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Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton

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The growth, diet and feeding strategy of five phytophil or phytolithophil species of Cyprinidae from the littoral habitats of Lake Balaton were investigated by examining their scales and foregut contents. The relationships between the total anterior radii of scales and the standard lengths were represented best by a power function for white bream *Blicca bjoerkna*, and linear functions for common bream *Abramis brama*, roach *Rutilus rutilus* and wild goldfish *Carassius auratus gibelio*, respectively. The backcalculated mean lengths for the first age groups of common bream, white bream and roach did not differ statistically from those obtained by direct observation on 0 group fish in late November 1995. Compared to other waters, common bream grows slowly, wild goldfish and roach rapidly, while the growth rate of white bream can be considered of medium speed in Lake Balaton. Common bream showed a generalized feeding pattern, consuming mainly chironomid larvae, detritus and *Corophium curvispinum*. Roach showed a clear shift between specialization for *Dreissena* and algae. Despite the dense population of *D. polymorpha* in the lake, the significance of the herbivorous adaptation of roach has not yet been made clear. Wild goldfish consumed mainly detritus but, in the open water region, it shifted to zooplankton. White bream preyed chiefly on *D. polymorpha*, but showed a mixed feeding pattern and utilized most of the available food resources. Carp had the most specialized feeding strategy and preyed mainly on *D. polymorpha*. According to the discriminant analysis, the five cyprinids exhibited significant food resource partitioning.

Key words: growth; feeding strategy; diet shift; resource partitioning; Cyprinidae; littoral zone.

INTRODUCTION

Lake Balaton is the largest shallow lake in Central Europe (surface area 593 km^2, average depth 3.2 m). Its trophic state varies from meso- to eutrophic along the longitudinal axis of the lake. During the last four decades, temporal variations in external nutrient loadings and primary productivity have resulted in profound environmental changes and alterations of its fish fauna. The natural shoreline (reed grass stands) has been limited to 110 km. The remaining shoreline (105 km) has been protected artificially with stones or concrete walls, thereby reducing the original spawning sites and nursery areas for fish. The water level has been regulated and its annual fluctuation does not reach more than 50 cm. Lake Balaton is an important tourist centre. Beside commercial fisheries, more than 100 000 sport fishermen visit the lake annually. Consequently, heavy human pressure and cultural eutrophication have changed the biological structure and functioning of the whole lake. Further information on the limnology of Lake Balaton is given by Bíró (1984).

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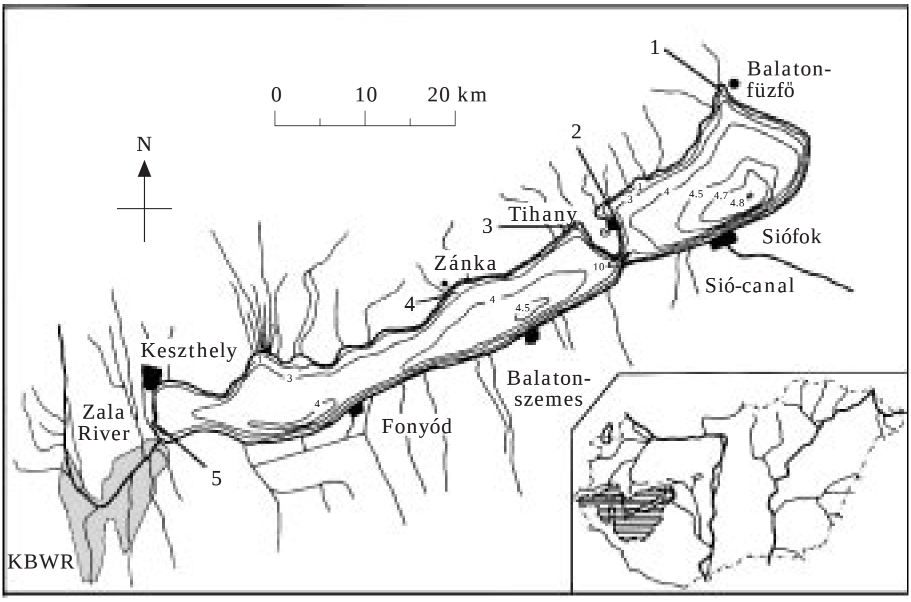

FIG. 1. Location of Lake Balaton in Hungary with indication of its drainage area (shaded). Sampling areas in the littoral zone of Lake Balaton: 1, Balatonfüzfö-bay; 2, Tihany; 3, Bozsai-bay; 4, Zánka; 5, area above the mouth of the Zala River.

Various studies have dealt with the growth and the diet of common bream *Abramis brama* (L.), the most common fish species in the open water areas of Lake Balaton (Pénzes, 1966; Bíró & Garádi, 1974; Tátrai, 1980; Bíró, 1991; Bíró *et al*., 1991; Dauba & Bíró, 1992). Recently, Simonian *et al.* (1995) described the diet and diet preference of three young-of-the-year (YOY) cyprinids in the littoral zone of Lake Balaton. However, the feeding and growth of the larger cyprinids in the littoral zone have been studied little. In contrast to the open water region, where common bream dominates, the fish fauna in the littoral zone consists mainly of white bream *Blicca bjoerkna* (L.), roach *Rutilus rutilus* (L.), carp *Cyprinus carpio* L. and wild goldfish *Carassius auratus gibelio* (Bloch). A recent study gave an overview of the long-term temporal variations that have taken place in the structure, dynamics, biomass and yield of 14 fish species, as well as in their food webs (Bíró, 1997). As the littoral fish species assemblages respond quickly to external effects, the aim of this paper was to study the growth, diet and feeding strategy of five coexisting littoral cyprinids in Lake Balaton.

MATERIALS AND METHODS

STUDY AREA

Samples were taken at 1–3·5 m depth from five sampling sites of the littoral zone along the Northern shoreline of the lake, in 1995–1996. These sites are located in various bays covered by *Phragmites australis* (Cav.) Trin. ex Stuedel stands (Fig. 1).

GROWTH STUDIES

For age and growth studies, fish were collected between March and November 1995. Adult specimens were caught with gillnets from the NE basin of Lake Balaton. 0 group fish were sampled by liftnet (mesh-size 5 mm) and dragnet (mesh-size 1·5 mm). Specimens of wild goldfish were obtained also from the commercial catches by an eel trap set in the mouth of the Sió-canal, the only outlet of the lake. Altogether 124 common bream (L = 28–325 mm, age groups 0+ to 10+), 167 white bream (L = 38–329 mm, age groups 0+ to 14+), 162 roach (L = 19·8–282 mm, age groups 0+ to 14+) and 340 wild goldfish (L = 61–314 mm, age groups 1+ to 7+) were collected for growth examinations. Standard length (L) was measured and length–weight relationships were calculated according to a power function. To study the early scale formation of fish, 8–20 mm common bream and roach larvae and juveniles were collected. To check the determination of the first year's growth, wintering YOY common bream, white bream and roach were sampled by liftnet in late November 1995 (20 individuals of each species). The differences between the direct measurement and the back calculated data for 0 group fish were assessed using Student's t-test.

Age determination and back calculation of growth were based on the annual ring structure of scales. Ten to 15 scales were taken from the left side of the body above the lateral line and below the insertion of the dorsal fin. After being cleaned in water, the scales were selected and dry mounted between slides. The annual rings and total radii of scales were measured in the anterior direction at 10 to 20 × magnification, using a profile projector. Relationships between the standard lengths of fish and the total anterior radii of scales were estimated using functional regressions (Ricker, 1975). The standard lengths were then backcalculated individually (Fraser, 1916, in Ricker, 1975). For the description of growth in length, von Bertalanffy's growth model (von Bertalanffy, 1957, in Ricker, 1975) was fitted to average backcalculated data. Instantaneous coefficients of growth in weight (G) were calculated using the Ricker (1975) model.

For the length–frequency assessments, multimesh gillnet samples taken in 1996 were standardized with PASGEAR computer software package (Kolding, 1996). The standardization was carried out for gear size (standard unit is a 20-m length of each gillnet panel), time (standard setting time is 120 min) and gear selectivity. Gear selectivity was assessed using a skew-normal function (Helser *et al*., 1991, 1994).

DIET ANALYSIS

Fish diet was studied by foregut content analysis. Collections were carried out from 4 April to 6 November 1996. Fish were caught by using multimesh gillnets (mesh-sizes 11, 14, 18, 24, 30, 40, 50, 65 and 80 mm), and by electrofishing (Smith-Root, Inc., Model 12 B electrofisher 400 W, 300–700 V, 60–80 Hz and 0·5–2 ms impulse width). Fishing was done in the most intense feeding periods of fish, during the morning and evening.

Gillnets were checked every half-hour or hour, depending on the water temperature, after which fish were measured immediately (standard length and weight were recorded) and dissected, their foregut being preserved in 10% formalin solution. Electrofishing was carried out for 30 to 60 min and the same treatment applied.

For the diet analyses, only larger (>14–15 cm) fish specimens were used. Young fish, which are largely zooplanktivorous, are not included in this paper. In total, 225 common bream (size range 55–950 g), 124 white bream (size range 93–310 g), 98 roach (size range 48–432 g), 105 wild goldfish (size range 442–1332 g) and 130 carp (size range 268–6170 g) were examined.

Gut contents were examined under a binocular microscope and food items were counted and identified to at least family, but sometimes to species, level. Some prey categories were combined into broader taxonomic or functional categories for quantitative comparisons. Food components were weighed when possible. In other cases, individual biomass was assessed according to length groups of the different prey taxa, or else the volumetric method was applied. Conversion of mean length to mean weight was done using length–weight relationships calculated for each prey taxon. Frequency of occurrence and biomass per cent of various prey taxa were determined according to Hyslop (1980).

Feeding strategy of fish was analysed following the graphical method of Costello (1990), modified by Amundsen *et al*. (1996). The terms between-phenotype (different

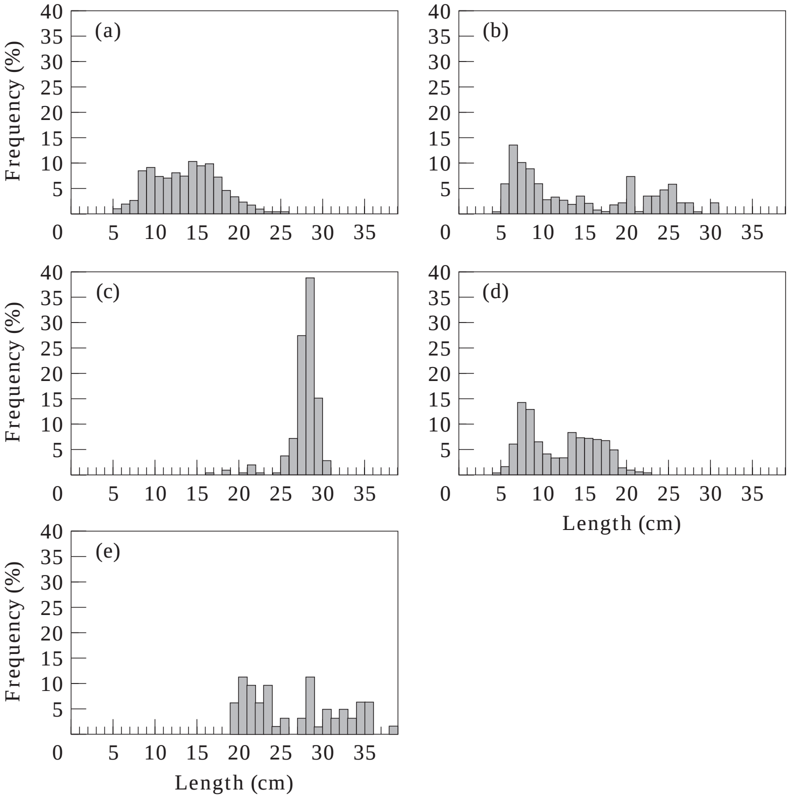

FIG. 2. Length–frequency distributions of cyprinids caught in Lake Balaton in 1996, standardized multimesh gillnet data. (a) Roach (n = 1538); (b) common bream (n = 1763); (c) wild goldfish (n = 211); (d) white bream (n = 2253); (e) carp (n = 63).

individuals specialized in different food types) and within-phenotype (most individuals consumed many food types) were used according to Amundsen *et al.* (1996) to describe the origin of the diet diversity.

ANALYSES OF FOOD NICHE BREADTH AND DIET DIFFERENCES

Diversity of diet was estimated using the standardized version of Levins' (1968) index of niche-breadth (B) and the gravimetric dietary proportions for 25 aggregated resource categories. Discriminant analysis was applied to the individual weight percentages of the 15 most significant food items as discriminant variables. The distinctiveness of species diet was measured directly by means of the Wilk's λ-criterion. The χ^2-test for Wilk's λ was used to test the significance of the overall difference between species-diet centroids. The relative importance of the original variables in separating species-diets was gauged by standardized weights (Tatsuoka, 1988).

RESULTS

SIZE DISTRIBUTION

The wild goldfish stock was dominated by large sized 6+- to 8+-year-old specimens in 1996 (Fig. 2). Younger age groups were scarcely represented in the littoral zone of Lake Balaton. Individuals aged 1+ or 2+ were found only in the eel trap catches, but in small numbers in 1995. The asymmetry in the size distribution of the introduced carp stock might be caused by the lack of natural recruitment.

LENGTH–WEIGHT RELATIONSHIPS

The length–weight relationships showed nearly isometric growth patterns for common bream ($W = 10^{-4{\cdot}702}L^{3{\cdot}005}$, $n = 126$, $r = 0{\cdot}997$), while for white bream ($W = 10^{-5{\cdot}212}L^{3{\cdot}267}$, $n = 146$, $r = 0{\cdot}997$), roach ($W = 10^{-4{\cdot}914}L^{3{\cdot}129}$, $n = 141$, $r = 0{\cdot}999$) and wild goldfish ($W = 10^{-4{\cdot}893}L^{3{\cdot}168}$, $n = 340$, $r = 0{\cdot}998$) these proved to be allometric.

GROWTH IN LENGTH AND WEIGHT

The relationship between the total anterior radii of scales (R) and the lengths (L) for white bream is best represented by a power function ($L = 66{\cdot}22R^{0{\cdot}687}$, $n = 146$, $r = 0{\cdot}966$), thus, the logarithmic form of the equation was used. The backcalculated logarithmic lengths were transformed to anti-log values. These relationships in common bream ($L = 89{\cdot}83R + 12{\cdot}51$, $n = 126$, $r = 0{\cdot}954$), roach ($L = 32{\cdot}64R + 9{\cdot}44$, $n = 141$, $r = 0{\cdot}991$) and wild goldfish ($L = 26{\cdot}70R + 28{\cdot}4$, $n = 160$, $r = 0{\cdot}988$) proved to be linear. Based on these relationships, the early scale formation was probable at 12·5 mm of common bream, 9·44 mm of roach and 28·4 mm of wild goldfish. These values were in agreement with those observed directly in common bream and roach fry. Their total scale formations have been observed between 10- and 14-mm standard lengths. No direct observations were made for YOY wild goldfish and white bream.

The measured data of YOY fish, collected in late November, did not differ from those obtained by backcalculations (*t*-test: NS) (Table I). According to the direct observations, YOY roach reached an average 48 mm (S.D. = ± 11·7), white bream 52 mm (S.D. = ± 5·2) and common bream 44 mm (S.D. = ± 7·3) standard length by late November 1995.

The theoretical values of L_∞ and W_∞ in von Bertalanffy's growth model seem to be realistic for the populations of common bream, white bream and roach (Table II). However, they have probably been overestimated for the wild goldfish population, because of the very rapid and balanced growth of wild goldfish in the first 7 years. The calculated von Bertalanffy's equations showed very close agreement with the calculated data ($r = 0{\cdot}9977$–$0{\cdot}9996$, $P < 0{\cdot}001$).

DIET COMPOSITION AND FEEDING STRATEGY

Rutilus rutilus

The food of roach by weight consisted mainly of benthic and periphytic molluscs, and *Dreissena polymorpha* (Pallas) (47·2%) and gastropods (14·5%) were dominant (Table III). Roach was occasionally herbivorous consuming algae (27·1%). According to the Amundsen *et al*. (1996) graphical method, roach preyed mainly upon Dreissena (Fig. 3). There was a high between-phenotype contribution to the niche width proportion belonging to other food types. Twenty-five per cent of roach adapted exclusively to an herbivorous feeding pattern. Along the artificial stony shoreline, roach fed rarely on bait (used by sport fishers), indicating high occasional specialization. The role of planktonic

TABLE I. Backcalculated lengths (L, mm), weights (W, g) and instantaneous rates of growth (G) in different age groups of roach, white bream, common bream and wild goldfish caught in the NE basin of Lake Balaton in 1995

Fish species			Age group									
			0+	1+	2+	3+	4+	5+	6+	7+	8+	9+
Roach (n=112)	L	Mean	47	83	117	151	178	203	223	236	242	253
		Min	35	64	89	125	159	184	203	215	227	235
		Max	58	99	142	179	210	230	247	259	262	271
		± S.D.	5·3	10·0	15·0	15·5	13·6	13·8	14·7	17·8	17·7	25·6
		Increase	47	36	34	34	27	25	20	13	6	11
	W	Mean	2·2	13·0	38·3	82·2	136	205	276	331	356	410
	G		—	1·76	1·07	0·78	0·52	0·41	0·30	0·17	0·08	0·14
White bream (n=127)	L	Mean	52	84	109	130	150	168	188	205	220	—
		Min	40	68	91	108	120	130	171	196	218	—
		Max	75	102	130	158	181	196	208	218	221	—
		± S.D.	7·1	8·0	8·1	9·3	10·7	13·1	9·2	8·0	2·7	—
		Increase	52	32	25	21	20	18	20	17	15	—
	W	Mean	2·7	12·0	28·4	50·9	79·9	117	166	220	274	—
	G		—	1·5	0·87	0·59	0·45	0·37	0·37	0·29	0·22	—
Common bream (n=121)	L	Mean	42	72	104	137	169	200	232	258	275	282
		Min	27	51	73	95	117	137	175	194	251	270
		Max	59	115	161	199	246	281	300	302	310	294
		± S.D.	6·3	13·8	21·6	27·2	32·8	39·0	34·4	25·6	23·0	16·7
		Increase	42	30	32	33	32	31	32	26	17	7
	W	Mean	1·5	8·4	26·0	58·7	109	181	270	359	431	461
	G		—	1·65	1·11	0·83	0·63	0·51	0·44	0·32	0·19	0·08
Wild goldfish (n=160)	L	Mean	64	106	157	201	237	267	287	—	—	—
		Min	39	74	127	167	197	238	263	—	—	—
		Max	86	152	197	246	284	310	312	—	—	—
		± S.D.	7·4	14·0	15·7	14·9	16·0	15·8	14·0	—	—	—
		Increase	64·0	42	51	44	36	30	20	—	—	—
	W	Mean	7·0	35·0	120	258	431	632	788	—	—	—
	G		—	1·60	1·26	0·78	0·52	0·39	0·22	—	—	—

TABLE II. The parameters of von Bertalanffy's growth model for cyprinids in Lake Balaton, 1995

	n	L_∞ (mm)	W_∞ (g)	K	t_0 (year)
Roach	112	319	831	0·160	0·026
White bream	127	359	1358	0·098	− 0·639
Common bream	121	501	2579	0·083	0·225
Wild goldfish	160	478	3801	0·129	− 0·015

n, Sample size.

TABLE III. The diet composition of cyprinids in the littoral zone of Lake Balaton (% wet weight)

	Roach	Common bream	Wild goldfish	White bream	Carp
Oligochaeta	—	5·6	—	0·1	2·0
Hirudinoidea	—	0·1	—	—	0·1
Copepoda	—	4·4	8·8	2·2	0·1
Cladocera	—	4·5	11·3	—	—
Leptodora kindtii	—	1·3	1·8	0·1	—
Ostracoda	—	0·4	0·2	—	—
Gammaridae	0·8	5·8	1·3	2·9	1·9
Corophium curvispinum	1·4	9·0	7·6	15·0	7·7
Asellus aquaticus	—	1·4	—	—	0·1
Jaera sarsi	—	0·3	—	—	—
Ephemeroptera larvae	—	0·1	—	—	—
Chironomidae larvae	0·1	30·7	0·7	3·4	6·4
Chironomidae pupae	—	5·7	0·4	3·6	0·3
Ceratopogonidae larvae	—	0·1	—	—	0·1
Trichoptera larvae	—	0·4	—	0·2	—
Micronecta spp.	—	—	—	1·7	—
Dreissena polymorpha	47·2	4·7	0·5	46·8	61·3
Gastropoda	14·5	0·3	—	1·6	1·1
Pisidium spp.	0·6	—	0·7	0·3	2·5
Detritus	2·3	17·3	43·5	3·3	13·7
Algae (filamentous)	27·1	—	—	2·2	—
Macrophyta	2·0	0·4	3·0	—	0·7
Bait material	3·3	7·3	—	14·4	1·9
Fish eggs	0·2	—	—	—	—
Other	—	—	—	2·3	—

and other benthic food items was very low and the diversity of the diet proved to be $B = 0{\cdot}102$.

Abramis brama

The diet of common bream was varied and mixed but comprised mainly benthic and zooplanktonic food items. Periphytic organisms were preyed on in

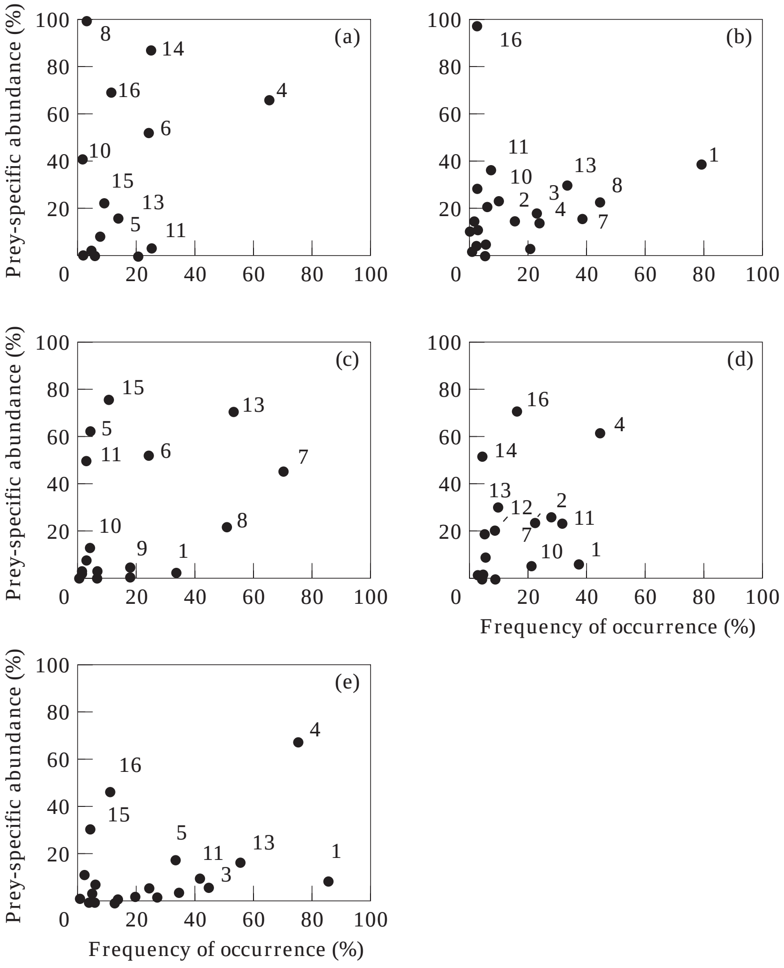

FIG. 3. Feeding strategy plots of cyprinids in the littoral zone of Lake Balaton: (a) roach ($n=98$); (b) common bream ($n=225$); (c) wild goldfish ($n=105$); (d) white bream ($n=124$); (e) carp ($n=130$). 1, Chironomidae larvae; 2, Chironomidae pupae; 3, Oligochaeta; 4, *Dreissena polymorpha*; 5, *Pisidium* spp.; 6, Gastropoda; 7, Copepoda; 8, Cladocera; 9, *Leptodora kindtii*; 10, Gammaridae; 11, *Corophium curvispinum*; 12, *Micronecta* spp.; 13, Detritus; 14, algae; 15, Macrophyta; 16, bait material.

spring only during the spawning period. By weight, the dominant food items were chironomid larvae (30·7%) and detritus (17·3%) (Table III). According to the feeding strategy analysis, a low within-phenotype component was detected. The most important prey groups were chironomids, occurring in >80% of the guts. However, their average contribution to the gut contents of this fish was moderate, indicating a generalized feeding strategy. Occasionally, high specialization was detected for the bait, which formed 7·3% of the total food by weight in the littoral zone. The rest of the diet came from many other food types, which were consumed rarely and in small amounts (Fig. 3). The diversity of the diet was relatively high, $B=0{\cdot}226$.

Carassius auratus gibelio

Wild goldfish consumed mainly zooplankton and detritus (Table III). Feeding on zooplankton was most expressed in the open parts of the littoral zone, while detritus dominated in the stony areas and reed grass stands. Copepods were the most common prey at a moderate level of specialization and formed 28·8% of the total food by weight. Cladocerans were less frequent and formed 12·9% [including *Leptodora kindtii* (Focke)] of the total diet by weight. Detritus, constituting 43·5% by weight of the diet, was found in more than half of the foreguts and a high specialization was observed for this food type. Wild goldfish occasionally showed a high specialization also for *Pisidium* spp. and macrophytes (Fig. 3). The diversity of the diet was relatively low, $B=0{\cdot}106$.

Blicca bjoerkna

Gut contents of white bream by weight consisted chiefly of *Dreissena polymorpha* (46·8%), *Corophium curvispinum* (G. O. Sars) (15·0%) and bait (14·4%) (Table III). Additional foods by weight were chironomid larvae and pupae in about 3·3%, gammarids, detritus and algae, respectively. Specialization occurred only for *Dreissena* in 45·5% of fish and some times for bait (in 16·7% of fish). The feeding strategy plots (Fig. 3) suggest a mixed feeding pattern, with varying degrees of specialization and generalization. The diversity of the diet exhibits an intermediate feature as compared to the other cyprinids, $B=0{\cdot}150$.

Cyprinus carpio

Dreissena polymorpha was the main food of carp, constituting 61·3% of its diet by weight. Detritus (13·7%), *Corophium curvispinum* (7·7%) and chironomid larvae (6·4%) were also important food components (Table III). According to the feeding strategy analysis, carp is strongly specialized toward *Dreissena*. Besides this specialization, a high within-phenotype component characterized its feeding strategy. Further specialization occurred only for bait, but this was not as clear as in the other species. Despite their small ratio in weight, chironomids were permanent components of the diet (Fig. 3). Among the cyprinids studied, carp showed the lowest diet diversity, $B=0{\cdot}051$.

RESOURCE PARTITIONING

According to discriminant analysis, the cyprinid diets were significantly different (for the four derived discriminant functions: $\lambda=0{\cdot}1499$–$0{\cdot}8382$, $\chi^2=770{\cdot}4$–$71{\cdot}66$, $P<0{\cdot}0001$) (Fig. 4). None of the four discriminant axes could be tied to a single food group. The most important food items appeared to be algae (axes 1 and 3), copepods (axis 2), detritus (axes 2 and 3), chironomid larvae (axis 3), cladocerans (axis 3) and *Pisidium* spp. (axis 4). The differences between the diet of roach, carp, common bream and wild goldfish are well represented along the first and second discriminant axes. The diet centroid of white bream could be separated best from those of the other species along the third discriminant axis. However, there were significant dietary overlaps among the various fish species occurring in the same habitat. The strength of their specialization indicated the partitioning of food resources, which resulted in

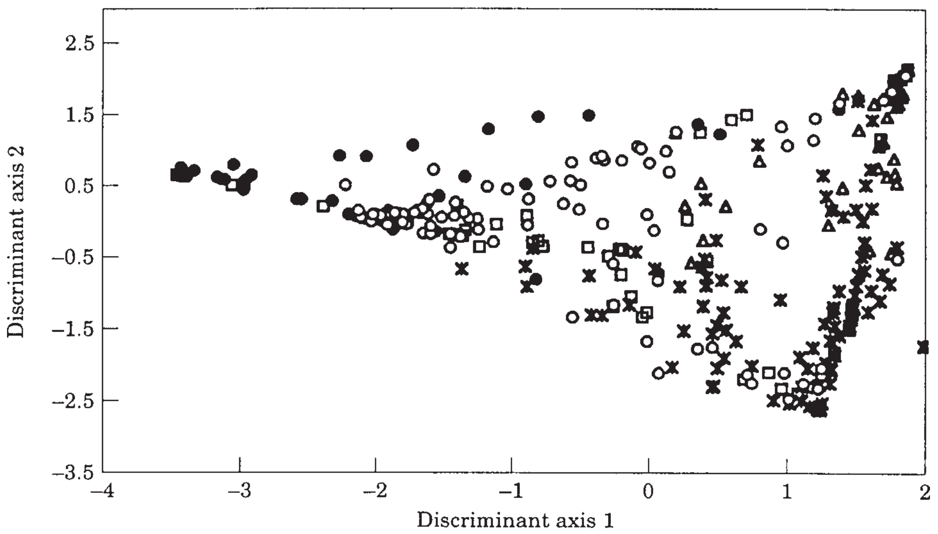

FIG. 4. The discriminant analysis plot along the first and second discriminant axes for the diet composition data of cyprinids in the littoral zone of Lake Balaton. ●, Roach; ✗, bream; △, wild goldfish; □, white bream; ○, carp.

interactive (niche) segregation (Nilsson, 1967) of species during certain periods. A dietary switch from zooplankton assemblages to benthic or littoral invertebrates occurred in all species in parallel with their increasing sizes and during seasonal migration between open water areas and littoral zones of different trophic state.

DISCUSSION

The growth rate of common bream has decreased since the 1960s (Pénzes, 1966; Bíró & Garádi, 1974; Dauba & Bíró, 1992) and this process is ongoing. Also, the actual growth of common bream in Lake Balaton is slower than in most other water bodies (Naiksatam, 1974; Shestopalova, 1977; Goldspink, 1978, 1981; Wright, 1990). This phenomenon could be explained partly by the negative size selection due to low fishing effort and mortality. From the 1950s to the end of the 1980s, on average more than 1000 tons of common bream were removed annually with seine nets. The 50% length retention of these nets for common bream was 19·5 cm on average (Bíró, 1978). It is thought that probable additional factors are some sublethal cyanobacteria toxins. These could be indicated by the huge amount of catarrhal secretions in the gut and the structural degradation resulting in light patches on the liver surface.

As compared to other water bodies (Kukuradze & Mariash, 1975; Sedlár *et al.*, 1976; Gudkov, 1985), the growth of wild goldfish is rapid in Lake Balaton. Roach in the NE basin of the lake also grow faster than in most other European waters (Zheltenkova, 1949; Frank, 1962; Holčik, 1966; Hellawell, 1972; Mann, 1973; Linfield, 1979; Pivnička, 1975; Baranova, 1984), while the growth rate of white bream can be considered as medium (Frank, 1962; Kirilyuk, 1991). The introduced carp also grew very rapidly. In European water bodies the annual growth rates have been regulated by several biotic and environmental factors (productivity, latitude, temperature, length of growing season), but in the shallow and warm Lake Balaton mainly by inter- and intraspecific mechanisms. Considering the long-term changes of the lake, the living conditions of all fish have altered significantly in space and time. As eutrophication became advanced (mid-1970s), the population density of the dominant cyprinids (e.g. common bream) and the stock size of their competitors increased [introduced eel *Anguilla anguilla* (L.), silver carp *Hypophthalmichthys molitrix* (Valenciennes), wild goldfish] and, consequently, their growth rate became stunted (early 1980s) (Dauba & Bíró, 1992). When the stock density decreased again (mid-1980s), their growth rate became faster, however, these populations started to show damped or undamped oscillations in the function of their natural recruitment and environmental perturbations. The causes of differences in growth rates are the variations both in stock density and food availability. Among cyprinids, these seem to be the crucial factors in Lake Balaton, while the growth and stock size of the top predator pikeperch *Stizostedion lucioperca* (L.) are basically food resource limited which has often been indicated by their self-regulating cannibalism (Bíró, 1997).

The growth rate of cyprinids in Lake Balaton was determined largely by the available food resources and their feeding strategies. Results obtained from discriminant analyses revealed significant differences in diet between the five cyprinids. According to these analyses, the most important food items discriminated among species' diet were *Dreissena*, algae, zooplankton, detritus, chironomid larvae and macrophytes.

According to Tátrai (1980), common bream weighing 125–434 g fed mainly on chironomid larvae (50–70% by weight) in Lake Balaton. Bíró *et al.* (1991) found that common bream, aside from chironomid larvae (17–83% by weight), consume significant amounts of zooplankton (22·3–68·2%) and molluscs (13–81%). Present results show that adult common bream did not specialize in any of the food resources but had a generalized feeding strategy.

The biomass of benthic invertebrates, mainly chironomid larvae, showed high annual and seasonal fluctuations in Lake Balaton. In 1995, the mean biomass of benthic chironomids ranged from 1·7 to 159·8 g m^{-2} (Specziár & Bíró, 1995), while in 1996, the average biomass was only 1·13–2·7 g m^{-2} in wet weight for the different areas of the lake. The overall benthic biomass showed an increase in this century, in parallel with eutrophication processes, as the mean abundance of *Chironomus plumosus* (L.) increased (Entz, 1965, 1966; Dévai *et al.*, 1979, 1984; Ponyi *et al.*, 1983; Perényi *et al.*, 1993; Specziár & Bíró, 1995). In Lake Balaton, chironomid larvae have become major components (17–82·9% by weight) of food only for common bream over 25–30 cm (Bíró, 1991). The increased biomass of benthic chironomids may be the main reason for the unchanged growth rate of common bream aged 6+ to 9+ (over 22–24 cm). The strong fluctuation of benthic biomass may have affected the feeding intensity and growth rate of common bream and caused significant differences in annual growth and competition with other fish species.

Wild goldfish feed differently from the other cyprinids. Where small particulate detritus is plentiful (along the stony shoreline and in the reed grass stands), they specialize on this food supply. In detritus-poor habitats (open water regions), they consume zooplankton. This non-native fish probably does not compete strongly for food with adults of native cyprinids in the littoral zone, which may explain its fast growth.

White bream consumes periphytic, benthic and planktonic food resources, and consequently shows a generalized feeding character. Along the shorelines, where periphytic components dominate, the competition for diet exists among white bream, roach and carp. In the open water regions, white bream and common bream compete for similar food resources. Roach and carp probably have an advantage over white bream in the littoral habitats. According to Berg *et al.* (1994) common bream in the open water has an advantage over white bream and roach due to its more effective filtering apparatus. White bream rarely preyed upon large mud-dwelling chironomid larvae and oligochaetes and only organisms living on the surface of the mud (small chironomid larvae, cladocerans, etc.) were consumed extensively. This indicates that white bream cannot dig as deeply into the mud as common bream or carp can.

The feeding of roach seems to be highly specialized. The reasons for shifts between its two main food types, periphytic molluscs and filamentous algae, are not properly known yet. According to the literature (Zheltenkova, 1949; Baranova, 1984), the high biomass of *Dreissenia polymorpha* or other small-sized molluscs provides the possibility for fast growth for roach in older age groups. Zheltenkova (1949) considers that pharyngeal teeth of roach are more suited to grinding molluscs than are those of its feeding competitors. However, herbivory of roach has been detected also in various water bodies, even in older age groups (Hellawell, 1972; Mann, 1973; Giles *et al.*, 1990).

Carp prefer to live in the shallow vegetated littoral habitat, which is rich in periphytic molluscs. They showed the most specialized feeding pattern, consuming Dreissena in large proportion. The observed rapid growth of carp is probably due to this food. In the open water areas, carp occurs rarely and has many strong competitors for benthic food resources, such as common bream, ruffe *Gymnocephalus cernuus* (L.), eel, etc. In natural waters, feeding of adult carp on zooplankton has been found rarely. As the natural recruitment of carp is insignificant, the population size is determined basically by the annual stocking and catch. However, the competition affects both its growth rate and condition.

Roach, white bream, wild goldfish and carp chiefly inhabit the narrow littoral zone of the lake and grow relatively well. However, common bream which inhabit mainly the open water region grow slowly in Lake Balaton, as compared to other waters. This discrepancy may arise from the differences in the food bases of the littoral and the open water regions. In the open water area, benthos and plankton are the only food bases available, since the submerged macrophyte stands disappeared in parallel with the planktonic eutrophication processes, whereas, the littoral region has more diversified fish food resources. The mostly regulated shorelines of the lake, protected by stones and concrete, have a rich periphytic fauna. The zooperiphytic biomass ranged annually between 12·9 and 359 g m^{-2} (stone surface) in 1995 and showed a summer maximum. The zooperiphyton by weight consists mainly of *Dreissenia polymorpha* (65·0–85·0%) and various amphipods (10·3–14·3%). The natural shorelines are usually covered by reed grass stands (1200 ha), which are also rich in periphytic fauna, especially zebra mussel *D. polymorpha* and *Corophium curvispinum* (our unpublished data). Due to their extensive coverage, reed grass stands provide more plentiful food bases for fish than those of stony shorelines. According to Bíró (1997), the littoral periphyton/zoobenthos fish food web mediates more energy to the fish than that of the planktonic food-web in the open water areas. Based on gut contents, artificial food (corn and cereal fodder, milling products) used by sport fisheries (to bait fish) play an important role in the diet and production of cyprinids in the littoral zone. The real significance of this food is not yet known and is probably underestimated because popular fishing places were avoided during sampling.

The phytolithophil common bream is one of the few fish species which spawns successfully along the stony shorelines of the lake. Owing to decreased fishing effort, its abundance in the open regions may increase and have negative effects because of its competitive advantages in relation to other species. If the shoreline regulations and the degradation of reed grass stands continue, interspecific competition will probably increase. The loss of spawning areas mostly affects the phytophil spawners.

Older age groups (6+–8+) dominated the age distribution of the non-native wild goldfish, which suggests low annual recruitment and possible immigration of individuals from other areas. The dominant age groups may have been born in Kis-Balaton Water Reservoir, or in the shallow SW basin of Lake Balaton, but this question has not yet been answered properly. The high abundance of the large (700–1300 g) individuals indicates a very high capacity of reproduction, which may imply the danger of its rapid invasion to the littoral region within a few years. Such an invasion may lead to increased interspecific competition. The degradation of the population composition of common bream and the increasing invasion of wild goldfish require the regulation of their stocks by using more selective fishing gear. The strict protection of the diversified natural shoreline sections would promote an increased spawning success of valuable and less competitive fish species in the highly eutrophic, shallow Lake Balaton.

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