

Abundance and horizontal distribution of Lake Constance pelagic whitefish (*Coregonus lavaretus* L.) during winter

By REINER ECKMANN

With 4 figures and 3 tables in the text

Abstract

On seven dates in winter/early spring 1989/90, hydroacoustic data were sampled in the main basin of Lake Constance with a single-beam echosounder. In the pelagic zone, acoustic backscattering is almost entirely due to pelagic whitefish during that time of the year. For each sampling date, whitefish abundance was estimated for three size-classes (from –32 dB to –52 dB) and the horizontal distribution of the stock was plotted. Total population estimates for all size-classes combined agreed extremely well among four surveys before and after spawning time, ranging from 5.3 to 5.9 million individuals. During spawning and in early spring only part of the population was accessible to acoustic sampling. Horizontal distribution patterns were very consistent among five surveys in winter, showing a pronounced density gradient increasing from the southwestern to the northeastern shore. Pelagic whitefish thus maintain their characteristic overwintering distribution pattern for at least three months.

Introduction

Acoustic methods are widely used for fish stock assessment, mainly in the marine environment. In recent years, these methods are becoming increasingly important for the study of freshwater fish communities. They have already been successfully employed in several studies to document vertical distribution and migration patterns and to assess the stock size of vendace and whitefish (BRANDT et al. 1991, BRENNER et al. 1987, DAHM et al. 1985, ECKMANN 1991, JURVELIUS & AUVINEN 1989, JURVELIUS & HEIKKINEN 1987, 1988, JURVELIUS et al. 1984, 1988, RUDSTAM et al. 1987).

In most of the studies that were conducted to estimate stock size, the lake was surveyed on one or two occasions, so the overall accuracy of the method could not be checked. In only one of these studies (JURVELIUS et al. 1984) was the acoustic data used to document the stock's horizontal distribution. Therefore, the aim of the present study was twofold: (i) to assess the stock of pelagic spawning whitefish in Lake Constance on several consecutive dates, and (ii) to map the stock's horizontal distribution during that time.

Traditional hydroacoustic techniques like the single-beam echosounder used in this study yield best results when only one species is present in the study area. Consequently, acoustic data were sampled during late autumn and winter months, i. e. around spawning time, because, according to own observations and those from fishery wardens, the pelagic of Lake Constance is inhabited almost exclusively by whitefish during that time of the year.

Materials and methods

Lake Constance (Bodensee), the second largest (to Lake Geneva) European prealpine lake, is the largest lake in Germany, situated at the German-Swiss-Austrian border. Its main basin has a surface area of 476 km², a

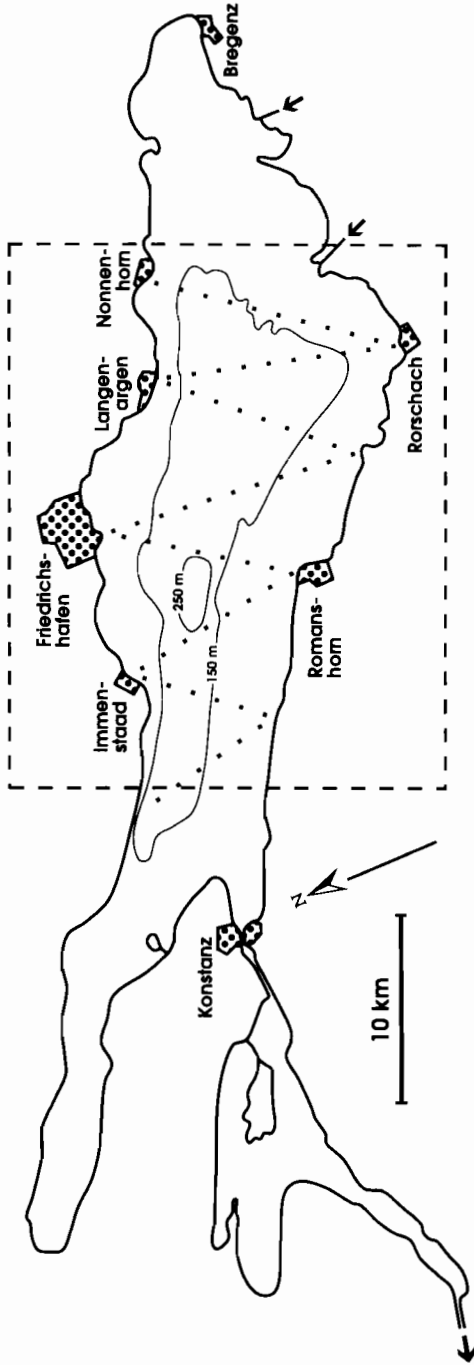


Fig. 1. Map of Lake Constance showing the transects for acoustic surveys (dotted lines) and the central part of the lake for which fish horizontal distribution patterns are depicted in Fig. 3 (hatched rectangular).

volume of 47.7 km³, a maximum depth of 252 m, and a mean depth of 100 m (GELLER & GÜDE 1989). The lake is warm-monomictic and has generally no ice cover in winter. Acoustic surveys can therefore be undertaken all year.

The fish fauna comprises about 30 species, but whitefish (*C. lavaretus*) and perch (*Perca fluviatilis*) are by far the most important economically. Fishing for whitefish is so intensive that generally only one or two year-classes are harvested at a time. Whitefish are present in two ecologically distinct forms in the main lake basin: Gangfisch, which spawn in shallow to medium-deep littoral waters, and Blaufelchen, which spawn close to the surface in the pelagic zone over water depths of up to 250 m (ECKMANN 1987, RUHLÉ 1986, VUORINEN et al. 1986). During the growing season, both forms probably co-occur as pelagic planktivores, but around spawning time mature and juvenile fish of both forms segregate according to their spawning sites.

A SIMRAD EY-M single-beam echosounder with 70 kHz working frequency was used. Ping rates were 182 and 91 min⁻¹ in the 60- and 120-m range, respectively, and time-varied gain (TGV) was set to 40 log R. The TVG function begins at two metres, so with the mounting of the transducer at one metre depth, fishes in the upper three metres are excluded from acoustic sampling.

The echosounder has a calibrated output, where the analog signals, internally shifted down to 10 kHz, can be recorded on an ordinary, high-fidelity tape recorder. Data tapes were digitized with an AD converter developed at Constance University electronics workshop. The current envelope was sampled every 0.1 ms. All information including ping number, depth, echo amplitude, and water depth was stored on hard disc in a personal computer. A system calibration was realized with a standard copper sphere (TS = -40.44 dB at 15 °C).

The directivity pattern of the circular transducer with 11.2° beamwidth at the -3 dB level was established. Ten 2-dB classes from -32 to -52 dB were considered in this study, and all echoes stronger than -32 dB were shifted down into the -33/-34 dB class. The target strength (TS) distribution was obtained by using the CRAIG and FORBES (1969) method to remove the effect of the beam pattern from the distribution of the echo amplitudes (cf. LINDEM 1983). All negative density values were set to zero.

When analyzing the data tapes with self developed software, single-fish echoes were sorted out, taking into account possible vertical and horizontal overlap of echosignals. In parallel, the energy (voltage squared) found in both single and multiple echoes was integrated. By assuming that the TS distribution of the single fish is representative of all fish, the total fish density was estimated. The water column from 3 to 60 metres was divided into five layers. When the number of single-fish echoes per transect in the uppermost layer (from 3 to 10 m depth) was less than 10, the calculated fish density was considered unreliable and was excluded from further calculations. TS (decibels) was transformed into fish length (L, centimetres) according to a relationship proposed by DAHM et al. (1985) for whitefish of Lake Constance: $TS = 20 \log L - 67.0$. To estimate the abundance for different size groups of whitefish, the ten 2-dB classes were pooled into three groups which correspond to total fish lengths of 56-35, 35-22, and 22-6 cm, respectively.

According to ELSTER (1944), the central part of Lake Constance (between Nonnenhorn, Rorschach, Friedrichshafen, and Romanshorn) is the main spawning area of Blaufelchen (Fig. 1). Acoustic data were, therefore, sampled along the transects shown in Fig. 1 starting at Nonnenhorn at the northeastern shore. Five surveys were done around spawning time of whitefish in 1989/90, and two in early spring 1990. Acoustic data were sampled at night. Boat speed was around 2.3 m·sec⁻¹, so it took from 8 to 9.5 hours to complete one survey. The pre-established transects could not always be covered completely due to harsh weather conditions. Furthermore, the two surveys in early spring started at Rorschach on the southeastern shore, thus omitting the easternmost transect, because at that time of the year the hours of darkness did not allow coverage of all transects during one night. The surveyed area thus ranged from 170 to 202 km² (Table 1). The littoral zone from the shoreline to about 60 m depth was excluded in this study, because the echoes from other species like perch and inshore spawning whitefish cannot be objectively distinguished from whitefish echoes. However, it is unlikely that the pelagic whitefish stock is underestimated in this way, because it appears from the recordings that pelagic whitefish do not enter medium depth waters where large shoals of overwintering perch and/or inshore spawning whitefish are observed at 30-50 m depth (Fig. 2).

Audio tape run was 45 min which represents 6.2 km transect length and 4095 or 8190 pings in the 120- or 60-m range, respectively. This corresponds to the maximum size of a data block, which was treated as one unit during software processing. Most tape recordings, however, were further partitioned to obtain sub-transects of fairly uniform fish density. This was done by a software routine after visual inspection of paper echograms. These subtransects that comprised from 701 to 8473 pings were then evaluated and areal densities for three size groups of fish estimated. For those subtransects that could not be evaluated due to excessive noise or "ghost bottom echoes", the fish density was grossly estimated from the paper recordings; total density was then distributed among the three size-classes according to the percentage size compositions

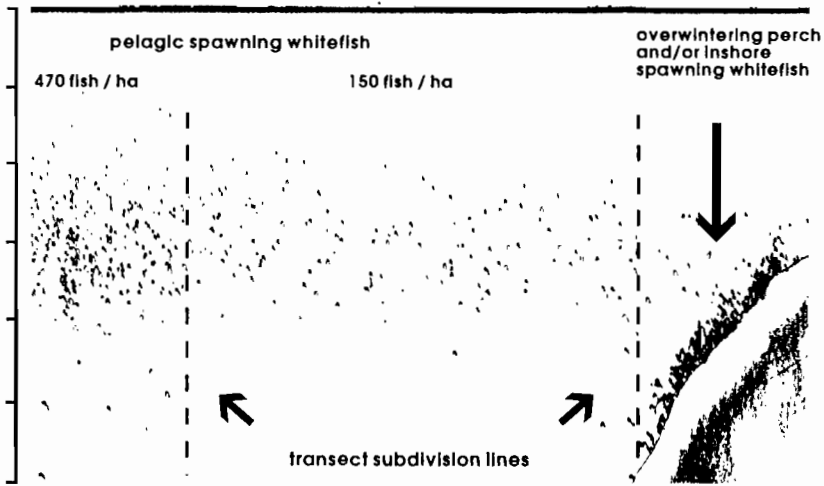


Fig. 2. Sample echogram showing inshore aggregation of overwintering perch and/or inshore spawning whitefish and abrupt changes of pelagic whitefish density in offshore waters. Vertical scale is 60 metres.

Table 1. Total transect length per survey [km], number of subtransects which were evaluated separately (no. of subtr. with interpolated density estimates), minimum/maximum area assigned to subtransects [km²], total area covered by survey [km²], minimum/maximum number of acoustic pings per subtransect, total number of acoustic pings in survey, minimum/maximum number of single-fish echoes per subtransect, total number of single-fish echoes in survey.

Date	tr. length	no. subtr.	min/max area	total area	min/max pings	total pings	min/max sfe	total sfe
8 Nov 89	68.0	31 (4)	1.28/15.98	185	716/3678	63 574	147/4039	29 052
18 Nov 89	80.4	34 (3)	1.77/13.51	212	885/3726	68 907	91/2300	26 320
10 Dec 89	70.7	24 (2)	2.20/28.33	186	1239/7438	60 241	163/2317	23 198
27 Dec 89	75.2	35 (4)	1.12/16.14	199	699/3162	63 260	443/4335	44 724
23 Jan 90	74.9	36 (6)	1.38/12.25	198	849/2839	58 216	363/6680	59 835
14 Mar 90	64.5	27 (4)	2.77/13.96	180	701/4237	52 767	212/3508	29 811
26 Apr 90	56.8	19 (6)	1.13/27.35	191	1159/8473	52 200	53/954	4 212

of the two neighbouring subtransects. Finally, isopleths of areal density were drawn by hand for all size-classes combined.

This method of splitting up transects in small subtransects reduces the number of single-fish echoes (sfe) per sample unit (min./max. number of sfe per subtransect: 53/6680, cf. Table 1). Since the Craig-Forbes method is believed to provide reliable fish density estimates only when the number of single-fish echoes per sample unit is sufficiently high (ideally > 1000 sfe; JURVELIUS & HEIKKINEN 1988, JURVELIUS et al. 1988, LINDEM 1983), this method of estimating total fish abundance might not be appropriate. Therefore, the precision of the method was checked in the following way. First, the average areal density for each survey was obtained as the mean density of all substances weighted by ping number per subtransect. Second, all subtransects of one survey were combined into one big sample unit by a software routine, and the overall mean density for these large sample units, which comprised from 52 200 to 68 907 pings (cf. Table 1), were calculated. The results are compared in Table 2.

For abundance estimates, each subtransect was considered representative for a trapezoid that is delimited on both sides by the bisector of the angle between two neighbouring transects and whose parallel

Table 2. Comparison of areal density estimates [no. of fish/ha]: mean density of all subtransects in one survey weighted by ping number per subtransect (mean density), overall density calculated from all transects in one survey combined into one single sample unit, and difference between both estimates in % of mean density.

Date	Size class	Mean density	Overall density	Δ [%]
8 Nov 89	large	70.0	69.1	+1.3
	medium	75.4	73.7	+2.3
	small	152.0	139.8	+8.7
	total	297.4	282.6	+5.2
18 Nov 89	large	55.2	56.1	-1.6
	medium	76.7	72.5	+5.7
	small	117.9	107.8	+9.4
	total	249.8	236.4	+5.7
10 Dec 89	large	31.6	33.5	-5.7
	medium	39.5	41.6	-5.0
	small	89.3	93.8	-4.8
	total	160.4	168.9	-5.0
27 Dec 89	large	55.8	55.8	± 0
	medium	74.2	72.1	+2.9
	small	172.8	158.8	+8.8
	total	302.8	286.7	+5.6
23 Jan 90	large	76.4	75.8	+0.8
	medium	94.2	94.9	-0.7
	small	134.9	122.9	+9.8
	total	305.5	293.6	+4.0
14 Mar 90	large	28.4	28.4	± 0
	medium	39.6	39.6	± 0
	small	139.3	130.9	+6.4
	total	207.3	198.9	+4.2
26 Apr 90	large	24.7	24.6	+0.4
	medium	53.3	47.2	+12.9
	small	87.3	69.1	+26.3
	total	165.3	140.9	+17.3

sides run perpendicular to the transect direction. These trapezoids were digitized and their areas determined. By multiplying trapezoid area with the corresponding fish density estimate and summing up over all trapezoids, the total fish abundance was obtained. This procedure is different from the commonly employed method, where mean areal abundance for the entire survey is multiplied by survey area. To assess the difference between both methods, a logarithmic transformation of the subtransect area density estimates was used to calculate weighted mean density (weighted by subtransect area) and symmetrical 95% confidence limits (JOHANNESSON & MITSON 1983) for each size group of fish. By multiplying weighted mean density with survey area, a second estimate of total abundance was obtained. Results of both methods are compared in Table 3.

Results

The density estimates for pelagic whitefish obtained in this study by the Craig-Forbes method are largely reliable, although the number of single-fish echoes per sample unit was lower than 1000 pings in 89 out of 177 subtransects. Mean total density estimates derived from the evaluation of short subtransects units deviated by only -5.0 up to +5.7% from those estimates

Table 3. Comparison of overall abundance estimates [no. of fish $\cdot 10^3$]: summed across all subarea abundances (areal sum), calculated from the logarithmic mean abundance for all subtransects weighted by subtransect area (log. mean), symmetrical 95% confidence intervals for log. mean abundance in % of log. mean (95% c.i.), and difference between both estimates in % of areal sum.

Date	Size class	Areal sum	Log. mean	95% c.i.	Δ [%]
8 Nov 89	large	1378	1673	54	+21.4
	medium	1418	1482	31	+4.5
	small	2746	2818	28	+2.6
	total	5541	5973	36	+7.8
18 Nov 89	large	1218	1678	66	+37.7
	medium	1656	1843	47	+11.3
	small	2461	2760	41	+12.2
	total	5335	6280	49	+17.7
10 Dec 89	large	611	622	25	+1.9
	medium	727	764	39	+5.0
	small	1708	1746	33	+2.3
	total	3045	3132	33	+2.8
27 Dec 89	large	1036	1071	37	+3.4
	medium	1403	1410	36	+0.5
	small	3418	3414	26	-0.1
	total	5856	5895	30	+0.7
23 Jan 90	large	1461	1419	40	-2.9
	medium	1788	1765	23	-1.3
	small	2485	2455	20	-1.2
	total	5734	5638	26	-1.7
14 Mar 90	large	589	634	51	+7.6
	medium	821	880	46	+7.1
	small	2749	2801	27	+1.9
	total	4159	4315	34	+3.7
26 Apr 90	large	407	400	160	-1.7
	medium	992	851	71	-14.2
	small	1429	1233	51	-13.7
	total	2828	2485	75	-12.1

that were based on all acoustic data per survey combined into one large sample unit. Only for the survey undertaken on 26 April 1990, where all subtransects contained less than 1000 single-fish echoes, the difference was +17.5% (Table 2). Thus, the subdivision of transects into smaller units affected the precision of the density estimates only slightly.

Abundance estimates were calculated by two differences methods, (i) by summing up the abundance estimates across all subareas, and (ii) by multiplying survey area with the weighted mean of the logarithmically transformed subtransect densities. The results of both methods differed by -12.1 up to +17.7% for all size classes combined, but no consistent pattern of deviation was apparent (Table 3). Since six out of 21 data sets of subtransect densities (mainly those for the large-sized fish) could not be normalized by taking logarithms ($P = 0.05$), only those abundance estimates which were obtained by the first method will be considered now.

Overall abundance estimates for all size classes combined agreed well among four surveys Nov. 8th, Nov. 18th, Dec. 27th, Jan. 23rd, ranging from 5.3 to 5.9 million individuals, while they were considerably lower for the other three surveys (Table 3). The most probable

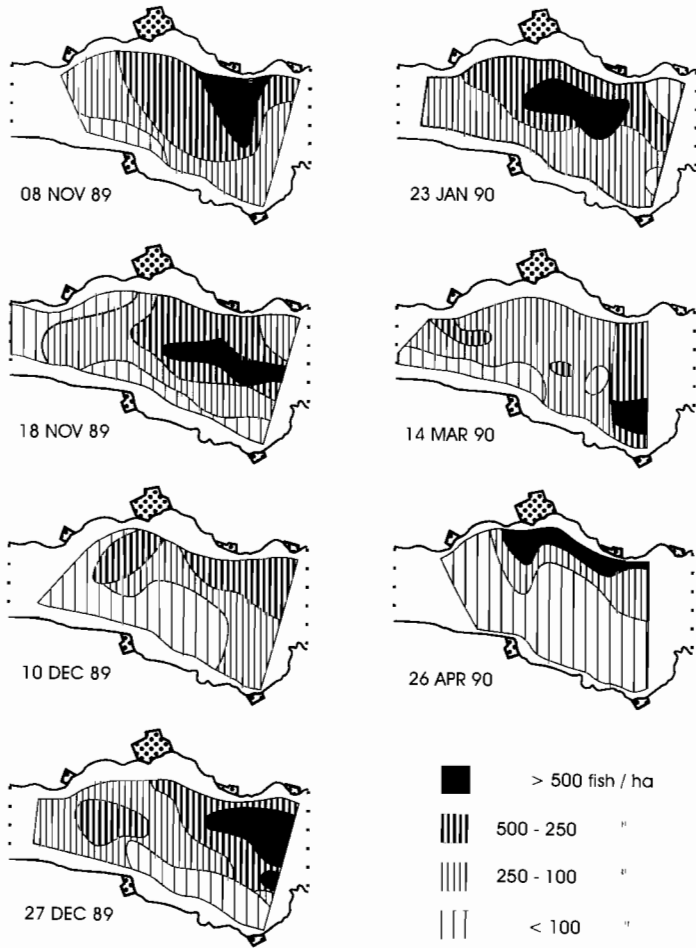


Fig. 3. Horizontal distribution of pelagic whitefish in the main basin of Lake Constance on seven dates in winter 1989/90. All size classes from -32 dB to -52 dB are combined.

reasons for the lower abundance estimates on December 10th, March 14th, and April 26th are the following. According to results from test fishing by fishery wardens, spawning activity of pelagic whitefish peaked on December 10th, 1989. During this time, mature whitefish concentrate in the uppermost metres of water (Fig. 4) where they cannot be detected by traditional hydroacoustic techniques (ECKMANN, 1991). This, however, does not explain, why the abundance of the small size class was also lower on that date. On March 14th, 1990, part of the whitefish population had probably moved already to the shallower eastern lake basin Bregenzer Bucht (cf. Fig. 3). Crustacean zooplankton blooms start earliest in the easternmost part of the lake (EINSLE, 1977), and whitefish catches are generally highest in this part of the lake in early spring. On April 26th, pelagic whitefish had ascended from their overwintering habitat to the lake surface (Fig. 4), where they were only partly accessible to hydroacoustic sampling.

The horizontal distribution of pelagic whitefish was very similar during late autumn and winter (8 Nov.–23. Jan.). They occupied the central lake basin and were always concentrated

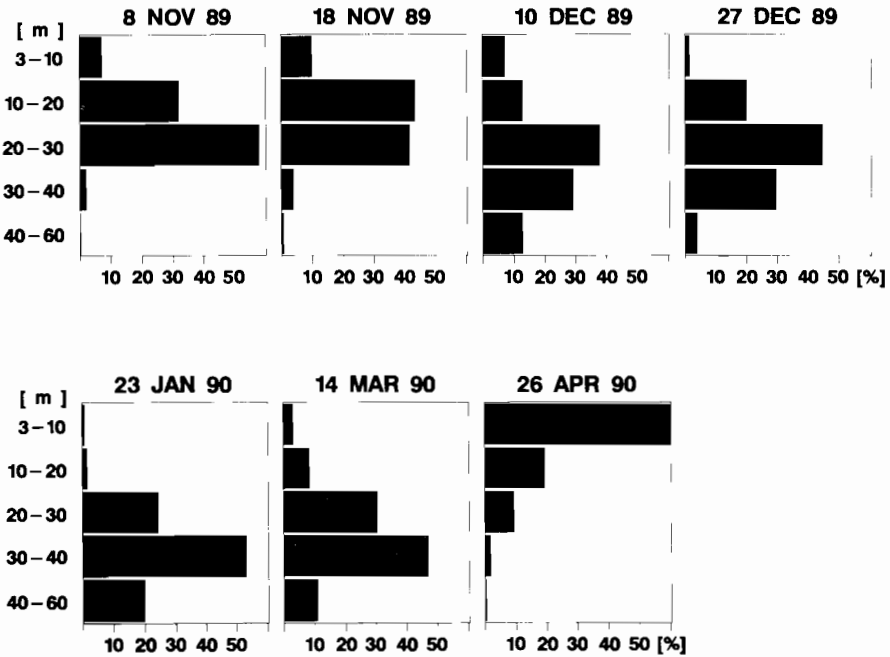


Fig. 4. Depth distribution of pelagic whitefish in the main basin of Lake Constance on seven dates in winter 1989/90. All acoustic data in one survey were evaluated as one sample unit, and all size-classes of whitefish were combined.

towards the northeastern shore (Fig. 3). Highest densities were observed in front of Nonnenhorn and Langenargen or in the very centre of the main basin, while lowest densities were observed in front of Romanshorn and Rorschach and towards the northwestern border of the main basin. These distribution patterns are the same for all three sizes classes. For each survey, subtransects were assigned rank numbers separately for large-, medium-, and small-sized fish according to fish density estimates, and rank numbers were tested against each other (three pairwise comparisons per survey). Spearman's rank correlation coefficient ranged from 0.546 to 0.935 and was significant at $p < 0.001$ ($n = 20$) or $p < 0.005$ ($n = 1$). Thus, the distribution patterns depicted in Fig. 3 are representative for the total whitefish population as well as for all three size-classes.

Discussion

It has already been shown in a previous study, that the reproducibility of whitefish abundance and size-class distribution estimates in Lake Constance is very good (ECKMANN 1991). Similar results have repeatedly been reported in the literature (JURVELIUS & HEIKKINEN 1987, JURVELIUS et al. 1984, LINDEM 1983). Under the conditions given in this study, highly consistent estimates of total abundance and size-class distribution of pelagic whitefish were obtained. The precision of the estimates was only slightly affected by dividing each survey in small subtransects of less than 1000 single-fish echoes (cf. Table 2). It was thus possible to map the horizontal distribution of whitefish with high precision. This would not have been

possible, had each survey been evaluated in units of shore-to-shore transects or in units of subtransects of uniform length, because changes in fish density along transects (cf. Fig. 2) would have been smoothed out in this way. Additionally, total fish abundance was estimated with better precision by summing up abundances across subarea units, because the calculation of mean abundance within one survey was biased because subtransect density or abundance values could not be normalized effectively. Therefore, whenever acoustic transects are spaced closely enough to map the fish's horizontal distribution, then the total abundance is better estimated as the sum of all subarea abundances rather than by multiplying total survey area with some biased mean abundance value. The disadvantage of the method adopted here is that no confidence limits for the abundance estimate can be given.

The symmetrical 95% confidence intervals based on logarithmic mean abundances are fairly large, ranging from 26 to 75% (cf. Table 3). They should, however, not be mistaken as an index of precision of abundance estimates based on the sum of the subarea abundances. Would the entire survey area be covered completely by acoustic transects and the fish distribution be heterogeneous, then the total fish abundance could be precisely indicated, yet there would still be a variance associated with the mean abundance. The confidence intervals presented in Table 3 are, therefore, rather an index of patchiness of distribution, and the total abundance estimates obtained in this study by summing up subarea abundances are probably much more precise than what is suggested by the broad confidence intervals of the logarithmic mean values.

Total abundance estimates on November 8th, November 18th, December 27th, and January 23rd agree extremely well (Table 3), and they seem to provide consistent estimates of the total pelagic whitefish stock in Lake Constance. On December 27th, highest fish densities were observed towards the easternmost boundary of the survey area. Since catches of pelagic whitefish are generally low in the eastern lake basin during that time of the year, it is most likely that only a minor fraction of the entire population was missed in this survey. Up to now, very little is known about the distribution of inshore spawning Gangfish after spawning time. They are often caught close to their spawning grounds in bottom-set gill nets until late January, but they disappear from this region later in winter. It is also largely unknown, at what time they move to inshore waters in late autumn prior to spawning. Inshore spawning whitefish, therefore, represent a potential source of error for the estimation of the pelagic spawning whitefish stock. The close correspondance among the abundance estimates on four dates before and after spawning time, however, suggests that these surveys, in which littoral waters were not considered for abundance estimates, in fact encompasses the pelagic whitefish stock only. This inference is not conclusive, but for the time being acoustic surveys around spawning time provide the best, instantaneously available estimates of pelagic whitefish stock size in Lake Constance.

During the fishing season 1990, 689 tons of Blaufelchen were caught (Fischereiforschungsstelle Baden-Württemberg, pers. comm.), which corresponds to 1.7 million individuals (average weight of legal-sized whitefish: 400 g). This figure is higher than the estimates for large-sized whitefish (unweighted mean abundance for the four surveys considered here: 1.3 millions), and lower than the mean abundance for large- and medium sized whitefish combined (2.8 millions). The discrepancy derives mainly from the uncertainty, what fraction of medium-sized whitefish will attain legal size (35 cm TL) and be harvested during the following growing season. This problem will remain unresolved until much more independent comparisons of acoustic stock estimates and catch data are performed. As a gross approximation of catches during the following growing season, the range between the estimated mean abundance for large-sized fish and for large- and medium-sized fish combined could be used.

The general horizontal distribution pattern observed during November, December, and January, when pelagic whitefish dwell in the main lake basin, agrees with previous findings of ELSTER (1944) as well as with today's experience of professional fishermen. The pronounced density gradient, increasing from the southwestern to the northeastern shore, however, has not been reported before. In earlier surveys during spawning time 1987, a similar decrease of pelagic whitefish abundance from the shore at Langenargen towards offshore waters had been observed as well (ECKMANN 1991). This gradient is representative of all three size-classes considered here, which is evidenced by the highly significant correlation among their distribution patterns. Neither proximate nor ultimate causes for this remarkably stable distribution pattern are known so far. As possible proximate causes, lake hydrography, physico-chemical as well as biological gradients, and sediment quality might be considered. Anyhow, the horizontal distribution of pelagic whitefish in Lake Constance deserves further investigation because it could serve as a model for pelagic whitefish in general. The lake is large enough so that horizontal distribution patterns are easily resolved for different size-classes of whitefish even with a single-beam echosounder, and the lake is just not too large so that the lakewide distribution can be mapped with good accuracy in reasonable time.

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Author's address:

R. ECKMANN, Institute of Freshwater and Fish Ecology, Department of Biology and Ecology of Fish, Müggelseedamm 310, D-12587 Berlin, Germany.