



## Diel and seasonal distribution of perch in Lake Constance: a hydroacoustic study and *in situ* observations

F. IMBROCK, A. APPENZELLER AND R. ECKMANN\*

Limnological Institute, University of Konstanz, PB 5560, D-78434 Konstanz, Germany

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A near-shore belt 50 km in length was surveyed parallel to the shoreline of Lake Constance, central Europe, with a single-beam echosounder five times between July 1993 and February 1994. The species and age composition of fish in the survey area was investigated by gillnet fishing and SCUBA-diving. In summer, the horizontal distribution of perch was patchy. Population density declined from east to west, and highest densities occurred in one shallow bay and close to ports and jetties at steeper shores. During daytime, perch stayed in the sublittoral zone between 3 and 15 m depth and between 2 and 6 m above the thermocline. Within this layer age classes were separated spatially: the relative number of young-of-the-year perch declined with depth whereas the relative number of adult perch (2+ and older) increased with depth. At dusk the fish migrated to the littoral zone, where they spent the night resting on the bottom. In winter, under almost homothermal conditions, perch of all ages were located between the 35 and 70 m depth contours, where they performed pronounced diel vertical migrations. They rested on, or close to, the bottom during daytime and ascended up to 20 m below the surface at night. During this season, horizontal distribution of perch was much more homogeneous than in summer

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Key words: *Perca fluviatilis*; horizontal distribution; vertical distribution; diel migration; hydroacoustics; echo sounding.

### INTRODUCTION

Lake Constance, shared by Austria, Switzerland and Germany, is the second largest, warm-monomictic European pre-alpine lake. It has a surface area of 500 km<sup>2</sup>, a volume of 47.7 km<sup>3</sup>, a maximum depth of 252 m and a mean depth of 100 m. Holomixis occurs in late winter at a temperature of 4°C. In its natural state, Lake Constance was oligotrophic. Due to anthropogenic eutrophication, the concentration of PO<sub>4</sub>-P during overturn reached a maximum of 87 µg l<sup>-1</sup> in the late 1970s. Since the beginning of the 1980s, the trophic status of Lake Constance has been decreasing (Geller & Güde, 1989) and it is currently mesotrophic.

During eutrophication adult perch *Perca fluviatilis* L. shifted their habitat from the littoral to the sublittoral zone. In parallel, their feeding habits changed from being mainly piscivorous to being planktivorous in summer and benthivorous in winter (Hartmann & Nümann, 1977). During most of the year juvenile and adult perch seem to be separated spatially (Wang & Eckmann, 1994). Gillnetting showed that the vertical distribution varies with season, the depth of maximum catch increasing from 6 to 10 m in summer to more than 40 m in winter (Hartmann & Nümann, 1977). Except for this general habitat shift,

\*Author to whom correspondence should be addressed. Tel.: +49-7531-882828; fax: +49-7531-883533; email: reiner.eckmann@uni-konstanz.de

little is known about the distribution of perch in this lake. Hartmann (1984) observed increasing commercial yields from west to east, but no data concerning the *in situ* horizontal distribution have been available so far. The aim of our study was to investigate the temporal and spatial dynamics of perch distribution in Lake Constance for a better understanding of the species' fundamental ecology. In addition, such data provide the necessary basis for abundance estimates and associated management decisions.

## MATERIALS AND METHODS

### SAMPLING METHODS

Echo surveying was made with a single-beam echosounder Simrad EY-M of 70 kHz working frequency equipped with a transducer of 11.2° beam width, which is described in detail by Jurvelius *et al.* (1984). The upper 3 m and the near-bottom layer (<0.5 m) were not accessible to analysis. Time-varied gain was set to 40 log R. The system was calibrated with a standard copper sphere. The analogue signals were recorded on a tape recorder (SONY TC-D5M stereo cassette recorder). These were digitized and stored on a PC. Data were analysed with special software developed at Constance University electronics workshop (Eckmann, 1991).

Fish signals were identified using bottom-set gillnets of 7, 10, 14, 28 and 32 mm mesh size. Net panels were 1.2 to 2 m deep and 12 to 25 m long. From July to October, the nets were set between 2 and 20 m water depth at dusk for periods of 10–30 min. In February and March 1994, gillnets were exposed during the night at 35 to 50 m depth. Total length (L) and wet weight of all fish were measured ( $n=472$ ) and related to age, which was read from the operculum ( $n=109$ ).

Light attenuation was determined for each month with a lux meter from stepwise measurements (1 m intervals), at the same location where diel migrations of perch were investigated (Fig. 1). From these data, light intensity for any depth was estimated from surface intensity, assuming an average surface loss of 7% (Schanz, 1983). Temperature profiles were measured with a temperature-depth-probe at four sites in the sublittoral zone and at one site in the pelagic zone (Fig. 1). We defined the depth of the thermocline as the depth having the steepest temperature gradient within a 5 m interval and then selected the 1 m interval with the greatest temperature difference.

Hydroacoustic investigations were complemented by SCUBA-diving on 18 occasions between April and August 1993 (total diving time 12 h 35 min). The presence and behaviour of perch were observed between 3 and 30 m depth at seven sites within the study area (Fig. 1). Each site was visited at least once during the day and once from dusk until dark. Additionally, on one occasion in September, a programmable underwater photo-camera (MINOLTA Dynax 7000i with flashlight NIKONOS SB3) took a series of photographs every 30 min from dusk until dawn at 4 m depth.

### ECHO SURVEY STRATEGY

The study was carried out in the near-shore areas of the north-western part of the upper lake's main basin and the eastern part of the fjord-like Überlinger See. To map the horizontal distribution of perch in this area, we had to consider their diel migrations and their depth distribution. Diel migrations were investigated once a month by surveying a transect of 2 km length (Fig. 1) every hour from late afternoon until next morning. To evaluate the depth distributions of perch, i.e. the two delimiting depth contours between which 90% of all fish signals were located, transects perpendicular to the shore were sampled monthly at five to six locations with high fish densities (Fig. 1). Horizontal sampling was then conducted between these depth contours along a 50 km stretch parallel to the shoreline at a speed of 7.8 km h<sup>-1</sup>. In July, August, September and October 1993 this was done during the day (light intensity >20 klx) and in February 1994 at night.

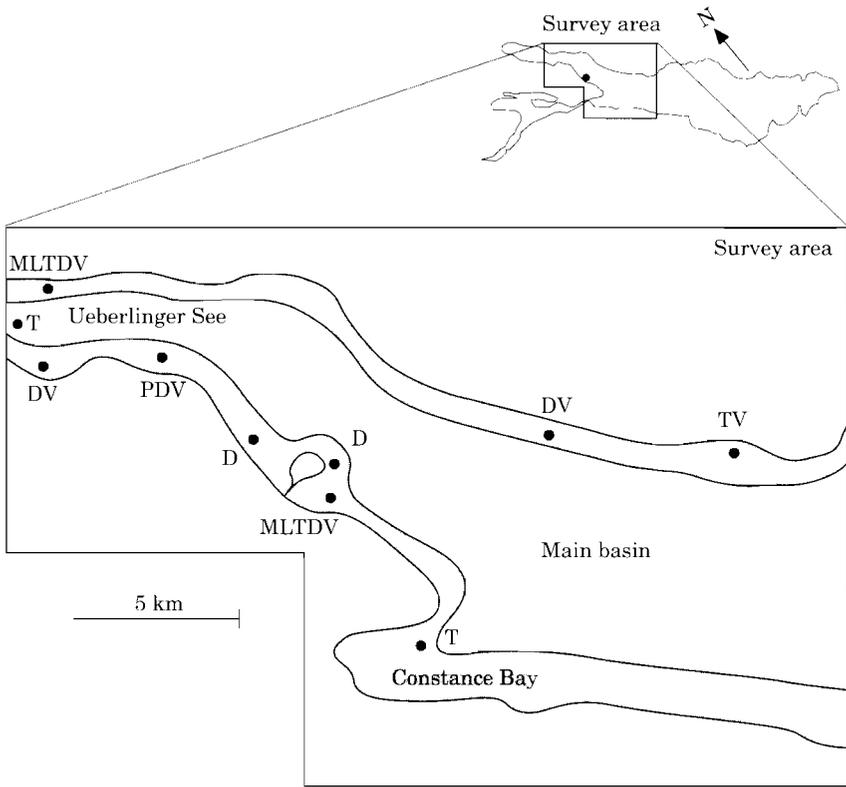


FIG. 1. Survey area and the sampling sites in Lake Constance. Grey area: near-shore belt covered by echo sounding parallel to the shoreline. M. transects parallel to the shoreline to investigate the diel migrations of perch; V. transects perpendicular to the shoreline to investigate the depth distribution of perch; L. light profiles; T. temperature profiles; D. diving grounds.

## DATA PROCESSING

After visual inspection of the echograms the shoreline was divided into segments according to changes in fish density. Abundance was calculated for each segment and then assigned to one of four classes:  $<100$ ,  $100-1000$ ,  $1000-10000$ ,  $>10000$  fish  $\text{ha}^{-1}$  surface area. Monthly horizontal distribution maps were constructed from these data. The absolute fish number of each segment was calculated by multiplying fish abundance with surface area. Surface area is the product of segment length and average width of perch schools. Segment length and width of perch schools were mapped by transects parallel and perpendicular to the shoreline and then calculated from the ping rate, the number of pings and the cruising speed. In summer, the school width levelled off at  $28 \pm 14$  m for bottom slopes  $>12\%$  ( $n=125$ ). Thus at all locations with slopes  $>12\%$  where school width had not been measured, we assumed this constant value. In winter, segment width corresponded to the distance between the 35 and 70 m depth contours.

For subsequent data analysis, the sublittoral zone was divided into two different shore types: locations with and without underwater structures in waters deeper than 3 m. Such structures were: wooden or stony ports, jetties, piers, moles or boulder areas. The extension of large ports along the shore was read from the echogram. The extension of segments with narrow structures was set to 100 m.

The shoreline was subdivided into sections of 500 m length. The percentage of fish contained in each of these sections was counted. The degree of horizontal aggregation was measured by the evenness-index, defined as:

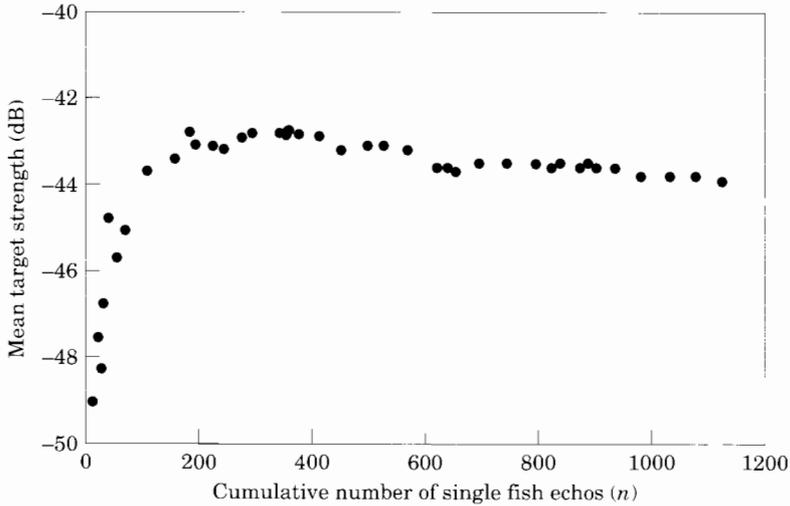


FIG. 2. Target strength estimated by the Craig-Forbes algorithm as a function of the number of single-fish echos.

$$E = - \sum (p_i * \ln p_i) * (\ln Z)^{-1}$$

where  $p_i$  is the relative number of fish in section  $i$ , and  $Z$  is the number of sections.  $E$  ranges from zero from maximal patchiness (i.e. all fish are concentrated in one section) to 1 for maximal evenness (i.e. each section contains the same number of fish). To assess the accuracy of abundance estimates by echo sounding, we compared 40 replicated samples for the same school: coefficient of variation was 61%.

### TARGET STRENGTH ESTIMATE

Total echo energy is the sum of echo energy of single fish echos (sfe) and echo energy of schools that are not resolved as single targets. The percentage contribution of echo energy of schools to the total echo energy was used to quantify the intensity of school formation. The target strength (S)\* of single fish was estimated by the Craig-Forbes algorithm (Craig & Forbes, 1969). Provided that  $sfe > 1000$ , this method produces reliable target strength estimates (Jurvelius *et al.*, 1988; Lindem, 1983).

In the present work, however, this condition was often violated because (i) in summer perch formed dense schools during daylight hours and single fish resolution was low, and (ii) to map the distribution of fish with high spatial resolution, it was often necessary to sample short transects of  $< 500$  m length. Consequently, many sampling units contained far  $< 1000$  sfe. Therefore, we sampled 40 replicated transects across a typical perch school. Mean S was estimated for increasingly larger sample units by cumulative addition of subtransects. At approximately  $> 300$  sfe, S levelled off at  $-43.4 \pm 0.4$  dB (Fig. 2). Thus, for transects with  $> 300$  sfe, the S distribution was considered reliable. For transects with  $< 300$  sfe, the S distribution of a larger sampling area that comprised the neighbouring transects and that contained  $> 300$  sfe was used. The estimated S distribution served to calculate fish number from total echo energy.

In early October, by the end of the growing season, maximum S was measured on four tethered perch of 10.0 cm (age 0+), 14.5 cm (age 1+), 22.0 cm (age 3+) and 25.0 cm (age 3+) total length. Each fish was exposed for 30 min in dorsal aspect without any tilt within the sound beam. From about 5000 S-values recorded for each fish, we chose the maximum S, supposing that this corresponds to the echo of the fish staying exactly in the

\*It is the journal's policy to avoid the use of multiple letters for mathematical symbols. The commonly used abbreviation for target strength (TS) was, therefore, changed to S, against the explicit will of the authors.

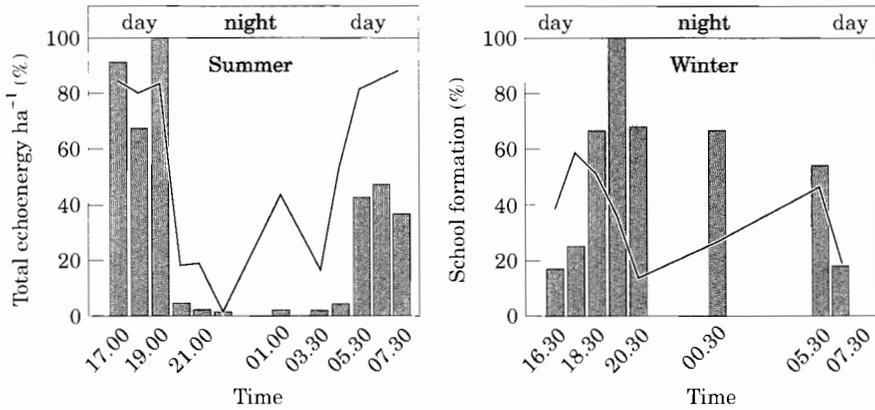


Fig. 3. Diurnal fluctuations of total echoenergy (bars) and intensity of school formation (lines) in summer (left panel) and winter (right panel). Maximum echoenergy measured during each survey period was set to 100%.

centre of the sound beam. This procedure had to be adopted because the exact position of a target in the sound beam of a single-beam sonar cannot be determined. Using this data, we established the following relation ( $n=4$ ):  $S=30.2 \log L - 74.8$ ,  $r=0.989$  [where  $S$  is maximum target strength (dB) and  $L$  is total length (cm)]. This  $S$ /length relationship together with the length/age relationship from gillnetting was used to identify the sizes and ages of perch observed by echo sounding. Limited by the resolution of the echo sounder ( $-52$  dB), perch  $<6$  cm could not be detected.

## RESULTS

In summer as well as in winter, perch between 6 and 31 cm (age 0+ to 4+) contributed between 93 and 97% of the total fish biomass and numbers of fish caught by gillnetting in the sublittoral zone of the survey area ( $n=472$ ). Therefore, we concluded that the signals on the echogram were related almost exclusively to perch. The bycatch comprised eight adult dace *Leuciscus leuciscus* (L.), 11 adult ruffe *Gymnocephalus cernua* (L.), one eel *Anguilla anguilla* (L.) and four adult coregonids *Coregonus lavaretus* (L.).

### DIEL MIGRATIONS AND BEHAVIOUR IN SUMMER AND WINTER

In summer, perch stayed in dense schools in the sublittoral zone during the day. Ninety per cent of the fish signals were found between the 6 and 30 m depth contours (5% and 95% quantil). Most fish were located at the 10 m depth contour. Between these depth contours, schools were observed between 3 and 15 m water depth (5 and 95% quantil, median: 6 m). Intensity of school formation reached very high values of  $93 \pm 7\%$  ( $n=79$ ). More than half of all schools maintained contact with the lake bottom ( $n=434$ ). Mean height of schools measured between 2 and 4 m. In some exceptional cases the height of large pelagic schools in Constance Bay reached up to 20 m. Length (extension parallel to the shoreline) and width (extension perpendicular to the shoreline) of schools did not differ significantly ( $n_1=229$  and  $n_2=163$ , respectively). School diameter fluctuated between 20 and 30 m. At dusk and light intensities of  $<100$  lx in 8 m depth, echo energy ha<sup>-1</sup> and intensity of school formation

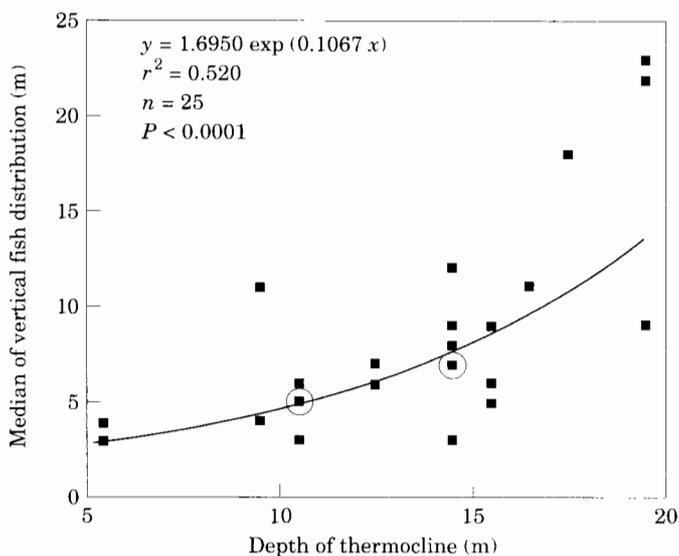


FIG. 4. Regression of the median vertical distribution of perch during day in summer and the depth of the thermocline.

declined dramatically. These values remained low at night and increased again at dawn [Fig. 3 (left panel)]. Direct observations by SCUBA-diving showed that by day perch were encountered from 1–30 m depth, but by night, only few individuals were seen deeper than 5 m. Further, at dusk, dense perch schools migrated inshore close to the bottom. In the littoral zone schools dispersed and the fish rested on the bottom during darkness. At dawn they showed a reverse migration to the sublittoral zone. Observations with the programmable underwater camera at 4 m water depth provided additional evidence for the fishes' nocturnal inactivity. Up to 47 perch per photograph were counted at dusk and dawn, suggesting high fish activity. But not a single fish was seen on 19 photographs during darkness.

In winter perch were detected by echo sounding between the 35 and 70 m depth contours. They spent the day close to the bottom, but at dusk they ascended into the pelagic region up to 20 m below the surface. During the night they were evenly dispersed within the water column. The nocturnal increase of echoenergy [Fig. 3 (right panel)] is due to this diel migration.

#### INFLUENCE OF WATER TEMPERATURE ON THE VERTICAL DISTRIBUTION OF PERCH IN SUMMER

Echo sounding data showed that between July and September, perch of all ages were present within the epilimnetic zone at water temperatures between 12.9 and 18.6° C. In October they stayed in waters of 10.8–13° C. These temperatures represent the median depths of the fishes' vertical distribution ( $n=25$ ). The median vertical distribution of perch was regressed on the depth of the thermocline by an exponential model (Fig. 4). From July until mid-October vertical distribution of perch and depth of the thermocline were significantly correlated. The centre of the fish schools was located between 2 and 6 m above the thermocline throughout the stratification period.

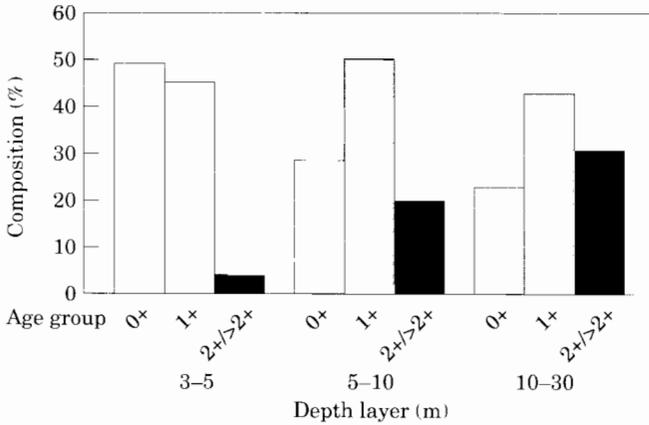


FIG. 5. Percentage composition by age of perch in three epilimnetic layers.

### SPATIAL SEGREGATION OF DIFFERENT SIZE CLASSES IN SUMMER

From July until mid-October different size classes of perch detected by echo sounding were separated spatially. From 3 to 30 m water depth, the relative number of young-of-the-year perch declined from 49.6 to 24.0%, whereas the relative number of adults (2+ and older) increased from 4.6 to 31.7% (Fig. 5). The relative number of 1+ perch was about 50% in all three strata (range 44.3–50.6%). In the water layer closest to the surface (3–5 m) mean S was significantly lower than in the two deeper layers, while between those two layers mean S was not significantly different (Lord Test) (Lozán, 1992).

### HORIZONTAL DISTRIBUTION OF PERCH IN THE SURVEY AREA

From July until mid-October, horizontal distribution patterns of perch were very similar [Fig. 6(a)]. Summer distribution was characterized by pronounced patchiness (evenness-index between 0.456 and 0.828). Abundances varied between 0 and 140 000 fish ha<sup>-1</sup>. Between 86 and 97% of all perch were concentrated in areas with fish densities >1000 fish ha<sup>-1</sup>. These areas contributed only between 15 and 45% to the length of the surveyed shore line [Fig. 7(a)]. Highest fish densities were always encountered close to ports and jetties. These sublittoral underwater structures were characterized by fish densities 8–65 times higher than shores without such structures (Table I). Constance Bay represented the only exception to this rule. In this region fish abundances reached high levels even further away from the shore.

In October, perch of all ages started to migrate towards the profundal zone. In February 1994 they were dispersed between the 35 and 70 m depth contours [Fig. 6(b)]. In contrast to summer, the horizontal distribution of perch was very homogeneous in winter (evenness-index between 0.835 and 0.928). Because the area that was inhabited by perch in winter (2000 ha) was about 10 times greater than in summer (200 ha), winter abundance was much lower, never exceeding 1000 individuals ha<sup>-1</sup>. Ninety-eight per cent of all perch were detected at sites with abundances between 100 and 1000 fish ha<sup>-1</sup>. These sites comprised two-thirds of the surveyed shoreline [Fig. 7(b)].

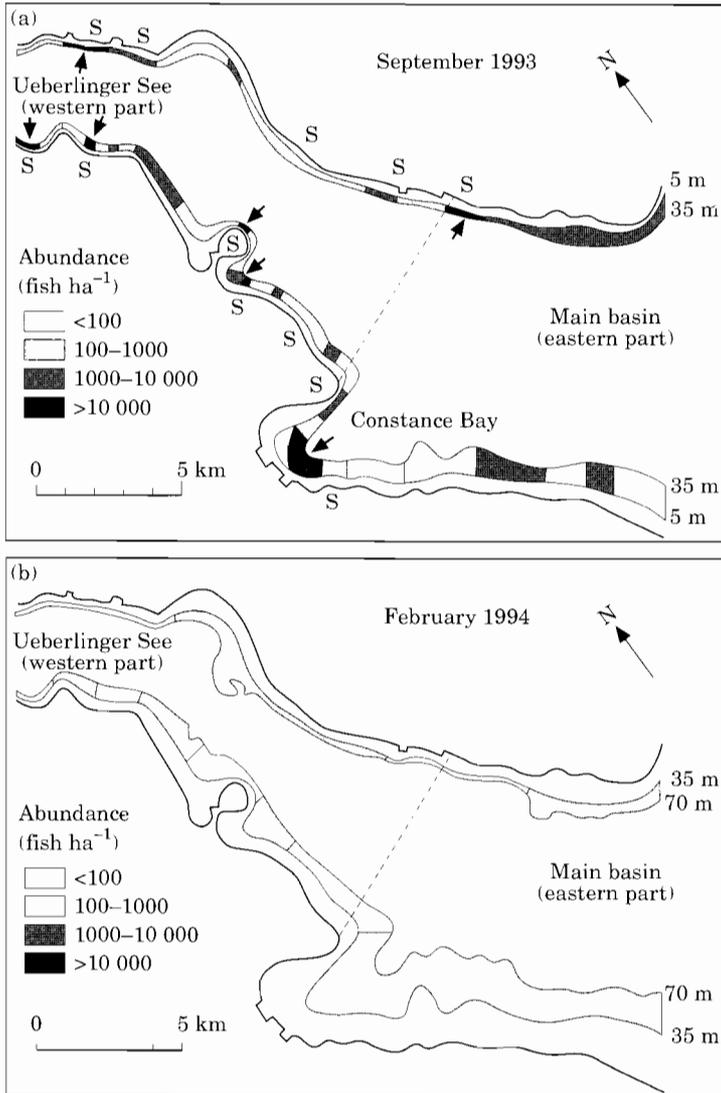


FIG. 6. Typical horizontal distribution of *Perca fluviatilis* in Lake Constance in (a) summer and in (b) winter. The dotted line divides the study area in a western and an eastern part. Arrows indicate sites with fish densities >10 000 fish ha<sup>-1</sup>. S indicates sublittoral underwater structures.

In both summer and winter, fish numbers per km shoreline were up to four times higher in the eastern part (main basin) than in the western part of Lake Constance (Überlinger See) (Table II). Only in October were more perch per km shoreline present in the western part.

## DISCUSSION

### TIMING OF HYDROACOUSTIC INVESTIGATIONS ON PERCH

The present study describes the diel and seasonal changes in behaviour of perch in Lake Constance. They were of fundamental interest to define best

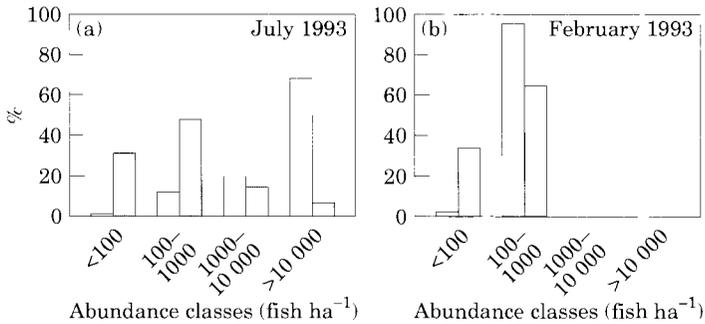


FIG. 7. Patchiness in distribution in (a) summer and (b) winter. Each shore segment is assigned to one of four abundance classes.  $\bar{\square}$ , Relative number of perch at sites belonging to the corresponding abundance class.  $\square$ , Relative length of the shoreline covered by the corresponding abundance class.

TABLE I. Mean perch abundances (fish ha<sup>-1</sup>)  $\pm$  S.E. at sites with and without underwater structures in the sublittoral of the survey area except Constance Bay

Month	With structure (mean $\pm$ S.E.)	Without structure (mean $\pm$ S.E.)	Factor
Jul.	8097 $\pm$ 2263 (n=12)	864 $\pm$ 209 (n=54)	9.4
Aug.	22 533 $\pm$ 9151 (n=12)	838 $\pm$ 104 (n=84)	26.9
Sep.	16 347 $\pm$ 4129 (n=12)	2016 $\pm$ 341 (n=80)	8.1
Oct.	20 438 $\pm$ 12 279 (n=12)	314 $\pm$ 50 (n=95)	65.1

At sites with underwater structures, fish density was measured directly in the school. At sites without underwater structures, abundance measurements are based on segments of 500 m length.

conditions for hydroacoustic investigations: since perch resting on the bottom or in shallow waters are not accessible by echo sounding, surveys should be carried out in summer in daylight and in winter at night.

In summer, at evening twilight, perch of all ages moved to shallow littoral areas where they dispersed and settled down until dawn. The transition from daytime activity to nocturnal inactivity has already been described by Hasler & Villemonte (1953). While changing to the nocturnal resting mode, the fish show a decreasing sensitivity to visual and mechanical stimuli (Helfman, 1979). Nocturnal quiescence might be a predator avoidance behaviour that reduces predation risk from nocturnally active enemies that perceive prey by mechanical stimuli. Young-of-the-year perch, however, are still vulnerable to predation by European eel *Anguilla anguilla* (L.), which is the most important predator in the shallow littoral zone of Lake Constance (Radke, pers. comm.).

Until now, the pronounced diel migrations in winter have not been described elsewhere in the literature. They seem to be characteristic for perch of Lake

TABLE II. Number of perch per km shoreline ( $\pm$  S.E.) in the western and eastern part of Lake Constance

Month	Western part (mean $\pm$ S.E.)	Eastern part (mean $\pm$ S.E.)	Factor (east/west)
Jul.	3772 $\pm$ 1232 ( <i>n</i> =50)	12 947 $\pm$ 5824 ( <i>n</i> =28)	3.4
Aug.	5923 $\pm$ 1856 ( <i>n</i> =60)	8129 $\pm$ 2227 ( <i>n</i> =43)	1.4
Sep.	9026 $\pm$ 2811 ( <i>n</i> =58)	38 449 $\pm$ 17 132 ( <i>n</i> =47)	4.3
Oct.	6525 $\pm$ 3644 ( <i>n</i> =58)	1323 $\pm$ 178 ( <i>n</i> =67)	0.2
Feb.	4589 $\pm$ 949 ( <i>n</i> =63)	17 865 $\pm$ 2207 ( <i>n</i> =53)	3.9

Abundance measurements are based on segments of 500 m length.

Constance and are the subject of further investigations (Eckmann, unpublished data).

#### VERTICAL DISTRIBUTION OF PERCH IN SUMMER

In summer the vertical distribution of perch schools was correlated to the depth of the thermocline. Throughout the growing season perch were present by day in an epilimnetic layer between 3 and 15 m depth, approximately 5 m above the thermocline. Accordingly, Hartmann & Löffler (1978) caught perch mainly between 6 and 10 m depth. Preferred temperature in laboratory and field distribution studies covers a wide range from *c.* 13 to 30° C (Hokanson, 1977). In Lake Constance, perch lived in relatively cold waters of 13–19° C. Here, they occupied a temperature niche intermediate between cyprinids and coregonids and they were located vertically between these two species (Hartmann & Löffler, 1978). Considering the fact that the epilimnetic water is oxygen saturated, it is unlikely that the vertical distribution of perch in the nearshore areas of Lake Constance is affected by oxygen gradients.

#### SPATIAL SEGREGATION OF DIFFERENT SIZE CLASSES OF PERCH

Our hydroacoustic data showed that different size classes of perch are separated spatially in summer. Young-of-the-year fish dominated in the littoral zone, whereas adults stayed mainly in the sublittoral. This segregation was interpreted as avoidance of cannibalism by Wang & Eckmann (1994). They found that the rate of cannibalism increased when juveniles and adults co-occurred in the sublittoral in late October. The proximate reason for this separation might be that young perch generally select higher temperatures (McCauley & Read, 1973; Hokanson, 1977) and thus the upper strata of the water column (Ferguson, 1958), or that they exploit different food resources.

#### HORIZONTAL DISTRIBUTION IN SUMMER

During the summer months the shallow Constance Bay was always inhabited by more than 10% of all fish detected in the survey area. In Lake Kinneret,

Israel, both fish and zooplankton were concentrated in zones where temperature and oxygen gradients were highest (Kalikhman *et al.*, 1992). In Lake Constance, these large pelagic perch schools next to the lake's outflow might be related to particular oxygen, temperature or food regimes as well. These parameters, however, were not evaluated in detail in this study. As Constance Bay belongs to the eastern part of the survey area, these fish schools contribute finally to the higher numbers of perch per km shoreline in the lake's main basin. But on a whole lake basis as well, Hartmann (1984) reported increasing yields from west to east. This might be due to the higher proportion of shallow bays in the eastern part, which are morphologically similar to Constance Bay. Large numbers of perch have also been reported for the shallow Bregenz Bay at the eastern end of the lake (Dahm *et al.*, 1985).

During the growing season perch aggregated preferentially close to sublittoral underwater structures at steeper shores in the north-western part of the lake. Large sublittoral areas without such structures were inhabited by few perch only. Echo surveys were conducted during daylight in summer, when perch formed dense schools, and during night in winter, when perch floated as single fish in the water column. The different degree of aggregation by day and night, however, is not the main reason for the seasonal changes of patchiness.

The apparent preference of perch for underwater structures at steeper shores in the north-western part of the lake has already been noted by fishermen and Scheffelt & Schweizer (1926). Such structures might serve as orientation marks or they provide shaded hiding places or refuge from predators. We did not evaluate the possibility that zooplankton might be more abundant at these sites.

Our observations during summer months showed that the heterogeneous distribution of perch was persistent and that the fish did not change sites or preferences. This is an indication for a possible site and school fidelity of perch as described for other lakes (Chikhova, 1973; Craig, 1974; Helfman, 1984). In our study, the furthest displacement of perch aggregations occurred along expanded boulder areas. But displacement was always <1 km from one month to another. In Lac Saint-Louis, Quebec, average distances travelled by marked yellow perch ranged from 1.9 to 3.9 km (Fortin & Magnin, 1972; cited by Thorpe, 1977). Aalto & Newsome (1990) support the hypothesis that perch in Lochaber Lake return to their natal location to spawn. If perch in Lake Constance form subpopulations, or even demes that exhibit reproductive isolation, should be the subject of further investigations.

#### HORIZONTAL DISTRIBUTION IN WINTER

With the beginning of autumnal mixing, perch started to migrate towards the profundal zone. This seasonal migration has been observed also in other lakes (Allen, 1935; Ferguson, 1958; Forney, 1971). In Lake Constance, the sites at which perch overwinter are not characterized by higher benthos abundances (Hartmann & Probst, 1995). We suggest that overwintering sites are selected mainly according to lake morphology, because we observed overwintering perch only on slightly declining but not on steeply sloping bottoms. The gradual return to the littoral zone started in winter and ended in late spring when perch spawn in shallow waters. This seasonal migration might ensure gonad growth and

gamete maturity that requires temperatures below 10° C. Optimal conditions for maturation occurred, when fish were exposed to 6° C or lower for 185 days (Hokanson, 1977). This corresponds to the winter period between late October and late April.

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