Ann. Zool. Fennici 33: 489–494
Helsinki 28 November 1996
ISSN 0003-455X
© Finnish Zoological and Botanical Publishing Board 1996

Piscivorous eels in Lake Constance: can they influence year class strength of perch?

Robert J. Radke & Reiner Eckmann

Radke, R. J. & Eckmann, R., Institute of Freshwater and Fish Ecology, Department of Biology and Ecology of Fish, Mueggelseedamm 310, D-12587 Berlin, Germany

Received 21 August 1995, accepted 28 February 1996

Research on predator-prey relationships in the littoral zone of Lake Constance showed that eels (*Anguilla anguilla* (L.)) were the most numerous piscivorous predators in the shallow water zones up to 3-metres depth in 1992. From July on fish was the most important component of the diet of eels. Perch (*Perca fluviatilis* L.), burbot (*Lota lota* (L.)) and bream (*Abramis brama* (L.)) were thwe most frequently consumed fish. As 61% of all identifiable fish the eels had consumed were perch, an attempt was made to estimate the impact of eel predation on the young-of-the-year (y-o-y) of the perch population. Consumption by the total eel population never exceeded the amount of perch fry consumed by adult, cannibalistic perch estimated in other studies, but it seems possible that eel predation could have an adverse influence on weak year classes. Further reoligotrophication of the lake might lead to even higher fish consumption by the eels due to declining benthic production and consequent increased predation pressure.

1. Introduction

Both species of perch (*Perca fluviatilis* L. and *Perca flavescens* Mitchill) are of great commercial and recreational interest (cf. Thorpe 1977); this has lead to a desire to understand the population dynamics of these two closely related species. Many studies have dealt with the problem of determining factors influencing year-class strength (e.g. LeCren 1955, Tesch 1955, Tarby 1974, Craig & Kipling 1983, Treasurer 1993). Despite evidence from experimental and field studies, that physical factors are important in influencing the recruitment success of perch (LeCren 1958, Clady & Hutchinson 1975, Hokansen & Kleiner 1975, Wang & Eckmann 1994a), predation by other species (Noble 1972, Kelso & Ward 1977, Nielsen 1980, Hartmann & Margraf 1993) or by cannibalistic perch (e.g. Popova & Sytina 1977, Treasurer *et al*. 1992) have been recognised as major factors structuring perch populations.

Perch in Lake Constance also show cannibalistic behaviour (Nümann 1939, Hartmann 1975), which has changed from a high rate of cannibalism prior to the eutrophication of the lake, to a low rate at the peak of eutrophication (Amann 1975, Krämer & Baroffio 1988), when even perch > 15 cm fed on zooplankton. Consumption by adult, cannibalistic perch has been quantified by Krämer and Baroffio (1988), but the effect of other potential predators is unknown. The aims of the present study were to determine the relative abundances of the piscivorous predators in the littoral zone of the lake, to quantify the food consumption by the most important of these predators and estimate the influence of predation on perch recruitment success in Lake Constance.

2. Material and methods

2.1. Sampling and diet analysis

Lake Constance is a large, deep, mesotrophic prealpine lake in southern Germany, with a surface area of 476 km^2, maximum depth of 252 m and a mean depth of 100 m. The four sampling sites in the northwestern part of the lake were representative of the different main types of the littoral zone to be found in the lake. Sampling took place biweekly from the end of April until mid-October in 1992. The following fishing gear was used: monofilament gill nets (32, 44, 50 mm stretched bar, length: 40 m, height: 2 m), trammel nets (10/150 mm, length: 10 m, height: 1 and 2 m), a fyke net, a trap net and electrofishing gear (EFKO: 7 kW, 300–600 V). Nets were exposed in the littoral zone from 1 to 3 m depth from one hour before sunset till one hour after sunrise, fyke and trap nets were emptied during the same morning. Electrofishing was carried out by wading along a 100 m stretch shoreline up to a depth of 1 m. Sampling in macrophyte beds, again by using electrofishing gear was done from a moving boat travelling for 30 min at low speed (< 0.5 m/s). The fish were killed, cooled with ice and immediately processed after completion of fishing to prevent further digestion of prey. Length of fish caught was measured to the nearest 0.5 centimetre (standard length (SL) and total length (TL), for eels (*Anguilla anguilla* (L.)) only total length). Digestive tracts were removed for analysis and preserved in 5% formalin-solution. Stomach contents were analysed under a stereoscopic microscope. Invertebrates other than insects were determined to species level, insects to order level. Irregularly occurring taxa, especially those of terrestrial origin were grouped as *various*. Fish were determined to species level and in the case of advanced digestion identified with the help of a bone collection (opercular, pharyngeal and vertebral bones).

For further quantitative analysis the method of reconstructed weight (Popova 1967) was applied. Prey items were counted, length was measured to the nearest millimetre and dry weight (DW, g) was then back-calculated from length-weight relationships. Lengths of partly digested prey items were back-calculated from hard part-length relationships (e.g. head capsule width, length of pharyngeal bone) and weight reconstructed as mentioned above. Length-weight and hard part-length relationships were obtained from literature if possible (Edmondson 1971, Adcock 1979, Geller 1989, Meyer 1989, Mehner 1990, Brendelberger pers. com.), or they were calculated from our own data for roach (*Rutilus rutilus* (L.)), bream (*Abramis brama* (L.)), dace (*Leuciscus leuciscus* (L)), chub (*Leuciscus cephalus* (L.)) and burbot (*Lota lota* (L.)). Hirudinea from the lake were sorted into suitable size classes, dried at 60°C, weighed and an average weight per size class was calculated.

2.2. Eel population estimate

As no estimates of the former or current size of the Lake Constance eel population were available, the size of the virtual eel population in 1992 was estimated with the help of data from fisheries statistics (Klein 1992), length at age data (Berg 1988) and our own length frequency data. The estimate was based on following assumptions:

a) Recruitment is constant for every cohort: This assumption is based on the continuous stocking of the lake with elvers

Table 1. Estimation of virtual 1992 eel population size in Lake Constance.

Age class	Length class (cm)	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	
8–9	48.2–52.9	12.3										
9–10	52.9–57.5	17.3	17.3									
10–11	57.5–62.2	21.4	21.4	21.4								
11–12	62.2–66.8	25.4	25.4	25.4	25.4							
12–13	66.8–71.4	11.4	11.4	11.4	11.4	11.4						
13–14	71.4–76.1	5.9	5.9	5.9	5.9	5.9	5.9					
14–15	76.4–80.7	1.9	1.9	1.9	1.9	1.9	1.9	1.9				
15–16	80.7–85.3	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2			
16–17	85.3–90.0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5		
17–18	90.0–94.6	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.7	**Total**
	Sum	100.0	87.7	70.4	49.0	23.6	12.2	6.3	4.4	2.2	1.7	**357.5**

=> virtual population size in 1992 is 3.575 times the catch in 1992.

and a resulting yield exhibiting little variance (average yield 1981–1990: 14 915 kg ± 3 168 kg (*S.D.*).

b) Natural mortality = 0%: This assumption seemed reasonable as mortality rates of eels in Lake Constance are not known and our estimate would tend to rather under- than overestimate the population size.
c) Fishing mortality of a specific age (length) class is equivalent to its proportion in the annual catch calculated from our length frequency data, e.g. the length class 48.5–52.9 cm which corresponds to eels from eight to nine years old, made up 12.3% of the total catch.
d) Lake Constance eels reach the harvestable size of 50 cm when they are approximately eight years old.
e) The population is dominated by resident female eels, which often stay in the lake for more than eighteen years (Berg 1988). As a result more than ten cohorts may contribute to the annual yield.

The total estimated, "harvestable" virtual eel population of 1992 was then calculated by adding the predicted catch in each subsequent year (which is the number of eels caught in the preceding year minus the number of eels in the youngest length class remaining) to the number of eels caught in 1992 (the calculation process is presented in Table 1). Maximum harvestable length class was assumed to be 90.0–94.6 cm, corresponding to eels of 17 to 18 years old. The average weight of an eel caught by commercial fishermen was 450 g. The annual yield of 14 915 kg is thus equivalent to approximately 33 000 eels caught annually. The virtual population of eels larger 48 cm would then be 3.575 times greater than this. To the estimated 118 000 harvestable eels living in the lake were added the 30.7% of the eel population which is smaller than 48 cm (from our own length frequency data), which results in a total estimate of approximately 170 000 eels. This is certainly an underestimate because: — a: natural mortality is disregarded, — b: number of silver eels leaving the lake is unknown, and — c: number of eels not appearing in the official catch statistics is unknown.

3. Results

3.1. Catch and diet analysis

Few fish were present in the littoral zone of Lake Constance in April but arrived in May and left it in October to move back to deeper water. During the whole time of the survey, eels were the most numerous predators (Table 2). No other predatory fish species except perch and chub were caught in larger numbers. Predatory species like pike (*Esox lucius* L.), pike-perch (*Stizostedion lucioperca* (L.)) and burbot were weakly represented in the littoral zone. Although the different fishing gear used does actually not allow direct comparisons of the catch results, we believe that our results are representative of the species frequencies in the lake, as fisheries statistics of the past ten years (Klein 1992) show very similar results. Only pelagic coregonids and perch (inhabiting the sublittoral zone in summer) show higher relative yields as compared to our catches. Further results presented in this paper thus concentrate on our findings of the eel diet analysis.

Identified prey items consumed by the eels revealed a great diversity of prey organisms, which varied throughout the survey depending on season and eel size. Despite the broad variety of consumed prey, neither planktonic organisms nor aquatic oligochaets could be found. On the other hand prey items of terrestrial origin were regularly encountered in small numbers (e.g. earthworms, caterpillars). Plant debris was thought to have been consumed accidentally, as it only appeared in small quantities

Table 2. Number of fish caught per species and month in the littoral zone of Lake Constance in 1992, with length range (*TL*).

Month	Eel	Perch	Chub	Pike	Burbot	Pike-perch
Apr.	1	–	–	–	1	–
May	69	31	6	1	4	1
Jun.	102	29	4	–	–	–
Jul.	128	36	8	5	1	–
Aug.	121	37	6	4	–	1
Sep.	70	18	3	3	2	–
Oct.	4	3	1	–	–	–
Total	495	154	28	13	8	2
	Length range (*TL*, cm)					
	21–98	13–30	15–55	16–80	14–36	20 + 30

Table 3. Frequency of occurrence (*F*) and proportion of biomass (*B*) of diet component per month in eel stomachs (Lake Constance 1992, only stomachs with contents are considered).

Month	Fish		Invertebrates		Number of stomachs examined
	F(%)	*B*(%)	*F*(%)	*B*(%)	
May	28.1	96.1	81.2	3.9	32
Jun.	23.0	92.5	82.4	7.5	74
Jul.	61.3	94.2	71.2	5.8	80
Aug.	78.0	98.9	53.6	1.1	82
Sep.	82.9	99.9	24.4	0.1	41
Oct.	100.0	100.0	–	–	2
Total	56.3	97.0	63.6	3.0	311

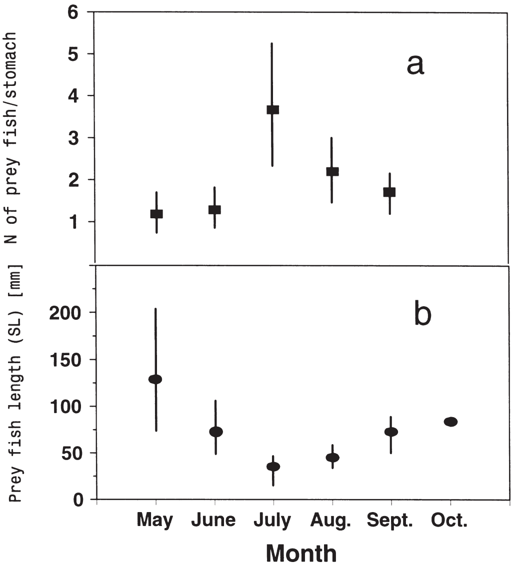

Fig. 1ab. — a: Average number of prey fish per eel stomach in a month (± *S.D.*), — b: Monthly average (median) length (*SL*) of prey fish consumed by eels in Lake Constance, 1992 (bars show 95%-confidence levels of median)

and always with animal remains. During the growing season the proportion of the eel population (frequency of occurrence; only feeding fish considered) feeding on fish rose continually from under 30% in May and June to more than 80% in September. Correspondingly the monthly proportion of fish biomass in the eel diet rose to nearly 100% in August and September (Table 3). This sharp rise is a result of the abundant y-o-y fish which became available in the littoral zone from July onwards. This fact becomes evident from analysis of the monthly mean prey fish length (*SL*) and the average number of fish per stomach of eels feeding on fish (Fig. 1). Mean prey fish length fell from over 120 mm in May to under 40 mm in July and then rose steadily until October, while the average number of prey fish per eel stomach rose from approximately one fish in May and June to nearly four fish per stomach in July falling again until October. Out of eight prey fish species identified in the stomach contents, perch was the most important contributor to eel diet both numerically and in terms of biomass (Table 4). Burbot was also frequently consumed and accounted for a third of the total fish biomass eaten by the eels. All other species (bream, ruffe (*Gymnocephalus cernua* (L.)), dace, roach and chub together made up less than 20% of all fish eaten and less than 4% of fish biomass consumed.

3.2. Predation estimate

To estimate the number of y-o-y perch consumed by the eel population in 1992, consumption was modelled using the diet analysis data, water temperature data and stomach retention times from Popova (1978). The number of perch consumed per month was calculated by assuming a stomach retention time (complete digestion and new filling) of three days in May and October (average temperature 13°C, 1 m below surface), of two days in June and September (average temperature 17°C) and one day in July and August (average temperature 23°C). Only that proportion of the whole eel population (including eels with empty stomachs) actually feeding on y-o-y perch was considered. We then calculated a lower estimate with the average number of y-o-y perch per stomach and month minus 1 *S.D.*, an average estimate and a higher estimate with the average number of y-o-y perch per stomach and month plus 1 *S.D*. Number of perch consumed in October was calculated using data from September as sample size in October was too small. In 1992 the total eel population in Lake Constance had thus consumed: 2.8 million (lower estimate), 9.9 million (average), 17.0 million (higher estimate), y-o-y perch until the end of October.

4. Discussion

Despite numerous studies on the diet of the European eel (cf. Tesch 1983, Deelder 1984) juvenile

Table 4. Number, proportion of fish biomass and length range (*SL*) of fish species consumed by eels in Lake Constance, 1992.

Fish species	*n*	Proportion of biomass (%)	Length range (mm)
Perch	250	61.7	25–135
Burbot	79	34.5	18–234
Bream	64	1.3	12–65
Ruffe	6	1.5	35–70
Dace	5	0.5	30–57
Roach	3	0.3	18–53
Chub	2	0.2	42 + 50

perch have so far only been reported from the Tjeukemeer (Netherlands) (De Nie 1987) and Lake Constance (Berg 1988) as a major contributor to eel diet. It remains unknown whether this is a consequence of ecosystem specific conditions or simply an effect of scientific interests. Juvenile perch seem to have two characteristics which render them vulnerable in two ways as prey for a nocturnal predator inhabiting the littoral zone such as the eel: firstly they move into the littoral zone after the pelagic phase and stay there from July until late Autumn (average 5.5 individuals per 100 m^2 from July to September (Fischer 1994)) and secondly they settle on the bottom after dusk and remain there inactively throughout the night (Wang & Eckmann 1994b). This might also be an explanation for low eel predation on cyprinids, which also occur in large numbers (average 45 individuals per 100 m^2 (Fischer 1994)) in the same habitat, but for which the behaviour to rest on the bottom at night has not yet been reported.

Perch population studies in Lake Constance are of great importance, as perch constitute the main commercial fish landings apart from whitefish (*Coregonus* sp.). Analysis of factors which affect recruitment success and their correlation with resulting cohort strengths has lead to several single and multi factor models which have been continuously modified according to new scientific findings (Hartmann 1981, 1982, Staub *et al*. 1987, Hartmann & Blank 1989). Common to all recent models is the assumption that predation by cannibalistic older perch is a major factor influencing recruitment success (Hartmann 1992, Tyutyunov *et al*. 1993, Staub *et al*. 1995). Krämer and Baroffio (1988) estimated from diet analysis data that the adult perch population in Lake Constance probably consumes 10 to 100 times its own number of the y-o-y perch stock annually. Correspondingly an average population of 5.2 million cannibalistic perch (data from 1971–1992, Staub *et al*. 1995) would consume from 52 to 520 million y-o-y perch. In contrast the average annual consumption by the eel population is less (9.9 million), on this basis eels would only consume between 1.9% and 19% of the number of y-o-y perch consumed by cannibalistic perch. In years with a small cannibalistic perch population (< 1 million), eel predation might even be as high as predation by adult perch. In 1992 the cannibalistic perch population was approximately 4.5 million, which means that 45 to 450 million y-o-y perch were consumed, and consumption by eels lay between 2.2% to 22% of the amount consumed by adult perch. The predicted virtual population size of the 1992 perch year-class is 2.5 million individuals (the cohort being only partly fished out). In this case the eel population had consumed approximately four times the amount of perch actually caught by the lake fishery. The interesting comparison of our consumption estimates to those of a bioenergetics model was not possible as published data on eel bioenergetics essential for such a calculation were insufficient.

From our findings we conclude, that eel predation might have a significant impact on weak year-classes of the Lake Constance perch population. It is important to note though, that low prey fish density might result in lower predation rates on y-o-y fish due to selective usage of other prey. On the other hand predation pressure could even be enhanced if the well documented oligotrophication (Tilzer *et al*. 1991) leads to a decline in zoobenthos production. Thus, further stocking with large numbers of eel elvers (> 0.5 million), as happened in the past (Berg 1988), justifies the consideration of eel predation in the newest perch population simulation models.

Acknowledgements. We would like to thank Mike Ladle for his valuable comments on the manuscript, Alfred Sulger for his invaluable assistance in all fishing operations and Miriam Schmid for her kind advice and help in laboratory work. This study was supported by the Deutsche Forschungsgemeinschaft within the special collaborative program (SFB 248) 'Cycling of matter in Lake Constance'.

References

Adcock, J. A. 1979: Energetics of a population of the isopod Asellus aquaticus: Life history and production. — Freshwater Biology 9: 343–355.

Amann, E. 1975: Nahrungsumstellung und Zunahme der Barsche (Perca fluviatilis) im Bodensee–Obersee infolge der Eutrophierung. — Österr. Fisch. 28: 72–76.

Berg, R. 1988: Der Aal im Bodensee. Axiology und Landwirtschaft (1). — Verlag Josef Margraf, Gaimersheim.

Clady, M. & Hutchinson, B. 1975: Effects of high winds on eggs of yellow perch Perca flavescens in Oneida Lake, New York. — Trans. Am. Fish. Soc. 104: 524–525.

Craig, J. F. & Kipling, C. 1983: Reproduction effort versus the environment; Case histories of Windermere perch, Perca fluviatilis L., and Pike, Esox lucius L. — J. Fish Biol. 22: 713–727.

De Nie, H. W. 1987: Food, feeding periodicity and con-

sumption of the eel Anguilla anguilla (L.) in the shallow eutrophic Tjeukemeer (The Netherlands). — Arch. Hydrobiol. 109: 421–443.
Deelder, C. L. 1984: Synopsis of biological data on the eel (Anguilla anguilla). — FAO Fisheries Synopsis No. 80, Rome.
Edmondson, W. T. 1971: Methods for processing samples and developing data. — In: Edmondson, W. T. & Winberg, G. G. (eds.), A manual on methods for the assessment of secondary productivity in freshwaters, IBP Handbook No. 17: 127–169.
Fischer, P. 1994: Litorale Fischbiozönosen in einem großen See – der Bodensee. — Dissertation, Universität Kiel.
Geller, W. 1989: The energy budget of two sympatric Daphnia species in Lake Constance: Productivity and energy residence times. — Oecologia 78: 242–250.
Hartman, J. 1975: Der Barsch (Perca fluviatilis) im eutrophierten Bodensee. — Arch. Hydrobiol. 76: 269–286.
— 1981: Prognose der Jahrgangsstärke beim Barsch Perca fluviatilis des Bodensees. — Fischwirt 31: 27–28.
— 1982: Fangprognosen für den Bodensee. — Fischwirt 32: 25–26.
— 1992: Kannibale Bodenseebarsch. — Österr. Fisch. 45: 51–54.
Hartman, K. J. & Margraf, F. J. 1993: Evidence of predatory control of yellow perch (Perca flavescens) recruitment in Lake Erie, USA. — J. Fish Biol. 43: 109–119.
Hartmann, J. & Blank, S. 1989: Jahrgangsstärke (Rekrutierung) beim Barsch (Perca fluviatilis) des Bodensees. — Österr. Fisch. 42: 160–164.
Hokanson, K. E. F. & Kleiner, C. F. 1975: Effects of constant and rising temperature on survival and development rates of embryonic and larval yellow perch, Perca flavescens (Mitchill). — In: Blaxter, J. H. S. (ed.), The early life history of fish: 437–448.
Kelso, J. R. M. & Ward, F. J. 1977: Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. — J. Fish. Res. Board Can. 34: 1655–1669.
Klein, M. 1992: Die Fischerei im Bodensee–Obersee im Jahre 1990. — Fischer und Teichwirt 1: 10–12.
Krämer, A. & Baroffio, C. 1988: Nahrungswahl und Kannibalismus beim Barsch (Perca fluviatilis) des Bodensee–Obersees. — Schweizer Fischereiwissenschaft 5: 3–4.
LeCren, E. D. 1955: Year to year variation in the year-class strength of Perca fluviatilis. — Verh. Int. Ver. Limnol. 12: 187–192.
— 1958: Observation on the growth of perch (Perca fluviatilis L.) over twenty-two years with special reference to the effects of temperature and changes in population density. — J. Anim. Ecol. 27: 287–334.
Mehner, T. 1990: Zur Bestimmung der Beutefischarten aus Fragmenten der Wirbelsäule bei der Nahrungsanalyse (Osteichthyes, Teleostei). — Zool. Anz. 3/4: 210–222.
Meyer, E. 1989: The relationship between body length parameters and dry mass in running water invertebrates. — Arch. Hydrobiol. 117: 191–203.
Nielsen, L. A. 1980: Effect of walleye (Stizostedion vitreum vitreum) predation on juvenile mortality and recruitment of yellow perch (Perca flavescens) in Oneida Lake, New York. — Can. J. Fish. Aquat. Sci. 37: 11–19.
Noble, R. L. 1972: Mortality rates of walleye fry in a bay of Oneida Lake, New York. — Trans. Am. Fish. Soc. 101: 720–723.
Nümann, W. 1939: Untersuchungen über die Biologie einiger Bodenseefische in der Uferregion und den Randgebieten des freien Sees. — Z. Fisch. 37: 637–688.
Popova, O. A. 1967: The 'predator-prey' relationship among fish (a survey of soviet papers). — In: Gerking, S. D. (ed.), The biological basis of freshwater fish production: 359–376.
— 1978: The role of predaceous fish in ecosystems. — In: Gerking, S. D. (ed.), Ecology of freshwater fish production: 215–249.
Popova, O. A. & Sytina, L. A. 1977: Food and feeding relations of Eurasian perch (Perca fluviatilis) and pikeperch (Stizostedion lucioperca) in various waters of the USSR. — J. Fish. Res. Board Can. 34: 1559–1570.
Staub, E., Büttiker, B. & Krämer, A. 1987: Grundlagen für Modellsimulationen zur Bewirtschaftung des Barsches (Perca fluviatilis L.) im Bodensee. — Schriftr. Fisch. Bundesamt Umweltschutz No. 40. Bern, Switzerland.
Staub, E., Gerster, S. & Krämer, A. 1995: Bewirtschaftung des Barsches (Perca fluviatilis L.) im Bodensee-Obersee. Teil III: Folgerungen für die Bewirtschaftung. — Mitteilungen zur Fischerei 54: 129–148.
Tarby, M. J. 1974: Characteristics of yellow perch cannibalism in Oneida Lake and the relation to first year survival. — Trans. Am. Fish. Soc. 103: 462–471.
Tesch, F.-W. 1955: Das Wachstum des Barsches (Perca fluviatilis L.) in verschiedenen Gewässern. — Z. Fisch. 4: 321–420.
— 1983: Der Aal: Biologie und Fischerei. — Verlag Paul Parey, Hamburg & Berlin.
Thorpe, J. E. 1977: Synopsis of biological data on the perch Perca fluviatilis Linnaeus, 1758 and Perca flavescens Mitchill, 1814. — FAO Fisheries Synopsis No. 113, Rome.
Tilzer, M. M., Gaedke, U., Schweizer, A., Beese, B. & Wieser, T. 1991: Interannual variability of phytoplankton productivity and related parameters in Lake Constance: No response to decreased phosphorus loading? — J. Plankton Res. 13: 755–777.
Treasurer, J. W., Owen, R. & Bowers, E. 1992: The population dynamics of pike, Esox lucius and perch, Perca fluviatilis in a simple predator-prey system. — Env. Biol. Fish. 34: 65–78.
Treasurer, J. W. 1993: The population biology of perch, Perca fluviatilis L., in simple fish communities with no top piscivore. — Ecol. Freshwat. Fish 2: 16–22.
Tyutyunov, Y., Arditi, R., Büttiker, B., Dombrovsky, Y. & Staub, E. 1993: Modelling fluctuations and optimal harvesting in perch populations. — Ecol. Model. 69: 19–42.
Wang, N. & Eckmann, R. 1994a: Effects of temperature and food density on egg development, larval survival and growth of perch (Perca fluviatilis L.). — Aquaculture 122: 323–333.
— 1994b: Distribution of perch (Perca fluviatilis L.) during their first year of life in Lake Constance. — Hydrobiologia 277: 135–143.