

Lake Constance fisheries and fish ecology

Reiner Eckmann and Roland Rösch

with 4 figures and 2 tables

Abstract: This paper summarizes changes in the fish species list and in fishery yields in Upper Lake Constance during the last century. Species richness has remained nearly unchanged since the end of the last century, although three species and one form of whitefish have been lost from the lake probably as a result of eutrophication and four other species have been introduced either accidentally or intentionally. Fisheries yields have increased since the 1950s because eutrophication enhanced fish production and fish stocks were exploited more intensively with highly efficient nylon nets. With increasing lake trophy during the 1960s and 1970s, the proportion of coregonids in commercial catches decreased, whereas the proportion of perch and cyprinids rose. The recent oligotrophication of the lake is reflected in an augmenting proportion of whitefish in commercial catches and an increasing age-at-capture. Lake whitefish (*Coregonus lavaretus*) and Eurasian perch (*Perca fluviatilis*) are commercially the most important fish species in Lake Constance. Their ecology has been studied intensively during the last decade, while most recently the littoral fish community has been included in our research activities. The effects of newly introduced and rapidly spreading ruffe (*Gymnocephalus cernuus*) on the native fish fauna are of special concern to fishery managers and will be a central topic of future research.

Long-term trends

Fish species occurring in the lake

The fish species list for the years prior to 1900 is compared with the present situation in Table 1. A total of 29 species presently occur in the lake (BERG 1993), which is about the same number as 100 years ago (KLUNZINGER 1892), although several remarkable changes have taken place during this time. Minnow (*Phoxinus phoxinus*) and bullhead (*Cottus gobio*), which were abundant in former times, disappeared from the lake. Both species are small-sized fish especially adapted to oligotrophic lakes (BERG 1993). At the beginning of this century, four forms of whitefish (*Coregonus* sp.) occurred in Upper Lake Constance (WAGLER 1941), while only two forms are currently found in considerable numbers, a pelagic spawning whitefish (local name: "Blaufelchen") and a nearshore spawning one (local name "Gangfisch"). A slow-growing deepwater form (local name "Kilch") has become extinct in the 1960s (KLEIN 1993).

Authors' addresses: R. Eckmann, Limnological Institute, University of Konstanz, D-78457 Konstanz, Germany, e-mail: Reiner.Eckmann@uni-konstanz.de. – R. Rösch, Fischereiforschungsstelle Baden-Württemberg, Mühlesch 13, D-88085 Langenargen, Germany.

Table 1. Fish species occurring in Lake Constance before 1900 and at present.

species	before 1900	at present (1992)
<i>Anguilla anguilla</i> (L.)	x	x
<i>Salmo trutta</i> L.	x	x
<i>Oncorhynchus mykiss</i> (Walbaum)		x
<i>Salvelinus alpinus</i> (L.)	x	x
<i>Coregonus lavaretus</i> L.		
Blaufelchen	x	x
Gangfisch	x	x
Sandfelchen	x	(x)
Kilch	x	
<i>Thymallus thymallus</i> (L.)	x	x
<i>Esox lucius</i> L.	x	x
<i>Rutilus rutilus</i> (L.)	x	x
<i>Leucaspis delineatus</i> (Heckel)	x	x
<i>Leuciscus leuciscus</i> (L.)	x	x
<i>Leuciscus cephalus</i> (L.)	x	x
<i>Phoxinus phoxinus</i> (L.)	x	
<i>Scardinius erythrophthalmus</i> (L.)	x	x
<i>Tinca tinca</i> (L.)	x	x
<i>Chondrostoma nasus</i> (L.)	x	x
<i>Gobio gobio</i> (L.)	x	x
<i>Barbus barbus</i> (L.)	x	x
<i>Alburnus alburnus</i> (L.)	x	x
<i>Blicca bjoerkna</i> (L.)	x	x
<i>Abramis brama</i> (L.)	x	x
<i>Rhodeus sericeus amarus</i> Bloch	x	
<i>Carassius carassius</i> (L.)	x	x
<i>Cyprinus carpio</i> L.	x	x
<i>Barbatula barbatula</i> (L.)	x	x
<i>Silurus glanis</i> L.	x	x
<i>Lepomis gibbosus</i> (L.)		x
<i>Perca fluviatilis</i> L.	x	x
<i>Stizostedion lucioperca</i> (L.)	x	x
<i>Gymnocephalus cernuus</i> (L.)		x
<i>Cottus gobio</i> L.	x	
<i>Gasterosteus aculeatus</i> L.		x
<i>Lota lota</i> (L.)	x	x

(x) = only very few specimen are caught actually

Of the fourth form, "Sandfelchen", only a few fish have been found recently (LUCZYNSKI et al. 1995). Bleak (*Alburnus alburnus*) was the most abundant species during the last century (KLUNZINGER 1892). In the 1980s, this species became nearly extinct, but in recent years the population seems to have recovered (BERG 1993).

The new species are three-spined stickleback (*Gasterosteus aculeatus*), rainbow trout (*Oncorhynchus mykiss*), pumpkinseed sunfish (*Lepomis gibbosus*), and most recently ruffe

(*Gymnocephalus cernuus*). The latter species was recorded for the first time in 1987 (BERG et al. 1989). The way of its introduction into the lake is unknown. Ruffe occurred in considerable numbers already in 1992 (HARTMANN 1993, FISCHER 1994), and it is now the most abundant species in shallow areas (RÖSCH & SCHMID 1996). A rapid spread of newly introduced ruffe in lakes outside of its natural range of occurrence has also been documented in lakes in Britain and the Great Lakes in North America (WINFIELD et al. 1997). During most of the year, ruffe in Lake Constance prey mainly on benthic organisms, but during the whitefish spawning period in early December, whitefish eggs form their main prey. Therefore, ruffe might influence reproductive success of nearshore-spawning whitefish. During the growing season, ruffe might compete with perch for benthic food resources, and this competition will likely increase with further oligotrophication of the lake (RÖSCH & SCHMID 1996).

Fisheries yield

The professional fishery has a long tradition in Lake Constance. At the beginning of this century, more than 400 professional fishermen were active, while in 1995 there were only about 150 (IBKF 1996). Fisheries statistics are based on annual reports of the IBKF, the International Commission for the Fisheries Management of Upper Lake Constance.

Fisheries yield does not necessarily reflect the fish biomass and species composition of a lake because only species of commercial interest are exploited intensively. In the case of Lake Constance, these are whitefish (*Coregonus lavaretus*) and perch (*Perca fluviatilis*) and to a lesser degree eel (*Anguilla anguilla*), brown trout (*Salmo trutta*), pike (*Esox lucius*), and pikeperch (*Stizostedion stizostedion*). Other species like the cyprinids roach (*Rutilus rutilus*), bream (*Abramis brama*), or dace (*Leuciscus leuciscus*) are caught only as bycatches. Therefore, their population dynamics and biomass are not well represented by the fisheries statistics.

Statistics of professional catches have been continuously available since 1909 (Fig. 1). Commercial exploitation can be divided into two main periods: the first lasted from 1909 to 1955 and the second from 1955 to the present. In the first period, annual yields did not exceed 700 tons and had a median of 415 tons. In 1956, the annual yield exceeded 1000 tons for the first time, and since then has not fallen below 750 tons. The median for the period 1956-1995 was 1104 tons. For whitefish, annual yields varied between 150 and 1400 tons. However, whitefish catches did not exceed 400 tons before 1955. A consistent feature of the yield is its high variability from year to year without obvious periodicity. One of the reasons for a more than doubling in the annual yield in 1956 compared to the previous year was a change in the fishing gear to highly effective nylon gill nets (NÜMANN 1972). Traditionally, whitefish were caught with a pelagic seine ("Klusgarn") or gill nets made from cotton (ELSTER 1944, NÜMANN 1972), for which the catch per unit effort (CPUE) was much lower than for nylon gill nets.

For cyprinid fishes, mainly roach and bream, maximum yields in the 1970s did not reflect the actual changes in population dynamics because at that time the cyprinid catch was subsidized by the state. This rendered the catch of cyprinids especially profitable. By the end of 1981, this subsidiary payment was stopped and in the following year cyprinid yields immediately declined to a much lower level. However, in recent years, the populations of cyprinids have decreased and during the summer of 1996, nearly no roach were caught in beach seine samples of juvenile fish (BLASEL 1997).

Prior to 1950, perch was an undesired species, but when professional fishermen adopted the technique of filleting, the market value of perch increased considerably (HARTMANN &

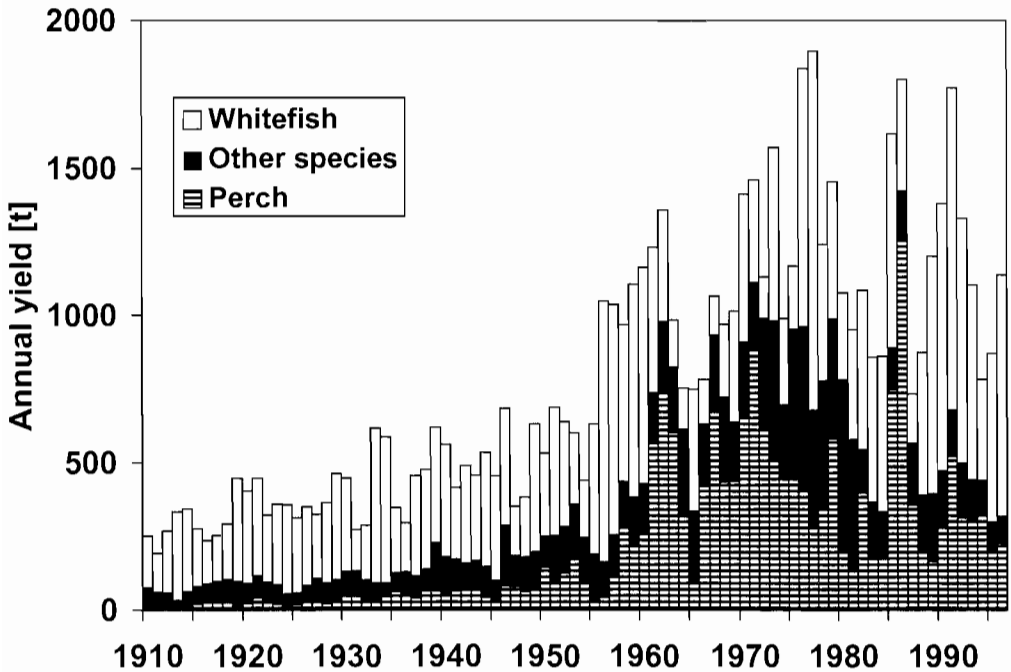


Fig 1. Fisheries yield (metric tons) in Upper Lake Constance from 1910 to 1996 for whitefish, perch, and all other species combined.

NÜMANN 1977). A gill net fishery developed and the perch population is now exploited very intensively (HARTMANN 1975).

During the period up to 1955, the annual commercial yield consisted mainly of whitefish with other species comprising less than 30% (Fig. 2). Beginning in the 1960s, the proportion of whitefish in the total yield diminished to less than 40% in certain years. However, during the last 15 years, the proportion of whitefish has increased and the proportion of perch decreased.

Age composition of the whitefish catch

To elucidate the changes in whitefish population structure, the age composition of whitefish in commercial catches is shown in Fig. 3. Prior to 1966, data are from NÜMANN (1972). Between 1966 and 1990, the data were kindly provided by the Institut für Seenforschung in Langenargen and for the years 1991-1996 data were taken from whitefish monitoring performed by the Fischereiforschungsstelle Langenargen. For the years before 1966, age composition is a mean composition for the whole year, whereas for the years 1966-1996, the age composition is given for August of each year. The month of August was chosen because in this month all year-classes that are caught in a given year are represented in the catch. In the 1930s, 3 to 5-year-old fish dominated the catches. Beginning in the 1950s, the mean age in the catch decreased, and in 1962 most of the fish caught were 1+ fish. With a change of the minimum mesh size from 38 to 44 mm in 1963, the mean age increased by roughly one year, but the

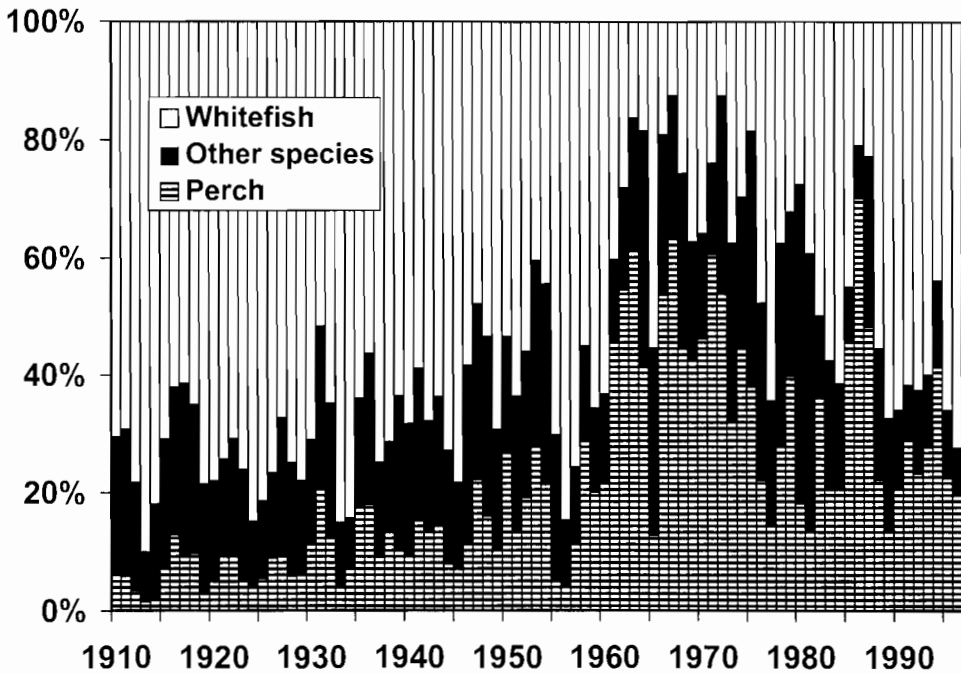


Fig. 2. The relative proportions of whitefish, perch, and other species combined in the annual fisheries yield.

average age of whitefish in the catch remained low. From 1970 to 1984, only one or two year-classes appeared in the catch, and few fish were older than 2+. In 1972 and 1975, even 1+ fish were big enough to be caught in gill nets of 44 mm mesh size. Beginning in 1985, fish in the catch were older again. Only a few specimens were 2+, most fish were 3+ or older, and no fish were caught as 1+. Since 1991, even 5+ fish have been caught. For the last years, a minimum of two year-classes have been represented in the catch.

Especially for whitefish, fisheries legislation is directed towards a sustainable yield, e.g., by reducing fishing intensity so that at least two year-classes are present in the catches. This measure failed during the peak of eutrophication in the 1970s and 1980s, but it seems to be working well under the present, more oligotrophic conditions.

Ecology of lake whitefish

In its pristine state, Lake Constance contained four different forms of whitefish (WAGLER 1941, NÜMANN 1972), while today only inshore spawning "Gangfisch" and pelagic spawning "Blaufelchen" are present in Upper Lake Constance. Professional fishermen differentiate these two forms using traditional criteria such as coloration of the dorsal region, pigmentation of fins, and body shape. Main component analysis of meristic and morphometric characteristics (RUHLÉ 1986), measurements of egg size (RÖSCH 1987), and biochemical genetic analyses (LUCZYNSKI et al. 1995, VUORINEN et al. 1986) have shown that both forms can only be differentiated at the

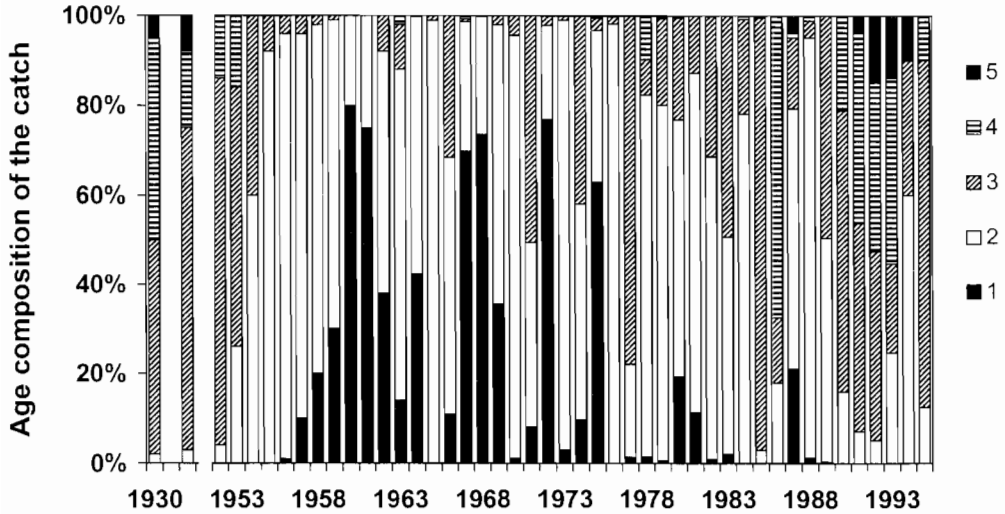


Fig. 3. Whitefish age composition in the catch. Up to 1963, minimum mesh size was 38 mm (knot to knot) and 44 mm thereafter.

population level and single specimens cannot be classified unequivocally. The larvae of both forms differ in a variety of traits: temperature dependence of embryogenesis (ECKMANN 1987), swimming behaviour after hatching and onset of food intake (RÖSCH 1988), yolk-sac volume at the time of hatching and rate of yolk resorption (ORTLEPP unpublished data, SIESSEGGER 1993), and growth rate (RÖSCH & DABROWSKI 1986). Both species are zooplanktivorous during their entire life and co-exist in the pelagic zone during the growing season.

Spawning and embryonic development

During the spawning period in late November/early December, the two whitefish forms are spatially separated. Gangfisch move towards the littoral zone where they spawn at 5 to 15 m depth, whereas Blaufelchen aggregate in the pelagic zone of the lake's main basin at water depths of more than 60 m. Lake Constance Blaufelchen are the only coregonids for which pelagic spawning has been reported. During spawning, Blaufelchen display vertical migrations of up to 50 m amplitude (ECKMANN 1991). They ascend at dusk and descend at dawn. Juveniles take part in these diel migrations, but only sexually mature specimens swim to the uppermost 10 m of water. Juvenile individuals as well as spent females halt their upward migration at a depth of 20-30 m and stay in this layer during the night. The vertical migration of the mature specimens to the uppermost water layers has been interpreted as a means to increase encounter probability among mature males and females. In contrast, diel vertical migration of the entire population is assumed to be a mechanism to avoid cannibalism on freshly spawned eggs that settle to the lake bottom at a speed of 1m/s (ECKMANN 1991). From the end of the spawning season in late December until the start of the next growing season in April, pelagic whitefish overwinter at a depth of 30-40 m and vertical migration ceases.

Blaufelchen spawning takes place within a short period of 3-5 days, whereas the Gangfisch spawning period lasts for more than a week, and ripe Gangfisch females may even be found in early January. The eggs of pelagic whitefish develop on the lake bottom at depths of up to 250 m, where temperature is constant at around 4 °C throughout the year. The embryonic development of Lake Constance whitefish (both Gangfisch and Blaufelchen) is the fastest among all coregonids that have been studied thus far. At an incubation temperature of 4 °C, larvae hatch after 70-80 days, i.e. in mid-February (ECKMANN 1987). The main lake basin rarely freezes over completely (once every 30 years since 875 A.D., the last time being in 1963 (KIEFER 1972)), so hatching cannot be synchronized with the time of ice-off, as is the case in many dimictic coregonid lakes. Turbellarians (NÜMANN & QUOSS 1972) and burbot (ELSTER 1944) are known to prey on whitefish eggs, so early hatching has been interpreted as an adaptive advantage that reduces this source of mortality (ECKMANN 1987). However, intensive predation of whitefish eggs by newly introduced ruffe (RÖSCH & SCHMID 1996, SCHMID 1998) represents a new situation whose effect on the whitefish stock is so far unpredictable.

Larval growth and survival

Hatched larvae ascend to the surface within a day or two (BRAUM 1964) where they do not encounter any predators at that time of year. Larvae prefer the warmest water available and consequently inhabit shallow waters along the shoreline or the upper layers of the lake's open water where their vertical distribution is clearly controlled by the vertical temperature gradient (ECKMANN 1989). Zooplankton abundance (mainly copepods) is low at the time of hatching, but BRAUM (1964) estimated that in the late 1950s/early 1960s zooplankton abundance was sufficient to meet the food requirements of the first feeding larvae. He concluded that whitefish larvae were not suffering from food shortage, and this conclusion was even more valid under the mesotrophic conditions in the 1970s and 1980s. In addition, whitefish larvae from Lake Constance have an outstanding capacity for starvation and only 50% of larvae reach the point-of-no-return after 50-60 days at 4 °C, so mortality due to food deprivation has been dismissed as an important factor for the control of year-class strength (ECKMANN & PUSCH 1991).

Subsequently, the alternative hypothesis that larval mortality is ultimately due to predation has been investigated. Since susceptibility to predation generally decreases with body size (MILLER et al. 1988), the growth of larval coregonids during their first weeks of life was studied by otolith and length-frequency analyses. Otolith analysis of larvae that had been reared under various temperature and food conditions in the laboratory clearly revealed that increments were deposited daily and that increment width and contrast were influenced by temperature and food regime (ECKMANN & REY 1987). Daily increment deposition was validated up to the age of 265 days in this study.

However, further analyses of larval otoliths with light and scanning electron microscopy demonstrated that, if larvae were reared at in situ temperatures of 4-6 °C, daily increments were only recognizable from 10 to 35 days after hatching. In larvae reared at 8 °C, increments were easily identified starting from the day of hatching. These results imply that whitefish larvae that hatch in the lake cannot be precisely aged (KLINK & ECKMANN 1992). As soon as water temperature increases in early spring, daily increments were recognizable and the growth history of larvae and juveniles could be reconstructed from increment analyses from that time onwards.

The otolith radius is linearly related to total body length in fish from 10 to 70 mm length (ECKMANN & PUSCH 1989). Daily growth rates can, therefore, be estimated from daily increment widths. In this way, the growth history of juvenile coregonids sampled in June 1987 was reconstructed for 70 days, from the beginning of April to the day of sampling. Otolith increment widths and, hence, absolute daily length increments clearly run parallel to the temperature in the uppermost water layer (measured at the depth of 2.5 m), while changes in zooplankton abundance were not consistent with changes in larval growth rate (ECKMANN & PUSCH 1989). As upper surface waters further warm up in June and July, the juveniles moved to deeper water to the location of their preferred temperature range of 12 to 15 °C.

Length-frequency analyses of larvae sampled in two consecutive years during spring provided additional evidence to support the concept that growth is mainly controlled by temperature and not by food abundance. In 1987, surface temperature increased about 10 days earlier than in 1986 from about 5 °C to almost 12 °C, and larval growth was advanced by almost 10 days in 1987. The alternative concept that an increase in zooplankton abundance in spring triggers the onset of larval growth was not supported by the zooplankton abundance data sampled at weekly intervals (ECKMANN & PUSCH 1989).

From the results of these independent analyses, it was concluded that the growth of coregonid larvae in Lake Constance starts at the moment that the surface temperature increases and that growth rates during April, May, and early June are controlled by temperature and not by food abundance. The influence of the time of surface warming on growth of larval whitefish can be demonstrated by a model calculation. If the observed temperature curve for spring 1987 is advanced by 5 days and larval growth is estimated as a function of temperature, then by mid-June the fish should be 50.9 mm long and weigh 786 mg instead of 47.8 mm and 638 mg (ECKMANN & PUSCH 1989). It is obvious from this model calculation that even a slight shift in the timing of spring warming can result in considerable growth differences. These may then translate into different survival probabilities.

A conceptual model for year-class strength

Multivariate regression analysis of whitefish year-class strength leads to a similar conclusion about the importance of spring temperature for survival of coregonid larvae in Lake Constance (ECKMANN et al. 1988). For a data set of 21 years (1962 to 1982), virtual year-class strength (y_{cs}) of Blaufelchen was treated as a dependent variable and regressed against density-dependent and density-independent factors. Meteorological conditions that are favourable for early thermal stratification (high amount of sunshine and low wind intensity in April) accounted for 41% of y_{cs} variance. The best fit of the regression was achieved after logarithmic transformation of y_{cs}. This indicates that y_{cs} increases in a non-linear fashion with rising surface water temperature. The number of larvae stocked into the lake from hatcheries ranged from 27 to 279 million individuals per year and accounted for another 18% of variance when it was added as a third independent variable. However, this relationship between stocking and y_{cs} became apparent only after the overwhelming influence of meteorological conditions had been removed from the data, whereas there was no significant direct relationship between stocking intensity and y_{cs}.

The virtual number of older conspecifics present in the lake at the time of larval hatching was negatively related to y_{cs} when this parameter was added as a fourth variable to the model.

Again, as in the case of stocking intensity, there was no direct relationship between ycs and the number of older conspecifics.

Throughout the analysis, no stock-recruitment relationship was apparent. This suggested that any possible relationship between parent stock size and ycs was overruled by other, more important factors. Crustacean zooplankton abundance in March and April did not contribute significantly to explaining ycs variance at any step of the model development. Furthermore, the lake's trophic state (measured as phosphorus concentration) had no detectable influence on the ycs of whitefish. The dramatic increase in phosphorus values from 1960 to 1979 was not accompanied by an increase in whitefish recruitment nor was ycs significantly lower during the years 1924 to 1939 when the phosphorus level was stable at approximately 4 µg/l (TRIPPEL et al. 1991).

Finally, based upon these two independent lines of evidence (otolith/length-frequency analyses and multivariate regression analysis), a conceptual framework for ycs control of Lake Constance whitefish can be outlined. Since the time of hatching is not controlled by surface temperature, larvae appear in the uppermost layers of water approximately at the same time each year. Food abundance is sufficient and the larvae are not subject to mortality by starvation. During their first weeks of life, however, when larvae live at temperatures of 4–6 °C, their growth rate is very low or even nil. As soon as the surface temperature starts to rise in spring, their growth rate increases and runs parallel to surface temperature until at least mid-June. Zooplankton abundance has no detectable influence on the growth rate during this time of the year. Since predation mortality is size-dependent, favourable weather conditions that allow for high growth rates will reduce predation mortality and ultimately lead to the establishment of a large year-class.

Does “unsuitable zooplankton” affect whitefish recruitment?

Living zooplankton is considered an optimal diet for fish larvae. In the hatcheries at Lake Constance, live zooplankton collected in the lake is routinely used for the prefeeding of whitefish and pike larvae before they are stocked into the lake (RÖSCH 1988). In feeding experiments using a dry diet for whitefish larvae, zooplankton was also used as the reference diet (KLEIFELD-KRIEBITZ & RÖSCH 1987, RÖSCH & APPELBAUM 1985, RÖSCH & DABROWSKI 1986).

However, in spring 1983, it was observed for the first time that rearing whitefish larvae on living zooplankton caught in Lake Constance resulted in massive losses, whereas parallel groups fed on dry diet or *Artemia* nauplii exhibited normal behaviour, growth, and low mortality (ECKMANN 1985, ECKMANN et al. 1986, RÖSCH 1995). A few days after the onset of food intake, some larvae showed a whitish intestinal content, their body was curved, and they swam near the water surface. These larvae stopped eating. Within a week after the occurrence of the first symptoms, losses amounted up to 100%. Juvenile whitefish were not affected by this plankton. Larvae exceeding 20 mm body length stopped growing, but resumed feeding as soon as suitable plankton was provided. The symptoms remained the same in all years when this phenomenon occurred. The unsuitable plankton was only found in the spring of certain years (Fig. 4).

When the phenomenon was reported for the first time in laboratory rearing experiments, a discussion started as to whether this phenomenon only occurred in the laboratory. For the years in which the problem occurred, year-class strength of whitefish was low (Fig. 4), even when a bigger year-class was expected based on a multivariate regression model (ECKMANN et

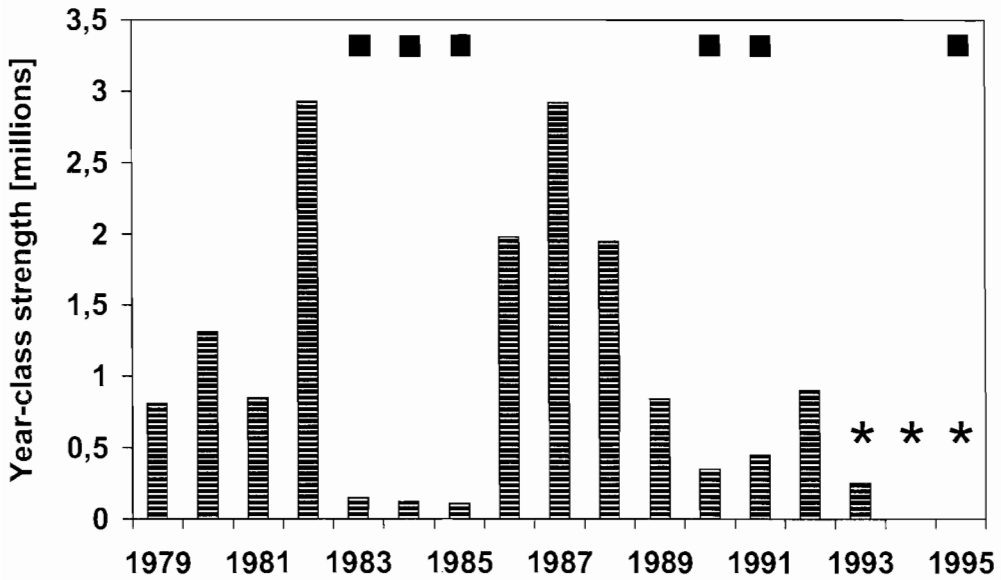


Fig. 4. Whitefish year-class strength in Lake Constance calculated by virtual population analysis. The years when "unsuitable zooplankton" occurred are indicated by ■. Year-classes that are not yet completely fished out are marked with an asterisk.

al. 1988). In May 1995, when the phenomenon occurred again, whitefish larvae caught in the lake showed the same histological damage as larvae fed on zooplankton in the laboratory (BURKHARD-HOLM & RÖSCH, unpublished data). The RNA/DNA ratios of whitefish larvae caught in the lake in spring 1991 were much lower than had been expected for larvae which exhibit normal growth, and they were comparable to the RNA/DNA ratios of larvae reared on unsuitable plankton (STEINHART & ECKMANN 1992).

The reasons for the occurrence of this phenomenon are thus far unknown (ECKMANN et al. 1986, RÖSCH 1995). However, it is the opinion of the authors that larval mortality due to unsuitable plankton has to be taken into account for explanations of whitefish year-class strength. Whether larvae of other species are also affected by unsuitable plankton in Lake Constance is unknown. Similar problems have not yet been reported for any other coregonid lake in Europe or North America.

Daily zooplankton ration of juvenile fish

Understanding zooplankton-fish interactions requires a qualitative determination of preferred food items depending on season and species of fish as well as quantitative measurements of daily rations. Larval and juvenile fish are planktivorous, but little is known about their daily rations. The methods used to determine the daily ration differ for in situ determinations (cf. ELLIOTT & PERSSON 1978) and for the determination of maximum values of food intake in laboratory experiments.

To determine maximum food intake, larvae and juveniles of whitefish and various cyprinid species (Table 2) were fed on living zooplankton under constant or varying temperatures

(MARMULLA & RÖSCH 1990, TROSCHER & RÖSCH 1991, HABERBOSCH 1992). The daily ration was determined as the difference between the amount of zooplankton added at the beginning and the amount remaining at the end of the experiment. The data were corrected according to losses in parallel tanks which contained the same amounts of zooplankton without fish (MARMULLA & RÖSCH 1990, TROSCHER & RÖSCH 1991, HABERBOSCH 1992).

For juvenile fish of all species investigated, the absolute daily ration increased with body weight. In terms of relative ration (daily ration expressed as % body dry weight), all species investigated showed a rapid increase up to a maximum value at small body sizes and a slower decrease beyond the maximum value. The body weight at which the maximum relative daily ration was attained was highest for whitefish with a dry weight of 137-231 mg (Table 2). In dace, this body weight was clearly lower, and the lowest value was observed in roach, bream, and bleak where the maximum daily ration was attained at a dry weight of 8 mg. The relative daily ration reached values of up to 40% in dace, up to 75% in whitefish, and even higher values in cyprinids (Table 2).

These results indicate the ability of juvenile fish to ingest high amounts of zooplankton within a short time. Whether zooplanktivorous fish influence zooplankton dynamics in Lake Constance is unknown at present. Due to a lack of quantitative data on the abundance of juvenile fish, a calculation of the overall "zooplankton grazing" capacity of the fish community is not possible. Even for whitefish, the number of juvenile fish cannot be calculated based on virtual population analysis because natural mortality rates of juveniles are unknown.

Ecology of Eurasian perch

The embryonic and larval phase

Eurasian perch spawn during May in the shallow littoral and sublittoral zone of Lake Constance. In the laboratory, the optimum temperature for survival from fertilization to hatching was 12-20 °C, while 16-20 °C was the optimum for survival from fertilization to the swim-up stage (WANG & ECKMANN 1994a). These temperature ranges are higher than those observed in previous studies on Eurasian and yellow perch (*Perca flavescens* Mitchill) from environments where water temperature during spawning and egg incubation was lower than in Lake Constance. Therefore, different optimum incubation temperatures were attributed to adaptations of different perch populations to the specific temperature range of their respective environment.

Table 2. Maximum daily rations for different fish species from Lake Constance.

species (temperature)	body dry weight [mg]	max. daily ration [% body dry weight]	author
dace (18 °C)	80	40	MARMULLA & RÖSCH (1990)
mixed group of cyprinids (18 °C)	8	230	MARMULLA & RÖSCH (1990)
whitefish (12 °C)	137	75	TROSCHER & RÖSCH (1991)
whitefish (various temp.)	231	79	HABERBOSCH (1992)

Two weeks after hatching in the littoral, most larvae were found in the pelagic zone, and they returned to the littoral zone as juveniles some weeks later (WANG & ECKMANN 1994b). The timing of the inshore migration was related to a decline in the pelagic zooplankton abundance which occurred at different times (early July 1990, late July 1991) in two consecutive years. As a result, juvenile perch were of different sizes at completion of the inshore migration in these two years (larger than 30 mm total length in 1990, larger than 40 mm in 1991). The hypothesis that inshore migration takes place at a certain size or ontogenetic stage was therefore rejected (WANG & ECKMANN 1994b).

At first feeding, perch larvae ingest small food items such as algae (only during the first days), rotifers, and nauplii, and they take increasingly larger items like copepods and daphnids as they advance in size (WANG 1994). When larvae were reared in the laboratory, there was a critical period during the second week after hatching, when both survival and growth were affected by temperature and food density. Under natural conditions in Lake Constance, temperature and food abundance during early embryonic and larval development of perch are highly variable from year to year. The most critical period of perch development, therefore, occurs in a stochastically fluctuating environment, and this probably affects survival of larval perch and, hence, year-class strength in an unpredictable fashion.

The juvenile and adult phase

After completion of their inshore migration, juvenile perch lived in shallow waters among stands of submerged macrophytes and fed on zooplankton and chironomid larvae (WANG & ECKMANN 1994b). When the submerged macrophytes had declined by late summer, these important hiding places for young perch disappeared, and juvenile perch switched to a different distribution and activity pattern. During the day, they aggregated in large shoals in shallow waters where food availability was low. They migrated offshore at dusk to feed on zooplankton, and returned to shallow waters again to rest on the bottom during the night. When autumnal mixing started in October, juvenile perch left the littoral zone and moved into deeper waters for overwintering (WANG & ECKMANN 1994b).

In contrast to young-of-the-year perch, older juveniles and adults lived in the sublittoral during the growing season. During the day, they stayed between the depth of 3 and 15 m, i.e., between 2 and 6 m above the thermocline (IMBROCK *et al.* 1996). Within this layer, age-classes were separated spatially, the relative number of adult perch increasing with depth. At dusk, perch of all size-classes migrated to the littoral zone where they spent the night resting on the bottom.

A hydroacoustic study along a 50 km belt near the shore demonstrated that horizontal distribution of perch was patchy in summer (IMBROCK *et al.* 1996). Between 86 and 97% of all perch were concentrated in areas with fish densities of more than 1000 fish/ha, which contributed only between 15 and 45% to the length of the surveyed shoreline. Highest densities were observed in a shallow bay and close to ports and jetties at steeper shores. Similar to juvenile perch, adults also moved into deeper waters for overwintering at the onset of autumnal mixing. In their overwintering habitat, juvenile and older perch were spatially separated.

During winter, the horizontal distribution of perch was much more homogeneous than in summer. They were located in a depth between 35 and 70 m where they performed pronounced diel vertical migrations. They rested on the bottom during the day and swam up to 25 m off the

bottom during the night. Light was the proximate cause of this regular vertical migration. Perch did not gain an energetic advantage by migrating in a homothermal water column, but they may have gained access to copepods in addition to their main diet of benthic invertebrates. It has been hypothesized that predator avoidance is the ultimate cause of diel migration: perch avoid piscivorous diving birds by resting on the bottom during the day and avoid burbot by swimming off the bottom during the night. The depth distribution of wintering perch gradually shifted to increasingly shallower depths by 0.25 m per day from January to May. As a result, perch lived at temperatures below 6 °C for about six months (ECKMANN & IMBROCK 1996).

In previous studies, the intensity of cannibalism in perch has been mainly attributed to the sizes and abundances of both young and adult perch and to the abundance of alternative food sources. However, our data suggest that cannibalism was predominantly related to distribution patterns of young and adults. During most of the year, such fish were spatially separated from each other, but as soon as they co-occurred in the same habitat, cannibalism took place. This happened at three different occasions: in early summer during the inshore migration when juveniles crossed the habitat of older perch, in autumn when juvenile perch foraged on zooplankton in offshore waters at dusk, and in early spring during the inshore migration of all age-classes after overwintering (WANG & ECKMANN 1994 b). These patterns may change considerably in the near future since the abundance of the submerged macrophyte *Potamogeton pectinatus*, which was very important as refuge for juvenile perch, is dramatically decreasing during the course of lake re-oligotrophication.

The littoral fish community

In small lakes, the littoral zone is an important fish habitat where fish abundance and diversity are often much greater compared to other lake zones (KEAST 1985, WERNER et al. 1977). Habitat and resource partitioning in the littoral zone are regarded as being key factors for the co-existence of fish species within the entire lake ecosystem. Most of these concepts, however, are based on studies of littoral fish communities in small North American lakes, and it is not yet clear if the same mechanisms are also valid for large, deep lakes. A detailed assessment with electric fishing and trammel nets of littoral fish species in Lake Constance provided new insight about the factors that control fish species composition, abundance, and distribution in a large lake (FISCHER 1994).

Spatial distribution of littoral species

The very shallow areas of a depth of less than 50 cm water were found to be of major importance for small species and juvenile fish, while submerged aquatic vegetation was not necessarily preferred as a habitat, even when available in deeper waters (FISCHER & ECKMANN 1997b). When comparing fish abundance among sites that differed in bottom slope, sediment type, bottom coverage with larger stones, and submerged macrophyte density, differences were often found to be more pronounced among depth strata than among sampling sites.

The above mentioned trend was most obvious in two benthic species, juvenile burbot (*Lota lota*) and stone loach (*Barbatula barbatula*, formerly *Noemacheilus barbatulus*) which were present in the littoral zone all year round and which always reached peak abundances in the most shallow of three depth strata (0-50, 50-150, 150-300 cm). The distribution of both species

among sampling sites was strongly correlated with the availability of gravel substrate and shelter provided by larger stones.

A strong preference for shallow waters was also observed in juvenile cyprinids (*Leuciscus leuciscus*, *Leuciscus cephalus*, *Abramis brama*) which, in contrast to the benthic species, were only found in the littoral zone during summer. The preference for shallow water of both juvenile cyprinids and benthic species is probably an adaptation to predation pressure from piscivorous fish that generally do not forage in very shallow water.

An alternative refuge from predators was provided by submerged macrophytes. These were preferred by juvenile bream as soon as this habitat became available during summer. This habitat shift was interpreted as a response to a change in bream body shape during ontogenetic development (FISCHER & ECKMANN 1997b). Juvenile bream become laterally compressed and high backed during their first summer which may lead to greater susceptibility to turbulence. This factor is of special importance in large lakes where wind forces may cause strong wave action and currents within shallow waters. Thus, both the availability of refuge areas and body shape appear to influence habitat choice in this cyprinid species.

A different distribution pattern was observed in perch and ruffe. Age 0 individuals of both species were mainly caught in deeper littoral areas within stands of submerged macrophytes, while older individuals were more abundant in open, non-vegetated areas. The occurrence of age 0 perch in the deeper littoral parts probably contributed to their greater vulnerability to predation by large eels and adult perch (RADKE & ECKMANN 1996) compared to juvenile cyprinids, which were not available to these predators as long as they remained in shallow waters.

Seasonal changes in species distribution

In addition to species-specific distribution patterns, total fish abundance, biomass, and species richness in the littoral zone varied significantly over the year (FISCHER & ECKMANN 1997a). Between-month comparisons revealed that in the spring-summer phase (May to September) abundance values were significantly higher compared to the autumn-winter phase (October to April). Separate canonical correlation analyses showed that different habitat variables influence the littoral fish community during the two seasonal phases. During the spring-summer phase, total fish abundance, biomass, and species richness were highly correlated with water temperature. When the data were compensated for the effect of water temperature, the importance of substrate coverage, lake level, and water depth became apparent. During the autumn-winter phase, however, water temperature and lake level were less important for fish abundance and biomass. During this phase, when the fish community was dominated by the benthic species burbot and stone loach, the habitat variables mean stone size, substrate type, and stone size range were most strongly correlated with fish abundance and biomass.

These results demonstrated that fish assemblages in a large lake are not dependent on a single factor, such as the often cited presence or absence of submerged macrophytes. The littoral fish community in large lakes is likely controlled by a much more complex set of factors as compared to small lakes. Since we still do not precisely know which temporal and spatial scales are important for fish community structure in the littoral zone of large lakes, our knowledge of habitat partitioning and resource use in these communities is still limited. The development of adequate field techniques that allow sampling with high temporal and spatial resolution, combined with analyses of single species-habitat relationships in the laboratory or in mesocosm

experiments, seems to be the most promising approach to the understanding of the complex in situ distribution and abundance patterns of littoral fish communities in large lakes.

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