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Spatial distribution of littoral fish species in a large European lake, Lake Constance, Germany

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With 9 figures and 5 tables in the text

Abstract: The spatial distribution and patterns of habitat use of littoral fish species in Lake Constance were studied using electric fishing and trammel net sampling to assess fish abundance and biomass in three depth strata at six different sampling sites within the littoral zone. Distribution differences among depth strata were found to be often more pronounced than among different sampling sites.

Juvenile chub (*Leuciscus cephalus*) and dace (*Leuciscus leuciscus*) were most abundant in the shallow areas of <50 cm water depth with maxima of 54.9 and 29.2 ind · 100 m^{-2}. Juvenile bream (*Abramis brama*) were collected mainly in the deeper littoral parts within areas of dense submerged aquatic vegetation with maximal abundances of 63.3 ind · 100 m^{-2}. Distribution of European eel (*Anguilla anguilla*) was found to be strongly dependent on the availability of adequate shelter. Dense accumulations of up to 61.7 ind and 40,000 g-wet · 100 m^{-2} were recorded within single samples at a boulder site. The benthic burbot (*Lota lota*) and stone loach (*Noemacheilus barbatulus*) also reached peak abundances in the shallow areas with up to 18.7 and 13.1 ind · 100 m^{-2}. The distribution of both species was strongly correlated with the availability of gravel substrate and shelter provided by larger stones.

All percid species were found mainly in deeper littoral areas. Juvenile perch and ruffe used areas of submerged aquatic vegetation as preferred habitat. Older individuals of both species seemed to avoid these areas and were caught in greater abundances and biomasses in open, unvegetated habitats.

The study shows a remarkably high temporal and spatial diversity in the littoral fish species of Lake Constance compared to many small North American lake ecosystems. The results also clearly demonstrate the importance of sampling with high spatial resolution for studies of littoral fish communities. Especially in large lakes, depth and size separation of fish species within single sampling sites may be as important for littoral habitat partitioning as distribution differences among different sampling sites.

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Introduction

It is well known that in small lakes the littoral zone is an important area for the fish fauna. Abundance and diversity here are often much greater compared to other lake compartments (KEAST 1985, WERNER et al. 1977) and habitat and food resources are normally more diverse (PIERCE et al. 1994). Most freshwater fish, including those regarded as typically pelagic, often use shallow areas for a short period of the year, either for spawning (GAFNY et al. 1992) or during larval and juvenile development (WERNER et al. 1977, SCHLOSSER 1982, WERNER et al. 1983, COPP 1992). Juvenile fish especially, use the littoral zone during the summer months in great abundance to accelerate their growth rates in the warm, highly productive shallow areas (CERRI & FRASER 1983, ALLEN 1982). Furthermore, the high structural complexity of the littoral zone significantly increases their protection from larger piscivorous predators (CROWDER & COOPER 1982, SAVINO & STEIN 1989, SCHLOSSER 1987, WERNER et al. 1983).

For many lakes, habitat and resource partitioning in the littoral zone are regarded as key factors in the coexistence of species within the entire ecosystem (WERNER et al. 1977, CROWDER & COOPER 1982, WERNER et al. 1983, ROSS 1986, GREENBERG 1991, LOBB & ORTH 1991). However, most of this knowledge is based on extensive studies of the littoral fish communities in small North American lakes and it is not yet clear if the same mechanisms are also valid for large, deep European lakes.

One goal of this study was a detailed assessment of littoral fish species in Lake Constance which is the second largest pre-alpine lake in Europe. As far as we know, there has been only one previous study of the littoral fish community in this lake (NÜMANN 1939) which, however, did not provide quantitative data. We sampled with electric fishing and trammel nets in three depth strata at each of six different sites in the western part of Lake Constance. Based on these data and the assessment of ten habitat parameters at the individual sites, we tested the hypothesis that habitat characteristics significantly influence species composition, abundance and biomass in the different habitats. To evaluate the importance of the individual habitat parameters for the fish species in detail, we applied canonical correlation analysis (HOTELLING 1936) to the habitat parameters for the eight most abundant fish species.

In this paper we specifically focus on distribution differences among sampling sites and depth strata during times of greatest abundance and biomass of the individual species. Changes in species composition due to seasonal changes of water temperature and lake level in Lake Constance are presented elsewhere (FISCHER & ECKMANN, in press).

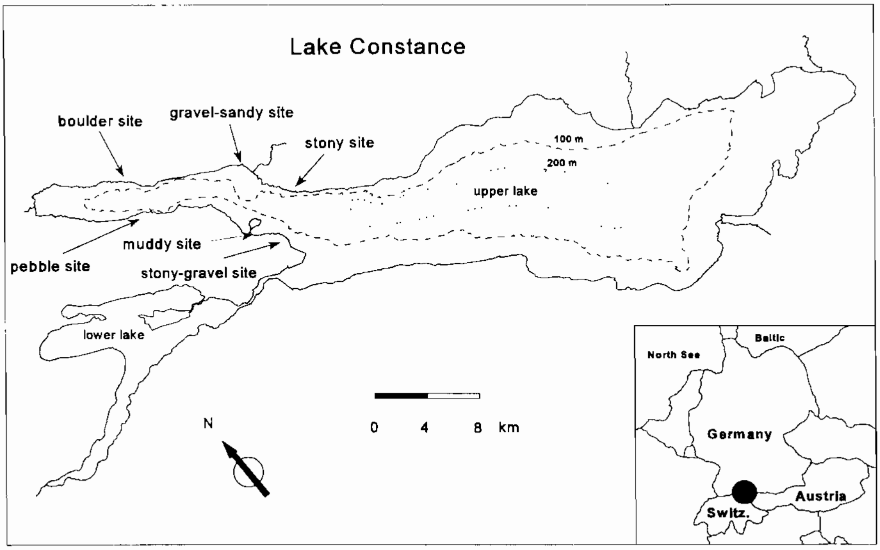

Fig. 1. Map of Lake Constance. The six sampling sites are marked with black arrows.

Material and methods

Study site

Lake Constance (upper lake) has a total surface area of 500 km^2, a mean depth of 95 m (maximum 254 m) and a shoreline length of 186 km. The littoral zone, according to JØRGENSEN (1990) and WETZEL (1983) the shallow-water zone from the shoreline to the lower boundary of the submerged aquatic vegetation, extends to a water depth of about 5 m during high water conditions in summer. Six sampling sites were selected in the northwestern part of the lake (Fig. 1). They ranged from extended littoral areas with low slopes and muddy sediments to artificial zones with large boulders in the very shallow areas, or shelf-like areas with pebbles and a pronounced drop at approximately 20 m from the shoreline (Table 1). Together, these six sampling sites represent a wide spectrum of the available types of littoral in Lake Constance and are therefore assumed to be representative of the littoral zone of the lake as a whole.

Field methods

Electric fishing was carried out from November 1991 until February 1993 during daytime: twice each month from April to December and monthly from January to March. Within each of the six sites, we sampled four times in each of the three depth strata, defined as "shallow" (0–50 cm depth), "intermediate" (50–150 cm depth) and "deep" (150–300 cm depth). For sampling the shallow and intermediate strata, the stationary generator part of the electric fishing device was placed on the beach and the anode and cathode were connected with 100 m long cables. In each of the two depth strata we en-

Table 1. Main geomorphologic parameters and density of submersed aquatic vegetation (SVA) at the six sampling sites (++ = deep littoral area completely covered with SAV, + = patches of dense SAV in deep littoral area, o = spare SAV coverage).

sampling sites	distance from shoreline to 5 m water depth (m)	mean slope (deg.)	%-area of sediment covered by stones larger ≈ 2 cm (%)	size range of stones (cm)	submersed aquatic vegetation (SAV)
stony site	25– 35	5.2	100	8–15	++
gravel-sandy site	250–300	1.0	40– 70	1– 7	+
boulder site	150–200	1.7	50–100	5–50	+
pebble site*	10– 20	1.2	30– 50	3–20	o
muddy site	350–400	0.8	0–100	3–10	+
stony-gravel site	180–240	1.4	100	0.5–10	+

* Because of a shelf-like littoral structure at the pebble site, the maximal water depth at this site was about 3 m.

closed four areas of about 50 m^2 each with nets (4 mm bar mesh, 1 m high in the "shallow" stratum and 2 m high in the "intermediate" stratum). We deployed the nets as carefully as possible, with only one or two persons in the water. When an escape reaction was observed in the fish, the procedure was stopped and another area in the same habitat and same depth was selected as an alternative sampling site. To remove the fish from an enclosed area, we sampled with the electro-shocker four times at 15 minute intervals (15 min sampling/15 min rest).

In the deep stratum, enclosure nets did not provide satisfactory data in preliminary samplings because of temporarily dense macrophyte vegetation. We therefore sampled this stratum from a boat without enclosure nets for the same time as we sampled in the shallower strata. This difference in sampling procedure resulted in larger sampling areas in the deep stratum which were, however, sampled less intensely. Therefore abundance and biomass values might be considered as biased and must be examined critically.

From April 1992 to May 1993, we also sampled with trammel nets (10.0 mm inner mesh (bar)/150.0 mm outer mesh (bar)) each time we performed electric fishing. We deployed two nets (20 m long, 1 m high) in each of the two strata "intermediate" and "deep" from one hour before sunset until one hour after sunrise. We defined the total catch per single net and night as CPUE (catch per unit effort) for abundance and biomass. We chose trammel nets for sampling because preliminary comparative experiments clearly revealed less size and species selectivity compared to monofilament gill nets.

Electric fishing and trammel net catches were anesthetized immediately after capture with 1,1,1-Trichloro-2-methyl-2-propanol (Chlorobutanol) and separated by day, sampling method, sampling site and depth strata. Small fish were preserved in 5 % formaldehyde, larger species such as eel (*Anguilla anguilla*) and pike (*Esox lucius*) were measured (total length TL and standard length SL) to the nearest millimeter and released. The weight of these individuals was back-calculated using length-weight relationships from previous data and from RADKE (1993). In the laboratory, all preserved fish were identified to species, measured (TL and SL, to the nearest millimeter) and weighed (wet) to the nearest 0.01 g.

Habitat measurements

Habitat structure within the littoral zone varied seasonally because of water level fluctuations caused by rainfall and meltwater runoff from the Alps. Therefore, it was necessary to measure all habitat variables (Table 2) on each sampling occasion. For the variables "substrate coverage" (percentage of sediment covered by stones larger than 2 cm), "mean stone size" and "stone size range", we made one initial detailed measurement by SCUBA diving. We placed rectangular PVC-frames (40 × 30 cm) on the substrate in five depth strata (0 to 5 m water depth) with five replicates in each stratum. The frames were photographed and the pictures evaluated for the variables "substrate coverage", "mean stone size" and "stone size range". Using this reference, visual assessments of these habitat parameters were performed for each sampling site and depth stratum on all subsequent occasions when electric fishing and trammel net sampling was conducted. To evaluate the species composition and density of submerged aquatic vegetation (SAV) we used SCUBA to count the shoot density of each species at the different locations once a month during the SAV growing season. Two divers counted the shoot density and assessed the SAV-species composition on PVC-pads along a total of four transects per site each from 5 m water depth to 0 m. Shoot density was counted within a small PVC-frame (20 × 20 cm) approximately every five meters along the transect. Based on these data, we defined a five level reference scale for subsequent visual estimations of density and species composition analysis of SAV. All habitat parameter assessments were done by the same persons over the entire sampling period.

Table 2. Habitat variables used to analyse fish abundance, biomass and distribution differences. Measuring procedure visual* is explained in the text.

Habitat variables	Measuring procedure and scales
water temperature	0, 100 and 300 cm water depth, measured to 0.1 °C
depth strata	shallow (0–50 cm), intermediate (50–150 cm), deep (150–300 cm)
substrate type	mud (0) – gravel (10), visual*
substrate coverage	percent area of substrate covered with larger stones, visual*
means stone size	diameter (cm), visual*
stone size range	diameter (cm), visual*
littoral width	from depth contours on 1 : 10,000 chart
SAV *Potamogeton pectinatus*	density (five level scale), visual*
SAV *Potamogeton perfoliatus*	density (five level scale), visual*
SAV *Chara* spp.	density (five level scale), visual*

Statistical analyses

Preliminary statistical analyses showed non-normal distributions in most of the untransformed, as well as log and square root transformed, catch data. We therefore rank-transformed abundance and biomass data of the individual fish species within each sampling unit (six sites with three depth strata each) and tested (Anova – Duncan's Multiple Range comparisons of Means) differences among sampling sites and among depth strata during phases when the individual species occurred in greatest abundances in the littoral zone (Table 3, months used in the analysis are marked with ●).

We used canonical correlation analyses (CCA), (HOTELLING 1936) based on monthly rank-transformed data in our evaluation of relationships between fish and habitat. To reduce the problem of autocorrelation in the input data set in the CCA (BORTZ 1985), we used the correlation coefficient r of individual habitat variables (temperature, depth strata, substrate type, substrate coverage, mean stone size, stone size range, littoral width, SAV (*Potamogeton pectinatus*), SAV (*Potamogeton perfoliatus*), SAV (*Characea*)) with the first canonical axis of the criterion variables (abundance, biomass) as recommended by SAS (1988). These values range from –1 to 1 and can be compared to each other by their absolute numerical value. Statistical procedures included SAS-ANOVA for depth and site distribution analysis of fish abundance and

Table 3. Occurrence of fish species per month (– = not collected, ○ = collected with only few individuals, ● = highly abundant at most sampling sites), mean length (TL) and length range (TL) caught by electric fishing (e) and trammel net sampling (t) in the littoral zone of Lake Constance during the period November 91 to June 93. The species *Pseudorasbora parva* (marked with an *) is originally an Asian species now common in aquaculture ponds in Europe.

Family	Species	Common name	Fishing gear	Month in which species was caught												Mean length (cm, TL)	Length range (cm, TL)
				J	F	M	A	M	J	J	A	S	O	N	D		
Salmonidae	*Salmo trutta* f. *lacustris*	lake trout	e, t	–	–		○				○				–	14.2	6.6– 0.5
Cyprinidae	*Rutilus rutilus*	roach	e, t	–	–	–	–	–	○	○	○	○	–	○	–	5.8	2.0– 9.0
	Leuciscus leuciscus	dace	e, t			○	○	○	●	●	●	○		–	–	6.0	1.9–24.3
	Leuciscus cephalus	chub	e, t	–	–	–	–	○	○	●	●	●	○	○	–	4.3	1.7–55.2
	Tinca tinca	tench	e, t	–	–	–	–	–	–	–	○	○	○	–	–	4.4	3.1– 6.7
	Gobio gobio	gudgeon	e, t	–	○	○	–	○	–		○		○			6.9	2.4–12.5
	Alburnus alburnus	bleak	e, t	–	–	–		–	○	○	○	○	–	–	–	7.5	1.5–17.1
	Abramis brama	bream	e, t					○	●	●	●	●	○	○	–	3.9	1.4–50.0
	Leucaspius delineatus	rain bleak	e	○	–	–	–	–	–	–	–	–	–	–		3.8	3.3– 4.2
	*Pseudorasbora parva**	barbel sp	t					○							–	10.6	–
Cobitidae	*Noemacheilus barbatulus*	stone loach	e, t	●	●	●	●	●	●	●	●	●	●	●	●	6.7	3.0 10.3
Anguillidae	*Anguilla anguilla*	European eel	e, t	–	–	○	○	●	●	●	●	●	●	○	–	24.0	7.7–83.0
Esocidae	*Esox lucius*	pike	e, t	–	–	–	–	○	–	○	○	–	–	–	–	48.1	15.5 86.0
Percidae	*Perca fluviatilis*	perch	e, t	–	–	○	●	●	●	●	●	●	●	○	–	9.1	2.9–30.3
	Stizostedion lucioperca	pike-perch	t		–		–					○				9.6	–
	Gymnocephalus cernuus	pope, ruffe	e, t	○			●	●	●	●	●	●	●	●	–	7.8	2.7– 8.5
Cottidae	*Cottus gobio*	bullhead	e	–	–	–	–		–	○	○	○				4.3	3.2– 6.0
Gasterosteidae	*Gasterosteus aculeatus*	three spined stickleback	e, t	–	–	–	○	○	–	○	○	○	○	○	–	5.4	2.0– 7.5
Gadidae	*Lota lota*	burbot	e, t	●	●	●	●	●	●	●	●	●	●	●	●	6.2	1.8 31.3

biomass and SAS-CANCORR for the analysis of relationships among individual species and habitat variables (SAS 1988).

Results

From a total of 33 fish species in Lake Constance (BERG & BLANK 1990), we found 19 species of nine families in the littoral zone (Table 3). Eight species occurred in greatest abundances in the electric fishing or trammel net catches at least during one period of the year (Fig. 2a, 2b).

Significant distribution differences in total fish abundance among sampling sites were found mainly from September to March (Fig. 3, upper graph). During this time, only burbot (*Lota lota*) and stone loach (*Noemacheilus barbatulus*) were caught in greater abundances in the littoral zone and dominated the fish community during most of that period (Fig. 2a).

In summer, European eel, the cyprinid species, chub, dace and bream and the percid species, European perch and ruffe successively dominated in the littoral zone and were caught in greatest abundances either by electric fishing or in the trammel net catches. During this period of the year, distribution differences among depth strata were highly significant (Fig. 3, middle graph) and no significant differences were found among sampling sites.

In addition to distribution patterns among sampling sites and depth strata, we found an extremely large variability in total fish abundance within our four replicates from each site and depth stratum. Variability of total fish abundance within replicate electric fishing samplings reached maximal CV-values (LOZÁN 1992) >300 % with an average value of about 150 % (Fig. 3, lower graph). This high variability occurred over the entire seasonal cycle, independent of total fish abundance, biomass and species composition.

Burbot and stone loach were caught in the littoral zone over the entire season. Integrated over all sampling sites, both species reached significantly higher abundance values (Table 4) in the "shallow" stratum where 61.8 % of all burbot and 90.2 % of all stone loach were caught. In both species, significant distribution differences were also observed among sampling sites.

Burbot were significantly more abundant at the stony, gravel-sandy, boulder and stony-gravel sites and reached comparatively lower abundances ($p<0.01$, Table 4) at the pebble and muddy sites (Fig. 4). Biomass distribution among sampling sites was similar. However, at the gravel-sandy site, higher abundance but comparatively low biomass values were observed. Length analysis revealed, that burbot caught at this site were significantly smaller (Fig. 5; $p<0.05$) compared to those caught at the boulder or stony sites.

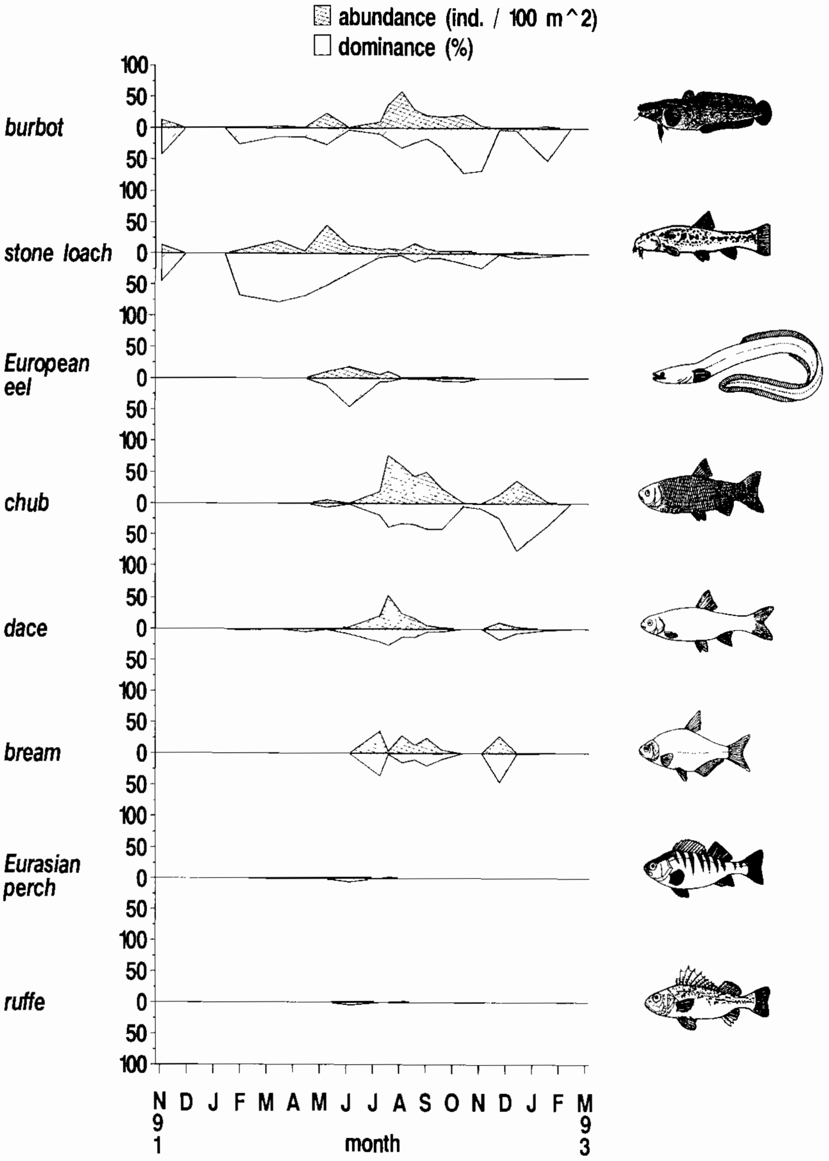

Fig. 2 a. Abundance and dominance values (percent of total catch abundance) of the eight most abundant fish species caught by electric fishing in the littoral zone of Lake Constance. Plotted are mean values integrated over all sampling sites and depth strata from November 91 to March 93.

Similarly, stone loach also reached high abundance and biomass values at the stony, gravel-sandy and stony-gravel sites (Fig. 4). However, significant distribution differences between burbot and stone loach were observed at the

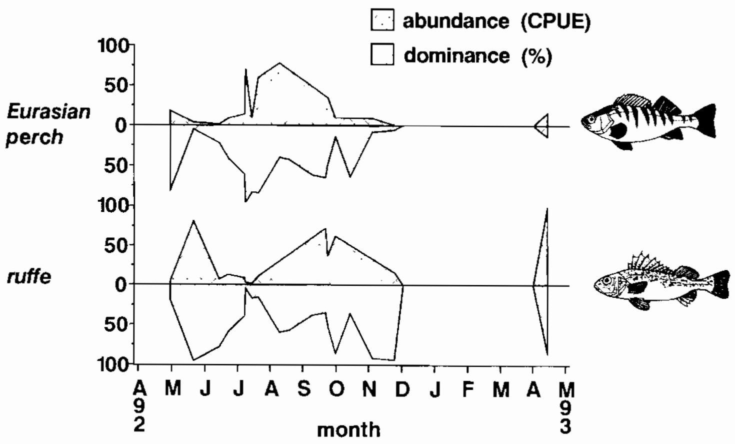

Fig. 2 b. Abundance and dominance values (percent of total catch abundance) of Eurasian perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) caught by trammel net sampling in the littoral zone of Lake Constance. Plotted are mean values integrated over all sampling sites and depth strata from April 92 to May 93.

Table 4. Significance levels of differences in abundance and biomass for electric fishing (e) and trammel net sampling (t) among sampling sites and depth strata; n. s. = not significant. Significance test: Anova-Duncan's Multiple Range comparsions of Means.

species	Fishing gear	among sampling sites		among depth strata	
		abundance	biomass	abundance	biomass
burbot	e	<0.01	<0.01	<0.01	<0.01
stone loach	e	<0.01	<0.01	<0.01	<0.01
European eel	e	n. s.	n. s.	n. s.	<0.01
chub	e	<0.01	<0.01	<0.01	<0.01
dace	e	n. s.	n. s.	n. s.	n. s.
bream	e	n. s.	n. s.	<0.01	<0.01
Eurasian perch	e	n. s.	n. s.	n. s.	n. s.
ruffe	e	n. s.	n. s.	<0.05	<0.05
Eurasian perch	t	n. s.	n. s.	n. s.	n. s.
ruffe	t	n. s.	n. s.	<0.01	<0.01

muddy and at the boulder site. At the muddy site, burbot occurred in comparatively low abundance and biomass values of 3.2 (± 1.3) ind · 100 m^{-2} and 6.5 (± 3.1) g-wet · 100 m^{-2}. Stone loach, in contrast, was collected with average values of 9.9 (± 7.1) ind · 100 m^{-2} and 25.1 (± 34.9) g-wet · 100 m^{-2} at this site and was therefore almost as abundant as at the gravel-sandy site. In contrast, at the boulder site, burbot reached comparatively high abundance and biomass values but fewer stone loach were caught with lower biomass.

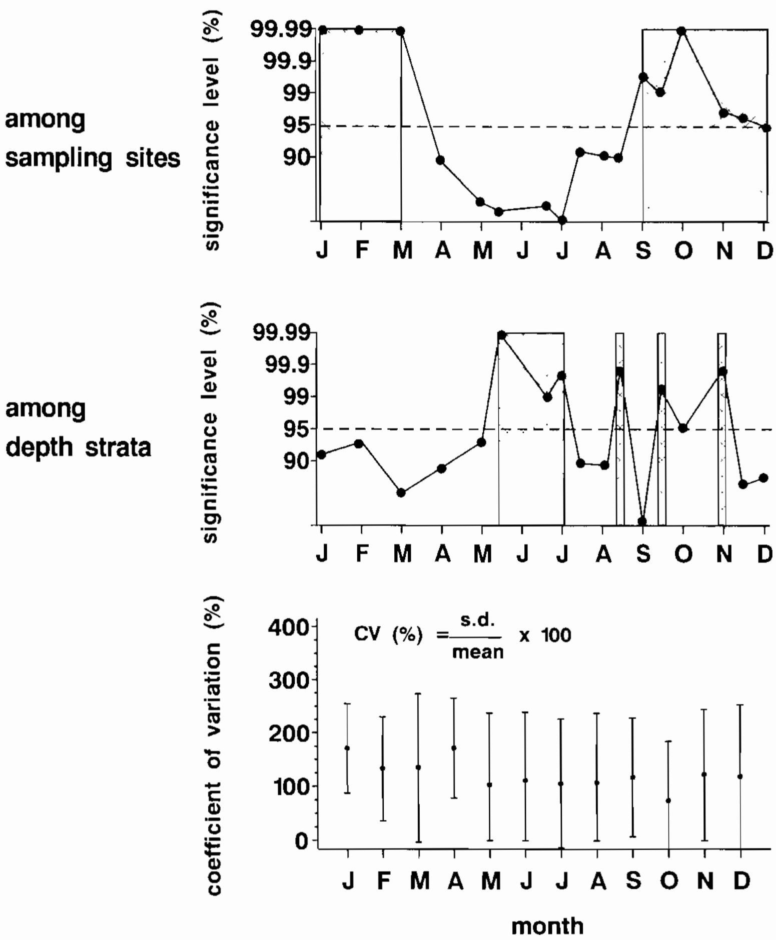

Fig. 3. Upper two graphs: Significance levels of distribution differences of total fish abundance among sampling sites (upper graph) and depth strata (middle graph). Sampling periods with significance levels above 95 % are marked as crosshatched areas. Lower graph: Variability within replicate electric fishing samplings, expressed as coefficient of variation (CV, Lozán 1992). CV-values were calculated separately for each sampling site and depth stratum and are plotted as mean values and standard deviations per month.

In the CCA (Table 5), the variable "substrate coverage" ranked highest with r = +0.61 for burbot and r = +0.59 for stone loach. In both species the variable "depth strata" ranked second with r = –0.44 and r = –0.55. Substrate coverage, with stones of various sizes in the shallow littoral areas, therefore, seems to be the most important habitat factor for burbot and stone loach.

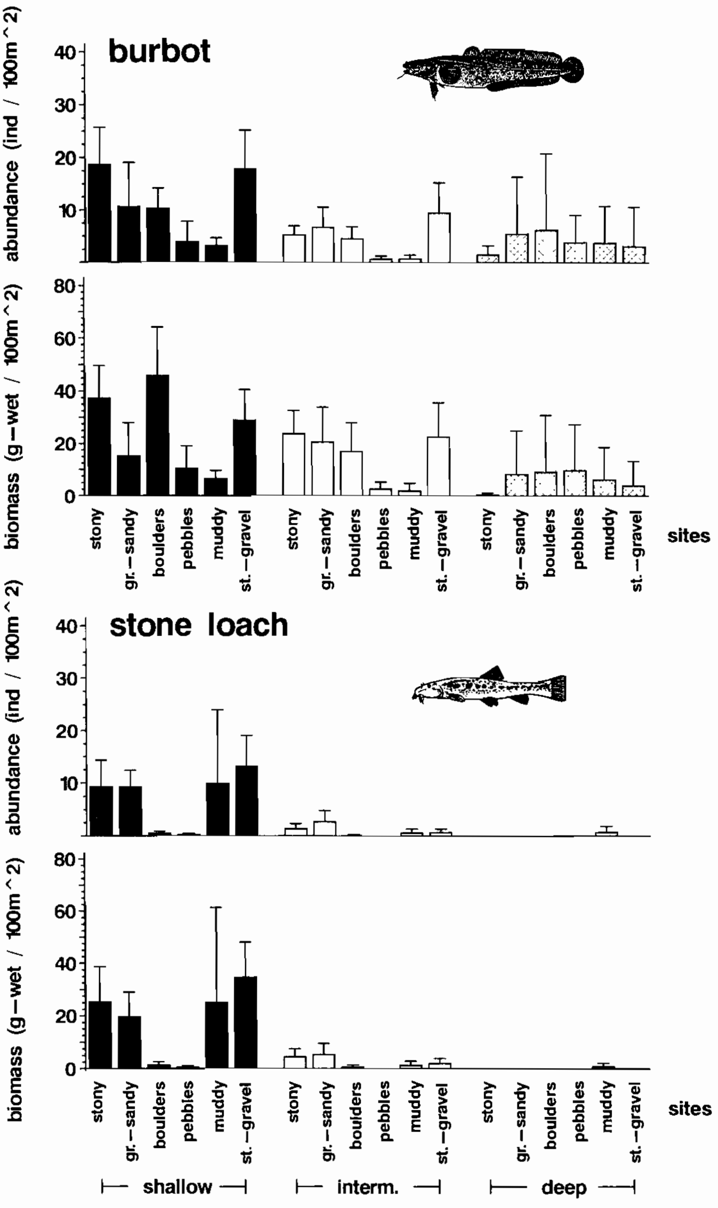

Fig. 4. Mean abundance and biomass values of burbot (*Lota lota*) and stone loach (*Noemacheilus barbatulus*) at the six sampling sites and three depth strata. Plotted are means and standard deviations integrated over the period November 91 to February 93.

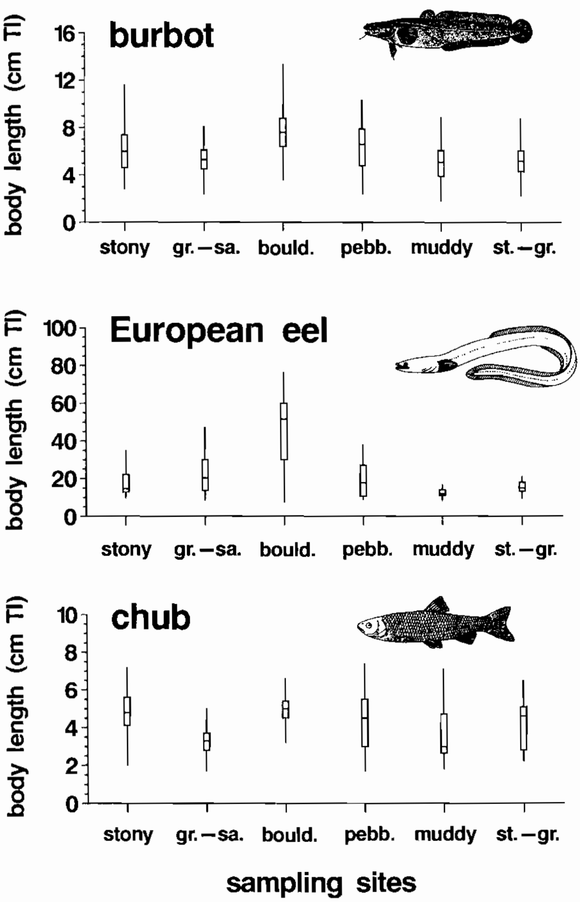

Fig. 5. Mean body length of burbot (*Lota lota*), European eel (*Anguilla anguilla*) and chub (*Leuciscus cephalus*) at the six sampling sites in the stratum "shallow". Plotted are the median, the 25th and 75th percentile (box) and the minimal and maximal values (whiskers), integrated over the period November 91 to February 93 for burbot, May 92 to October 92 for eel, and July 92 to September 92 for chub.

Both species clearly differed in the variables "substrate type", "mean stone size", and "littoral width". "Substrate type" and "mean stone size" reached comparatively high values for burbot but not for stone loach. In contrast, "littoral width" ranked higher in stone loach but not in burbot. The low r-values of the two variables "substrate type" and "mean stone size" for stone loach may explain the observed high abundance and biomass values of this species at the muddy and gravel-sandy sites, two sites with completely different substrate characteristics (Table 1).

Eels (*Anguilla anguilla*) were collected in greatest abundances in the littoral zone from May to October (Fig. 2 a). The highest biomass values were

Table 5. Canonical correlation for fish species in the littoral zone of Lake Constance. Correlation coefficients r of the multivariate independent predictor variables to the first canonical axis of the multivariate dependant criterion variables are shown. Input data for the electric fishing sampling are ranked over month. Because of less replicates in trammel net sampling, input data for Eurasian perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) caught by trammel nets are combined and ranked from May to Sept. Further explanations in text.

	electric fishing								trammel net
	burbot	stone loach	European eel	chub	dace	bream	Eurasian perch	ruffe	Eurasian perch and ruffe
input data integrated over:	month	month	month	month	month	month	month	month	May to Sept.
r^2	0.67	0.69	0.46	0.55	0.47	0.37	0.43	0.43	0.69
pr>f	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
variance explained by canonical axis I	94.6	96.9	68.9	92.0	87.9	77.3	75.8	68.3	66.4
criterion:									
abundance	0.99	0.99	0.90	0.99	0.99	0.99	0.98	0.90	0.90
biomass	0.98	0.99	0.99	0.98	0.99	0.97	0.88	0.74	0.97
predictor:									
temperature	0.00	0.16	0.05	0.06	0.04	0.12	0.03	0.05	0.08
depth strata	−0.44	−0.55	−0.17	−0.42	−0.28	−0.07	−0.15	−0.11	0.24
substrate type	0.29	0.08	0.23	0.17	0.20	0.03	0.11	0.07	−0.48
substrate coverage	0.61	0.59	0.34	0.31	0.35	−0.05	−0.12	−0.18	−0.20
mean stone size	0.13	−0.06	0.21	0.00	0.03	0.03	0.20	0.19	0.34
stone size range	−0.10	−0.20	0.01	−0.12	−0.12	−0.03	0.14	0.16	0.33
littoral width	−0.01	0.24	0.03	−0.17	−0.16	−0.12	−0.11	−0.03	0.33
SAV (*Chara* spp.)	−0.10	−0.20	0.01	−0.12	−0.12	−0.03	0.14	0.23	−0.24
SAV (*P. pectinatus*)	−0.22	−0.25	−0.14	−0.27	−0.29	0.03	0.30	0.20	−0.15
SAV (*P. perfoliatus*)	−0.20	−0.18	−0.12	−0.22	−0.25	0.02	0.08	0.02	−0.01

recorded at the boulder site in 0 to 50 cm water depth (Fig. 6). There, a narrow band of large stones (diameter 30–50 cm) became inundated in spring with rising lake level. At this site, mean abundance and biomass values of 13.3 (± 22.0) ind $\cdot$ 100 m^{-2} and 3231 (± 5241) g-wet $\cdot$ 100 m^{-2} were found, with maximal values up to 61.7 ind $\cdot$ 100 m^{-2} and 40,000 g-wet $\cdot$ 100 m^{-2}. Distribution of eels was only significantly different ($p<0.01$) among depth strata and only for biomass (Table 4). The high biomass values recorded at the boulder site were mainly due to large individuals with a size range of about 40 to 75 cm length (Fig. 5), aggregating in the shallow stratum. Small eels (size range 10 to 20 cm) were caught at various locations. Most (63.6 %) eels <20 cm TL were obtained at the muddy and stony sites. Only 4.1 % of all eels <20 cm TL were found at the boulder site where most of the large eels were caught. In August and September, with increasing density of SAV, eels of various size classes were caught at almost all sampling sites either in the intermediate or deep

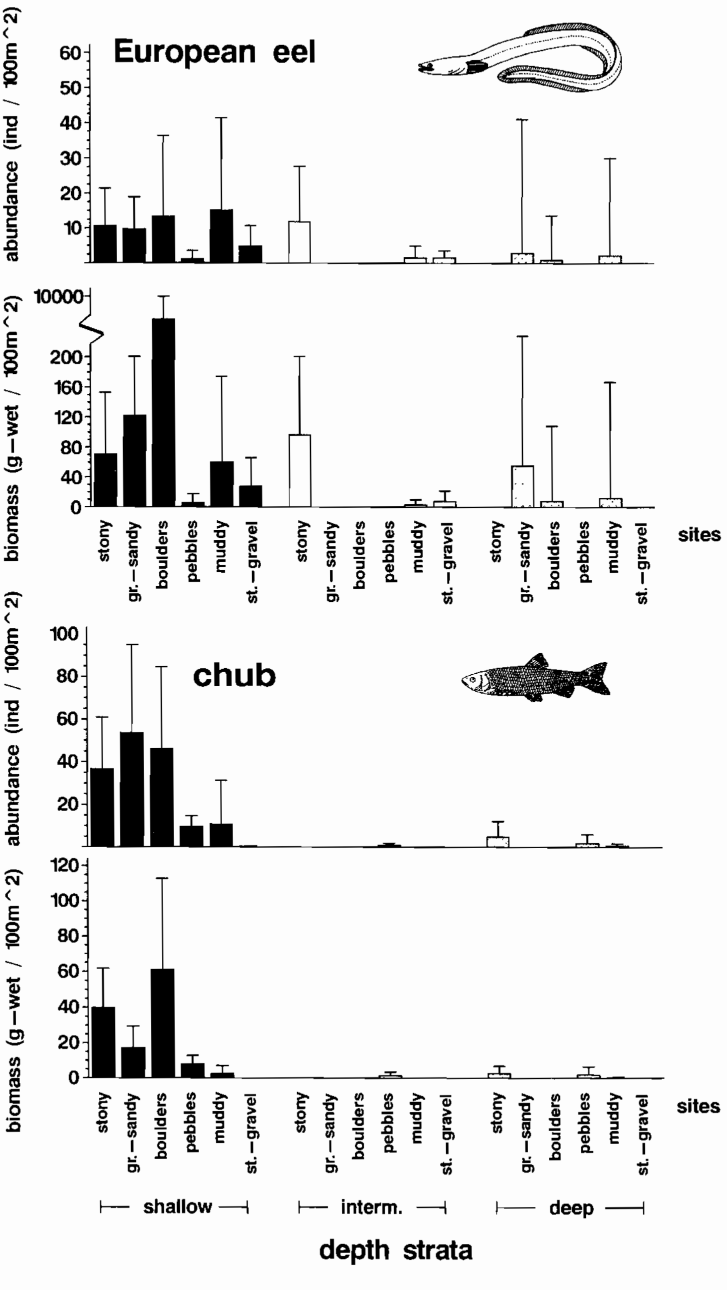

Fig. 6. Mean abundance and biomass values of European eel (*Anguilla anguilla*) and chub (*Leuciscus cephalus*) at the six sampling sites and three depth strata. Plotted are means and standard deviations integrated over the period May 92 to October 92 for eel and July 92 to September 92 for chub.

strata. However, mean eel abundance and biomass per $100\,m^2$ still remained highest in the shallow areas of the boulder site for large individuals (40–75 cm TL) and in the shallow stratum at the muddy site for small individuals (10–20 cm TL).

In the CCA (Table 5), all r values for the habitat variables remained lower for eel than for burbot and stone loach. The variable "substrate coverage" ranked highest with $r = +0.34$. The variables "substrate type" and "mean stone size" ranked second and third. The variable "depth strata", however, only reached a value of $r = -0.17$.

From late June to October, the littoral fish community in Lake Constance was characterized by juvenile cyprinids and percids of various size classes. Age 0 chub (*Leuciscus cephalus*) were caught in the littoral zone in greatest abundances from July to September (Fig. 2 a). 96.5 % of all chub were caught in the shallow areas <50 cm water depth. Significant differences ($p<0.01$) in chub abundance and biomass were also observed among sampling sites (Table 4). High abundance values of 36.5 to $54.9\,\text{ind} \cdot 100\,m^{-2}$ were observed at the northern stony, gravel-sandy and boulder sites. Significantly lower values were recorded at the southern pebble, muddy and stony gravel sites (Fig. 6). Similar distribution differences among northern and southern sampling sites were also recorded for chub biomass.

Like burbot, chub reached high abundance but low biomass values at the gravel-sandy site. Length analysis revealed that 98.3 % of all chub collected in the littoral zone belonged to age-class 0. However, with an average body length of 3.3 cm (Fig. 5), age 0 chub caught at the gravel-sandy site were significantly smaller than age 0 chub caught at the northern boulder and stony sites. The variable "depth strata" ranked highest in the CCA (Table 5), with $r = -0.42$. This shows the importance of shallow areas for age-class 0 chub in general. A comparatively high r value of the variable "substrate coverage" ($r = +0.31$) additionally indicates a preference for areas with high substrate coverage of stones within the shallow areas. The negative values for all three SAVs indicate that juvenile chub seem to avoid areas with dense SAV, especially those with high densities of *Potamogeton pectinatus* ($r=-0.27$).

Dace (*Leuciscus leuciscus*) were collected in the littoral zone in greatest abundances from June to August (Fig. 2 a). Dace distribution was similar to that of chub but differences among sampling sites and depth strata were not significant (Table 4). Length analysis of dace revealed different size classes in the individual depth strata. With an average length of 8.2 cm TL (Fig. 7), dace caught in the intermediate stratum were significantly larger ($p<0.01$) than those caught in the shallow or deep strata. In the CCA (Table 5), the variable "substrate coverage" ranked highest for dace with $r = +0.35$. In contrast to chub, "depth strata" only ranked third. As for chub, all three SAV variables had negative values.

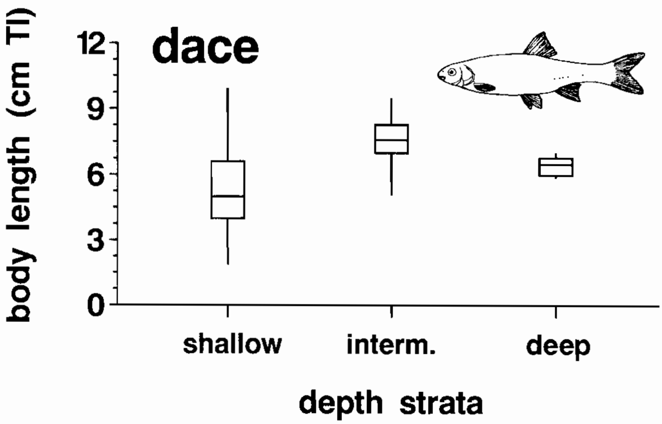

Fig. 7. Mean body length of dace (*Leuciscus leuciscus*) in the three depth strata integrated over the six sampling sites. Plotted are the median, the 25th and 75th percentile (box) and the maximal and minimal values (whiskers), integrated over the period June 92 to August 92.

Bream (*Abramis brama*) were caught in greatest abundances from June to September (Fig. 2a). Distribution differences for bream were found to be significant among depth strata ($p<0.01$) but not among the sampling sites (Table 4). However, distribution differences among depth strata were different among different periods of the year. During the "non SAV growing season" (May to Jul.), 74% of all bream were caught in the shallow stratum (Fig. 8). From August to October, when dense stands of SAV were present in the deeper littoral areas, 61.2% of all bream were caught in the "deep" stratum. In contrast to dace, no significant differences were recorded for total length of bream in the different depth strata. In the CCA, none of the substrate variables reached high r values (Table 5) but the three variables "SAV (*P. pectinatus*)", "SAV (*P. perfoliatus*)" and "depth strata" were no longer negatively correlated to abundance and biomass. The generally low r values for all habitat parameters indicate that age 0 bream have the most variable distribution of the cyprinid species in Lake Constance. On the other hand, the positive r value of the SAV variables indicates that age 0 bream preferably use areas with dense SAV as habitat when available in the littoral zone.

Perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernuus*) were caught in greatest abundances and biomass from April to November by electric fishing and by trammel net sampling (Fig. 2a, 2b). With an average length of 4.8 (± 2.1) and 5.5 (± 1.5) cm TL, perch and ruffe caught by electric fishing were significantly smaller ($p<0.001$) than those in the trammel net catches (mean TL = 9.7 (± 2.5) cm for perch and 8.0 (± 1.4) cm for ruffe).

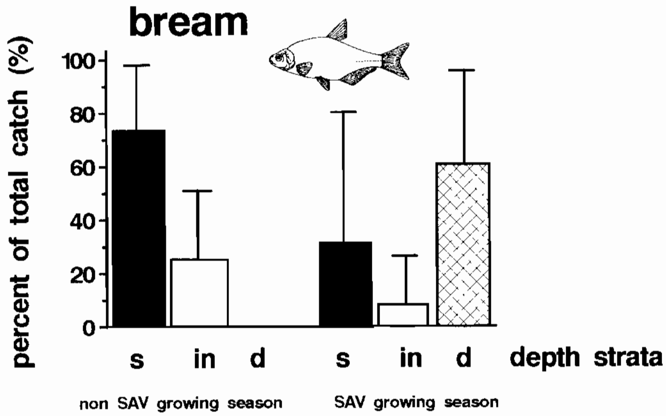

Fig. 8. Percent of total catch of bream (*Abramis brama*) in the three depth strata (s = shallow; in = intermediate; d = deep), integrated over the six sampling sites. Plotted are means and standard deviations during months with no or only spare SAV in the littoral zone (May to July; non SAV growing season) and during the months August 92 to October 92 (SAV growing season) when dense stands of SAV were present in the deep stratum.

In the electric fishing catches, neither perch nor ruffe showed significant differences in abundance or biomass among sampling sites. Among depth strata, only ruffe distribution was significantly different ($p<0.05$, Table 4). Most (87.8 %) ruffe were caught in the deep stratum with maximal values of 9.9 (12.7) ind $\cdot$ 100 m^{-2} and 31.0 (46.9) g-wet $\cdot$ 100 m^{-2} at the boulder site (Fig. 9). Similar results were obtained in the trammel net catches where 74.9 % of all perch and 61.2 % of all ruffe were caught in the deep stratum. Distribution differences in the trammel net catches were significant ($p<0.01$) only for ruffe among depth strata (Table 4). Maximal values of 71.4 (± 27.4) ind $\cdot$ $CPUE^{-1}$ and 408 (± 378.7) g-wet $\cdot$ $CPUE^{-1}$ were recorded at the boulder site (Fig. 9). The CCA for perch and ruffe for electric fishing and trammel net catches gave contradictory results. In the electric fishing catches, the SAV variables ranked highest for both species (Table 5). R values of +0.30 for "SAV (*P. pectinatus*)" in perch and of +0.23 for "SAV (*Chara* spp.)" in ruffe indicate a stronger positive relationship between SAV and perch and ruffe compared to other species. However, this is valid only for associations of *P. pectinatus* and *Chara* spp. but not for *P. perfoliatus*.

A separate CCA for the trammel net catches showed different habitat variables to be important for larger perch and ruffe. The variable "substrate type" ranked highest with $r = -0.48$. "Mean stone size", "stone size range" and "littoral width" ranked second and third with comparatively high values of +0.34, +0.33 and +0.33. In contrast to the electric fishing catches, in the trammel net

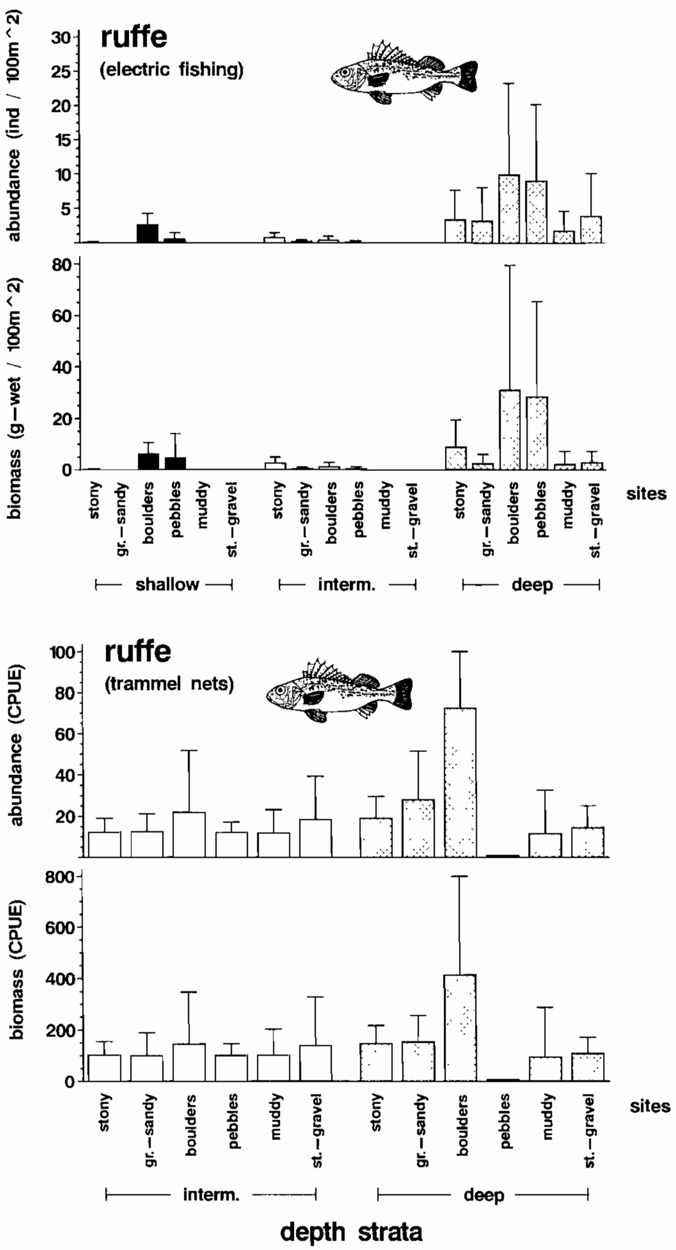

Fig. 9. Mean abundance and biomass values of ruffe (*Gymnocephalus cernuus*) caught by electric fishing (upper graph) and trammel net sampling (lower graph) at the six sampling sites and three resp. two depth strata. Plotted are means and standard deviations integrated over the period May 92 to October 92 for electric fishing and April 92 to November 92 for trammel net sampling.

catches, both species showed negative r values for all SAV variables. This indicates that larger perch and ruffe seem to prefer open areas in the deeper littoral as habitat and, in contrast to the juveniles, avoid areas with dense aggregations of SAV.

Discussion

Habitat-species interactions in aquatic environments are rarely characterized by simple low factorial models (VINCE et al. 1976, CROWDER & COOPER 1982, TONN & MAGNUSON 1982, LODGE et al. 1988). In many studies, scattered results are more characteristic than clear distribution differences, and significance levels are generally low (PIERCE et al. 1994). A complex relationship was also found for the littoral fish community in Lake Constance. Our data reveal complex site and depth dependent distribution differences often combined with a strong effect of body size.

In most North American lakes, submersed aquatic vegetation is assumed to be very important for small or juvenile fish (WERNER et al. 1977, BAKER & ROSS 1981, WERNER et al. 1983, RAHEL 1984) and body size is mainly discussed with respect to predator-prey interactions between relatively small prey within dense patches of SAV and large predators outside (MITTELBACH 1986, DEVRIES 1990, LYONS 1991). Our data indicate a more complex relationship among individual fish species and their habitat in Lake Constance. In this lake, the very shallow areas (<50 cm water depth) are of major importance, especially for small species and/or juvenile fish and SAV is not necessarily preferred as habitat even when available in deeper littoral areas.

RUIZ et al. (1993) described a similar size-related depth distribution of fish species in Chesapeake Bay, USA. Similar to our results from Lake Constance, they found small individuals more often in the very shallow areas compared to deeper parts. COPP (1990) also made similar observations in the Upper Rhone River, France. He found juvenile fish of particular species and length more often in the very shallow areas compared to adjacent deeper waters. We therefore postulate that mechanisms regulating littoral fish communities in large European lakes are probably more comparable to shallow water fish communities in estuarine ecosystems or floodplain channels than to small North American lakes. Large lakes, estuaries and floodplain channels have in common that vegetation in the deeper areas is often more scattered or even absent, and turbulences in the shallow areas are higher due to wind and wave action. This may prevent larger predators, with greater susceptibility to hydrodynamic forces, from using shallow areas as habitat and feeding areas and thus provide refuge in these highly productive areas especially for small and juvenile fish.

Another important result of the study was the high variability of the abundance and biomass values within most of our replicates. Variability among replicate electric fishing or trammel net samplings within a single site and depth stratum were often higher than among different sites or depth strata. However, this high variability was consistent over the entire sampling period within all sites and depth strata. Benson & Magnuson (1992) made similar observations in their studies of littoral fish in northern Wisconsin lakes (USA). In replicate seine hauls at sampling sites within lakes, they often found a higher variability among replicates than among different sites or lakes. Pierce et al. (1994) discussed this observation in detail and postulated, that this variability is not a result of inadequate sampling design but an effect of using real quantitative abundance and biomass data for littoral fish community studies instead of the commonly used presence/absence information. We too hold that the observed high variability in our replicates is not a result of inadequate sampling design because we explicitly tried to avoid disturbance during our field sampling. Furthermore, the high variability within most of our replicates was consistent over the entire season, all sites and depths and, most important, independent of the total amount of fish caught per sampling. Even when species richness and fish density were low during winter and benthic species, with low escape potential, dominated, variability was as high as among the replicates in summer. Therefore, our data seem to support the hypothesis of Benson & Magnuson (1992) and Pierce et al. (1994) who postulated that small-scale distribution patterns within single habitats, smaller than most of our commonly used fishing gears can sample, are probably very important but more or less unknown in littoral fish assemblages. However, without detailed knowledge of the temporal and spatial scales within which these patterns occur, a detailed evaluation of their importance for habitat partitioning among littoral fish species is problematic. The development of sampling methods to resolve such patterns should therefore be one of our major goals in future studies of littoral fish communities.

Integrated over the entire sampling period, we discriminated a permanent and a temporary group within the littoral fish community of Lake Constance. The permanent group is composed of the two benthic species burbot and stone loach, which were found in the littoral zone throughout the year, even in winter when water temperatures dropped below 4 °C and ice partly covered the shallow littoral zone. CCA showed that both species mainly use shallow areas with a high percentage of substrate coverage as habitat. Lyons (1987) reported a similar distribution pattern for two small benthic fish species in Wisconsin lakes, darter (*Etheostoma exile*) and mottled sculpin (*Cottus bairdi*). As in Lake Constance, these two were the only abundant benthic species in the littoral zone, and they were also found mainly in waters <1 m deep. Lyons (1987) interpreted this restriction to the shallow areas as a result of the lower predation risk there compared to deeper areas and by the use of shallow areas as spawning sites. Stone loach in Lake Constance do use shallow areas for spawning but burbot migrate from the littoral zone to deeper adjacent areas while still juvenile, at a length of about 12 cm, and spawn in water >50 m deep (NÜMANN 1939). Therefore, the availability of spawning sites might explain the preference of stone loach for shallow areas but not for burbot. The restriction of juvenile burbot to shallow areas is more likely to be the result of lower predation risk and greater availability of shelter in these areas.

Both species showed similar distribution patterns among sampling sites except for the muddy site. There, only stone loach were found in greater abundances. This specific site is characterized by a low slope and muddy sediment in the shallow areas. WELTON et al. (1991) showed that for stone loach, food availability is a strong trigger for habitat selection and may overrule substrate preferences. Furthermore, stone loaches prefer chironomids as their main food source (WELTON et al. 1991). Because chironomids are normally more abundant in muddy sediments compared to gravel-sandy or stony areas (UHLMANN 1982), food availability may be the reason for the comparatively high abundance of stone loaches at the muddy site.

Besides burbot and stone loach, European eels, the cyprinids chub, dace and bream and the two percids Eurasian perch and ruffe were also caught in great abundance in the littoral zone but in different habitats. Each of these species was found in the littoral zone only during a restricted time of the year but then dominated the fish community.

Similar to LYONS (1987), we found many age 0 cyprinids restricted to the shallow areas <50 cm deep or to areas of dense submerged aquatic vegetation. In contrast, larger individuals such as adult perch and ruffe were caught in either intermediate or deeper areas. The use of shallow areas as refuges for small or juvenile fish when large predators are present in deeper adjacent areas is well known in freshwater as well as in estuarine systems (HECK & THOMAN 1981, BAIN et al. 1988). However, shallow areas are mainly regarded as alternative habitats when SAV is absent from deeper zones or when its density is low. As in the investigations of RUIZ et al. (1993), we found the highest abundances of small fish (mainly age 0 chub and dace) in shallow areas during the entire season, even in the months with dense SAV in deeper littoral areas. As already postulated by RUIZ et al. (1993), our data indicate that shallow waters may be a preferred habitat especially for small fish, even when dense SAV is available in deeper areas. Greater protection from the larger predators, which are mainly present in the deeper littoral areas in Lake Constance, seems to be the most probable reason for this observed distribution. Like chub and dace, age 0 bream were collected in the shallow areas too, when no SAV was present in deeper areas. However, with increasing density of SAV during summer, bream distribution shifted from shallow to deep areas, especially to areas with dense stands of *P. perfoliatus* at the stony site.

We assume that this habitat shift was a response to the availability of cover by SAV in the deeper water and to a change in body shape during ontogenetic development. In contrast to juvenile chub and dace, juvenile bream become laterally compressed and high backed during their first summer. This change in body shape may lead to much greater susceptibility to turbulence, especially in large lakes where wind forces may cause strong wave action and currents in the shallow areas. When the amount of energy spent on adjusting body position in shallow turbulent water increases, deeper areas with dense SAV may be the best alternative habitat. There, water turbulence declines to comparatively low levels and SAV provide more protection compared to open, nonvegetated areas.

Up to now, hydrodynamic forces have barely been recognized as factors influencing habitat selection and distribution patterns in littoral fish species. Such forces may result in decreased feeding success and growth rates (GIBSON 1994), but to our knowledge there are no direct measurements of the effects of turbulence on habitat selection. In littoral zones, where wind and wave action often cause strong turbulent hydrodynamic forces, these factors should be considered as environmental variables that influence habitat availability and, thus fish distribution.

In addition to the three cyprinids, European eels, Eurasian perch and ruffe were also caught in greater abundances. Eels were caught at almost all sites and depth strata within the littoral zone but were separated by size classes.

Small eels (<20 cm TL) occurred in greatest abundances in the shallow areas, medium-sized eels (20 to 50 cm TL) in the intermediate zone, and large eels (>50 cm TL) in the shallow or in the deep areas. BERG (1988) and TESCH (1973) classified the European eel as a generalist species, able to use a wide variety of habitat types. Our data partly support this for Lake Constance. However, the observed accumulation of large eels up to 40,000 g-wet $\cdot$ 100 m^{-2} in the shallow areas at the boulder site show that eels strongly prefer a very specific habitat type. Large stones with a diameter of 30–50 cm providing interstitial caves and shelter seem to exactly fit the habitat requirements of large eels in Lake Constance and may explain the extremely high densities of eels at this specific site.

The Eurasian perch and the ruffe differed from all other species in their depth distributions. Both species were never found in greater abundances or biomasses in the shallow areas. Age 0 individuals were mainly caught in deeper littoral areas within stands of dense submerged aquatic vegetation. Older individuals were more abundant in open nonvegetated areas. RADKE (1993) and WANG (1994) showed that age 0 perch are more often preyed upon by large eels and adult perch than age 0 cyprinids. The distribution of juvenile perch mainly in the deeper littoral parts probably contributes to this greater vulnerability to predation compared to juvenile cyprinids. Adult perch, on the other hand, are known to use the littoral in Lake Constance mainly during the night for resting, and stay in the pelagic zone during the day (IMBROCK et al. 1996). Thus, open nonvegetated areas in the littoral zone are probably more safe for resting adult perch compared to densely vegetated areas because large predators such as eel and pike are often found closely related to areas with dense SAV.

Conclusions

It is apparent that fish assemblages in the littoral zone of Lake Constance are not dependent on a single factor such as the often cited presence or absence (in small North American lakes) of macrophytes. Our results show that littoral fish communities in a large European lake may be far more complex when compared to small aquatic ecosystems. Most species seem to have very specific patterns of habitat use and, if available, accumulate within these sites in high densities. Especially for small fish, the "shallow water" (0–50 cm water depth) habitat seems to be a strongly preferred habitat, overruling many other substrate variables. However, our knowledge of habitat partitioning in littoral fish communities of large lakes is still limited and, most importantly, we often do not know the scales and spatial distances which are important for community structure in the littoral zone.

We assume that we sometimes did not manage to adequately sample distribution patterns within habitats which prevents a more detailed insight into littoral fish community structure. The development and application of adequate field techniques, combined with the analysis of single species – habitat relationships in laboratory experiments, therefore seems to be the most promising approach to understanding the complex in situ relationships in littoral fish communities of large lakes.

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