet för miljöförändringar som potentiellt kan kräva riktad förvaltning.

Content

1. Introduction

Ecosystem-based fish and fisheries management aims at handling impacts of fishing and other human activities on aquatic ecosystems (Bianchi and Skjoldal 2008). For proper management of fish populations and fisheries, it is important that estimates of fish abundance, recruitment and development over time are accurate and precise. This may be difficult as the distribution of fish is heterogeneous and governed by shifting habitat preferences through life-span, variation in habitat suitability within and across years as well as during migration. Precise and cost-effective sampling thus requires knowledge of habitat use over the season and for different ontogenetic life stages (Wootton 1998). Factors that influence habitat selection can be divided in ultimate (long-term, functional) and proximate (short-term, immediate response) cues (Noakes 1992). Aggregations of fish may have different causes such as light conditions, beneficial temperature and oxygen levels, but also depend on biotic factors such as food availability, competition, predator avoidance and spawning (Clark and Levy 1988, Neilson and Perry 1990, Helfman 1993, Fréon and Misund 1999). Fish may be forced by physical factors to occupy a discrete water volume, referred to as the habitat volume (Clark et al. 2004). Temperature is considered one of the most important factors for habitat selection in fish, as body temperature in most fish is governed by the surrounding water temperature. Water temperature also affects oxygen levels (Grow et al. 2022), which is another key determinant for fish metabolism. Fish are sensitive to temperature differences and can detect variations in temperature smaller than 0.1° C (Hoar and Randall 1979). This allows fish to orientate towards water volumes with favorable temperatures, e.g., for metabolic needs (Batty 1994). Most lakes in the temperate region are stratified through the warm season. The upper layer, the epilimnion, is separated from the colder bottom water, the hypolimnion, by the metalimnion at a depth mainly determined by the heating of the sun and the mixing power of winds (Boehrer and Schultze 2008, Jacobson et al. 2013). The metalimnion is often referred to as a boundary for lake fish habitat selection (Northcote and Rundberg 1970, Clark and Levy 1988). This thermal stratification is commonly present for several months in temperate lakes and is likely the driver of annually repeated distribution patterns observed in temperate and boreal regions (e.g. Helfman 1993, Fernö et al. 1998).

Vendace (*Coregonus albula*) inhabits freshwater and weak brackish waters across northern Eurasia (Enderlein 1981, Kullander et al. 2012). It is a pelagic, zooplanktivorous species (Northcote and Hammar 2006). The thermal habitat selected by adult vendace is colder water, not exceeding 18° C, while young-of-the-year vendace can be found in the warmer water in the meta- and epilimnion (Northcote and Rundberg 1979, Hamrin 1986). In Lake Peipsi (Estonia/Russia), that exhibits unstable summer stratification, vendace avoided areas with a water temperature above 18-19° C (Jaani 1996, Kangur et al. 2020). Through the period of thermal stratification, adults are hence found below the metalimnion (Hamrin 1986, Jurvelius et al. 1988, Mehner et al. 2010). It has been suggested that adult vendace do not cross the thermocline (Helland et al. 2010), but Lilja et al. (2015) observed, with hydroacoustics, that probable vendace temporarily crossed the thermocline into water of 22-23° C. Accordingly, Hamrin (1986) found that young-of-the-year vendace migrated into the epilimnion during night while adults did not move further than into the metalimnion. The European Inland Fishery and Aquaculture Advisory Commission (EIFAAC; 1969) states that temperatures of 23-24° C are lethal for vendace. Mehner et al. (2007) followed the vertical migration of vendace *(C. albula)* and Fontane cisco (*Coregonus fontanae)* over 10 months and suggested that diel vertical migration in these species was a genetically fixed behavior as they found no correlation with food, predators or bioenergetic advantages. For the North-American cisco (*Coregonus artedi*), a similar and closely related species, Rudstam and Magnuson (1985) estimated preferred temperature to 12° C. An oxygen level of 3 mg/l has been suggested as the lower limit of the habitat for cisco (*C. artedi*; Jacobson et al. 2010, Grow et al. 2011).

As fish distribution is governed by habitat suitability, the choice of habitat is a key interest when estimating population size and distribution (Kramer et al. 1997, Fréon and Misund 1999, Bianchi and Skjoldal 2008, Jacobson et al. 2010, Grow et al. 2011). Fish – and especially pelagic fish - live their lives in a three-dimensional environment, why pelagic fish distribution needs to be analyzed from both a horizontal and a vertical perspective. Thus, the behavior of pelagic fish plays a major role in population size and stock assessment surveys using hydroacoustic technology, and may be a bottleneck in interpreting the acoustic data (e.g. Fernö and Olsen 1994, Fréon and Misund 1999, Godö et al. 2014).

Living in a restricted habitat volume during part of the year may facilitate accurate sampling for "ground truth", i.e. a representative sample of fish by trawling used to interpret acoustic signals. However, the restricted habitat volume also put the species at risk of bottleneck intra-specific competition, over-fishing and consequences of environmental changes.

This study investigates how seasonal variation in thermal habitat can be used to facilitate stock assessment of vendace - a cold water species – and improve precision in the estimates of population size. We also discuss future scenarios of climate change based on a previous 45-years environmental perspective. The study was conducted in Lake Mälaren, where the vendace population drastically decreased in the early 1990s, potentially caused by over-fishing in combination with recruitment failure (Nyberg et al. 2001).

2. Material and methods

2.1. Lake Mälaren

Lake Mälaren was chosen as study area as the lake is extraordinary heterogeneous with many discrete bays and basins separated by narrow sounds (Figure 1). It is the third largest lake in Sweden with an area of 1 114 km^2 and a water volume of 14.3 km^3. The average depth is 13 m and maximum depth 76 m. L. Mälaren is an important water reserve for about two million people that live around the lake and as such, water quality and ecological status have been monitored for a long period of time (Anonymous 2013). From west to east, the general pattern is increasing bottom depths and decreasing nutrient levels. L. Mälaren holds 34 different species of fish (Degerman et al. 2001, Beier et al. 2015). The total annual catch in the commercial fishery is about 270 tons (mean for 2016-20) and presently mainly focused on pikeperch (*Sander lucioperca*). Until the early 1990s, vendace was a commercially important species, fished mainly for the roe. The fishery on vendace more or less stopped after a drastic decrease in the catches, from a mean annual catch of 156 tons (1970-1989) to 36 tons 1990 and decreasing thereafter. The decline in the landings of vendace was caused by an equally drastic decrease in population size (Nyberg et al. 2001). The present day fishery is still small (10 tons 2021). Regular recruitment and increasing population size over the last decade indicate that the vendace population in L. Mälaren is slowly recovering.

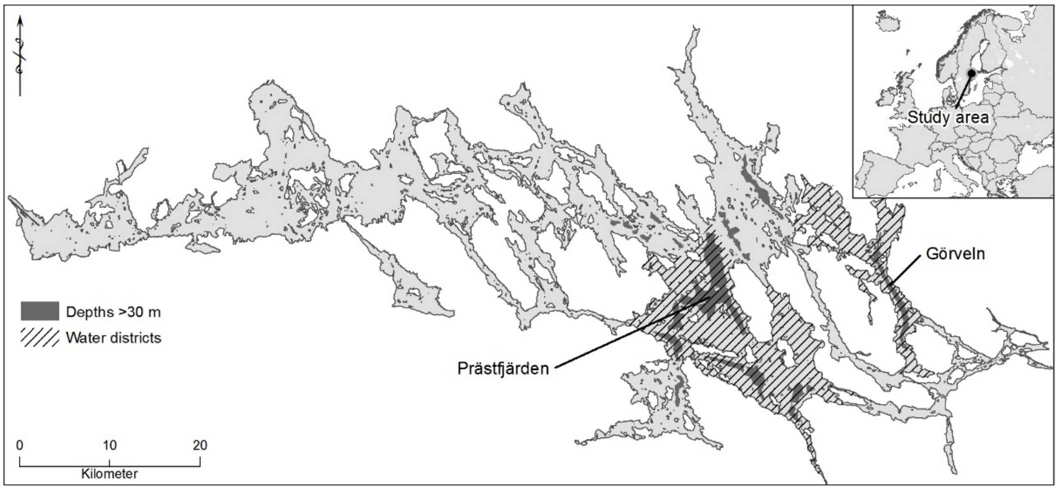

Figure 1. Lake Mälaren is the third largest lake in Sweden (1,114 km^2) and a water reserve for two million people. It has an extraordinary heterogeneous morphology and bottom topography with the largest depths in the eastern parts.

2.2. Thermal habitats for vendace

Through the period of thermal stratification in L. Mälaren (July-October; Anonymous 2013), the habitat for cold-water fish like vendace is confined to the hypolimnion. The water volume of this thermal refuge was calculated from depth data compiled from digital charts (Swedish Maritime Administration) and completed with depth data from hydroacoustic surveys and other activities recording depth data. Datasets were processed (ArcGIS 10.2.2) to estimate areas and water volumes along a depth gradient. Data on areas and water volumes at different depths were extracted in 5 m layers (Table 1). Parts of L. Mälaren where exchange of migrating vendace was not probable (mainly the basin Ekoln) were excluded in Table 1. Assumed available habitats (depths >30 m) were determined from temperature preferences of yearling-and-older vendace (e.g. Rudstam and Magnuson 1985, Hamrin 1986, Helland et al. 2010), depth profile temperature data (Figure 4) and frequency of vendace in trawl catches at different depths (Table 2, Figure 2). The assumed available habitats are visualized in Figure 1. The preferred thermal habitat volumes were confirmed by the absence of yearling-and-older vendace in the trawl catches from two other surveyed areas shallower than 30 m (thus lacking hypolimnion, not shown).

Table 1. Areas and water volumes in 5 m depth layers. Lake Mälaren, Sweden.

Depth (relative surface, m)	Area (km^2)	Volume (km^3)	Volume portion (%)
0	1114	10.703	
5	680	6.572	61,4
10	447	3.830	35,8
15	207	2.411	22,5
20	140	1.561	14,6
25	96	0.979	9,1
30	64	0.579	5,4
35	39	0,328	3,1
40	25	0.172	1,6
45	15	0.076	0,7
50	7	0.023	0,2
55	2	0.002	0,02

Table 2. Cumulative, depth stratified trawling results through 2011-14 for the basins Prästfjärden and Görväln (L. Mälaren, Sweden) for young-of-the-year (0+) and yearling-and-older (>0+) vendace.

Trawling depth	Number of vendace 0+	Number of vendace >0+	Number of trawl hauls
5-10 m	1	0	6
15-20 m	1	3	1
20-25 m	49	48	5
25-30 m	0	48	1
30-35 m	46	563	3
40-45 m	1	407	3

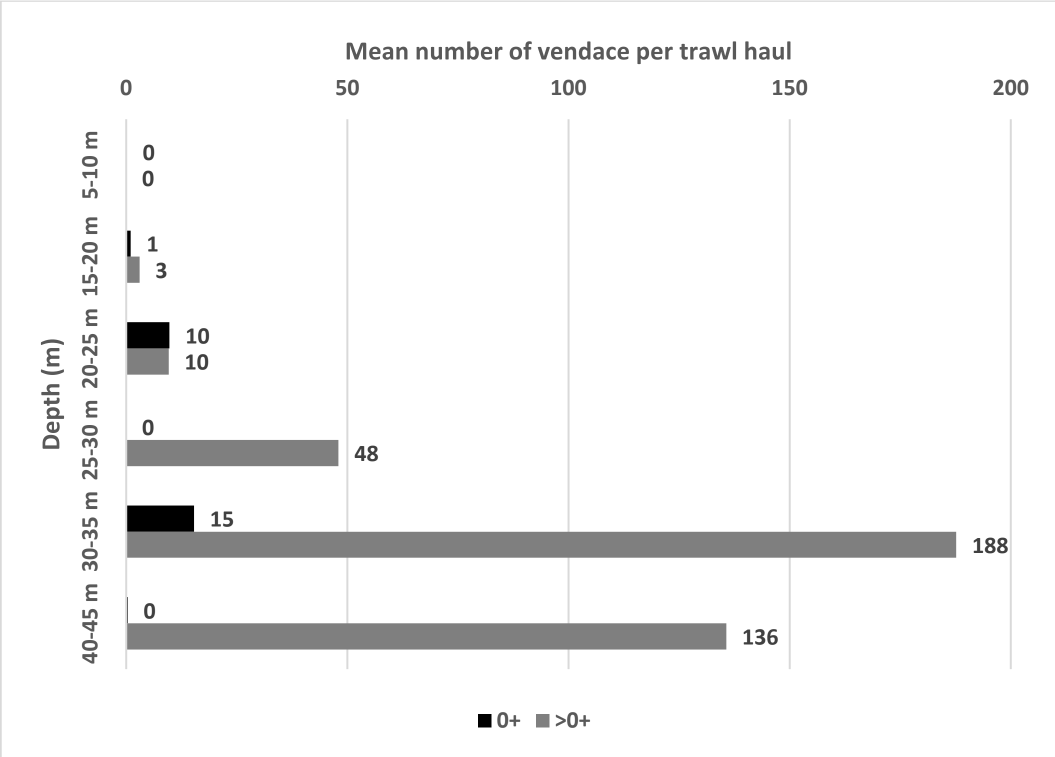

Figure 2. Mean number of vendace per depth stratified trawl hauls through 2011-14 for the basins Prästfjärden and Görväln (L. Mälaren, Sweden) for young-of-the-year (0+) and yearling-and-older (>0+) vendace.

2.3. Hydroacoustics

Hydroacoustic fish monitoring surveys supported by midwater trawling were performed in late September to early October in 2011-2014 in the basin Prästfjärden, and in 2011 and 2013-2014 in the basin Görväln (Figure 1). The surveys were performed in darkness, starting one hour after sundown and stopping at the latest one hour before sunrise.

The hydroacoustic data were collected along transects using a hull-mounted transducer (Simrad ES120-7C) and echo sounder Simrad EK60. The echo sounder was calibrated according to recommendations by Foote et al. (1987) and the manufacturer (Simrad). Pulse length was set to 0.512 ms and power to 150 W. The ping rate was 3 pings/s. The threshold for target strength of single echo detections was set to -60 dB to include small, young-of-the-year fish. Data sets were processed to allow for comparing the results of vendace densities from the whole basin Prästfjärden with the corresponding results from areas restricted to vendace habitat volumes in this basin and the basin Görväln. Such habitat volumes were determined for areas with bottom depths ≥30 m considering the thermal stratification, the temperature preferences of yearling-and-older vendace and frequency of vendace in trawl catches at different depths (Table 2). In 2011, a survey was performed that covered all presumed vendace thermal habitat volumes (Figure 1).

2.4. Midwater trawling

Midwater trawling data was used as ground truth, i.e. to assign species composition and size distribution to the hydroacoustic data. Trawling speed was 2.5 knots. The trawl hauls were limited to 10 minutes due to high densities of fish. The trawl mouth opened 5 m × 12 m (height × width). The cod-end was partitioned into two bags with mesh-size 5 and 7 mm, respectively, allowing retention of juvenile fish. The trawl hauls were performed the same night as the corresponding hydroacoustic data were collected to be representative for basins and depths. Due to the thermal stratification, the trawl hauls in each basin were performed in three depth strata; the shallow part of the water column (5–10 m), around the metalimnion (usually 10–20 m) and in the hypolimnion (>20 m). Trawl catches were identified to species and individually measured for total length and weight. If the number of individuals of a certain species exceeded 300, a random subsample of 100 juveniles and 200 adults were measured per each trawl haul. The total catch of each species in each trawl haul was weighed. The trawl catch composition, i.e. species, size proportions and – for target species like vendace – the proportion of young-of-the-year (0+) and yearling-and-older (>0+) were assigned to the hydroacoustic densities for each basin. In this process, trawl data from each basin was partitioned into classes (species, individual fish lengths, geo-position, fishing depth, and bottom depth). Fish lengths (total length) were transformed to target strengths based on Love (1971) and CEN (2014). Species and size-groups within species from the trawl data were matched with densities for corresponding size-groups in the hydroacoustic data, extracted in intervals (elementary distance sampling units determined to avoid auto-correlation) and layers (5 m). The final density for one species, or size-group within a species, for a discrete basin was calculated from the mean of intervals and sum of layers. In order to restrict an estimate to the presumed thermal habitat volumes for vendace, i.e. the hypolimnion according to literature, and temperature and trawling observations, density was also calculated using data only from areas where bottom depths were 30 m or more.

Classification of vendace as young-of-the-year juveniles (0+) and yearling-and-older (>0+) was based on annual size-distributions in the trawl catches and experience of age determination from scales and otoliths (Figure 3). The abundance of vendace included zero values, displayed a significant positive skew and was $\log_{10}x+1$-transformed in the statistical analysis.

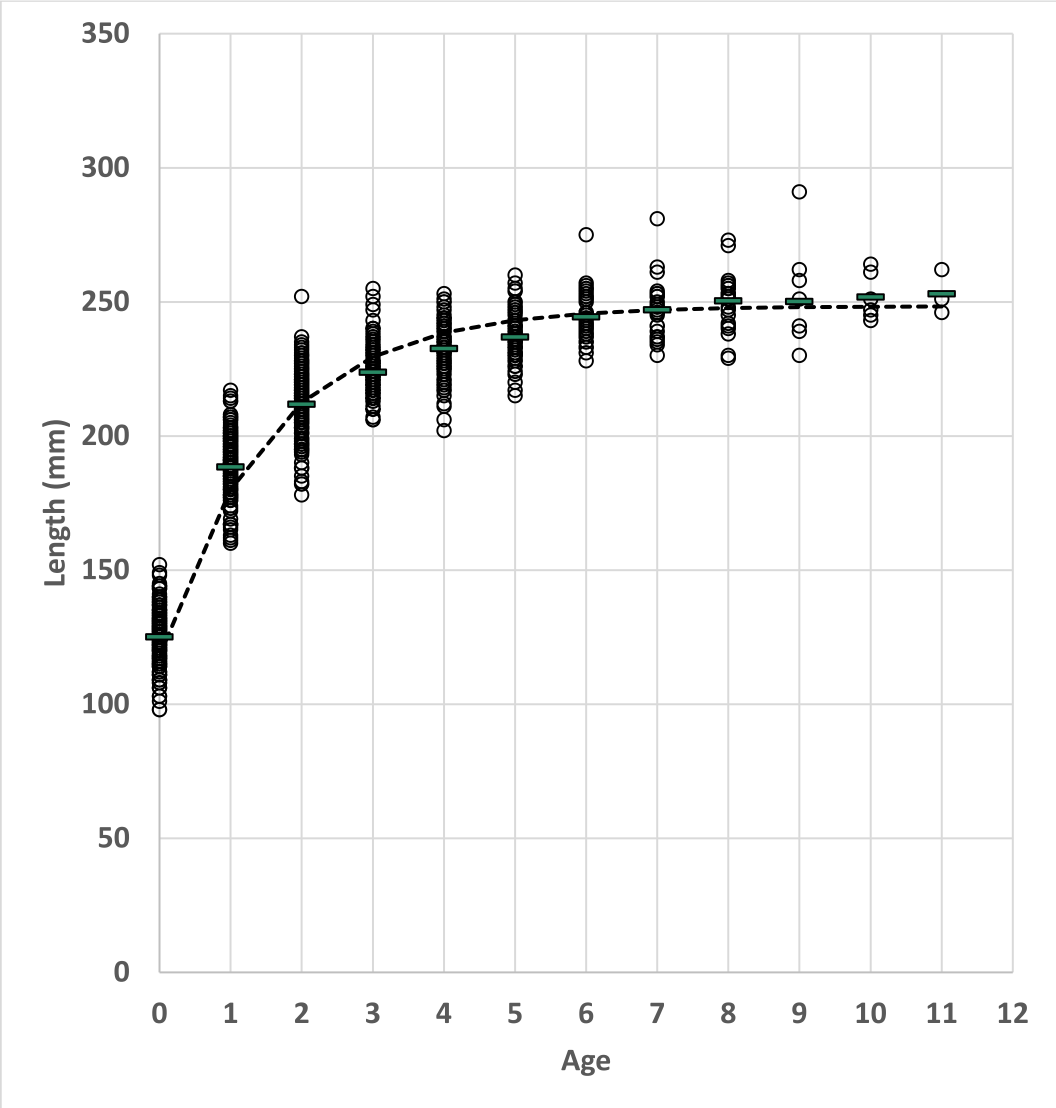

*Figure 3. Length at age for vendace (*Coregonus albula*) in L. Mälaren, Sweden. Bars mark mean length and dotted line growth curve with L_{inf} (v Bertalanffy). Data from trawl catches in September 2008-17.*

2.5. Temperature profiles

Water temperature profiles were taken in combination with the hydroacoustic data collection and trawling with a probe (SST CTM208, software SDA v. 1.83, SST GmbH) at each surveyed basin for each year (Figure 4). The water temperature was registered every 0.5 m from surface to the bottom at the actual position, which was chosen to include hypolimnion temperatures.

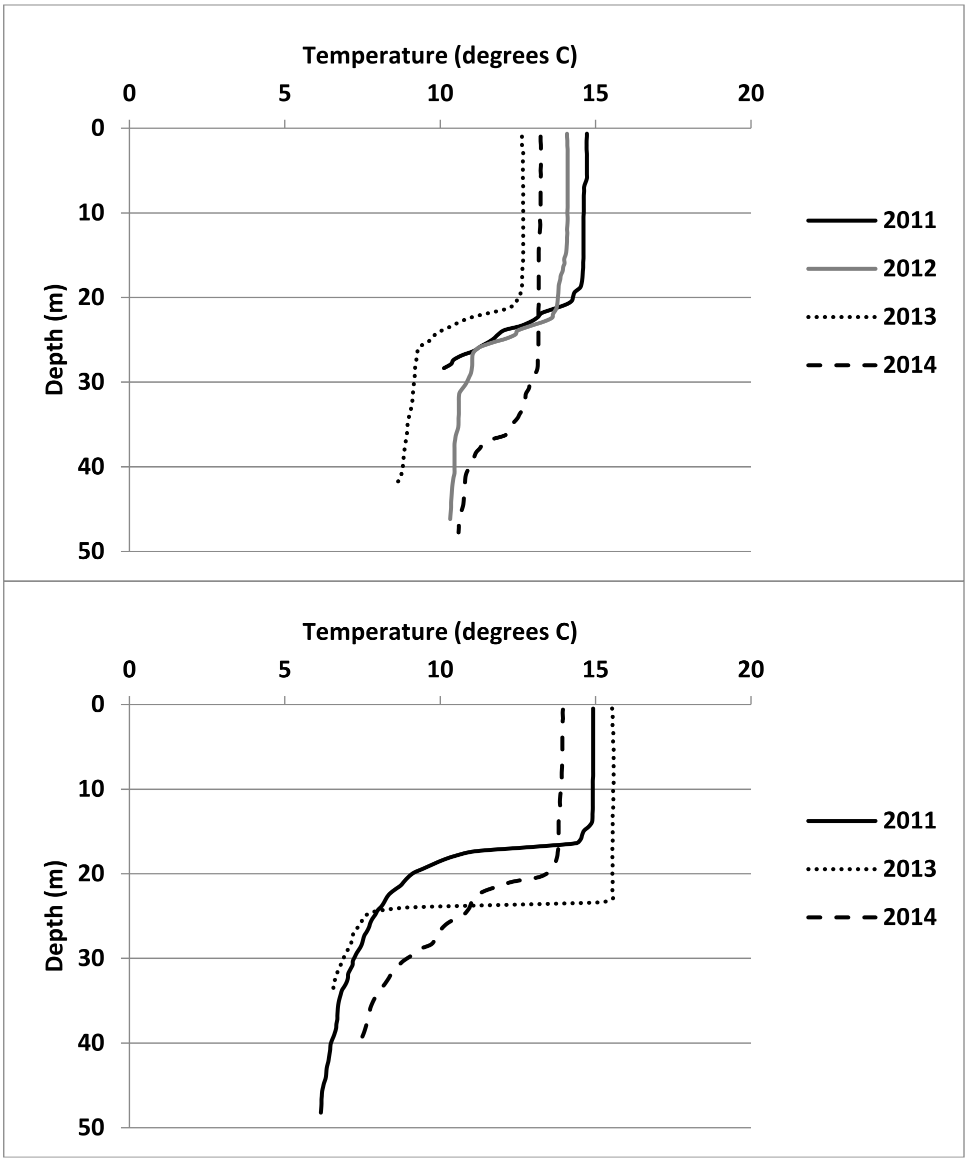

Figure 4. Water temperature profiles for the period 2011-2014 in Prästfjärden (upper) and Görväln (lower), Lake Mälaren (Sweden). Temperature profile data were collected through the period 20 September to 2 October.

3. Results

The estimated abundance and variation of yearling and-older vendace from hydroacoustics and trawling, expressed as mean densities with confidence interval (95 %) and coefficient of variation for Prästfjärden (2011-2014), Görväln (2011, 2013-14) and all areas with vendace thermal habitat volume (2011), are presented in Table 3. In Görväln, the areas surveyed with hydroacoustics already fulfilled the criterion of bottom depths of 30 m or more (i.e. as thermal habitat volume) because of the bottom topography of this basin. Abundance estimates from the survey in 2011 covering all areas with the habitat volumes for vendace were calculated accordingly (Table 3, Figure 1).

One consequence of the restricted thermal habitat volume for vendace during the stagnation period July-October was that practically the whole population (yearlings-and-older) was aggregated in relatively small areas of the lake (5,4 % at 30 m depth; Table 1). This observation was confirmed by trawling results 2011-2014 in the corresponding areas (Table 2, Figure 2). A drastic increase in abundance was observed from 30 m depth. The hydroacoustic abundance (HA; log10(x+1)) of vendace in September 2012-2014 was significantly correlated to depth (m) and water temperature (C; Equation (1); Linear regression, $r^2_{adjusted}=0.57$, Anova $F_{2,721}=189.2$, $p<0.001$).

HA (log10) = 1.073 + (0.050*Depth) - (0.057*Temperature) (1)

Water temperature profiles for 2011-2014, collected in the period September 20 through October 2 before the annual temperature stratification had been broken, showed differences between basins and between years for the same basin. Results are shown for each year and separately for the two basins Prästfjärden and Görväln (Figure 4).

The results on vendace densities showed consistently reduced variation when datasets including assumptions on vendace thermal habitat volumes were used, i.e. when temperature/depth post-stratified data were used in the analyses (CV; Table 3). The stratified results on densities still varied between areas and years, which could be expected as thermal habitat volumes differ between areas and years depending on the annual variation of thermocline depth and thereby temperatures. In Prästfjärden 2011-2014 density did not differ significantly between stratified and un-stratified results (t-test, t=-0.77, df=6, p=0.467) whereas the decrease in corresponding CV was significant (t-test, t=4.26, df=6, p=0.005).

Table 3. Mean densities (number/km^2) of vendace in two separate basins - Prästfjärden (2011-2014) and Görväln (2011, 2013-14) - and for all areas containing suitable habitat volumes for vendace (2011) in L. Mälaren, Sweden. Results are presented as regularly processed (no depth stratification, i.e. all depths) and temperature/depth stratified. Abbreviations: P (Prästfjärden), G (Görväln), nd (no data), CI (confidence interval 95 %), CV (coefficient of variation), N (EDSU) (number of elementary distance sampling units).

Basin/Area	**Density**	**2011**	**2012**	**2013**	**2014**
Prästfjärden,					
no depth stratification	Density	24000	154200	153100	92600
	CI	72	480	298	262
	CV (%)	84	76	60	91
	N (EDSU)	30	23	37	40
Prästfjärden >30 m	Density	30100	231500	179200	146500
	CI	405	494	270	297
	CV (%)	53	39	43	50
	N (EDSU)	9	13	31	23
Görväln (>30 m)	Density	208200	nd	283600	144200
	CI	252	nd	869	284
	CV (%)	21	nd	49	36
	N (EDSU)	11	nd	10	13
All-deep-areas, no					
depth stratification	Density	93200	nd	nd	nd
	CI	168	nd	nd	nd
	CV (%)	74	nd	nd	nd
	N (EDSU)	64	nd	nd	nd
All-deep-areas					
(>30 m)	Density	155400	nd	nd	nd
	CI	301	nd	nd	nd
	CV (%)	53	nd	nd	nd
	N (EDSU)	29	nd	nd	nd

4. Discussion

In general, seasonal aggregations of fish in restricted habitat volumes can be hazardous for the population because of increased exposure to predators, fishery or environmental disturbances. However, the situation may lead to that a large proportion of the population is gathered at a relatively small and predictable area. Such a situation may therefore be capitalized on for an assessment of the size of a whole population. As a larger proportion of the population is detected at a smaller area, the use of information on thermal habitat limits is likely to give more accurate and precise measures of population size at lower survey costs. Using this approach, the vendace population in L. Mälaren in 2011 could be estimated to about 9 million individuals (yearling-and-older) representing 736 tons (calculated from mean weight of yearling-and-older vendace in 2011).

The reported commercial landings of vendace from L. Mälaren recent years have been low (average over 2012-21 was 6.6 tons). However, in the light of the landings before the collapse of the vendace population in L. Mälaren in the early 1990s, with annual average landings of 150 tons, the risk of overfishing could have been imminent with annual harvests of 20 % of the population biomass, given it was of the same magnitude as recently assessed.

For assessment of population size, such aggregations can also be used to decrease survey effort by minimizing the area to be monitored. For surveys that cover larger areas than known thermal habitats, data processing and analysis should be stratified for areas and depths for more accurate and precise measures of population size (Adams et al. 2006).

Vendace temperature preferences and choice of habitat (young-of-the-year juveniles excluded) through the period of summer stagnation will affect populations differently depending on the depth and the morphology of lakes. In lakes with a mostly homogeneous morphology and large depths, vendace can remain in areas that hold large volumes of cold water in the hypolimnion. In lakes with heterogeneous morphology and varying depths, like L. Mälaren, vendace have to adjust their choice of habitat to areas that offer the preferred conditions (Hamrin 1986, Jurvelius et al. 1988, Mehner et al. 2010). In L. Mälaren, the summer stagnation with thermal stratification lasts from July to October (Anon., 2013) with some minor variation between years. Through this period, for the vendace population in L. Mälaren, a temperature preference of ≤12° C (Rudstam and Magnuson 1985, Mehner et al. 2010) reduces the potential thermal habitat volume with over 90 % to only one km^3 or less (Table 1), depending on annual variation.

Through these periods of restricted thermal habitat volume, seasonally resulting in locally very high vendace densities, vendace experience reduced oxygen levels in the hypolimnetic habitat (Anon. 2013) and presumed food depletion during the summer growth period. Furthermore, the thermal habitat volume in discrete areas show inter-annual variation caused by differences in wind exposure that establish the depth of the thermocline. Thus, the habitat volume in a discrete area may differ from one year to another.

Many freshwater fish species in temperate and boreal regions that prefer cold-water experience seasonally decreased habitat volumes. Climate change may impair their situation through these periods (e.g. Jacobson et al. 2013). Hypothesized future prospects of increasing water temperatures through longer periods might increase the duration of lake stratification and potentially decrease the suitability of the habitat volume further due to oxygen depletion. Contrary, increased brownification might induce a more shallow warming of the water and result in a more shallow thermocline and increased habitat volume. However, increased total organic matter (TOM) from decomposition processes would result in decreased oxygen levels, especially in the hypolimnion through the period of stagnation, which would again decrease the habitat volume.

In the case of thermal habitat volumes for vendace in L. Mälaren, a weak increase in mean water temperatures has been observed from 1995 (data from Prästfjärden 1965-2011; Anon. 2013). Data on surface and bottom temperatures (in August) were available for the same period. The mean difference between surface and bottom temperatures, when data were grouped 1965-1987 and 1988-2011, showed a weak increase in two out of three basins that hold cold-water habitats July-October (Anon. 2013). Bottom oxygen levels from Prästfjärden showed an annually recurrent decrease during the stagnation period July to October. The lowest mean oxygen level (October) was not below 5 mg/L, but occasional levels down to 2 mg/L have been noted, i.e. clearly below the lower limit of 3 mg/l suggested by Jacobson et al. (2010) for cold-water species. However, Anon. (2013) concluded that future oxygen levels were not likely to decrease to critical levels, as TOM was low and expected not to increase in these areas. Watercolor (brownification) experienced only a weak increase 1965-2011 in the eastern, deeper parts of L. Mälaren (Anon. 2013).

The natural environment for fish allows for distribution in three physical dimensions, but with time as a fourth dimension, which needs to be considered when management surveys are planned (Fréon and Misund 1999, Simmonds and MacLennan 2005). Hydroacoustic technology enables studies of fish in all these dimensions, but fish behavior still needs to be accounted for in the planning process and in interpreting acoustic data and the results on fish abundance and distribution (Fernö and Olsen 1994, Fréon and Misund 1999, Adams et al. 2006). When applicable, accuracy and precision in estimations of stock size can be improved through a stratified design of hydroacoustic surveys and by properly assigning the ground truth data – usually from midwater trawling for pelagic species – to the hydroacoustic data (Adams et al. 2006, Yule et al. 2009 and 2012).

The results showed considerable variation in vendace densities between basins within the same year. The results also varied depending on the strategy that was used for survey planning, analyses and assigning ground truth to the hydroacoustic data (Table 3). The depth of the thermocline determined the thermal habitat volume for each basin separately, and could vary between basins the same year as well as between years (Figure 4). Consequently, to achieve the most accurate estimate on local and total abundance for a discrete year, all basins with vendace thermal habitat volumes should be surveyed with proper timing. Data on temperature profiles should be collected for each surveyed basin to determine the actual habitat volume. Finally, the assigning of ground truth data to the hydroacoustics and the following analyses should be temperature/depth stratified and include only actual vendace habitat volumes to improve the precision of the estimate.

4.1. Conclusions

By introducing stratification to the design of hydroacoustic surveys supported by midwater trawling, seasonal aggregations of fish in temporally restricted thermal habitat volumes can be used to lower survey effort and improve precision in estimates of population size. When surveys cover larger areas, including restricted habitat volumes, data should be stratified in post-processing and analysis. Temporally restricted habitat volumes may induce risks for the populations to over-fishing and sensitivity to environmental changes that potentially call for directed management.

5. Acknowledgements

We are grateful for support from the Institute of Freshwater Research, Department of Aquatic Resources, Swedish University of Agricultural Sciences, and for the supportive work by the crew of R/V Asterix. We sincerely thank reviewers for constructive suggestions and Teresa Soler for the layout. The Swedish Agency for Marine and Water Management, grant numbers 71336 and 71337, financed the study.

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