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Collapse and recovery of the European smelt (*Osmerus eperlanus*) population in a small boreal lake — an early warning of the consequences of climate change

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We used warm summer temperatures as an analogue of climate change to estimate the potential impacts on a population of smelt (*Osmerus eperlanus*) in a boreal lake. A combination of hydroacoustics, seine and gillnet catches with temperature and dissolved oxygen profiles was used to study the changes in the abundance, vertical distribution and age structure of the smelt population. Smelt were squeezed between their temperature and dissolved oxygen tolerance limits during most summers. Conditions in 2002 were, however, extreme and mean surface-water temperatures exceeded 21 °C while at the same time waters below 6 m had low (< 0.5 mg l^{-1}) dissolved oxygen concentration. Pelagic fish density during summer declined from 5000 to 200 fish ha^{-1}. However, some young-of-the-year smelt survived in 2002, leading to a recovery in abundance to 4500 fish ha^{-1} by 2004. A similar recovery is not likely if the high temperature and low oxygen conditions persist during critical periods over a generation time.

Introduction

Future scenarios of global warming resulting from increasing atmospheric greenhouse gas concentrations anticipate increases in average annual air temperature of 2–4 °C, with more intense warming occurring in northern latitudes (IPCC 2007). These kinds of increases have important implications for aquatic ecoystems, particularly small boreal lakes (Forsius *et al*. 2010), since the distribution and movements of many aquatic organisms are related to the timing of seasonal temperature cycles, which are strongly affected by atmospheric temperature and winds. Lakes in temperate and boreal regions of the world are generally dimictic and exhibit strong thermal stratification during the summer months. During stratification, the epilimnion is warm, well mixed, and oxygenated and the hypolimnion is cold and cut-off from mixing and reoxygena-

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tion by the temperature gradient in the thermocline. Fish distributions during stratification typically reflect thermal preferences and tolerances, with coldwater fish (e.g., coregonids, salmonids) in the hypolimnion and cool water fish (e.g., cyprinids, percids) in the epi- and metalimnion (Jurvelius 1991, Vašek *et al*. 2009, Rydell *et al*. 2010). Decreased recruitment in cold-water fish species and increased recruitment of cool-water species (Casselman 2002, Winfield *et al*. 2008, 2010), changes in distributions and loss of populations (Sharma *et al*. 2007, Lehtonen 1996), and changes in growth potential of certain fish species (Brandt *et al*. 2002) have all been reported as the potential impacts of the climate change on the northern freshwater ecosystems.

Eutrophication as a result of increased nutrient loading due to poor land-use practices in catchment areas is common in many boreal lakes. Over 2000 lakes are currently classified as eutrophic in Finland (Tammi *et al*. 1999). The increased nutrient supply accelerates primary production and the rate of oxygen-consuming decomposition, leading to more rapid and prolonged oxygen depletion in the hypolimnion. Appropriate water temperature and dissolved oxygen (DO) levels, which generally varies with local climate, is among the most important attributes of habitat quality affecting survival of fish in lakes (Tonn 1990, Jackson *et al*. 2001, Lucas and Baras 2001). Hypoxia is more likely in lakes where water is slow moving, poorly mixed, and is rich in nutrients (e.g. Kramer 1987). Consequently, the combination of increasing water temperature and decreasing dissolved oxygen levels in eutrophic lakes may significantly increase the risk of local extinctions of some fish species (Magoulick and Kobza 2003). Yet, there are only few recent studies of oxygen and temperature combination in relation to climate or other long-term changes (Jones *et al*. 2008, Elliott and Bell 2011).

The European smelt (*Osmerus eperlanus*) is a short-lived (usually 1–3 years) pelagic omnivore and is a key species in the pelagic food web of many temperate and boreal lakes (Ivanova 1982, Nyberg *et al*. 2001, Sandlund *et al*. 2005). This makes smelt a good species for the study of population abundance changes in response to changes in environmental conditions. Maturity occurs typically at the age of 2 years and smelt spawn during the spring in tributaries or shallow littoral areas when water temperature is between 4 and 8 °C (Nellbring 1989). Embryos hatch 10–20 days after spawning. There are only a few estimates of European smelt abundances in small lakes owing to the absence of recreational and commercial catch data and the low catchability of smelt in standard gillnet sampling (Olin and Malinen 2003, Olin *et al*. 2008). Peltonen *et al*. (1999) stated that echo sounding gives more reliable estimates of smelt stocks than gillnet sampling especially small smelts having low catchability with the multimesh gillnet.

During the summer of 2003, central Europe was exposed to an unusually severe heat wave, which also directly affected the hydrology of many lakes (Jankowski *et al*. 2006). In Finland, temperature in lakes was in the end July even 4–6 °C higher than average. However, in 2002 the warm period was even longer, surface water temperatures being 2–3 °C higher than average till the end of August (Korhonen 2007). The main objectives of this study were to describe the population responses of European smelt in a small boreal lake to warmer than normal summer temperatures. We used these data and findings as an analogue of the likely effects of climate change on coldwater fish population in a small boreal lake ecosystem. In this study, we explore whether the thermal niche–dissolved oxygen squeeze hypothesis (Coutant 1985) could explain the observed substantial reduction in population abundance of smelt during the summer of 2002 in the study lake.

Material and methods

Study area

Alvajärvi is a lake located in central Finland (62°19´N, 25°43´E) and has a surface area of 200 ha, maximum depth 16.5 m and mean depth 3.8 m (Fig. 1). The lake discharges into the Päijänne system, but upstream fish migrations are blocked by a hydroelectric dam about 10 km downstream from Alvajärvi. Several small lakes upstream of Alvajärvi are connected by creeks. The lake is dimictic and the main basin is

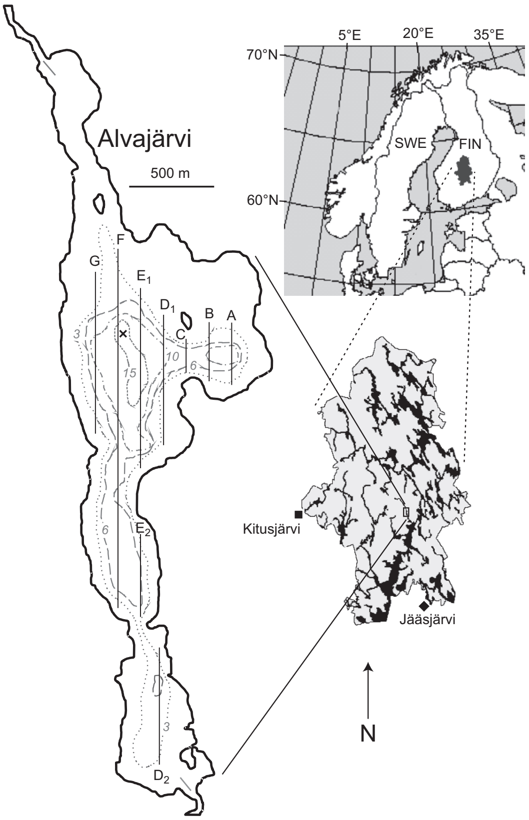

Fig. 1. Location of Alvajärvi, Kitusjärvi and Jääsjärvi in central Finland. The bathymetric map (isobaths in metres) of Alvajärvi shows the hydroacoustic transects (A–G) and the main basin sampling site for hydrologic data (×).

fully stratified by late summer. The average chlorophyll-*a* concentration during the summers 2001–2006 at 2 m depth was 19 μm l^{-1}. Thus, the lake is eutrophic as a result of nutrient loading from agriculture in the watershed. Water colour is high (average 146 mg Pt l^{-1}), average pH is 6.9 and Secchi depth 1.1 m. European smelt is the dominant planktivorous fish in pelagic areas. Main predatory species are perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*) and pike (*Esox lucius*). Other common fish species in the lake include roach (*Rutilus rutilus*), white bream (*Abramis bjoerkna*), common bream (*A. brama*), and bleak (*Alburnus alburnus*). European smelt undergoes diurnal vertical migrations in boreal lakes (Horppila *et al*. 2000), even during the stratified period (July–September). Aggregations of older smelt inhabit the hypolimnion during daytime and ascend to warm epilimnetic waters at dusk and dawn for feeding. During night, smelt are dispersed throughout the hypolimnion, even in areas with relatively low oxygen concentrations (Malinen *et al*. 2005).

Hydroacoustic data

Echo sounding data were collected with a calibrated single-beam 70-kHz Simrad EY-M echo sounder (full beam angle 11°, pulse duration 0.6 ms, ping rate 3 pings s^{-1}, time-varied gain $40 \log R$). During data collection carried out at the end of August or the beginning of September annually from 2001 to 2006, N–S transects established in the main basin were followed using a global positioning system (GPS) (Fig. 1). Because of the diurnal vertical migration pattern of smelt, hydroacoustic data collection was commenced at least one hour after sunset. Each survey took about one hour. Echo counting (MacLennan and Simmonds 1992) was used to estimate smelt density and distribution because smelt are uniformly dispersed at night and most of the acoustic scatters are single fish. A vertically aimed transducer approximately 0.5 m below the surface on a side of the boat was used for all surveys. All acoustic data were collected at a constant boat speed of 7–8 km h^{-1}. Analysing threshold value of target strength was set to –56 dB. In the years 1994 and 1997, the echosounding protocol was similar apart from the location of transects. During these two years, the survey was done by sailing along a zigzag route in the areas with depth > 3 m for about one hour without fixed transects. The covered area of the lake was however about the same as in 2001–2006.

Hydroacoustic data were recorded onto audiocassette tapes, which were then digitized. Fish target strength, density and vertical distribution in 1-m-depth layers starting from the depth of 2 m below the transducer were analyzed using the HADAS software (ver. 3.3) (Lindem 1990). Reference voltages recorded at the beginning of each tape were used to adjust system gains. Echoes with target strengths (TS) ≥ –56 dB were interpreted as fish and fish TS distributions were compiled using the Craig and Forbes (1969) deconvolution technique to eliminate the effect of the beam pattern. We used the TS–length relationship reported by Peltonen *et al*. (2006), $\mathrm{TS} = 23.4 \times \log_{10}L - 68.7$ dB (L = total length in cm), to convert our target strength distributions to length distributions and *vice versa*.

Catch samples

Smelt were sampled for aging, not for abundance estimates, from the main basin of the lake (depth > 10 m) with a purse seine (length = 100 m and height = 8 m; 6 mm minimum mesh size from knot to knot) in August 2001 (one haul) and September 2004 (5 hauls). In 2001, sampling was done after sunset and in 2004 before sunset, in the afternoon. Age of all smelt in these samples was estimated using otoliths. In addition, a set of 20 monofilament nylon vertical multimesh gillnets (1.5 m height × 30 m length) was used to estimate the density index of other fish species in the lake. Gillnets had 9 mesh sizes (10, 12, 15, 20, 25, 30, 35, 45 and 50 mm from knot to knot) in 9 3.3-m-long panels. The lake was sampled once annually in August from 2001 to 2006. Gillnets were placed in the lake using a stratified random sampling design with depth layer as the main blocking variable and were left soaking for approximately 24 hours. Average catch per unit effort (CPUE) in the test fishing was used as an index of abundance of species besides European smelt, which were not caught with gillnets.

Water temperature and dissolved oxygen

Water temperature and dissolved oxygen data were collected from Alvajärvi twice per month between May and September in 2001 and 2002 and once per month from 2003 to 2006. Winter samples were collected from under the ice in March. Oxygen content (mg l^{-1}) was measured using YSI meter in 2001 and Winkler titrations in other years. All samples were taken at 2-m intervals from 0 to 12 m, at one station in the deepest portion of the main basin (Fig. 1). We used a linear interpolation over depth to match hydrologic and hydroacoustic data for equal depth layers. Similar interpolation was done over time between sampling points. Since water temperature in Alvajärvi is not regularly monitored, we obtained surface water temperature data from two nearby lakes in central Finland monitored by the Finnish Environmental Centre to assess long-term trends in water temperature in this geographical region. Surface temperatures from June to September in Jääsjärvi (61°34´N, 26°8´E) and Kitusjärvi (62°16´N, 24°2´E) were obtained for the 1971 to 2006 period and 11-year moving averages were calculated (data from the Hertta database of the Finnish Environment Institute). Jääsjärvi and Kitusjärvi are 80 km southeast and 90 km west of Alvajärvi, respectively.

Statistical analysis

Mean fish density was estimated for each acoustic transect, taking into account its depth profile by weighing the average density from each depth layer with the number of pings received from that layer. Because vessel speed was constant, the number of pings was used to approximate the length of sampling unit (transect). Thus, the mean density ($\bar{y}$) of smelt in the main basin was calculated as the weighted mean of transects, using the numbers of pings as the weighting factor. The variance of arithmetic mean density ($\mathrm{Var}(\bar{y})$) was calculated as (Shotton and Bazigos 1984):

$$\mathrm{Var}(\bar{y}) = \frac{\sum_{i=1}^{n}\left[(y_i - \bar{y})^2 \times \mathrm{ping}_i\right]}{\sum_{i=1}^{n}\mathrm{ping}_i \times (n-1)}\,, \qquad (1)$$

where y_i is the fish density in the ith sampling unit, ping_i is the number of pings in the ith sampling unit, and n is the number of sampling units. The 95% confidence intervals (CI) for the mean fish densities were calculated assuming the density was Poisson-distributed (Jolly and Hampton 1990, Malinen and Tuomaala 2005). Thus, the end points of the 95% confidence limits were given by

$$\bar{y}\left[1 + \frac{\mathrm{Var}(\bar{y})}{\bar{y}^2}\right] \pm 2\sqrt{\mathrm{Var}(\bar{y})}. \qquad (2)$$

Results

Acoustic surveys of Alvajärvi carried out in

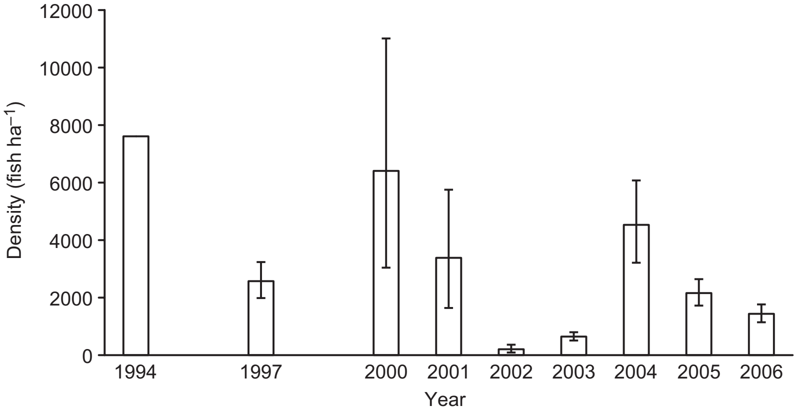

Fig. 2. Pelagic fish density (fish ha^{-1}) in Alvajärvi based on hydroacoustic surveys in 1994, 1997 and 2000–2006. Every survey was performed at night. Whiskers show the 95%CI (not established in 1994).

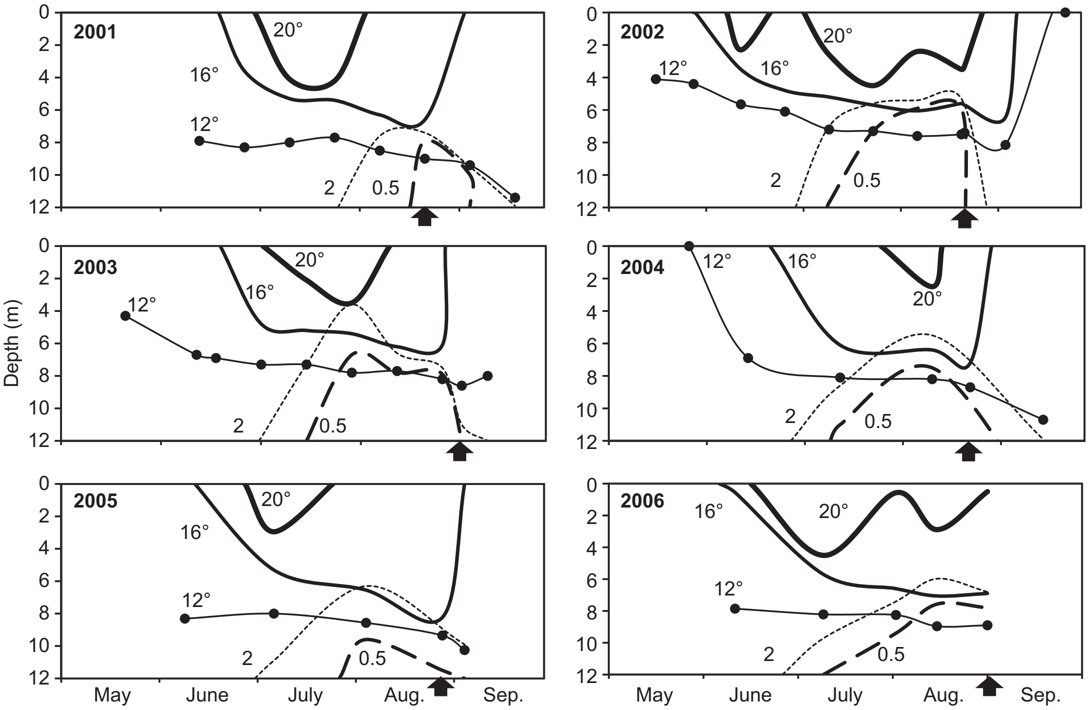

Fig. 3. Temperature (°C, solid-line isopleths) and dissolved oxygen concentration (mg l^{-1}, dashed-line isopleths) in Alvajärvi during the summers 2001–2006. Only temperature isopleths for temperatures 12, 16 and 20 °C and dissolved oxygen contours for concentrations 0.5 and 2 mg l^{-1} are presented. Black circles in 12 °C isopleths indicate the sampling points. Black arrows indicate the time of echo sounding.

1994 and 1997 estimated mean pelagic fish densities of 7600 and 2600 fish ha^{-1}, respectively (Fig. 2). Since 2000, the acoustic survey had been carried out annually and estimates of fish densities ranged between 200 and 6400 fish ha^{-1}, with the lowest estimate reported in 2002. Prior to 2002, mean pelagic fish density across the surveys was 5000 fish ha^{-1} and after 2002, estimated pelagic fish density rapidly recovered to 4500 fish ha^{-1} by 2004

The main basin of Alvajärvi was strongly stratified during the summers from 2001 to 2006 (Fig. 3). Stratification developed in May and disappeared during the first half of September by autumn turnover. In July, the epilimnion continued to warm up and the zone of water with DO

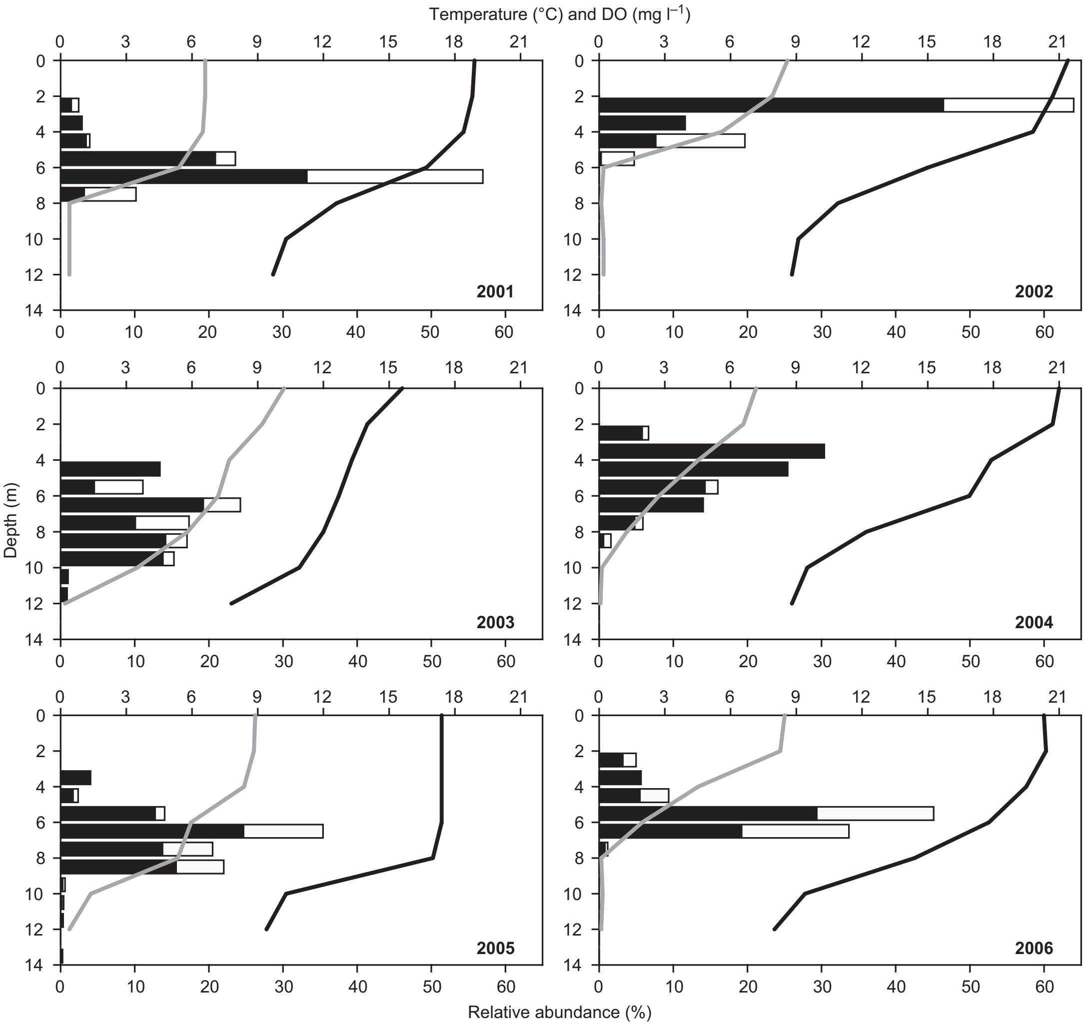

Fig. 4. Vertical distribution of fish at night in Alvajärvi in years 2001–2006, and temperature (grey line) and dissolved oxygen (DO, black line) profiles on each hydroacoustic sampling date. Black sections in bars indicate fish smaller than about 6 cm (< –50 dB) in total length and white sections larger fish.

concentrations < 2.0 mg l^{-1} in the hypolimnion increased so that for much of August, hypolimnetic waters had low oxygen concentration (Fig. 3). During late winter, DO was always higher than 4.7 mg l^{-1} at depths from 6 m to surface. The vertical fish distribution during acoustic surveys was clearly related to the presence of low oxygen concentration in the hypolimnion and high temperatures in the epilimnion since fish were detected in acoustic data only in DO over 2 mg l^{-1} (Fig. 4). Fish density was always greatest in the thermocline (Fig. 4) which was located in depth from 2 to 4 m in 2002 and 2004 but 5 to 7 m in other years. The temperature in thermocline was typically 12–18 °C, except during the summer of 2002 when it was about 21 °C which coincides with the very low fish density (Fig. 2). Opposite to other years, in 2002 the isopleths of 0.5 mg l^{-1} DO were located in the epilimnion (6 m) at the temperature exceeding 16 °C. Thus, in 2002 the hypoxic conditions (DO < 0.5 mg l^{-1}) in the thermocline forced smelt to occupy habitats with higher temperature and closer to the surface than in other years.

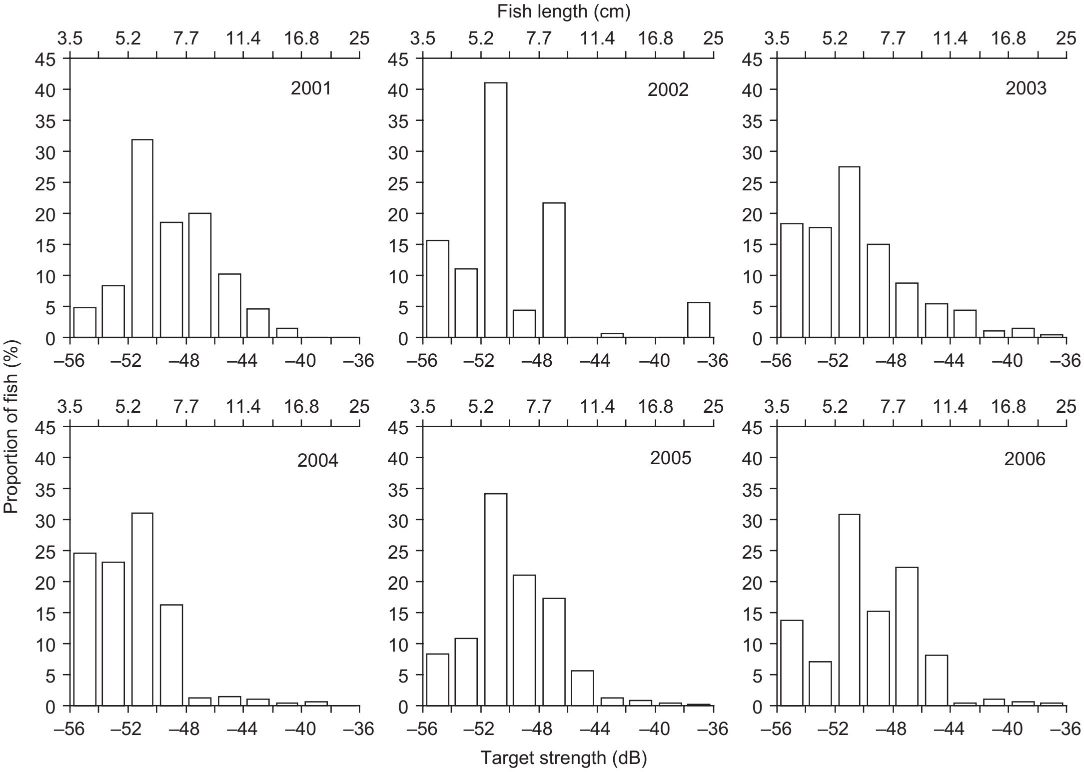

Fig. 5. Target strength distribution of hydroacoustic estimates of fish size (TS ≥ –56 dB) from Alvajärvi in years 2001–2006.

In 2001, the total length of smelt sampled by the seine ranged from 72 to 95 mm, and all (*n* = 31) belonged to the age-group 1+. Seine catch was purely smelt. Two age-groups of smelt (*n* = 11) were found in the 2004 seine catch: fish with total lengths between 53 and 60 mm belonged to the age-group 0+ (73% of the sample), and fish between 92 and 99 mm in total length belonged to the age-group 1+ (27% of the sample). In this catch, the proportion of smelt was 3% of fish under 10 cm in total length, perch (41%) and pikeperch (45%) being the most common species. Target strength (TS) distributions compiled for each acoustic survey showed a change in shape from 2001 to 2006 (Fig. 5). In 2001, TS was widely distributed with no clear skew with mean TS of about –50 dB (63 mm in length). However, the 2002 TS distribution was strongly skewed towards smaller TS in the –52 to –56 dB range. This skewed distribution remained through 2004, while in the following summers greater proportion of larger targets was detected. For example, in 2004 the majority (79%) of the detected fish targets were smaller than –50 dB; in 2005, 53% of targets were ≤ –50 dB in size, but the density was about 50% lower than that in the previous year (Figs. 4 and 5), consistent with the low abundance of the 0+ age-group in 2005. The highest proportion in the TS distribution occurred in the TS class of –52 to –50 dB each year, which translates roughly to fish with length from 5 to 7 cm, respectively.

Roach and perch were the most common species in gillnet catches in Alvajärvi (Table 1). White bream, bream, bleak and pikeperch were also captured, but their relative abundances were much lower than the abundance of roach and perch.

The average surface temperature during May–September in Jääsjärvi and Kitusjärvi increased by 1–2 °C between 1990 and 2006 (Fig. 6). The summer of 2002 was the warmest summer in both lakes during the period of record for which monitoring data are available.

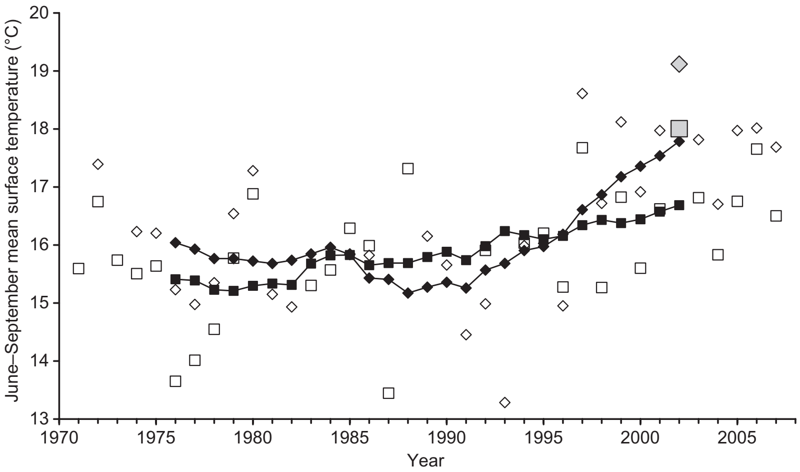

Fig. 6. Mean surface-water temperature (June–September) in two Finnish lake, Jääsjärvi (61°34´N, 26°8´E) (white diamonds) and Kitusjärvi (62°16´N, 24°2´E) (empty squares) from 1971 to 2006. Eleven-year moving averages for Jääsjärvi (solid line and black diamonds) and Kitusjärvi (solid line and black squares) are shown in the center years of the calculation periods. The warm summer of 2002 is highlighted (grey square and diamond). Original data from the Hertta database of the Finnish Environment Institute.

Discussion

In acoustic studies of multispecies fish communities, species identification of targets is an important yet difficult task. In case of Alvajärvi, the conclusion that the vast majority of the targets consisted of smelt was based on behavior in relation to temperature and gill-net and seine catches. In Finnish lakes, meta-hypolimnetic distribution in open water during night is typical only for vendace and smelt (Jurvelius 1991) but there is no vendace in Alvajärvi. In gill-net catches, in deep areas (> 5 m), CPUE was low as compared with that in shallower areas and consisted mainly (71%–100%) of fish over 9 cm in total length (T. Keskinen unpubl. data). Gill net is not suitable for monitoring smelt stocks (Peltonen *et al*. 1999) and thus smelt was not found in gill-net catch. In seine catch of 2001 carried out during dusk, smelt was the dominant species and that sample represented well the fish community observed by echosounding. In 2004, samples were taken during daylight and thus there were also other species present. High numbers of pikeperch (< 10 cm TL) were from intensive stocking (29 ind. ha^{-1}) done 9 days before sampling. Put together, our data on fish community and its vertical distribution imply convincingly that the fish observed after dusk by echosounder were mainly smelt.

Table 1. Average catch per unit effort (CPUE, g and ind. net^{-1}) of six common fish species in Alvajärvi based on August gillnet samples from 2001 to 2006.

Species	2001		2002		2003		2004		2005		2006	
	g	ind. net^{-1}	g	ind. net^{-1}	g	ind. net^{-1}	g	ind. net^{-1}	g	ind. net^{-1}	g	ind. net^{-1}
Roach	515	22.0	623	32.6	537	24.8	653	30.8	338	15.4	843	37.6
Perch	318	15.7	925	58.0	236	14.8	357	22.0	258	12.8	447	20.8
Pikeperch	118	0.5	211	1.3	113	0.6	85	0.6	237	1.3	216	0.7
White bream	68	1.0	205	4.3	371	6.4	439	14.8	174	4.6	114	3.3
Common bream	24	0.4	180	4.0	153	1.3	76	0.5	118	2.2	146	1.7
Bleak	50	3.6	138	9.8	21	1.3	92	5.9	38	2.4	113	4.0

The thermal niche–dissolved oxygen hypothesis (Coutant 1985) proposes three mechanisms which can regulate fish population abundance: (1) direct mortality owing to thermal or respiratory stress, (2) decreased fecundity of adults residing in marginal habitat, and (3) increased rates of indirect mortality (e.g. starvation, disease, predation and overfishing). In temperature-gradient experiments, adult European smelt (2+ and 3+ years old) showed preference for the water temperature of 12 °C, and this preference did not vary with season (Ivanova 1982), and smelt was observed to avoid temperatures over 14–15 °C (Dembiński 1971). Thus, during summer the preferred temperature for smelt in Alvajärvi was found between depths of 8–10 m (Fig. 3). Other factors being equal or at least not limiting, we would expect to find smelt occupying these waters as a result of behavioural thermoregulation. The acute hypoxia sensitivity of European smelt is not known, but they reportedly prefer waters with oxygen concentrations higher than 5 mg l^{-1} (Moeller and Scholz 1991). In Alvajärvi, the low DO concentration seemed to limit the occurrence of smelt at the depths of preferred temperature in August. According to our acoustic data, the highest fish densities were detected mostly in a depth stratum with water temperatures from 12 to 18 °C and dissolved oxygen higher than 2 mg l^{-1} during August of every surveyed year, except in August 2002 (Fig. 2) when no fish were observed in water layers with temperatures below 16 °C and the fish density was extremely low. Conditions in August 2002 were probably lethal or at least very harmful to European smelt in Alvajärvi because, opposite to other study years, the 0.5 mg l^{-1} DO isopleth was located in a warmer water layer than 16 °C for about two weeks. However, in Lake Hiidenvesi smelt could tolerate the conditions of hypolimnion with DO < 2 mg l^{-1} in 14 °C which is in accordance with the observations in Alvajärvi (Malinen *et al*. 2005).

The worst environmental conditions in Alvajärvi (low dissolved oxygen, high temperatures) for adult European smelt usually occur in August. Smelt survival during this critical period may be an important mechanism regulating population density in small boreal lakes. The diurnal vertical migration of European smelt owing to their feeding behaviour, requires fish to enter the warm epilimnion for short periods so there must be some tolerance for short-term exposure to relatively high temperatures. As the water column warms above optimal temperatures, smelt move downward seeking cooler water until they are stopped by low oxygen concentrations. Lehtonen (1996) proposed that smelt is a species likely to suffer from climate warming. Occurrence of water temperatures ≤ 20 °C is suggested critical for a smelt population in Lake Peipsi (Estonia/Russia border) (Kangur *et al*. 2007). Exceptionally high temperature in 2002 coupled with the wider depth range and prolonged duration of anoxia in Alvajärvi created unfavourable environmental conditions for smelt in August. Although we do not have any direct observations of mortality, we infer from the observed changes in pelagic fish densities (Fig. 2) and TS distributions (Fig. 5) that substantial mortality of especially older smelt (> 0+) occurred during summer stratification period. Mass mortalities of smelt in several shallow Russian lakes also occurred during the warm summer of 1972 (Ivanova 1982). The ultimate reason for mortality is speculative, but physiological stress and predation together may be important factors. Smelt usually avoid highly illuminated environments, utilizing the epilimnion at dusk. However, in the summer of 2002, smelt were forced to occupy the epilimnion during daylight hours because temperature and oxygen conditions at greater depths probably exceeded their physiological tolerance. Physiological stress combined with unfavourable illumination very likely decreased the ability of smelt to avoid their main predators (perch and pikeperch) and as a consequence mortality increased and the stock collapsed. According to gillnet fishing (Table 1), the stocks of perch and pikeperch are abundant and occupy the whole lake area. Both these species use smelt as a prey (Keskinen and Marjomäki 2004, Haakana *et al*. 2007) and, as cool water species, their food consumption increases sharply with temperature (Bergman 1987, Keskinen *et al*. 2008). Thus, increased predation due to unfavourable environmental conditions is a potential reason for smelt stock collapse in 2002. Data from other lakes in central Finland show that year 2002 was the warmest in the study period (Fig. 6).

Different fish species and age-groups have different strategies and abilities to survive unfavourable environmental conditions (Kramer 1987, Jackson *et al.* 2001). Young-of-the-year (age 0+) European smelt seem to show preference for higher water temperatures than older year-classes (≥ 1 year of age) (Ivanova 1982, Vinni *et al.* 2004, Malinen *et al.* 2005). As a result of these ontogenetic differences in temperature preference, 0+ smelts may inhabit the uppermost epilimnion during the summer while older fish are found in deeper waters. These ontogenetic differences in temperature preferences produce a depth separation of age groups, which reduces the potential for cannibalism on 0+ smelt (Vinni *et al.* 2004) and the potential for mortality due to hypoxia since the young-of-the-year fish inhabit a depth stratum (epilimnion) that remains well oxygenated throughout the summer. The observed fish densities indicated that European smelt population in Alvajärvi recovered in terms of abundance within two years after the collapse in 2002. We hypothesize that this relatively quick recovery was possible because mortality in 2002 was greatest in fish > 1+ years old, which led to an increase in the recruitment of 0+ fish by 2003 due to decreased competition. Also in 2002, part of the age-group 0+ was possibly near surface (0–2.5 m) and thus was not detected by echosounder. The lifespan of smelt in shallow Russian lakes is 1–2 years and the smelt populations of these lakes are distinguished by a simplified size–age structure and sharp fluctuation in the abundance of individual year-classes (Ivanova 1982). According to our target strength distributions (Fig. 5), fish detected in the years after the collapse (2003 and 2004) were clearly smaller than those in the year prior (2001) or three years later (2005). Based on these findings, we suggest that there were ontogenetic differences in smelt survival related to age-specific temperature preferences in the population. This hypothesis is also supported by the age distributions of seine samples in 2001 and 2004. The post spawning mortality in smelt is often high (Nellbring 1989). We do not have data on the spawning stock age structure in Alvajärvi but based on the seine samples, smelt older than 1+ are rare. This could indicate that post spawning mortality is high in third year of their life, 1+ smelt in August representing spawning stock of the next spring. Thus, the unfavourable conditions in 2002 have probably been responsible of the spawning stock collapse and led to observed changes in abundance and size distribution.

Observed fish densities in Alvajärvi were in most years somewhat higher than smelt densities reported by Jurvelius *et al.* (2005) in 5 south boreal lakes (460–2000 ha^{-1}) indicating dense smelt population in Alvajärvi. Other species did not show any clear changes in abundances based on gillnet CPUE (Table 1). The higher average CPUE in 2002 was probably due to enhanced vulnerability of cool-water species (perch, cyprinids), resulting from increased activity associated with the warmer than usual epilimnetic waters in August (Linløkken and Haugen 2006, Olin *et al.* 2008). Thus, the observed collapse of the smelt population was not a consequence of increased abundance of predatory fish, because these changes were not observed. However, increased predation likely was a contributing factor because these predatory species would have been focused more on smelt due to spatial and temporal overlap resulting from the unfavourable environment conditions for smelt and their weakened ability to avoid predation.

Blumberg and Di Toro (1990) estimated that, owing to climate warming, the loss of dissolved oxygen in the epilimnion and hypolimnion of Lake Erie's central basin could be 1 mg l^{-1} and 1–2 mg l^{-1}, respectively, coupled with an increase in the volume of the anoxic zone in the lake. Also epilimnetic temperature and duration and intensity of stratification in summer will increase with increased temperature in hypolimnion (De Stasio *et al.* 1996). These kinds of predictions are in good accordance with our results because during the summer of 2002, the volume of hypoxic water in Alvajärvi was clearly larger than during other years. Furthermore, although the thermocline was not deeper in 2002 (this depth is primarily a function of wind-induced spring mixing), the thermal gradient was much steeper in 2002 than in other years, and water temperatures exceeding 20 °C were observed for an extended period in the summer. This is in accordance with De Stasio *et al.* (1996) who concluded based on simulations that in most cases thermocline will became shallower in small north-temperate lakes. Overall observations in Alvajärvi are consistent with the typical consequences of climate change observed in other temperate and boreal lakes (Hondzo and Stefan 1993, Schindler *et al*. 1996, Jankowski *et al*. 2006, Forsius *et al*. 2010).

We presented a case study of the response of a European smelt population in Alvajärvi to a record warm summer in 2002 as an analogue of potential impacts of future climate warming on pelagic fish populations in small boreal lakes. There is an increasing evidence of the linkages between climate and aquatic environments consistent with climate warming scenarios during the last decade (e.g. Schindler *et al*. 1996, Salinger 2005). Over the past 30 years, which saw an increase in average annual global air temperature, mean surface-water temperatures in two Finnish lakes show also an increasing trend, reaching their highest values during the summer of 2002, the hottest summer on record to date (Fig. 6). Our results demonstrate that owing to species-specific temperature and oxygen requirements, global warming may restrict pelagic habitat availability for European smelt populations in small closed lakes in temperate and boreal regions. If these restrictions are temporary as in 2002, then smelt populations will probably recover rapidly. However, if the changes persist over the longer-term (e.g. one generation time of smelt) then the long-term viability of smelt populations in many small lakes will be imperilled, i.e. climate change will enhance the risk local of extinction for these species.

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