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– an indicator of population sensitivity to environmental and climate stressors

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Abstract

Smelts play a key role in the pelagic ecosystem of large lakes in northern Europe and North America. In numbers, they often dominate the open water. In large lakes in Scandinavia (including Finland), European smelt (*Osmerus eperlanus* L.), a cold-water glacial relict, is commonly the most important prey for piscivorous fish species, but also acts by ontogenetic shifts as a predator on zoo-plankton, small crustaceans, fish larvae, mysids and occasionally – with increasing size - fish. Furthermore, the large numbers of smelt in the open water are important competitors to other planktivorous fish. Due to the diverse life histories and biological interactions of smelt in large lakes, its role in the food-web structure is expected to be variable. Smelt population dynamics, recruitment, size and age structure, growth, life history and mortality were analysed and compared for five Swedish lakes that varied in size, depth, morphology, trophic status and latitude to understand the varying life histories and roles in lake food-webs. The results showed that in shallow, eutrophic lakes smelt stayed small and short-lived, and populations experienced high mortality. In deeper, colder and less nutrient-rich lakes, smelts grew larger and older, and might shift to a piscivorous trophic level. By ontogenetic adaptions smelt seems to uphold high abundance and recruitment over a wide range of ecosystems, but in shallow lakes without cold water refuges smelt populations run the risk of collapsing on the occasion of extremely warm summers with drastic consequences for their predators and lake ecosystems.

Sammanfattning

Nors spelar en viktig roll i det pelagiska ekosystemet i stora sjöar i norra Europa och Nordamerika. Till antal dominerar de ofta i öppet vattnet. I stora sjöar i Skandinavien (inklusive Finland) utgör europeisk nors (*Osmerus eperlanus* L.), som är en kallvattenart, ofta det viktigaste bytet för rovfiskar. Genom ontogenetiska skiften är nors även en predator på djurplankton, små kräftdjur, fisklarver, pungräkor och - med ökande storlek - fisk. Därtill är nors genom sin höga numerär ofta en betydelsefull konkurrent till andra planktonätande fiskarter. På grund av varierande livshistoria och biologiska interaktioner i de stora sjöarna, varierar norsens roll i näringsväven. Norsens populationsdynamik, rekrytering, storlek och åldersstruktur, tillväxt, livshistoria och mortalitet analyserades och jämfördes för sjöar med varierande storlek, djup, morfologi, trofisk status och latitud för att förstå variationen i livshistoria och de skiftande rollerna i sjöars näringsvävar.
Resultaten visade att i grunda, eutrofa sjöar förblev norsen småvuxen och kortlivad, och dessa populationer uppvisade hög mortalitet. I djupare, kallare och mindre näringsrika sjöar blev norsen större och äldre, och kunde övergå till en trofisk nivå som fiskätare. Genom ontogenetiska anpassningar verkar nors kunna upprätthålla hög täthet och rekrytering i ett brett spektrum av ekosystem, men i grunda sjöar, utan tillgång till områden med kallvatten, riskerar norspopulationer att kollapsa vid extremt varma somrar med drastiska konsekvenser för rovfiskar och sjöars ekosystem.

Innehållsförteckning

1. Introduction

European smelt (*Osmerus eperlanus* L.) is found in marine and brackish coastal areas, estuaries and inland boreal and temperate lakes. The lacustrine European smelt (hereafter smelt) – originally a landlocked glacial relict (Ekman 1922) - occur in lowland lakes once covered by the sea during previous glaciation events in northern Europe (Scandinavia, the Baltic region and Russia). Smelt is primarily a pelagic species. To avoid predation and optimize foraging, smelt perform diel vertical migrations which may vary depending on the type of lake, and age and size of the smelt (Nellbring 1989, Hammar et al. 2018).
As smelt is abundant – often even numerous – in lakes where it occurs (Nyberg et al. 2001, Axenrot et al. 2013, Hammar et al. 2018), it plays a key role in the pelagic ecosystem (Sandlund et al. 2005) acting both as a competitor for zoo-plankton, small crustaceans, mysids, fish larvae and fish, and as prey for piscivorous fish (Nellbring 1989, Sandlund 2017, Hammar et al. 2018). Food competing pelagic fish species are mainly vendace (*Coregonus albula*), whitefish (*Coregonus spp.*) and sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*; Nilsson 1979, Northcote and Hammar 2006). In freshwaters, smelt is an important prey species for several large piscivores, e.g. perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*), brown trout (*Salmo trutta*), landlocked Atlantic salmon (*Salmo salar*) and Arctic char (*Salvelinus alpinus*; Nilsson 1979, Heikinheimo et al. 2002, Keskinen & Marjomäki 2004, Hammar et al. 2018, Eloranta et al. 2019). Hence, smelt has been introduced in many lakes to improve prey availability for salmonid species attractive to recreational fishing. However, as shown by e.g. Sterligova & Ilmast (2017) and Eloranta et al. (2019), smelt can change the food web and fish community in lakes where it has been introduced. This has been shown also for lakes in North America regarding the closely related rainbow smelt (*Osmerus mordax*; Mercado-Silva et al. 2006).

The lacustrine European smelt is found in lakes with contrasting morphometry and trophic status. However, smelt is a cold-water species and long-lasting periods of high water temperatures (>20°C) have been observed to negatively affect the abundance of smelt in shallow lakes that lack cold-water refuges (Kangur et al. 2007). Dembinski (1971) found that smelt avoided water temperatures above 14-15° C. According to a literature review by Nellbring (1989) smelt show habitat segregation based on age and size. In summer, yearling-and-older smelt avoid high temperature water layers by migrating to colder water below the thermocline, if available (Power & Attrill 2007, Hammar et al. 2018).

Differences in limnological conditions (Nellbring 1989), climate and fishing pressure (Arula et al. 2017) have been suggested to result in growth, size and sexual maturation differences in smelt. In fish in general, age/size at maturity can be a trade-off between growth potential and predation risk (e.g. Roff 1984). With high mortality at early age/small size, natural selection will favour early maturation (De Roos et al. 2006, Arula et al. 2017). Limiting environmental conditions causing increased mortality may also result in early maturation (Sutherland et al. 1986). Thus, the age/size at sexual maturation in smelt vary among populations. In shallow and warm lakes, like Lake Peipsi (Estonia/Russia), life span of smelt is 1-2 years (Kangur et al. 2007), postulating early maturation, whereas in the cold and deep Lake Vättern (Sweden) 12-years-old smelt have been found (Hammar et al. 2018). In general, the maximum length of lacustrine smelt is <150 mm, but occasionally some individuals grow well over this length by shifting to fish diet (Sandlund 2017, Hammar et al. 2018). Smelts are also known for stunted populations adapting to assumable unfavourable conditions by increasing the reproduction rate, i.e. through sexual maturation at an early age and small size - characteristics often associated with high mortality (Nellbring 1989). Thus, smelt occupies variable positions in the food webs of lakes that offer different habitat characteristics (Nilsson 1979, Nellbring 1989, Sandlund 2017).

Despite the role as key species in the pelagic ecosystem in most lakes where it occurs, knowledge is often incomplete about smelt abundance, stock status, biology and ecological importance. The reason for this is probably that smelt is not a commercial species – at least not nowadays in most countries (Jurvelius et al. 2005). Historically, smelt was fished for human consumption and could be an important contribution to food protein (e.g. Degerman 2007).

Data on smelt for this study was obtained from the five largest Swedish lakes. Important for the study was that smelt is not fished in these lakes, but commonly regarded as an important prey species for large piscivores. In four of the lakes, smelt populations have shown little trends in population size, but large annual variations in recruitment (Nyberg et al. 2001, Sandström et al. 2014, Hammar et al. 2018). In the fifth lake, L. Storsjön (Figure 1), smelt was introduced in 1977 and has shown an increasing abundance since then (Axenrot et al. 2013). The lakes vary considerably in habitat characteristics (size, depth, morphometry, temperature regime and nutrient status). Lakes Vänern, Vättern and Storsjön and the basins Prästfjärden and Ekoln (in L. Mälaren) are dimictic, i.e. with a thermocline developing during summer and early autumn separating warm and cold water, while L. Hjälmaren and the basin Granfjärden (L. Mälaren) are polymictic, thermally mixing from surface to bottom (Figure 1). Four of the lakes are situated in southern Sweden with similar climate and one (L. Storsjön) in the middle part of Sweden in a colder climate zone at a higher altitude. Thus, these lakes constitute a field laboratory that enables studies of how large scale physical and edaphic conditions affect smelt populations and their ontogeny.

The aim of this study was to examine how ontogenetic variations in different populations of European smelt associate with lake characteristics and ecosystem conditions, and thus may be an indicator of smelt populations vulnerable to environmental perturbations and climate changes.

2. Material and methods

2.1. Study areas

The five largest lakes in Sweden allow for public recreational fishing and therefore are subjected to governmental management of the fish populations. To maintain this management, the fish stocks in the lakes are surveyed through standardized gill netting and hydroacoustics supported by midwater trawling. The five lakes are Vänern, Vättern, Mälaren (represented by three basins in this study*)*, Hjälmaren and Storsjön (Figure 1). The study lakes vary extensively in characteristic metrics (Table 1) and climate. While the annual average air temperature is circa 7° C for the four southern lakes it is 3.8° C for L. Storsjön (average 1991-2020; SMHI 2023).
Smelt is indigenous to these lakes except for Lake Storsjön where it was introduced in 1977 (Axenrot et al. 2013). There is commercial fishing of varying extent in the lakes mainly focussed on large piscivores, signal crayfish (*Pacifastacus leniusculus*, introduced) and vendace. In Lake Vänern the main predators on the smelt are landlocked Atlantic salmon, brown trout, pikeperch and European perch (Nilsson 1979), in Lake Vättern Atlantic salmon (introduced, stocked), Arctic char and European perch, and in Lakes Mälaren and Hjälmaren pikeperch and European perch (Degerman et al. 2001). In Lake Storsjön brown trout and to some extent lake trout (*Salvelinus namaycush*. introduced) are the main predators.

2.2. Data collection

The data collection and stock assessments – using hydroacoustics and midwater trawling – have been ongoing since the early 1990s. For this study, smelt determined to age (otoliths) from the period 2011-13 were used for lakes Vänern, Vättern and Mälaren. Lake Hjälmaren was surveyed 2015, 2019 and 2020 and smelt determined to age these years were used for analyses. Data from a survey in Lake Hjälmaren in 1989 was also used as a reference. The latest survey in Lake Storsjön was in 2011 which also included determination to age for smelt. Previous surveys in this lake have not included determination of age in smelt.

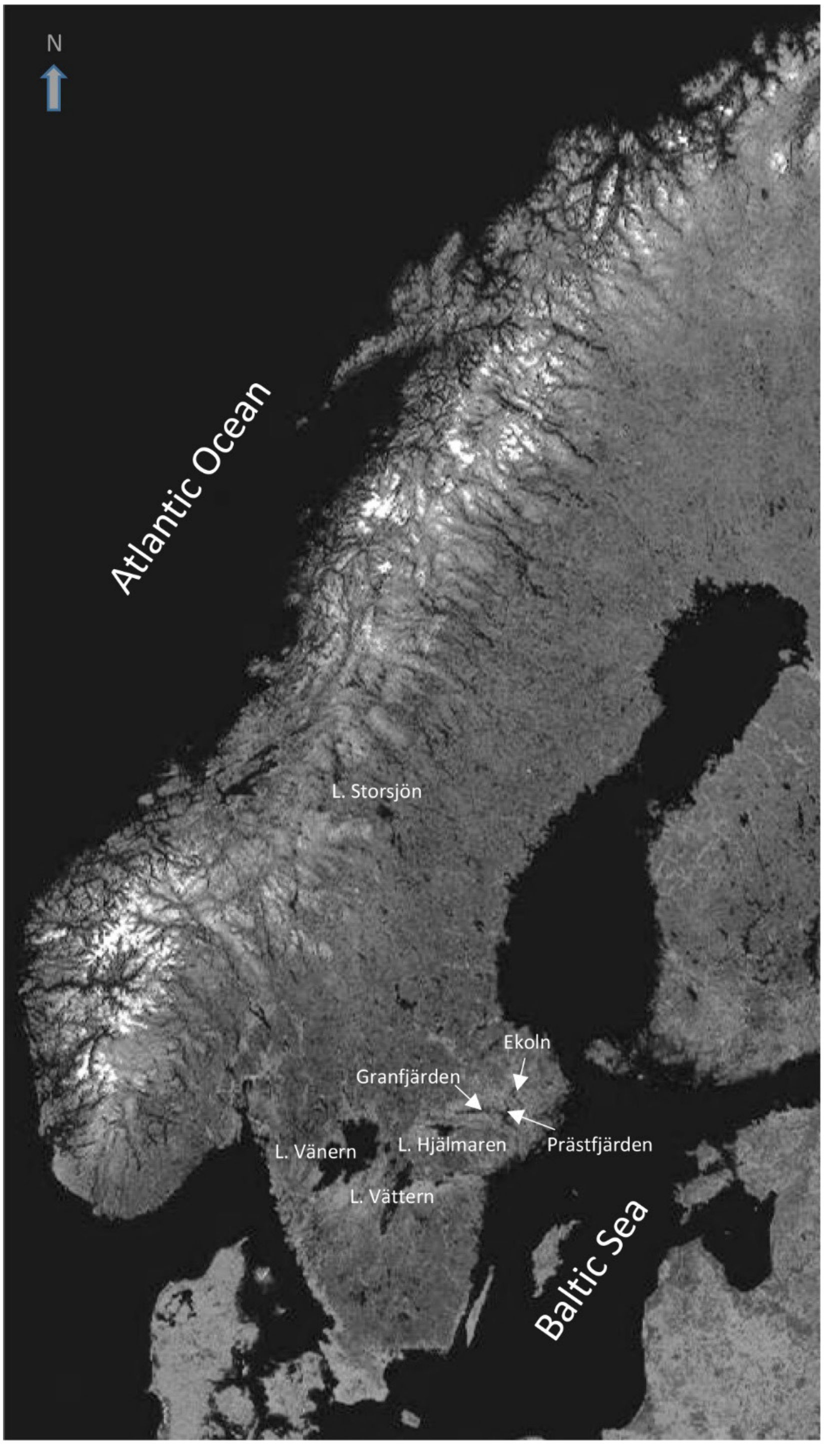


Figure 1. The Scandinavian Peninsula with the lakes/basins included in the study. The basins Granfjärden, Prästfjärden and Ekoln are parts of Lake Mälaren.

2.2.1. Midwater trawling data

Midwater trawling was performed the same night as the geographically corresponding hydroacoustic data were collected and considering subarea differences in depths. Trawling speed was 3 knots. The trawl hauls over the years have lasted for 20-30 minutes in lakes Vänern and Vättern, as well as in L. Storsjön (Axenrot et al. 2013), commonly dominated by smelt. In L. Mälaren and Hjälmaren the trawl hauls have lasted for 10 minutes because of high densities of fish, mainly smelt. The trawl mouth opened 5 x 12 m (height x width). The cod-end was partitioned into two bags with mesh-sizes 5 and 7 mm allowing retention of juvenile fish.

At the time of the surveys (August and September), lakes/basins that are deep enough are thermally stratified which has importance for the spatial structure of the fish community. Consequently, the trawl hauls in each subarea with thermal stratification were performed in three depth strata; the shallow part of the water column (5-10 m), around the thermocline (usually 10-20 m) and below the thermocline (>20 m). For subareas with bottom depths down to approximately 50 m, one trawl haul per depth stratum was performed (i.e. usually a total of three trawl hauls per subarea). For subareas with bottom depths over approximately 50 m the deepest stratum (hypolimnion, >20 m), representing the predominant water volume, was generally covered with 1-3 more trawl hauls depending on the size of the subarea. The total catch of each species in each trawl haul was weighed.

From the trawl catches, a random subsample of smelt (n=200) was measured for total lengths for each subarea (four in Lake Vänern, three in Lakes Vättern, Hjälmaren and Storsjön). A size-representative subsample of smelt (n=70) from each subarea was measured for length and weight, and determined to age using otoliths. Smelt were usually caught in sufficient numbers to fill these quotas.

To further analyse possible variations among smelt populations in the different lakes/basins, data on length (total length, TL), weight and age from the collected samples were used to calculate

- Maximum individual length among sampled individuals (Max L, mm)
- Asymptotic length (L_{inf}; von Bertalanffy growth function)
- Growth (K-value; von Bertalanffy growth function)
- Growth first year (TL of 0+)
- Condition for sampled individuals (PCA), 0+ and 1+ (Table 3); Fulton´s condition factor (Ricker 1975, Nash et al. 2006)
- Mortality1 (Chapman & Robson 1960)
- Mortality2 (Hamel 2015)

2.2.2. Hydroacoustic data

Assessments of smelt abundance, biomass and recruitment success for the different lakes/basins were based on long-term time-series data from hydroacoustics and midwater trawling. The timing of the surveys was chosen to enable inclusion of young-of-the-year smelt in the hydroacoustic results. For the principal components analysis (PCA), mean abundance per hectare of young-of-the-year smelt (0+) was used as an index of Recruitment, and mean biomass (kg) per hectare for yearlings and older (>0+) was used to represent Biomass for available years (see Data collection).

The hydroacoustic surveys were performed at night, in darkness, with an index of coverage (Aglen, 1983) ranging between 4 and 5 in all lakes. The hydroacoustic data were collected using a hull mounted 38 kHz (7°) transducer with echo sounder EK60. In Lake Hjälmaren, data from a hull mounted 120 kHz (7°), with a shorter nearfield than 38 kHz, was used because of little depth. The echo sounders were calibrated according to recommendations by Foote et al. (1987) and the manufacturer (Simrad). The threshold for target strength of single echo detections was set low, usually from -60 dB, to include small, young-of-the-year smelt.

The midwater trawling data were used to assign species composition and size distribution to the hydroacoustic data. The trawl catch composition, i.e. species, size proportions and – for target species like smelt – the proportion of 0+ and >0+ were assigned to the hydroacoustic densities for corresponding depth strata for each subarea. In this process trawl data from the different strata in a subarea were partitioned into classes (species, individual fish lengths, trawl geo-position, fishing depth, and bottom depth). Fish lengths (TL) were transformed to target strengths based on Love´s equation (1971). 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 autocorrelation) and layers (5 m). The final density for smelt (0+ and >0+) for a discrete subarea was calculated from the mean of intervals and sum of layers.

2.2.3. Data processing and statistics

The hydroacoustic data were processed in Sonar5-Pro (ver. 6.0.3), calculations and Anova statistics were performed in MS Excel (2016), Pearson statistics in SPSS and PCA statistics in Jump 16.0.0. For related parameters that showed high pair-wise Pearson correlation (>80 %), one or more of the parameters were removed from the final PCA data set. For the Principal Components Analysis parameters were log transformed in case of wide and skewed ranges.

3. Results

There were large differences between lakes in maximum and asymptotic (L_{inf}) lengths of smelt, with the largest maximum and asymptotic lengths in the largest and deep L. Vänern, and the smallest, respectively, in the shallowest and second smallest L. Hjälmaren (Tables 1 and 2). Maximum age followed a similar pattern with 10 years in L. Vänern and Storsjön, but normally only 1 year in L. Hjälmaren.

The lowest growth rates were observed in L. Vänern and the basin Ekoln (L. Mälaren), having the largest maximum and asymptotic lengths. The highest growth rates were observed in L. Hjälmaren for the stunted population with lowest maximum age, and for the basin Prästfjärden (L. Mälaren; Table 2). Growth in the first year (total lengths), i.e. from young-of-the-year (0+) to yearling (1+) sampled in August/September, differed between lakes (Anova $p<0.001$; Figure 2). First year growth was smallest in the polymictic basin Granfjärden (L. Mälaren) and highest in L. Storsjön, with the coldest climate. The polymictic and shallowest L. Hjälmaren showed medium growth the first year together with large and deep L. Vättern and the basin Prästfjärden (L. Mälaren).

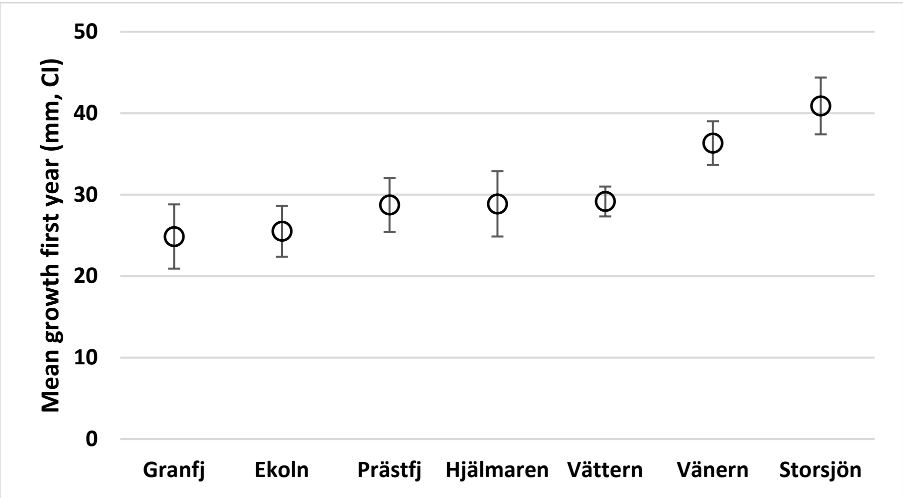


Figure 2. Mean growth first year calculated from trawled smelt in August (L. Vänern) and September (the rest of the lakes/basins). The basins Granfjärden, Prästfjärden and Ekoln are parts of Lake Mälaren. Confidence intervals (CI) 95 %.

In Lake Hjälmaren smelt showed the markedly highest mortality followed by the basin Granfjärden (L. Mälaren), both shallow and polymictic. The lowest mortality was observed in deep lakes where smelt reached large maximum length and high maximum age (Tables 1 and 2).

Table 1. Characteristics of the lakes included in the study. In Lake Mälaren the basins included were Granfjärden, Prästfjärden (including S and N Björkfjärden) and Ekoln. Each of these basins was treated as separate waterbodies. Air temp corresponds to average annual air temperature during 1991-2020. Depths are given in meter, altitude in meters above sea level and air temperature in degrees C. Secchi depth and phosphorus levels were averages for August-September 2011.

Lake /basin	Latitude (North)	Longitude (East)	Area (km^2)	Altitude (m)	Mean depth (m)	Max depth (m)	Air Temp (C)	Secchi depth (m)	Phosphorus (µg/l)
Vänern	58.835	13.242	5650	45	27	106	7.5	5.0	6
Vättern	58.274	14.450	1910	88	40	128	7.4	15	4
Mälaren/ Granfjärden	59.492	16.553	77	0.7	10	30	7.0	1.2	44
Mälaren/ Prästfjärden	59.396	17.391	320	0.7	17	63	7.3	3.0	20
Mälaren/ Ekoln	59.744	17.615	36	0.7	15	37	7.3	2.3	48
Hjälmaren	59.236	15.802	483	22	6	20	7.0	1.0	58
Storsjön	63.197	14.343	456	293	17	74	3.8	10	4

Table 2. Characteristics of smelt populations in the studied lakes/basins. Max L is the largest total length recorded in this study, L_{inf} the asymptotic length, Growth is the K-value of the von Bertalanffy equation, Max Age is the recorded oldest individual, Condition is the average calculated Fulton condition factor, Mortality1 and Mortality2 are calculated according to Chapman & Robson (1960) and Hamel (2015), respectively. Biomass is the weight (kg) of smelt per hectare and recruitment is the number of young-of-the-year smelt per hectare based on estimations from hydroacoustic and trawling data.

Lake/ basin	Max L (mm)	L_{inf} (mm)	Growth	Max Age	Condition	Mortality 1	Mortality 2	Biomass	Recruit-ment
Vänern	295	353	0.138	10	0.48	0.48	0.54	11.580	2984
Vättern	166	142	0.392	7	0.42	0.67	0.54	2.744	1996
Mälaren/ Granfjärden	155	144	0.403	3	0.45	1.35	1.8	17.526	25901
Mälaren/ Prästfjärden	240	148	1.073	5	0.46	0.63	1.08	37.867	2660
Mälaren/ Ekoln	261	166	0.113	6	0.49	0.62	0.9	32.154	18113
Hjälmaren	126	120	0.945	1	0.47	2.3	2.7	1.619	2359
Storsjön	207	156	0.466	10	0.46	0.57	0.54	2.261	509

The largest smelt biomass (kg per hectare) was observed in the basins Prästfjärden and Ekoln (L. Mälaren) characterized by high total-phosphorous content in combination with large shallow areas and access to deeper parts. Despite high levels of nutrients in L. Hjälmaren, the biomass of smelt was low (Tables 1 and 2).

Recruitment (number of young-of-the-year per hectare) was very high in the basins Granfjärden and Ekoln (L. Mälaren), both eutrophic. The lowest recruitment was observed in the oligotrophic and cold-water dominated lakes Storsjön and Vättern (Tables 1 and 2).

Young-of-the-year (0+) smelt were considerably smaller in L. Storsjön, situated in a colder climate (at higher latitude and altitude), but showed the fastest growth the first year (Table 3, Figure 2). Yearling (1+) smelt reached the largest lengths in polymictic, nutrient-rich L. Hjälmaren, where smelt also showed the lowest maximum age and the highest mortality (Tables 1-3).

Table 3. Mean total length (mm) and Condition (Fulton condition factor) for young-of the-year (0+) and yearling (1+) smelt.

Lake/basin	Mean length 0+ (CI 95%)	Condition 0+	Mean length 1+ (CI 95%)	Condition 1+
Vänern	58.7 (±1.6)	0.459	95.0 (±1.5)	0.460
Vättern	58.9 (±1.6)	0.466	88.0 (±1.0)	0.414
Granfjärden	64.9 (±1.9)	0.443	89.8 (±2.4)	0.455
Prästfjärden	66.4 (±2.4)	0.439	95.2 (±1.6)	0.473
Ekoln	68.3 (±1.7)	0.482	93.9 (±2.3)	0.500
Hjälmaren	66.7 (±2.7)	0.448	101.8 (±1.2)	0.478
Storsjön	43.6 (±2.0)	0.302	84.5 (±2.7)	0.454

Recruitment failures were observed L. Hjälmaren and the basin Granfjärden (L. Mälaren) after the unusually warm summer of 2018 in southern Sweden (SMHI 2024). Recruitment of smelt was observed to be unusually low in the polymictic basin Granfjärden (Figure 3; Rogell & Axenrot 2022). Trawling results from surveys in polymictic L. Hjälmaren in 2019 and 2020 showed recruitment failure in 2018 as a lack of 1+ and 2+ smelt in 2019 and 2020, respectively, and a strong dominance in numbers of 2+ smelt in 2019 (i.e. recruited in 2017) and 1+ in 2020 (i.e. recruited in 2019; Table 4; Axenrot & Rogell 2021).

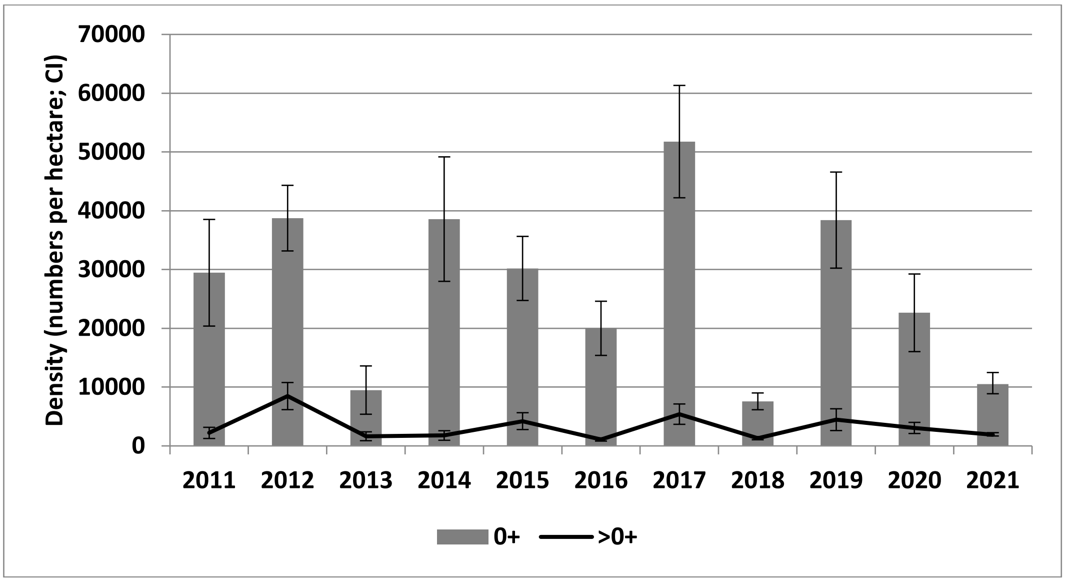


Figure 3. Estimated densities per hectare of young-of-the-year (0+) and yearling–and-older (>0+) smelt based on hydroacoustics supported by trawl data in the basin Granfjärden, L. Mälaren. Confidence intervals (CI) 95 %.

All variables included in tables 1-3 were tested for correlation (Pearson bivariate correlation; Table 5). Latitude, Altitude and Air temperature were significantly correlated (>±0.82, p<0.05) and only Air temperature was retained for further analyses. Mean and Max depth were also significantly correlated (0.96, p<0.001) and the latter was kept. Secchi depth and Phosphorous level were correlated (-0.79, p<0.05), but both were kept. Growth, Biomass and Recruitment were not significantly correlated to other variables. Mortality1 and Mortality2 were significantly correlated (0.97, p<0.001), and only Mortality2 was kept. Condition and Condition 1+ were also significantly correlated (0.90, p<0.01), and Condition was kept. All remaining variables were kept for further analyses.

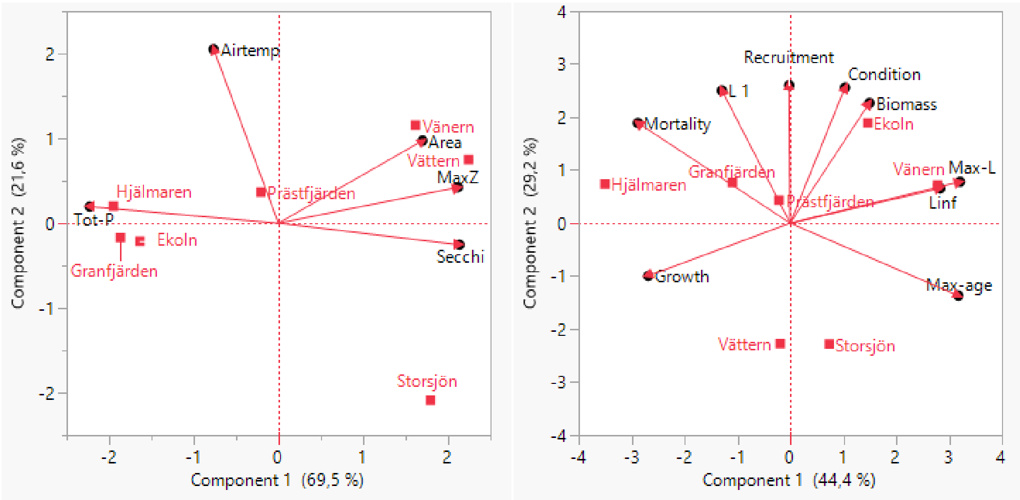
Table 4. Frequency per age class of smelt in Lake Hjälmaren 2019 and 2020. Data from midwater trawling in September both years.

Age	n (2019)	Frequency (%)	n (2020)	Frequency (%)
0	2	3,2	17	12,1
1	2	3,2	123	87,9
2	56	90,3	0	0,0
3	2	3,2	0	0,0

To visualize the most important correlations among the kept variables principal component analyses (PCA) were performed using the reduced data set for lake/basin and smelt characteristics, respectively. For lake/basin characteristics the first two axes explained 88.5 % of the variation (Figure 4a). For smelt characteristics the first two axes explained 66.9 % (Figure 4b).

Table 5 Bivariate correlation between included variables (Tables 1-3) given as Pearson r (the product moment correlation coefficient). Significant correlations denoted with bold and asterisk (p<0.05, ** p<0.01, *** p<0.001).*

	Lat	Lake area	Alt	MeanZ	MaxZ	Air temp	Secchi	Tot-P	L max	Linf	L mean	Growth	Max age	Mortality1	Mortality2	Biomass	Recrt	L 1+	Cond 0+	Cond 1+
Latitude																				
Lake area	-0.34																			
Altitude	**0.82***	-0.01																		
MeanZ	-0.33	0.56	0.19																	
MaxZ	-0.17	0.66	0.34	**0.96*****																
Air temp	**-0.97*****	0.28	**-0.92****	0.19	0.03															
Secchi	0.12	0.24	0.63	**0.84***	**0.84***	-0.31														
Tot-P	-0.2	-0.54	-0.59	**-0.78***	**-0.90****	0.31	**-0.79***													
L max	0.04	0.52	-0.04	0.26	0.33	0.11	-0.05	-0.4												
Linf	-0.18	**0.92****	-0.04	0.34	0.46	0.20	0,00	-0.43	0.74											
L mean	-0.74	-0.20	**-0.97*****	-0.30	-0.48	**0.85***	-0.66	0.72	-0.07	-0.16										
Growth	-0.18	-0.29	-0.34	-0.44	-0.41	0.20	-0.42	0.37	-0.27	-0.36	0.44									
Max age	0.38	0.57	0.62	0.60	0.73	-0.40	0.60	**-0.85***	0.68	0.62	-0.73	-0.61								
Mortality1	-0.18	-0.34	-0.30	-0.62	-0.66	0.13	-0.48	0.75	**-0.77***	-0.45	0.39	0.54	**-0.84***							
Mortality2	-0.2	-0.42	-0.44	-0.74	**-0.78***	0.20	-0.66	**0.84***	-0.68	-0.46	0.53	0.61	**-0.92****	**0.97*****						
Biomass	-0.17	-0.26	-0.56	-0.22	-0.29	0.39	-0.51	0.23	0.52	-0.01	0.57	0.21	-0.14	-0.34	-0.10					
Recruitment	-0.13	-0.36	-0.47	-0.39	-0.54	0.26	-0.52	0.57	-0.08	-0.16	0.46	-0.36	-0.38	0.12	0.24	0.40				
L 1+	-0.52	0.09	-0.68	-0.43	-0.45	0.59	-0.67	0.62	-0.02	0.09	0.72	0.71	-0.59	0.59	0.65	0.2	-0.08			
Cond 0+	**-0.93****	0.21	**-0.90****	0.16	-0.03	**0.98*****	-0.31	0.40	0.09	0.15	**0.86***	0.11	-0.41	0.14	0.21	0.37	0.34	0.57		
Cond 1+	0.13	-0.29	-0.37	-0.73	-0.74	0.10	**-0.82***	0.66	0.33	0.01	0.47	0.34	-0.29	0.19	0.35	0.58	0.29	0.47	0.16	
Condition	0.18	-0.10	-0.21	-0.54	-0.48	0.03	-0.68	0.4	0.56	0.40	0.24	0.11	0.04	0.02	0.12	0.38	0.15	0.51	0.09	**0.90****



(a) *(b)*

Figure 4. Principle component analysis (PCA) of (a) lake characteristics (Table 1) and b) smelt characteristics (Table 2). Only the first two axis are shown, explaining 91.1 and 73.6 % of the variation, respectively.

The lake characteristics grouped the lakes in two distinct categories, and one lake/basin in a transition zone in-between. Large, deep and chiefly nutrient poor lakes with high visual clarity formed one group (L. Vänern, Vättern and Storsjön, Figure 4a). These lakes were all dimictic and thus provided cold water through the period of thermal stratification. The other group comprised smaller, shallower and more nutrient rich lakes/basins (L. Hjälmaren and the basins Granfjärden and Ekoln, Figure 4a). Two of these were polymictic (L. Hjälmaren and the basin Granfjärden), but the basin Ekoln was dimictic holding small volumes of cold water through the period of thermal stratification. The basin Prästfjärden, in-between the two groups (Figure 4a), was also dimictic, holding small volumes of hypolimnetic cold water through the thermally stratified period, but differed from the basin Ekoln in being considerably less rich in nutrients. The vertically separated position of Lake Storsjön in the PCA graph (Figure 4a) could be explained by the high latitude (Figure 1) resulting in low annual average air temperature.

The smelt characteristics showed that high mortality and growth were well correlated and symptomatic for the shallow and polymictic Lake Hjälmaren and the basin Granfjärden (Figure 4b). Smelt growing to large size and reaching high age were correlated and typical for the large, deep and dimictic lakes (Lakes Vänern, Vättern and Storsjön, Figure 4b). High biomass and condition factor were correlated for the eutrophic, dimictic basins Prästfjärden and Ekoln while the PCA results for Recruitment and L1 (length of yearling smelt) showed correlation with lake Hjälmaren and the basin Granfjärden (Table 5, Figure 4b). The vertically separated position of Lake Vättern could be explained by low biomass and condition factor in a nutrient-poor, ultra-oligotrophic lake. The position of Lake Storsjön could partly be explained the same way as L. Vättern, but also by small yearling smelt because of the high latitude resulting in significantly later spawning, hatching and thus time for growth the first year (Figure 4b).

4. Discussion

In general, the smelt populations in all lakes/basins showed high abundance and recruitment success. Life histories of smelt among the studied lakes/basins varied and depended on habitat characteristics and ecosystem conditions.

The large, deep and clear-water lake characteristics correlated with smelt that grew old - up to 10 years - and large (Max L and L_{inf}). Smelt in these lakes did not show fast growth as young-of-the-year (0+; Tables 2 and 3), but did so the second growth season (sampled in August/September; Figure 2). Mortality in these lakes was considerably lower than in lakes/basins without access to cold water, as smelt might shift habitat to avoid high epilimnion temperatures and grow out of an exposed predation window (Cowan et al. 1996, Hammar et al. 2018). Our stable isotopes analyses (^{15}N; not published) separated large (>150 mm) and smaller smelt indicating that larger smelts were piscivorous occupying a higher trophic level (Sandlund et al. 2005). Piscivory by large smelt is a well-established trait and Hammar et al. (2018) found that small fish dominated the food of smelt >150 mm. For some lakes, e.g. L. Vänern, this ontogenetic diet shift resulted in a sigmoid growth curve that affected the K value (von Bertalanffy growth function) for the parameter Growth to be lower than expected (Table 2). In the large, deep and ultra-oligotrophic L. Vättern (Table 1), parameters Max L and L_{inf} showed low values compared to the other large lakes as well as the smaller lakes/basins with access to deep cold-water habitats. In L. Vättern, Hammar et al. (2018) recorded smelt well over 150 mm caught in the hypolimnion in bottom-set gillnets for test-fishing, while mid-water trawling in the hypolimnion (this study) did not catch smelt >166 mm. A possible explanation is that large smelt in L. Vättern avoid open water because of high predation risk as a result of extraordinary high Secchi depth (Table 1) in the presence of several daylight active predators, as Atlantic salmon, Arctic char and brown trout as well as diving birds like cormorant (*Phalacrocorax carbo*) and goosander (*Mergus merganser*).

Lake Storsjön belongs to the same group of large and deep lakes, but is situated in a colder climate (Table 1) than the other lakes in this study and outside the indigenous range for smelt in Sweden. The small size of young-of-the-year smelt is explained by late ice break-up and cold water temperatures in spring that result in late spawning with small size and low condition index in early autumn for young-of-the-year smelt (0+; Table 3). Despite small size as 0+ as well as early ice-cover and late ice break-up, growth from 0+ to 1+ was high (Figure 2) indicating good food availability, which could possibly be an effect of weak food competition for an introduced species. The high maximum age and low mortality may be explained by few predators in open water in L. Storsjön (Axenrot et al. 2013).

Another group of lakes/basins were small, shallow, polymictic and rich in nutrients. Here, smelt showed fast growth as 0+, but slow (Granfjärden) or intermediate (Hjälmaren) growth from 0+ to 1+, high mortality and short life spans of only a few years (Tables 2 and 3, Figure 2). The shortest life span was recorded for smelt in L. Hjälmaren. Age determination from otoliths showed only young-of-the-year (0+) and yearlings (1+) in the trawl catches in 2015 (Axenrot 2018). A previous survey in 1989 and trawling results from 2015, 2019 and 2020 show that smelt in L. Hjälmaren over long time, with few exceptions, were maximum two years old (2+; Pettersson 1989, Axenrot & Rogell 2021). These findings suggest that smelt in this type of lakes spawn as early as 1+, as reported by Nellbring (1989). As smelt spawn in spring (in late April in L. Hjälmaren) the individual smelt needs to become sexually mature and invest energy in building gonads in their first year. To survive predation pressure in these lakes/basins, smelt invests energy in rapid early growth while simultaneously allocating energy to develop gonads for spawning by age 1+. This unique ontogenetic situation occurs in shallow, polymictic, and eutrophic lakes. In the absence of cold-water habitats to optimize continued growth, smelt in these lakes appear as stunted populations that must sexually mature, produce gonads and spawn early, even in their first year of life (Nellbring 1989, Sandlund et al. 2005, Power & Atrill 2007, Kangur et al. 2007, Arula et al. 2017, Hammar et al. 2018). Growth from 0+ to 1+ differed between the two polymictic L. Hjälmaren and the basin Granfjärden (Mälaren) in that growth was faster in L. Hjälmaren (Figure 2). A possible explanation could be that smelt in L. Hjälmaren need to spawn already as yearlings (1+) to preserve the population while the basin Granfjärden is not isolated to the rest of L. Mälaren and fast growth in early life may not be crucial for preserving the population. The high densities of young-of-the-year smelt in the basin Granfjärden (L. Mälaren), as shown from hydroacoustics and midwater trawling time-series data (Figure 3), were likely to cause high intra-specific food competition which could explain the slower growth from 0+ to 1+ (Figure 2). The relatively low biomass of smelt despite high densities in the basin Granfjärden and L. Hjälmaren (Table 2) might be explained by the small size of individual smelt and relatively shallow depth (i.e. less water volume).

Between these two groups of lakes there was a third group that consisted of small, predominantly shallow, relatively nutrient rich and dimictic lakes/basins

(Prästfjärden and Ekoln). Sufficient depth was available in parts of the lakes/basins allowing smelt access to hypolimnetic cold-water during the thermally stratified period in summer to early autumn. Here, smelt showed a more regular growth and life history, i.e. individual smelt became 5-6 years old and continued to grow over 120 mm (Table 2). Mortality was considerably lower than in lakes/basins without access to cold water. Still, maximum age was lower than in the large and deep lakes possibly because of high production enhancing predation and higher mortality. Size or age at sexual maturity and gonad development were not specifically studied, but considering the observed maximum age of smelt in this type of lakes/basins they were not forced to invest in both growth and gonads their first year of life.

Growing to a large size to avoid predation and probably - by size - produce more offspring, as well as having a long life-span with several spawning opportunities can be assumed to be beneficial both for the individual smelt and for the population. This kind of life history was observed for smelt in the large, deep and clear-water lakes, naturally low in nutrients and with access to large volumes of hypolimnetic cold water through the period of thermal stratification. When such conditions were fulfilled, smelt showed the longest life-span and grew to a size where some individuals could become piscivorous which further would enhance individual survival and recruitment success (Nellbring 1989, Sandlund et al. 2005, Sandlund et al. 2017, Hammar et al. 2018). The opposite, i.e. very short life-span allowing for only one spawning through life, and small size – even at sexual maturity - was found for the growth stunted smelt in the smaller, shallow, polymictic and nutrient-rich lakes/basins. Young individuals generally have higher temperature tolerance than older and larger ones (Hamrin 1986, Nellbring 1989, Hammar et al. 1996; LaFrance et al. 2005). Hence, smelt were able to sustain the population in warmer lakes by adapting to reproduction at young age and small size. Sexual maturity and spawning at age 1+ were observed to have negative effects on growth but should also negatively affect fecundity. Recruitment failures were observed in L. Hjälmaren and the basin Granfjärden after an unusually warm summer in 2018 (Figure 3; Axenrot & Rogell 2021). The life history of smelt in this type of lakes/basins bring on vulnerable population dynamics where merely one single year of unsuccessful recruitment might lead to a population collapse (Kangur et al. 2007, Arula et al. 2017). In the other lakes/basins where smelt grew older, a single year of unsuccessful recruitment would normally not be a threat to the whole population.

The future perspective of continued climate warming forms a threat to smelt populations that today live on the brim of possible ontogenetic adaption in shallow, polymictic lakes with high nutrient load (Kangur et al. 2007, Keskinen et al. 2012). Higher summer temperatures will enhance unfavourable conditions for smelt, as increased evaporation leading to lower water levels causing further increase in water temperatures (e.g. Eklund et al. 2017). Primary production may increase, including cyanobacteria, as well as decomposition consuming more oxygen which may lead to lack of oxygen in deeper strata. This will produce problems for smelt both in nutrient rich lakes without thermal stratification (e.g. L. Hjälmaren) and in nutrient rich lakes/basins with restricted hypolimnion areas. In lakes large enough to offer a large pelagic zone, smelt is commonly the most important prey species for large piscivorous fish in Scandinavian, Baltic area and Russian lowland lakes. Consequently, smelt population collapses are liable to induce drastic changes in large piscivore populations with negative consequences for commercial and recreational fisheries, and bring about lake ecosystems changes.

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