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Distribution and diel vertical migration of Eurasian perch (*Perca fluviatilis* L.) during winter

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The distribution and migration patterns of overwintering perch were studied by hydroacoustics and gill netting in Lake Constance, central Europe. In autumn, perch left the littoral and moved to deeper waters for overwintering. They lived at temperatures below 6°C for about six months. In January, perch were present between the 42 and 69 m depth contours. Their distribution then shifted to increasingly shallower depths by 0.25 m per day, and they returned to the littoral in early May where adults spawned in late May. During winter, perch performed diel vertical migrations, resting on the bottom during day and swimming up to 25 m off the bottom during night. Light was the proximate cause of this regular vertical migration. Perch did not gain an energetic advantage by migrating in a homothermal water column, but they may have gained access to copepods in addition to their main diet of benthic invertebrates. It is hypothesized that predator avoidance is the ultimate cause of diel migration in overwintering perch which avoid piscivorous birds by resting on the bottom during day and avoid burbot by swimming off the bottom during night.

1. Introduction

The distribution and migration patterns of lake-dwelling *Perca* species during the growing season are generally well known. Soon after hatching in spring, larvae are dispersed in the pelagic zone from where they return to the littoral as early juveniles some weeks later (Coles 1981, Whiteside *et al*. 1985, Post & McQueen 1988, Treasurer 1988). In the littoral, young-of-the-year form schools during the day, feed throughout the day or at twilight, and rest on the bottom during the night (Emery 1973, Hasler & Villemonte 1953). As thermal stratification breaks down in autumn, they move to deeper waters for overwintering, from where they return to the littoral next spring (Wang & Eckmann 1994). This regular migration between summer and winter habitat is also displayed by older juveniles and adults. Besides the general observation that perch overwinter in deeper waters, little is known about their behaviour during this time of the year. Lake Constance, a warm-monomictic prealpine lake in southern Germany, offers the possibility of monitoring fish distribution during winter because the lake freezes only rarely (Kiefer 1975).

During a routine hydroacoustic survey on Lake Constance in winter 1989–1990 it was observed that dense fish aggregations were present at 50 m depth during the night, while they were absent during the day. Further observations suggested that these distribution patterns resulted from regular vertical migrations of fish between the bottom and the open water. These fish were suspected to be overwintering perch, and a study was initiated to investigate their distribution and daily migration behaviour during winter. The specific aims of this study were: (i) to identify the species in question, (ii) to test the hypothesis that light is the proximate cause of diel migration, (iii) to define the depth contours between which these fish overwinter, and (iv) to estimate their daily vertical migration amplitude

2. Material and methods

The study was carried out near the island Mainau at the southwestern shore of Ueberlinger See, a fjord-like basin at the northwestern end of Lake Constance. The lake is 500 km^2 large and up to 254 m deep, it is mesotrophic, and the most abundant fish species are whitefish (*Coregonus* ssp.) and Eurasian perch (*Perca fluviatilis* L.) (cf. Eckmann 1991). The sediment is sandy at the study site, and the lake bottom falls off to more than 100 metres at about 1 km distance from the shore. During the growing season from late May to late October, Eurasian perch are fished with bottom-set gill nets between 5 and 25 metres depth. Commercial fishing for perch continues throughout winter in waters from 40 to 80 metres depth, but yields are much lower than in summer. In early winter (Dec./Jan.), inshore spawning whitefish are also caught in the sublittoral between 5 and 20 metres depth.

Fish were sampled with bottom-set gill nets of 10 to 38 mm bar mesh and 1.5 to 2-m height. Nets were exposed between a 20 and 60-m depth in February/March 1991, 1992, and 1994. Fish were identified to species, measured and weighed. Subsamples were taken for age determination by opercular bones (1994 samples) and stomach content analyses (1991 and 1992 samples). Macrozoobenthos samples (four replicates) were taken during the day with a bottom grab of 225 cm^2 cross section from a 20, 40, and 60-m depth in February 1991 and in March 1992. In parallel, zooplankton was sampled with a vertically towed closing net in 20-m intervals from a 60-m depth to the surface. Samples of benthos and plankton were preserved in 5% formalin for later analyses. Temperatures were read from isopleths that are based on continuous recordings with thermistor chains and from additional temperature profiles. These data were sampled in the central part of Ueberlinger See (D. Ollinger, Limnol. Inst., Univ. Constance, pers. comm.).

Hydroacoustic data were sampled on 13 occasions in winter 1990/91 along a west-east transect. The transect started in a shallow bight between the island Mainau and Konstanz-Egg above the 10-m depth contour and ended at approximately 1 500 m distance above the 100-m depth contour (cf. IGKB 1990). At 2.1 m/s cruising speed one sampling lasted for about 12 minutes. In total, 118 transects were sampled. Additional data were sampled during 9.5 hours while the boat was anchored above 20, 30, 40, 50, and 60-m depths. A single-beam echosounder Simrad EY-M with 70 kHz operating frequency was used. TVG was set to 40 logR. The system was calibrated with a standard copper sphere. Perch smaller than 6 cm (– 52 dB) were not considered in single-fish analyses. Details on data acquisition and processing are reported in Eckmann (1991).

For analysing the spatial distribution of fish in the water column, the acoustic energy (receiver voltage squared) from single and multiple targets was integrated along subtransects which each comprised a 10-m depth interval (eg from 20 to 30 m, 30 to 40 m bottom depth etc.). The length of each subtransect in metres was estimated from mean cruising speed, ping rate and the number of pings in that transect. Each subtransect was further subdivided vertically in cells of 2 m thickness. Echo energy was calculated in arbitrary units per cubic metre for each cell. Finally, a value proportional to fish biomass (arbitrary units/m^2) was calculated for each cell.

The echoes from occasionally encountered gill nets were excluded from the analyses only when these echoes were clearly separated from fish echoes. Otherwise, the complete transect was discarded. In most surveys, some scattered targets were observed in pelagic waters during daylight hours (Fig. 1a). They were generally located farther offshore and closer to the surface than the vertically migrating targets. During night surveys, these targets were still present in offshore waters and were excluded from further analyses after visual inspection of the echograms.

The spatial distribution of the vertically migrating, densely aggregated targets was characterized by calculating the median and 5% and 95% percentiles of the echo integrals in both horizontal and vertical directions. To this end, the echo integral for each subtransect was obtained by summing fish biomass estimates (units/m^2) across all depth cells and multiplying the sum with the subtransect length. The echo integral for each 2-m depth layer was obtained by multiplying fish biomass estimates for each cell with cell length and summing across all subtransects. These values (in units/m) which are proportional to fish biomass per metre shoreline allow comparison of the spatial distribution of fish in both vertical and horizontal directions within and between surveys.

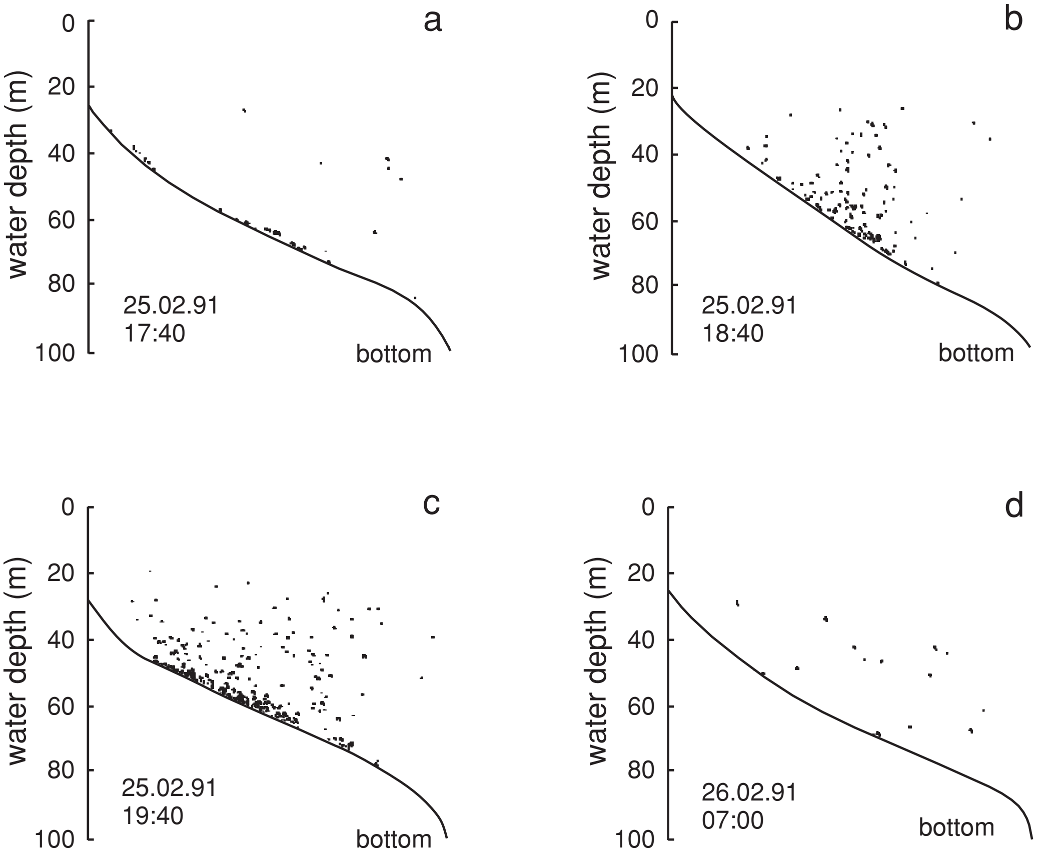

Fig. 1. Echograms sampled in the shore region of Lake Constance/Ueberlinger See showing diel vertical migration of overwintering perch. Local sunset and sunrise times were 18:01 and 7:13 hours.

3. Results

Bottom-set gill nets yielded 394 perch of all age classes from 0 to 4, one ruffe (*Gymnocephalus cernuus* (L.)) and one Arctic char (*Salvelinus alpinus* (L.)). A professional fisherman who operates in the study area with gill nets of 32 mm bar mesh reported some by-catch of inshore spawning whitefish until late January. Afterwards, whitefish were only found in the pelagic and his catch consisted of perch only. Therefore, it is concluded that the vertically migrating targets come almost exclusively from perch.

Overwintering perch swam off the bottom at dusk and returned to the bottom at dawn (Fig. 1). Only a small fraction of the perch population could be detected by echo sounding during the day. Since the theoretical vertical resolution limit of the EY-M sounder is 44 cm (1 450 m/s sound speed, 0.6 ms pulse length), most fish either rested on the bottom or swam close to the bottom during the day. During the night, mean echo energy increased about tenfold as compared to the maximum daytime values. Only part of the targets were observed at considerable distance from the bottom, but about 50% of the total echo energy was confined to a narrow layer above the bottom (Fig. 1).

On nine occasions between 22 January and 2 April 1991, acoustic data were sampled continuously from before sunset until complete darkness (between 7 and 24 transects per survey). For each survey, echo energy per transect was plotted against median time of the transect and the time when 50% of the mean nighttime echo energy was reached was estimated by interpolation. When these data for all nine surveys were regressed on local sunset time (Fig. 2), the slope was not significantly different from 1 (*t*-test,

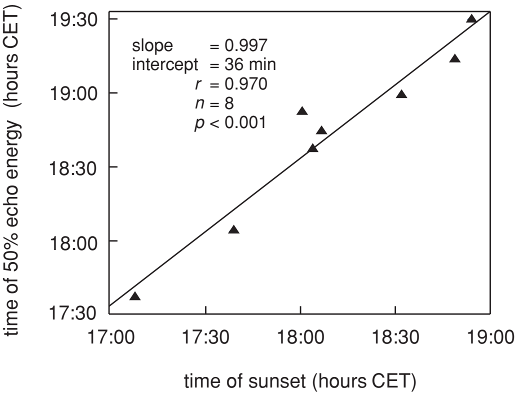

Fig. 2. Regression of the time when 50% of the average nighttime echo energy due to vertically migrating perch were reached on local sunset time. Data were sampled from 22 January (local sunset time 17:08) to 2 April (local sunset time 18:54).

$p < 0.001$) and the intercept was 36 minutes. It was concluded that decreasing light intensity is the proximate cause for the perch's evening ascent from the bottom into the open water. The fish returned to the bottom at dawn, but data were not collected to test the hypothesis that increasing light intensity is the proximate cause for the morning descent to the bottom.

It was further speculated that those fish that live at greater depth during the day start to ascend into the open water earlier than those fish that live at shallower depth. To evaluate this hypothesis, the depth contour was determined that corresponds to the nighttime population gravity centre (PGC), i.e. where 50% of the population stay over a deeper bottom and 50% over a shallower bottom. Then, two depth intervals were defined by the depth contours that are 5 and 15 m above and 5 and 15 m below the PGC. For both intervals the time when 50% of the mean nighttime echo energy was reached was estimated by interpolation. In six out of eight cases, fish from the deeper bottom ascended about eight minutes earlier, but this difference was not significant (sign-test, $p > 0.05$).

Echograms which were sampled while the boat was anchored revealed that fish located off the bottom during the night stayed at the same water depth for considerable time. Traces from individual targets could be tracked for up to three minutes between a 40- and 50-m depth ($n = 61$), during which time target depth fluctuated less than 2 m. Simultaneously, other targets sank towards the bottom. This was most obvious within the last few metres above the bottom where many individual targets could be tracked until they could not be resolved from the bottom contour. These observations could be made any time of the night.

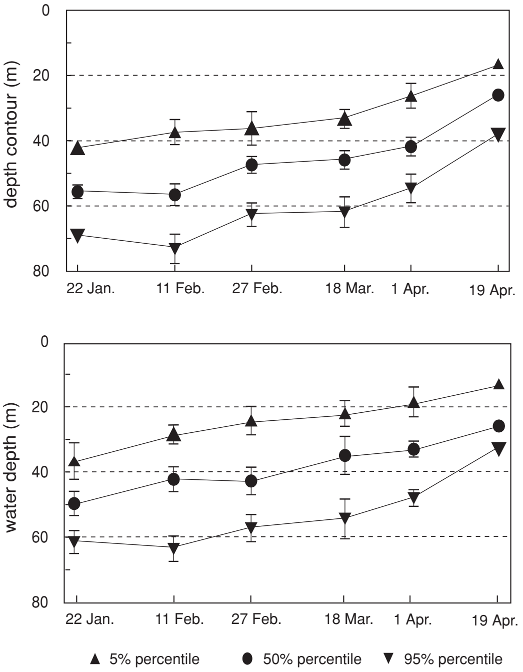

Fig. 3. Depth contours that delimit the bottom area over which perch were located during night (upper panel), and water depth range inhabited by perch during night (lower panel). For each date, the 5, 50, and 95% percentiles and their standard deviations are shown. Numbers of evaluated transects per date from 22 January to 19 April were 3, 5, 14, 3, 25, and 2.

The sinking velocity was determined for two fish which sank from 10 to 40 m and from 22 to 32 m at mean speeds of 9.3 and 4.5 m/min, respectively. Sinking velocity increased for the first fish from 6.7 m/min (10–15-m depth) to 18.3 m/min (30–35 m depth) and then decreased again to 11.2 m/min, while for the second fish it increased from 3.9 to 5.2 m/min. The ascent of fish from the bottom into the open water could not be documented in this way. To estimate the mean speed of the upward migration, the distance between the bottom depth at the PGC and the upper boundary (5% percentile) of the nighttime distribution was divided by the time between the start of the evening ascent and the time when 50%

of the nighttime echo energy was reached. The average speed of the upward migration calculated for eight surveys was 21.7 (*S.D.*) m/min.

In January, perch lived between the 42 and 69 m depth contours (Fig. 3, upper panel). These limits corresponded to the 5% and 95% percentiles of the echoenergy in a horizontal direction from inshore to offshore, averaged over all night transects. Until the end of March, perch continued to inhabit a depth contour interval of about 30 metres (5% and 95% percentiles). During that time, their horizontal distribution gradually shifted to shallower depths by approximately 0.25 m per day. At the beginning of April they lived between the 26- and 55 m-depth contours. During April, when the PGC was located above the 40 m depth contour and the fish inhabited a more steeply inclined bottom region, the upward shift of their horizontal distribution increased to about one 1 m per day. They lived between the 17- and 38-m depth contours on 19 April (Fig. 3, upper panel).

The maximum daily vertical migration amplitude remained constant from January to late March. The upper boundary of the fishes' nighttime vertical distribution, which was estimated for each subtransect as the upper 5% percentile of the total echo energy in this subtransect, did not depend on bottom depth. This means that fish at the PGC ascended to 24 m from the bottom, and those at the 5% and 95% percentiles ascended to 9 and 38 m. Since the horizontal distribution gradually shifted to shallower depths from January to late March and the vertical migration amplitude remained constant, the nighttime distance between the upper boundary of the fish and the water surface decreased from 35 to 19 m (Fig. 3, lower panel). During April the daily vertical migration amplitude decreased. Thus, by mid-April, when perch were located between the 17- and 38-m depth contours, they ascended to about 10 to 15 m below the surface. This corresponded to a maximum vertical migration amplitude of only 12 m at the PGC.

Zooplankton and zoobenthos abundances were similar in 1991 and 1992. Copepods (mainly *Cyclops* and *Eudiaptomus*) dominated in zooplankton samples numerically by more than 99%. Their abundance decreased from 2 100–3 000 ind/m^2 in the 0–20 m layer through 1 000–1 400 ind/m^2 (20–40 m) to 800–1 100 ind/m^2 in the 40–60-m layer. Zoobenthos was composed of Tanypodinae, Chironominae, and *Tubifex* sp. Since the latter species was never found in perch stomachs, it is not considered any further. Tanypodinae abundance decreased from 1 380–1 600 ind/m^2 at 20 m depth through 300–400 ind/m^2 at 40 m to 135–190 ind/m^2 at a 60-m depth. Chironominae were most abundant at a 40-m depth (1 150–1 260 ind/m^2) and less abundant at 20 m (150–1 000 ind/m^2) and 60 m (270–320 ind/m^2) depth.

Stomach contents of perch were similar in 1991 ($n = 60$) and 1992 ($n = 37$). Copepods were generally found in low numbers, except three specimens which contained up to 150 copepods per stomach. Chironomids were the main diet of overwintering perch. Between three and five chironimids were counted per stomach.

4. Discussion

The behaviour of lake-dwelling Eurasian perch during winter has, to our knowledge, never been studied before by hydroacoustics. It is well known that perch migrate from the littoral to greater depth in autumn when thermal stratification breaks down and in lakes that do not freeze over, such as Lake Constance, professional fishermen know by experience at what depth perch overwinter and how they gradually return to shallower waters in spring. The precise distribution and behaviour of perch during winter, however, are largely undocumented.

The autumnal migration of perch to deep waters is faster than their backward migration to shallow waters in spring. Wang and Eckmann (1994) observed that 0+ perch left the shallow littoral of less than 10 m depth in Lake Constance within two weeks during October 1991. Another two weeks later they had completely disappeared from areas less than 25 m deep. From November onwards, 0+ and older perch could only be sampled with bottom-set gill nets between 30 and 60 m depth. In addition, hydroacoustic studies that were conducted during whitefish spawning time in 1989/90 (Eckmann 1991) revealed that perch lived between a 30- and 60-m depth by the beginning of December. Although the precise pattern of the perch's retreat from the littoral has not been documented by hydroacoustics, it is assumed that they migrate to deeper regions within two months or even less, whereas their gradual re-

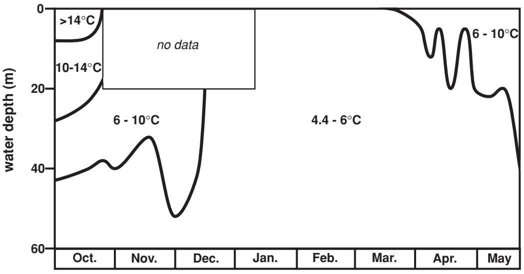

Fig. 4. Vertical distribution of temperature in the central part of Lake Constance / Ueberlinger See during winter 1990/91. (No. data available in the upper 20 m from 25 October to 10 January due to technical failure.)

turn to the littoral lasts for over four months from January to early May.

Perch require winter temperatures of 6°C or lower during at least 185 days to attain complete sexual maturity in the following spring (Hokanson 1977) which may be the reason they migrate to deeper regions for overwintering. Temperature data collected in the central part of Überlinger See (Fig. 4) allow estimation of the temperatures that perch experienced during winter 1990/91. The 6°-isotherm fluctuated around a 40-m depth in October and November 1990 and then rose towards the surface during December. At the beginning of January 1991, the water column was almost homothermal down to 40–80 m. Holomixis occurred during mid-February at 4.4°C, after which thermal stratification started to build up again in March. During April, the 6°-isotherm sank to about a 20-m depth, and surface temperature increased to 10°C in early May. Therefore, perch lived at temperatures below 6°C from November 1990 until the end of April 1991. It was only in late April/early May, when perch invaded the littoral zone, that they encountered temperatures above 6°C. The fast retreat of perch to deeper waters in autumn and their gradual return to shallow waters thus assures that they live at temperatures below 6°C during about 6 months from November until late April.

Data on vertical temperature distribution do not provide any evidence that the gradual return of perch to shallow water is controlled by increasing temperature. From January to late March, the depth contours between which 90% of the perch population lived shifted to shallower depth at an average rate of 0.25 m per day. Water temperature, however, changed in a dissimilar way. During January and February, the water column was generally homothermal from 20 m down to 80 m with temperatures decreasing from 5.2°C on 24 January to 4.3°C on 28 February. During March, temperatures between a 20- and 60-m depth were constant at 4.4°C. They increased to 4.6–5.2°C by the beginning of April and to 4.8–5.8°C by 30 April. It is obvious that perch moved to shallower depth with both decreasing (Jan./Feb.) and increasing (Mar./Apr.) temperatures. Thus, the hypothesis that perch use water temperature as an orientation cue for their gradual return to the littoral is not supported by the present data. In a large and deep lake like Lake Constance, the general time course of water temperature is fairly predictable. It is, therefore, conceivable that perch do not need to respond to actual temperature changes but rather use a different mechanism that assures that they arrive at a certain time (late April/early May) in the littoral zone. There, they might use temperature to trigger spawning, which generally occurs in May during a short interval of only two weeks (Wang & Eckmann 1994).

Diel vertical migration is widespread in fish. There are three hypotheses that account for the ecological significance of this behaviour (Levy 1990): the bioenergetic hypothesis, the foraging strategy hypothesis, and the predator avoidance hypothesis. The bioenergetic hypothesis predicts that vertical migrants experience different temperatures whereby they achieve metabolic benefits and, ultimately, increased growth rates. This hypothesis can be dismissed in the present case, because vertically migrating perch experienced temperature differences of only 0 to 0.6°C from January until early April. It was only by mid-April, that the temperature difference between the upper and lower 5% percentiles of the perch's nighttime distribution exceeded 1°C.

The foraging strategy hypothesis is partly supported by the present data. Chironomids are the main diet of overwintering perch in Lake Constance. Tanypodinae that are carnivorous and live on the sediment surface were strongly selected over Chironominae that live buried in the sediment (unpubl. data). But three out of 97 perch contained up to 150 copepods in their stomachs. Copepods dominate the zooplankton community of Lake Constance from January to April. They show no distinct vertical migration during that time, and their population gravity centre is located at about a 20-m depth (Stich 1989). Our own data show that copepod abundance increased towards the surface. Vertically migrating perch might, therefore, gain access to higher abundances of copepods and use this food resource in addition to benthic food. The observation that only three out of 97 perch had consumed appreciable amounts of copepods is consistent with our hydroacoustic data. These data suggest that only a small part of the population ascends to shallow waters at dusk, while about 50% are located within a narrow layer parallel to the bottom.

The predator avoidance hypothesis provides an additional explanation for the observed migration pattern without contradicting the foraging strategy hypothesis. Fish that stay in the open water during the day are potentially threatened by piscivorous birds. Goosander (*Mergus merganser*) which overwinter on Lake Constance, attack their prey from below, so the risk of predation is less for a fish that rests on the bottom during the day. Besides goosanders, cormorants (*Phalocrocorax carbo*) may visit the lake in large flocks during winter. Both species are accidentally captured in commercial gill nets at depths of 25 or 30 m. Predation risk from piscivorous birds could, thus, be the reason for the daytime resting on the bottom of overwintering perch.

The dusk ascent of those perch that stay near the bottom during the night might be a reaction to the presence of burbot (*Lota lota* (L.)) in this lake. Burbot are active during night and forage close to the bottom. They feed at temperatures as low as 4°C and live between a 40 and more than 50-m depth in Lake Constance during winter (Hartmann & Löffler 1978, Nümann 1939). Nümann (1939) reported that burbot indeed feed on small perch during winter, and Guthruf *et al.* (1990) observed in Lake Biel that the diet of burbot may consist up to 90% of 0+ and 1+ perch from November to January. Swimming off the bottom during the night can, therefore, be interpreted as an adaptive strategy that reduces the risk of being preyed by burbot.

Fish that swim off the bottom during the night might be transported away from their daytime resting area by horizontal currents. Overwintering perch, however, seem to stay within the water column that is delimited by the depth contours between which they live during the day. This might be achieved by regular sinking to the bottom during the night and monitoring the associated pressure changes by stretch receptors in the swimbladder wall. This hypothesis is compatible with our hydroacoustic observations that some targets were floating apparently motionless at the same depth for up to three minutes while others sank to the bottom. Even those fish which swim far off the bottom (from 10 to 30 m) seem to return to the bottom during the night. It was not possible during stationary sounding to track individual fish after they had sunk to the bottom. We can, therefore, not speculate about how long an individual perch rests on the bottom before it ascends again, nor whether this individual will ascend to a similar water depth as before.

Different size classes of perch probably ascend to different depth strata during the night because for larger fish it might be less profitable to feed on small-sized prey like copepods. This hypothesis can be tested by comparing target strength distributions among different depth strata. In vertically migrating fish that move over several tens of metres within minutes, such a comparison provides little information because swim bladder volume and tilt angle vary continuously. Therefore, only maximum target strength values (grouped in 2 dB intervals) in a layer close to the upper and in a layer close to the lower boundary of the perch's nighttime distribution were compared but no consistent trend was found. Thus our data suggest that perch of – 36 to – 38 dB, which corresponds to a total length of 16.5 to 19 cm (Imbrock et al. 1995), are found near the bottom as well as some 20 or 30 m above the bottom.

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