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Vertical distribution and swimming speed of pelagic fishes in winter and summer monitored *in situ* by acoustic target tracking

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We studied the swimming speed and vertical distribution of fish under ice from March to April and in open water in August. Fish were surveyed with a downward facing stationary 120 kHz split beam echo-sounder in a boreal lake. A commercial trace tracking software was used to estimate the depth, speed and size of fish. Most fish in the study area were smelt (*Osmerus eperlanus*) and vendace (*Coregonus albula*). In March and April, fish were detected under the ice around the clock, whereas in August only a few fish were detected during daytime. Fish were typically detected between 12 and 19 m depth and they swam from 5 to 50 cm s^{-1} i.e. 0.5 to 3 body lengths s^{-1}. The effect of sunrise and sunset on the under-ice swimming depth and speed became more marked with increasing day length. In summer, the effect on depth was not so evident. In March–April there was a shift towards day activity, which persisted in August. Changing illumination seemed to account for most variation in the swimming depth and speed of fish.

Introduction

Changing light intensity, water temperature, feeding and predation have been proposed to explain the habitat selection, migrations and activity of pelagic planktivorous fishes (e.g. Dembinski 1971, Shvetsov *et al*. 1983, Bergman 1984, Vuorinen 1986, Clark and Levy 1988, Jurvelius *et al*. 1988). Monitoring of fish migrations is essential in studying habitat selection of fish in relation to abiotic and biotic environmental gradients. In order to be able to estimate the bioenergetic costs of this behaviour, an estimate of the swimming speed of fish is an important parameter. For decades, hydro-acoustics has been used to estimate size of fish stocks and their spatio-temporal distributions (e.g. Dembinski 1971, Jurvelius *et al*. 1984, Steinhardt and Wurtsbaugh 1999). Presently, target-tracking techniques using split beam transducers provide a tool for studying e.g. swimming speed, direction and the acoustic size of the fish (dB) in situ (e.g. Arrhenius *et al*. 2000, Mulligan and Chen 2000). In situ behavioural studies are sometimes more relevant than experimental set-ups, e.g., in bioenergetic research. Hydro-acoustics has proved to be cost-efficient, and it produces rapid, continuous, real-time and often high resolution results.

In the northern parts of the Eurasian and North American continents, lakes are often covered with ice in winter. The ice gives "shelter" against winds and low air temperature; it also reflects and absorbs solar radiation and thus makes illumination conditions different from those in summer. There have been relatively few studies on fish behaviour under ice in lakes (e.g. Pavlov *et al*. 1986, Presnyakov and Borisenko 1993, Steinhard and Wurtsbaugh 1999, Tolonen 1999, Jurvelius *et al*. 2000). Knowledge of under-ice fish behaviour is relevant in itself and its importance may grow when we have to evaluate the ecological effects of climatic warming.

Typically, vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*) make up the vast majority of the fish biomass in the pelagic areas of boreal Finnish lakes. These two plankton feeders are essential prey species for predators like pike-perch (*Sander lucioperca*), brown trout (*Salmo trutta*), endangered land-locked salmon (*Salmo salar*) and the Saimaa ringed seal (*Phoca hispida saimensis*) (Peltonen *et al*. 1996, Valkeajärvi *et al*. 1997, Kunnasranta 1999, Auvinen *et al*. 2004). Vendace is by far the most important target for commercial Finnish lake fisheries, with annual catches being usually 6000 tonnes (Auvinen *et al*. 1990).

In the present work, we studied seasonal and diurnal patterns in the vertical distribution and the swimming speed of fish under ice in winter and during the ice-free season in summer. We expected that there would be a considerable difference in the swimming speed of fish between day and night, and that fish move faster in summer than under ice in winter due to differences in temperature.

Materials and methods

Study area

Vuokalanjärvi (62°14´N, 29°09´E) is an 18-km^2 lake in eastern Finland. Its mean depth is about 10 m, and the depth in the study area was 20 m. In the study period from 6 March to 5 April 2000, the ice was 60 cm thick with a further 35 cm of snow on it. The air temperature varied between –11 and +6 °C during this period, and the number of daylight hours grew from 11 to 15 hours per day. In the summer study period in August, the air was ca. 20 °C warmer and daylight was 17 hours long.

In March–April the water temperature was 1.5 °C at 1-m depth below the ice, and reached its maximum, 3.5 °C, at 19-m depth. Oxygen concentration decreased from 14 mg l^{-1} to 2.5 mg l^{-1} between these depths. During the ice-free season in August, the temperature in the water column is usually between 15 and 18 °C in weakly stratified lakes like this, the coolest water being in water layers near the bottom. Water colour in the surface layers of the study lake was ca. 35 Pt mg l^{-1} (Regional Environmental Centre for South Savo, unpubl. data).

In Vuokalanjärvi, pelagic fish catches (Lehtonen *et al*. 1998) are dominated by vendace, whitefish (*Coregonus lavaretus*), small perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*). Pike (*Esox lucius*), burbot (*Lota lota*), brown trout and large perch are the most abundant predators.

Light intensity (W m^{-2}) was measured with a CTD sonde (SBE 19 Seacat Profiler, Licor LI-193SA Spherical Quantum Sensor) in neighbouring Kermajärvi (62°25´N, 28°40´E) on 12 April 2000. Water colour in this lake was ca. 25 Pt mg l^{-1} (Regional Environmental Centre for South Savo, unpubl. data). The calibrated CTD sonde was out of service before that date, and during these measurements the snow had already melted on the ice. However, we considered it was important to obtain some figures of the light intensity under ice. In the measurements, the depth of darkness (= 1 W m^{-2}) was monitored.

Echo-survey and data-processing

A downward-facing 120 kHz split-beam echosounder (Simrad EY500, ES120-7F transducer, 7° beam width, pulse length 0.3 ms) was used. Its pingrate was 2 pulses s^{-1}. Because we were interested only in fish larger than ca. 5 cm, echo tracks with mean target strength (TS) larger than –56 dB were considered in this analysis. To separate fish echoes from the lake bottom, the data collection was stopped ca. 1 m above the bottom.

The transducer, mounted at the same site in a hole in the ice or a motionless boat, was calibrated using the Simrad lobe program and a 23 mm copper sphere with TS of –40.4 dB. We assumed the TS–size (cm) relationship to be $TS = 20\log L - 67$ (Bagenal *et al.* 1982). Altogether ca. 100 hours of data were collected. The data were processed with EP500/trace tracking software (version 5.3, Simrad). The minimum number of consecutive traces for accepting a fish track was set to 4, the allowed depth window between consecutive traces to 50 cm, and the maximum number of consecutive missing pings in a series of traces to 1. The tracking software gave a direct output of estimated speed.

There are two reasons why the fish track data collected are a biased sample of the fish population. Firstly, due to the conical shape of the sound beam, the probability of a randomly moving fish encountering the beam is linearly proportional to the beam radius, which is proportional to the depth. Secondly, because in the software the maximum number of pings per fish track is fixed to 10 and thus the 11th ping starts a new track, the number of traces detected from a fish is inversely proportional to its speed and directly proportional to beam radius and the depth. Therefore, in the estimation of averages from the data these biases were corrected by weighting each observation with factor speed $\times$ depth^{-2}. Despite the correction, especially the near surface average speed may be underestimated because the minimum number of detections from a fish for accepting a trace was set to 4. For example at 5-m depth the beam width is ca. 60 cm, and the fish that are moving faster than 15 cm s^{-1} are excluded even when they cross the beam centre.

In addition to this, targets with zero speed or speeds higher than 1 m s^{-1}, which might include echoes from several fish within one dense fish shoal, were excluded from the estimations of average speeds. The number of excluded tracks was << 1% of the total number of tracks. Also all $TS > -41$ dB were excluded to reduce the risk of including multiple echoes from one fish. This exclusion was ca. 15% of the total number of echoes. While the conical beam shape decreases the sample volume in the upper depth layers, the upper edge of the vertical movements of fish cannot be measured without bias. However, we consider that a comparison between study periods can still be made.

Exploratory fishing

We used a 10-m high seine (cod-end mesh size 8 mm knot to knot) to sweep the bottom of a 12 ha area. This took 3.5 h and started at sunrise on 8 March 2000. The species and size composition of the catch was derived from sub-samples. The total catch was determined for each species separately. A fisherman's dog ate the seine catch sample caught in August.

Statistical analysis

The statistical significance of the differences in hourly averages of speed and depth of the targets was evaluated by weighted least squares ANOVA (SPSS 11.0) using the factor speed $\times$ depth^{-2} to weigh the observations. The speed data was ln-transformed prior to the analysis.

Results

Vendace accounted for 40% of the specimens in the winter seining catch sample (total 641 fish). The percentages for smelt and whitefish were 55 and 4, respectively. The mean length was 16.8 cm (range 14–19 cm) for vendace, 9.3 (6–12) for smelt, and 25.4 (17–33) for whitefish. Smelt formed a distinct length-group and had no overlap with the other species. Fish longer than 14 cm were coregonids and the proportion of vendace was about 90%.

Fish traces were typically detected in the depth layer from 12 to 19 m (Fig. 1). On 6–8 March, an ascent of fish was detected beginning somewhat before sunrise, and a descent began around 18:00, half an hour before sunset. There was a clear distinction in the swimming depth of fish between day and night (ANOVA: Tukey $p < 0.05$). On 20–22 March, a clear ascent of fish was detected at around 05:00, an hour before sunrise, and a descent an hour later (ANOVA: Tukey $p < 0.05$). The same pattern, though weaker, was

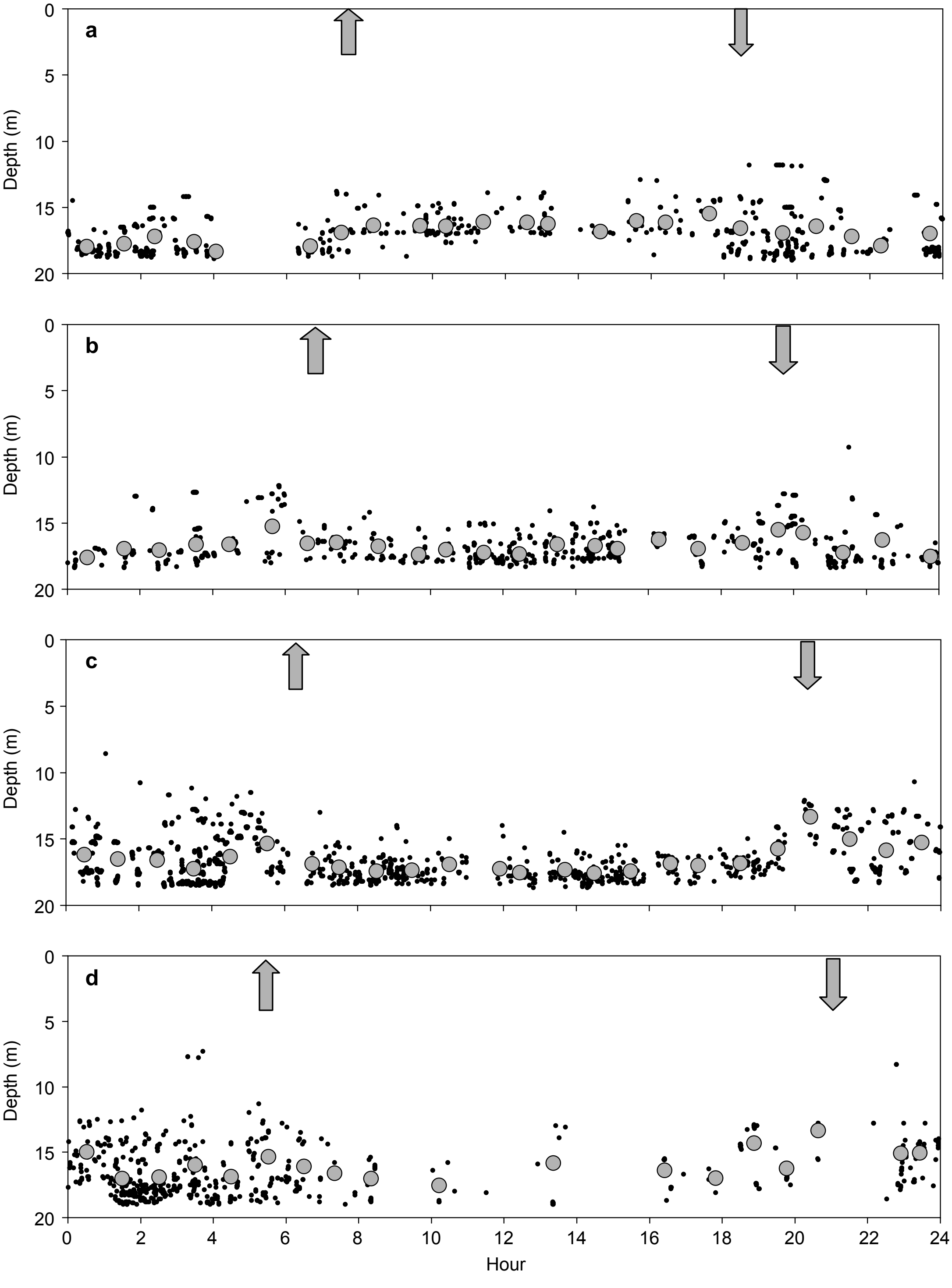

Fig. 1. Diurnal changes in the mean swimming depth (m) of fish during (**a**) 6–8 March, (**b**) 20–22 March, (**c**) 3–5 April and (**d**) 17–18 August 2000. Black dots indicate individual measurements and grey dots the hourly average depth of fish during each hour. Sunrise and sunset are marked with arrows. The echo sounder was not monitoring from 4 to 6 o'clock in part **a**.

found at 19:00 during sunset. In April, swimming depths during the hours of sunset and evening were clearly different from the daylight hours (ANOVA: Tukey $p < 0.05$). During dark hours, fish were in April detected somewhat higher than in March. In summer, no clear ascent took place around sunrise or sunset.

Fish swam typically between 5 and 50 cm s^{-1} (Fig. 2). Under ice some fish were almost motionless during the night, while in August only a few fish moved slower than 5 cm s^{-1}. The distribution of horizontal direction of fish movement was uniform in all study periods. In March, there was a small change in the average speed around sunrise or sunset. In April, however, a decrease in the speed began an hour before sunset. The average swimming speed of fish was higher during the day than at night (ANOVA: Tukey $p < 0.05$). In August, the swimming speed was for four hours around noon higher than during the other hours (ANOVA: Tukey $p < 0.05$). In March, there was practically no difference in the swimming speed between day and night (Table 1). However, a slight tendency towards higher daytime activity was seen on 20–22 March. At that time the snow began to melt on the ice and it increased the light penetration into the water. At the beginning of April as well as in August the swimming speed was clearly higher during daylight hours than during the dark hours. The average speed was ca. twice as high in August as under the ice in March–April.

In March–April, in the ice-covered lake, acoustic target strength distribution showed that larger fish were monitored during daylight than in darkness. In August, the situation was reversed. Larger fish tended to move faster than smaller ones both under ice (Spearman $r = 0.508$, $p < 0.001$) and in summer (Spearman $r = 0.276$, $p < 0.001$). Exploratory seining under ice showed that the larger fish (ca. –44 dB i.e. 15 cm) were vendace and the smaller ones (ca. –48 dB i.e. 10 cm) smelt. The average swimming speeds under ice ranged mostly from 0.5 to 3 body lengths per second. Speed relative to body length was about the same in August.

Light intensity measurements showed that darkness, i.e. one W m^{-2}, was between seven and six meters from noon until one hour before sunset one week after the end of the echo-sounding in April. Darkness reached the water surface by sunset.

Discussion

Our data indicate that on a seasonal basis the increasing light intensity has a marked influence on the swimming speed of vendace and smelt. An interesting question for future studies is how much swimming behaviour is affected through physiology e.g. melatonine synthesized by pineal gland (Porter *et al.* 2001) and how much it is dependent on foraging and predator-prey relations in the aquatic community.

Low temperature and the scarcity of sunlight together with isolation from the atmosphere make under-ice conditions radically different from summer conditions. Mixing in ice-covered lakes is caused by through-flow currents, oscillations of the ice, and convection currents induced by heat flow from the sediments or by solar radiation penetrating the ice (Bengtsson 1996). In our study area, there was no through-flow and obviously most of the mixing was caused by penetration of solar radiation in winter. During the echo-surveys the air temperature variation was small and the wind was weak, and thus ice movements causing noise in the water were small. The wind was also weak in the summer sampling period. Thus we concluded that winter and summer echo-surveys could be compared in spite of the differences in the seasonal weather.

In March–April the number of daylight hours increased during the study period from 11 to 15 hours. In summer the day-length was ca. 17 hours. There was less light in the water column under snow and ice than in summer, particularly for low sun angles during March–April. It is well known that vision is the main sensory ability

Table 1. Average swimming speed (cm s^{-1}) of monitored fish in 2000.

Date	*n*	Day		Night	
		Mean	SD	Mean	SD
6 March	925	11	2.2	12.4	3.7
20 March	946	13	5.4	12.4	8.1
3 April	1800	19.6	7.8	9.6	4.2
17 August	645	26.1	12	19.6	5

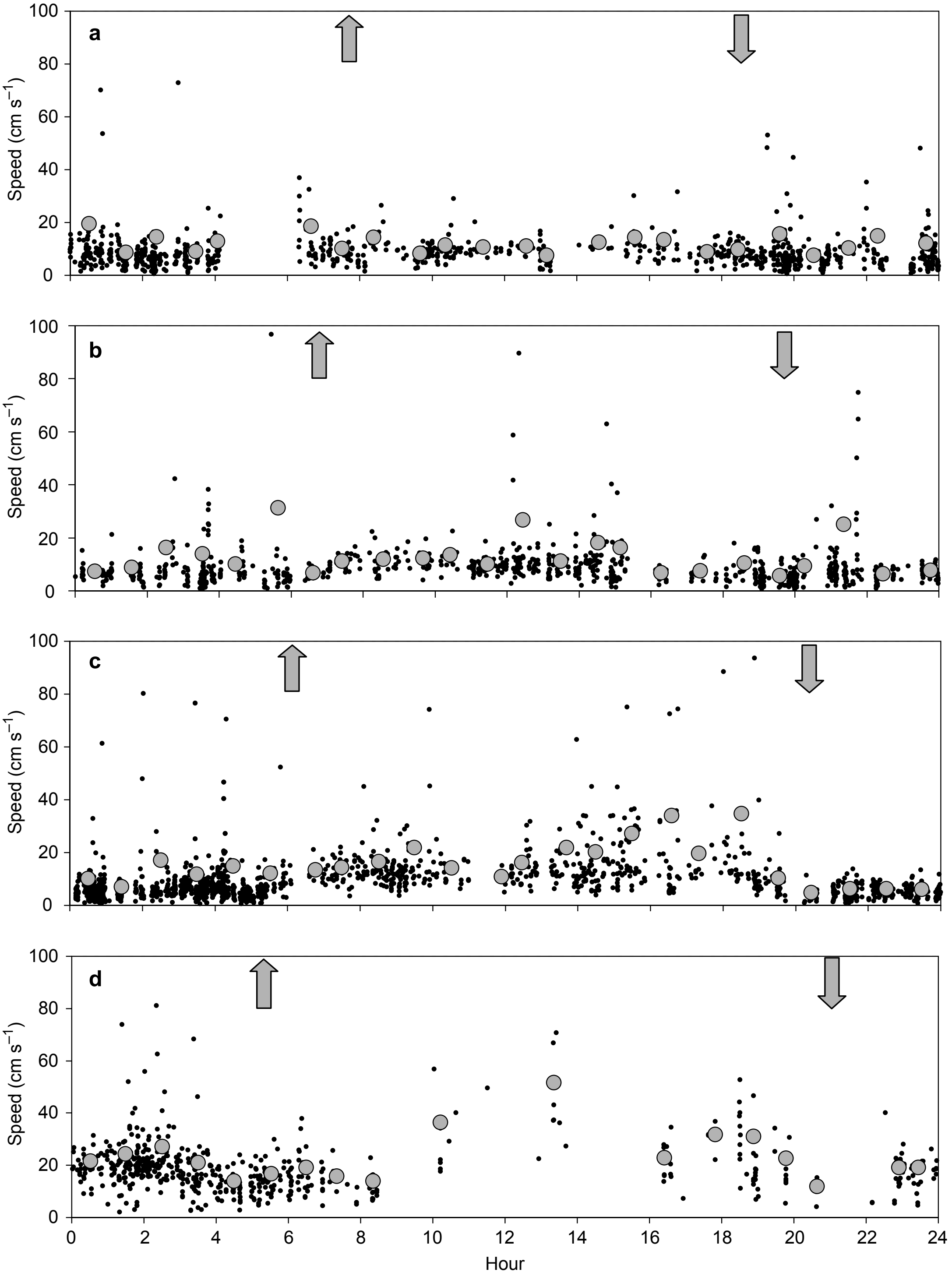

Fig. 2. Diurnal changes in the hourly mean swimming speed (cm s^{-1}) of fish. For specifications *see* Fig. 1.

governing the formation and maintenance of fish shoals, and that in general shoals break up when the light intensity falls below a certain level (Ellis 1956). Much of the diurnal variation in the shoaling behaviour and swimming speed can be assumed to take place when the solar illumination decreases and fish lose visual contact with their neighbours, causing the shoals to disperse. This happens after sundown under ice, and in the darkness the swimming speed also decreases. The reverse happens at dawn. These phenomena were not so clear in summer. In the future, we consider it important to make a bottom-up echosounding to study also the fish movements in the coldest water layer just below the ice.

Feeding is a good reason for plankton feeders like vendace and smelt to swim faster in daylight than in darkness. Previous under-ice studies (Jurvelius *et al*. 2000) strengthen the belief that vendace and smelt shoal during the day and disperse during the night. The same behaviour is typical also in summer (e.g. Jurvelius *et al*. 1988). In bright light conditions these fish shoal and this might be adaptive behaviour towards predators. On the other hand, if zooplankton school in light and vendace caught plankton by sight, fish schooling could also increase the foraging success of vendace in daylight.

Our estimates of the average swimming speed of smelt and vendace correspond closely to the speed of brook trout (*Salvelinus fontinalis*), yellow perch (*Perca flavescens*) and alewives (*Alosa pseudoharengus*) estimated by split beam hydro acoustics and underwater video cameras (Arrhenius *et al*. 2000). Preliminary results under ice by Jurvelius *et al*. (2000) strengthen the opinion that the speed of free-swimming lake fish is usually between 0.5 to 2 body lengths s^{-1}. We could not distinguish echoes from different species, but Jurvelius *et al*. (2000) concluded that the under-ice swimming speed of vendace and smelt was almost the same in daylight, but that smelt swam faster at night than in daylight while vendace swam slower.

The swimming speed of fish was lower during winter under ice than in summer. The lowest average swimming speeds were found in the darkest hours under ice in April, and the highest at noon in August. The hourly average speeds reached their maximum during the day and were at a minimum around sunset and dawn in winter and summer. In March the day and night swimming activities were almost the same. The increasing solar radiation in April caused the echo-surveyed fish to manifest clear day activity. This activity pattern was also seen in August. Previous echosoundings have shown that a considerable proportion of fish might live in dense schools on the bottom during the day in August (Jurvelius *et al*. 1988). Maybe fish that swam further away from the bottom in August had to swim faster in order to avoid predators. Those fish that stayed close to the bottom may have remained quite stationary. Unfortunately, there is not much we can say about the activity of those fish.

Fish swimming speed is a crucial component of bioenergetics models where metabolic losses are a function of swimming speed (e.g. Hanson *et al*. 1997). Split beam acoustics can be used to study the vertical and temporal distribution as well as the swimming speed of fish under ice in winter and in open water in summer. As Torgersen and Kaartvedt (2001) stressed, split beam target tracking may be used to study fish migrations *in situ*, without the constraints and possible artefacts of an experimental set-up. This method is also aided by the automatic and time-efficient data collection and processing. Split beam trace tracking can be a powerful tool to study how fish are responding to environmental changes such as the engine noise of trawlers and wastewater entering the study area. In future studies, it would be important to clarify how light affects the behavioural mechanism of fish.

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