



Long-term development of fish populations in the Římov Reservoir

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Abstract The inshore fish community of the Římov Reservoir in the Czech Republic was evaluated over 21 years using shore seining at night. The development of the fish community was divided into two separate phases: a highly dynamic and unstable phase dominated by perch, *Perca fluviatilis* L., was replaced by an extremely stable cyprinid phase dominated by roach, *Rutilus rutilus* (L.), and bream, *Abramis brama* (L.). The abundance of both these species oscillated during the cyprinid phase, but with decreasing amplitude. The proportion of piscivorous fish species such as asp, *Aspius aspius* (L.), pike, *Esox lucius* L., and pikeperch, *Sander lucioperca* (L.), increased slightly with time but remained low. The biomass of large Cladocera was negatively correlated with fish biomass only

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during the perch phase. The Shannon–Weaver index of diversity increased during the fish community succession, mainly because of greater evenness amongst the species.

KEYWORDS: biodiversity, cyprinids, perch, reservoir, stability, succession.

Introduction

Long-term studies of reservoir fish communities are necessary to determine the key factors that influence community structure. In heavily managed systems such as reservoirs, it is also necessary to establish a baseline for management recommendations (e.g. to predict future productivity of the fisheries; Gido, Matthews & Wolfinbarger 2000).

Construction of reservoirs provides the possibility of studying lentic ecosystem through a gradual succession of their biotic assemblages. Kubečka (1993) divided the development of fish communities in reservoirs of Central Europe into five phases according to the change in dominant fish species during reservoir ageing: (1) a riverine species phase; (2) a pike, *Esox lucius* L., phase; (3) a perch, *Perca fluviatilis* L., phase; (4) a transient perch-cyprinid phase; and (5) a cyprinid dominated phase.

The initial phase of the fish fauna's development in newly impounded European reservoirs has been described in many publications (e.g. Holčík & Pivnička 1972; Starmach 1986; Vostradovský, Křížek, Albertová, Růžička & Vostradovská 1989; Kubečka 1993; Tereshchenko & Nadirov 1996; Seďa & Kubečka 1997; Tereshchenko, Trifonova & Tereshchenko 2004). However, there are few studies describing the long-term sequence of events in reservoir fish fauna (Starmach 1986; Pivnička 1992; Tereshchenko & Nadirov 1996; Gido *et al.* 2000).

This study evaluated the development of fish community in a South Bohemian impoundment, the Římov Reservoir, over a 21-year period between 1985 (7 years after the reservoir filling) and 2006. The following questions were examined. (1) Are there any long-term changes of reservoir fish community in terms of species composition, abundance and biomass? (2) Does the reservoir fish community show a successive change to cyprinid dominance? (3) Is there long-term effect of stocking piscivorous fish species into the reservoir? (4) Are there changes in biomass of large cladocerans that correlate to long-term changes in reservoir fish community?

Study site

This study was carried out in the canyon-shaped Římov Reservoir, a deep, narrow impoundment in

South Bohemia, Czech Republic (about 170 km south of Prague, 48°50' N, 14°30' E), constructed for drinking water storage and flood control. The reservoir was built in 1978 by damming the River Malše.

The maximum area of the Římov Reservoir is 210 ha; maximum volume is 33.10^6 m³; the maximum depth 45 m with a mean depth of 16 m. The length of the reservoir is 12 km and the maximum surface altitude is 471 m asl. The mean theoretical retention time is approximately 92 days. The average annual inflow ranged from 2.63 to 10.8 m³ s⁻¹ (SD = 1.95) during 1985–2005.

The reservoir is dimictic, with summer stratification usually lasting from April to September. The littoral zone is without submerged aquatic macrophytes because of the steep banks and water level fluctuations (Hladík & Kubečka 2004). The trophic status of the reservoir is mesotrophic to eutrophic, with phosphorus and chlorophyll *a* concentrations decreasing towards the dam (Seďa & Devetter 2000). Phytoplankton is almost permanently phosphorus limited (Vyhnálek, Komárková, Seďa, Brandl, Šimek & Johanišová 1991; Nedoma, Porcalová, Komárková & Vyhnálek 1993) and the mean annual chlorophyll *a* biomass range was 4.7–28.0 µg L⁻¹ (mean = 11.5 µg L⁻¹; SD = 5.8) from 1985 to 1998 (Komárková, Komárek & Hejzlar 2003).

Regular sampling focusing on the inshore fish community started in 1985, seven years after the reservoir was filled, although Vostradovská & Vostradovský (1983); Kubečka (1990); Seďa & Kubečka (1997) described the initial development of the fish community in the Římov Reservoir during the first 7 years after filling (1978–1984). Trout; *Salmo trutta* L., and *Oncorhynchus mykiss* (Walbaum), dace; *Leuciscus leuciscus* (L.), chub; *Leuciscus cephalus* (L.), and grayling; *Thymallus thymallus* (L.), which had been dominant in the river before filling, were replaced by perch, roach, *Rutilus rutilus* (L.), and bream, *Abramis brama* (L.), during the first 3 years after filling. The new colonisers had very strong recruitment in this initial phase: roach in 1979–1981, bream in 1980 and 1981 and perch in 1979–1982. The biomass of these species peaked in 1982, at 600–700 kg ha⁻¹. Perch was the dominant species, representing over 70%, roach represented 20% and bream only 4% of the total fish biomass.

Biomaniipulation measures were carried out mainly between 1983 and 1989. These included: (1) drying out

Table 1. Mean per year of abundance (n) and mean biomass per hectare and year ($\text{ha}^{-1} \text{yr}^{-1}$) (BPA) for stocked piscivorous species in 5-year period. Mean biomass of predators (kg ha^{-1}) in night inshore fish community in 5-year period

Period	Pikeperch		Pike		Asp		Sum of all		BPA
	n	kg ha^{-1}	n	kg ha^{-1}	n	kg ha^{-1}	n	kg ha^{-1}	(kg ha^{-1})
1984–1988	8680	1.5	2435	5.3	3800	2.4	14915	9.21	0.92
1989–1993	12000	1.9	760	2.9	540	1.2	13300	5.95	0.85
1994–1998	9300	3.7	894	4.5	1600	5.0	11794	13.22	0.89
1999–2003	2500	2.8	4238	1.9	9200	5.8	15938	10.48	1.09
2004–2006	4892	2.3	1757	6.1	6227	1.6	12876	9.97	0.91

spawned eggs of cyprinid species by lowering the water level; (2) catching perch with fyke-nets during the spawning period; and (3) removing adult fish with shore seines. Regular stocking of piscivorous fish species was carried out throughout the entire history of the reservoir (Table 1).

Material and methods

Fish were caught by shore seining at night. Římov Reservoir has been regularly netted since 1985, although data for the years 1990 and 2003 were not available. Only fish aged 1 year and above were considered in this study. The nets ranged in length from 50 to 200 m, their height was 4 m, and stretched mesh size 10 mm. Fish were sampled each summer (June to September) at six sites situated between the dam and the inflow. Catch data were presented as catch per unit area, calculated according to Kubečka & Böhm (1991) (biomass or abundance ha^{-1}).

Zooplankton was collected every 3-weeks at the deepest station near the dam, by vertical hauls using an Apstein plankton net (mesh size = 200 μm). The hauls were taken from the bottom to the surface and at least two hauls were pooled into one sample. The sample was divided into three size fractions using sieves with mesh sizes of 0.71 mm and 0.42 mm (Seda & Dostálková 1996). The biomass of all zooplankton fractions was measured as protein nitrogen by the biuret reaction (Blažka 1966).

Statistical analysis

Piscivorous fish species in the reservoir were represented by pikeperch, *Sander lucioperca* (L.), pike and asp, *Aspius aspius* (L.). Perch was not included among the piscivores (although adult perch can be piscivorous) because stomach analyses of Římov perch in the mid-1980s indicated that fish were rarely consumed (Kubečka, Seda & Matěna 1998). The abundance of each piscivorous species relative to the number

Table 2. Parameters of the correlation between population development of three predatory species with their stocking and the age of the reservoir. The dependence was tested for abundance of three main predators individually and abundance and biomass of the sum of predators

	Pikeperch	Pike	Asp	Sum of predators	
				Abundance	Biomass
b	3.120	0.101	0.210	0.066	0.201
P -level for b	0.005	0.835	0.686	0.890	0.361
c	0.002	0.000	-0.000	0.000	-0.007
P -level for c	0.031	0.967	0.654	0.637	0.504
r^2	0.430	0.005	0.015	0.016	0.063
Durbin–Watson for autocorrelation (P -level)	0.092	0.764	0.842	0.672	0.884

stocked and the relationship between the age of the reservoir and the abundance of piscivores (individual species and abundance and biomass all three species together) were examined. The amount of piscivorous fish in the total catch was tested against stocking the previous year, because stocking usually took place in autumn. A linear model was developed: $A = a + (b \times T) + (c \times n)$, where A is abundance of piscivorous species, T is time (year), n is number of stocked piscivorous fish and a , b , c are constants. A Durbin–Watson test (Durbin & Watson 1951) showed no autocorrelations in all data sets (Table 2) and thus the least square regression was used to test of any relationship.

Zooplankton of the size fraction > 0.71 mm consisting completely of large cladocerans (mainly daphnids) was in focus of this study. Vašek, Kubečka & Seda (2003) showed that this zooplankton fraction was the preferred prey of the dominant fish species. Total fish abundance and biomass were tested against the annual mean, spring mean (March to June) and summer mean (July to October) biomass of the large Cladocera fraction. The relationship between the age of the reservoir and cladoceran biomass mean and annual

Table 3. Parameters of the correlation between the fish abundance and biomass with the biomass of Cladocera > 0.71 mm and the correlation of total zooplankton biomass and the biomass of Cladocera of > 0.71 mm with the age of the reservoir. The analyses were restricted to the cyprinid phase (1991–2005)

Fish	Spring mean of Cl > 0.71 mm		Summer mean of Cl > 0.71 mm		Annual mean Cl > 0.71 mm		Total zooplankton biomass
	<i>n</i>	<i>B</i>	<i>n</i>	<i>B</i>	<i>n</i>	<i>B</i>	
b	1.055	0.960	-0.420	-0.060	0.598	0.540	-0.940
<i>P</i> -level for b	0.026	0.043	0.880	0.833	0.073	0.103	0.753
c	0.002	0	0.001	0	0.001	0	0
<i>P</i> -level for c	0.13		0.347		0.189		
d	0	0.048	0	0.024	0	0.031	0
<i>P</i> -level for d		0.250		0.380		0.300	
<i>r</i> ²	0.370	0.320	0.120	0.110	0.273	0.226	0.008
Durbin–Watson for autocorrelation (<i>P</i> -level)	0.340	0.740	0.580	0.230	0.250	0.844	0.580

mean biomass of total zooplankton were also examined. This test was restricted to the phase of cyprinid dominance in the reservoir. The methodology was the same as with the piscivorous species. Models were as follows: $C = a + (b \times T) + (c \times A)$; $C = a + (b \times T) + (d \times B)$, where C is cladoceran biomass, B is fish biomass and a , b , c and d are constants. The Durbin–Watson test was not significant (Table 3).

The Shannon–Weaver index (H') of diversity, the equitability index (J) and number of species were used to describe changes in species composition and evenness. The relationship between the age of the reservoir and these three factors were tested. The Durbin–Watson test detected autocorrelation at case of the Shannon–Weaver index ($P = 0.04$) but not for equitability index ($P = 0.26$) and number of species ($P = 0.124$). The Generalised Least Square method was used for trend detection of the Shannon–Weaver

index and least square regression for the equitability index and number of species.

Results

Development of dominant fish species

The dominant fish species were roach, bream and perch throughout the sampling period. They represented over 70% of the total fish abundance almost every year (Fig. 1). The study period was divided into two separate phases (Figs 2 & 3). Perch was dominant in the first phase between 1985 and 1988 (perch phase), while roach and bream replaced perch thereafter (cyprinid phase). Total fish biomass was two to fourfold higher in the perch phase than in the cyprinid phase (highest in 1985–409 kg ha⁻¹). In 1988, the perch population collapsed. In 1989, perch abundance

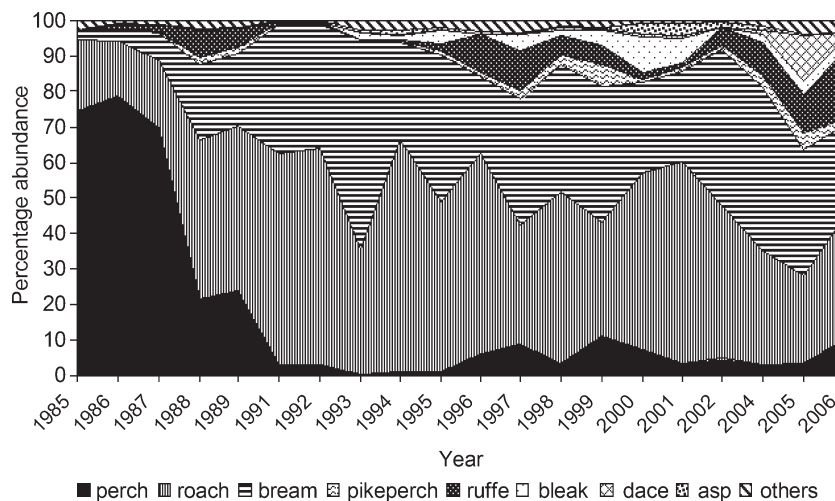


Figure 1. Composition of the night inshore fish community in Řimov Reservoir during the sampling period.

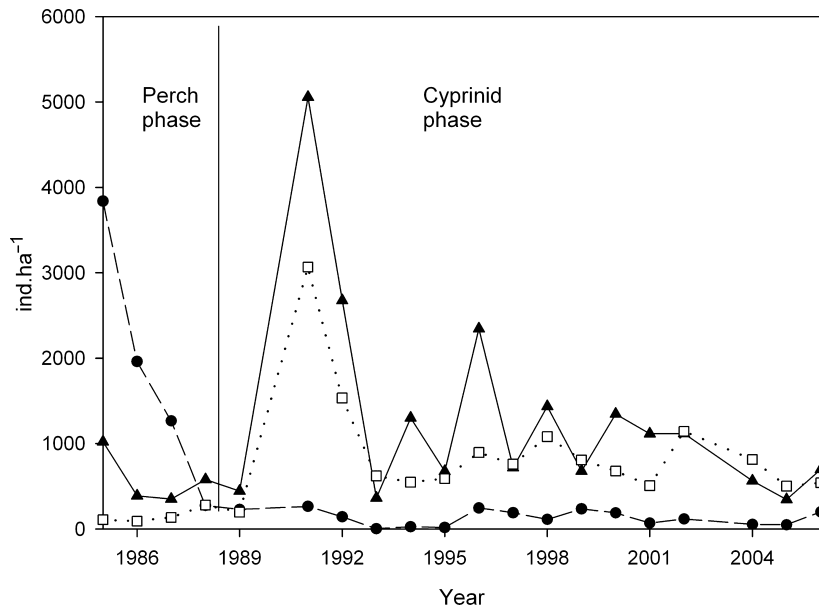


Figure 2. Shifts in abundance of perch (dashed line), roach (solid line) and bream (dotted line) in Římov Reservoir.

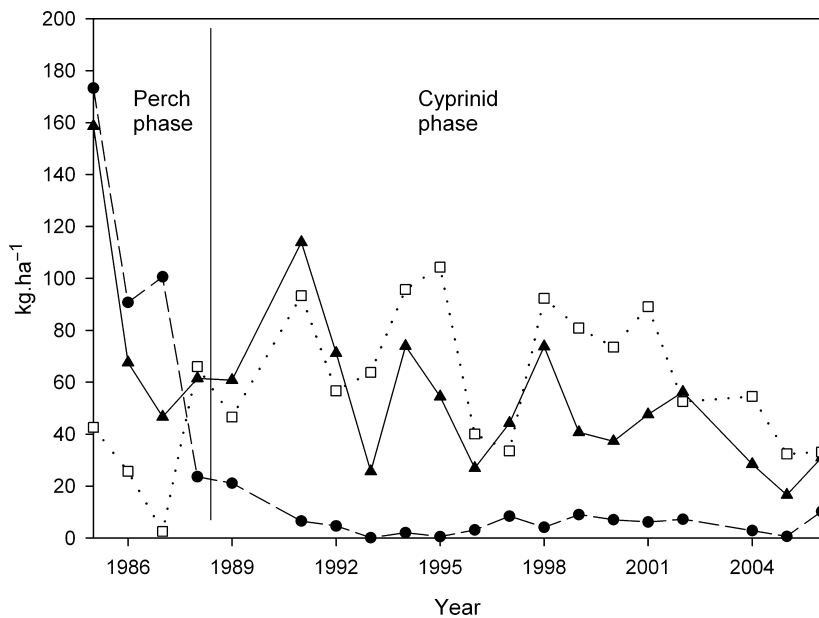


Figure 3. Shifts in biomass of perch (dashed line), roach (solid line) and bream (dotted line) in Římov Reservoir.

was 87% lower than in 1985 (Fig. 2). The total fish biomass in 1989 decreased to less than one-third of that in 1985 because of this event (Fig. 3).

In 1988–1989 the fish community shifted from a perch phase to a cyprinid phase. Since then, bream and roach have dominated the fish community with the former species usually prevailing in biomass and the latter in abundance (Figs 2 & 3). No statistical

difference was found between abundance (Unpaired *t*-test of annual means; $t = 1.435$, $P = 0.159$) and biomass (Unpaired *t*-test of annual means, $t = -0.219$, $P = 0.828$) of bream and roach in the cyprinid phase. Their abundance seemed to be, to a large extent, synchronised (the correlation of their abundance over the cyprinid phase expressed as the Spearman $r_s = 0.643$, $P = 0.01$; Fig. 4). The abundance and

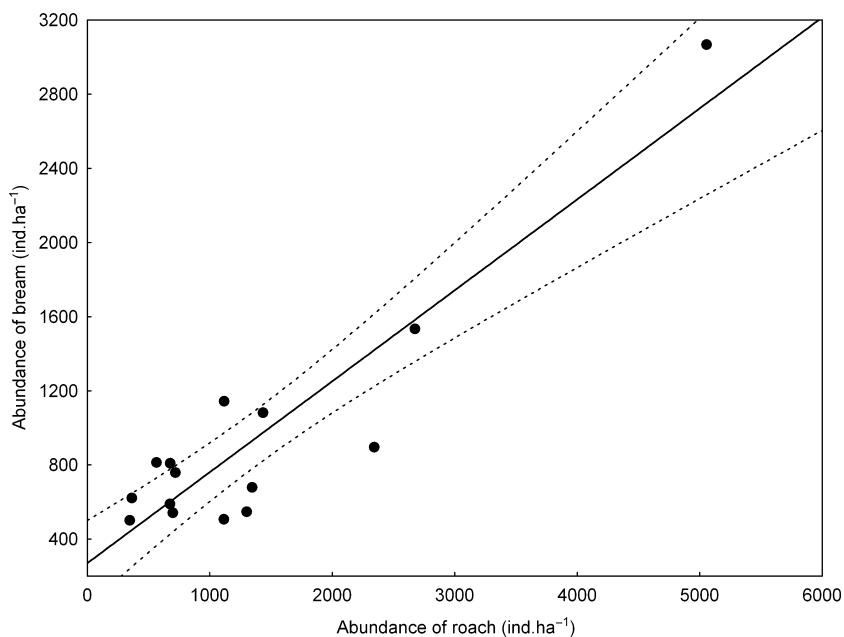


Figure 4. Relationship between abundance of roach and bream in the cyprinid phase (Roach abundance = $27.068 + 0.49055 \times$ bream abundance) in Římov Reservoir. Dashed line indicates confidence interval (95%).

biomass of both species oscillated throughout the cyprinid phase from 1989 to 2006. The biggest amplitude was after the perch collapse in 1991. Bream and roach had a very strong year class in 1990, which was especially evident through a large increase in abundance in 1991. The populations of the two species decreased very rapidly after this 1991 peak. Every 2 or 3 years thereafter their abundance increased again, but

with diminishing amplitude (Fig. 2). The proportion of perch remained low throughout the cyprinid phase (Figs 2 & 3).

Development of populations of piscivorous fish

In Římov Reservoir, the mean proportion of piscivorous species (pikeperch, pike and asp) was low, around

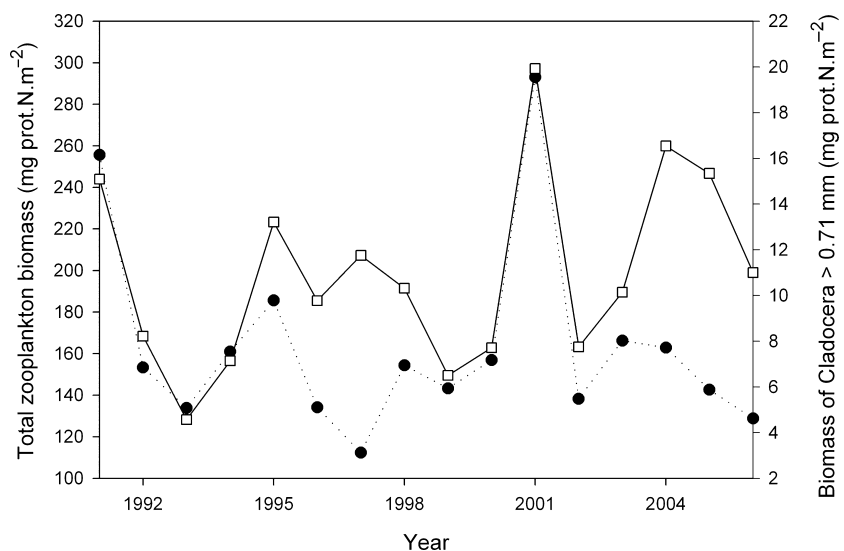


Figure 5. Shifts in total zooplankton biomass (solid line) and biomass of Cladocera > 0.71 mm (dotted line) during the cyprinid phase in Římov Reservoir.

3% of abundance and 7% of the biomass in the reservoir during the cyprinid phase. The abundance of piscivores slowly built up and increased 2.5 times over 15 years (1991–2006), mainly caused by an increasing pikeperch population, which was dependent on the number of pikeperch stocked in the previous year (Table 2). Pike, asp and the sum of all three piscivores were not dependent on the number of individuals stocked (Table 2).

Zooplankton-fish interaction

No relationship was found between abundance or biomass of fish and biomass of Cladocera > 0.71 mm (Table 3). The spring mean of Cladocera > 0.71 mm biomass increased linearly during the cyprinid phase, but not the summer mean of Cladocera > 0.71 mm biomass or the annual mean of total zooplankton biomass (Table 3). The annual mean biomass of Cladocera > 0.71 mm and total zooplankton biomass was stable with minor fluctuations during the cyprinid phase (Fig. 5).

Development of fish diversity

Eighteen species of fish and one hybrid (*Abramis brama* × *Rutilus rutilus*) were caught in the reservoir. The average number of species detected in a particular yearly sampling was 12. The Shannon–Weaver index ($r^2 = 0.514$, $P > 0.001$) and the equitability index ($r^2 = 0.611$, $P > 0.001$) were significantly correlated with the age of the reservoir but no trend was found for number of species ($r^2 = 0.006$, $P = 0.748$) (Figure 6a–c).

Discussion

The development of the fish community between 1985 and 2006 was divided into an unstable perch phase and a stable cyprinid phase. The transition between these two phases was very fast, with perch ceasing to dominate in 1988–1989 (Figs 2 & 3). Two factors contributed to this change: fyke nets removed about 20 kg ha⁻¹ of perch every year during the perch phase (Seďa & Kubečka 1997) and an unidentified disease appeared in the perch population in 1988 (Seďa & Kubečka 1997). At that time perch was sensitive to disease because the population was composed mainly of 6–7 year old individuals, which were highly stressed by lack of prey (Kubečka *et al.* 1998). This allowed cyprinids to become dominant, although a strong recruitment of perch was found in some years (Vašek, Kubečka, Matěna & Seďa 2006). In contrast to perch,

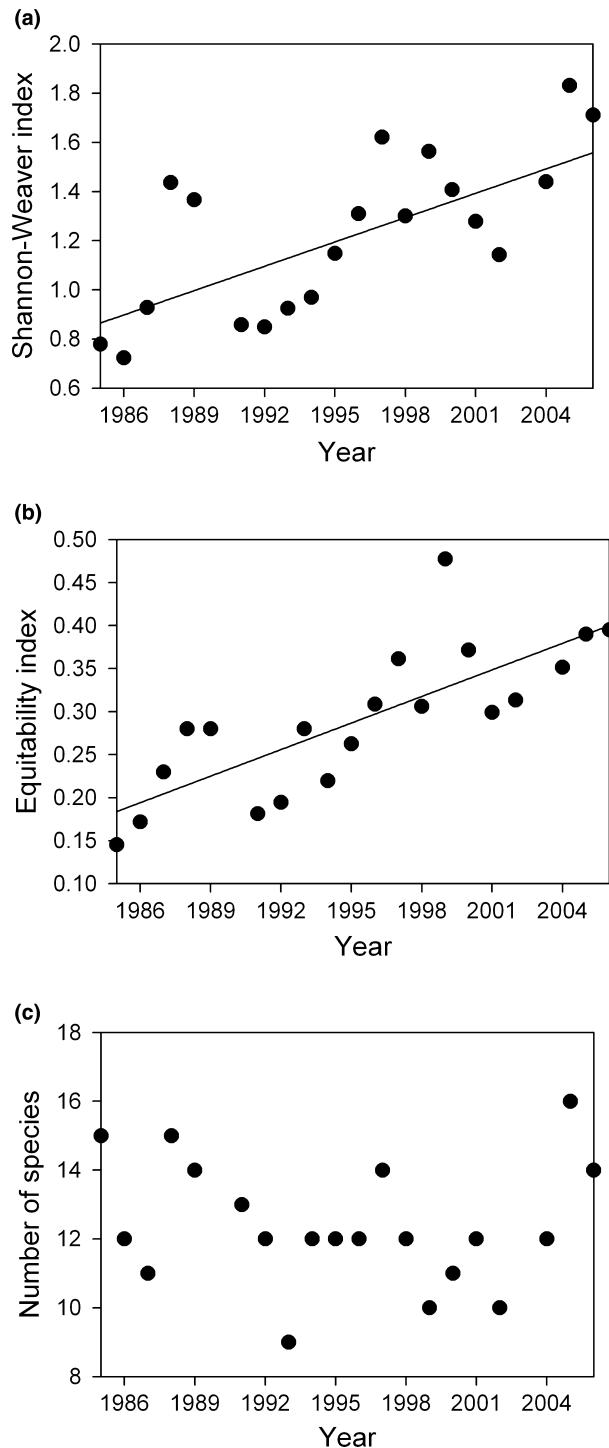


Figure 6. Relationships between the age of Řimov Reservoir and the (a) Shannon–Weaver index ($y = 0.033x - 64.64$); (b) equitability index ($y = 0.01x - 20.24$); and (c) number of fish species.

cyprinid species are better adapted to utilise food resources under eutrophic conditions, since both roach and bream are able to feed on zooplankton as adults,

and roach is also able to utilise algae whilst bream can feed on chironomid larvae burrowed in soft sediment (Johansson & Persson 1986). In Římov Reservoir, which is a eutrophic water body, perch foraging abilities and consequently abundance thus seem to be more limited than foraging abilities of cyprinids.

The highest fish community biomass was recorded in 1985 and apparently reflected initial boom in fish productivity that usually occurs in a newly-flooded environment (Holčík 1989; Tereshchenko *et al.* 2004). During the cyprinid phase, roach and bream had similar abundance dynamics resembling dampened oscillations of decreased amplitude. Their populations stabilised relatively quickly after the perch collapse. Although changes in biomass of large Cladocera correlated with the development of reservoir fish stock during the perch phase in 1980s (Seda & Kubečka 1997), no correlation between biomass of large Cladocera and fish stock was found during the cyprinid phase. This can be accounted for by the relatively stable cyprinid populations throughout the past 15 years, which exerted constant feeding pressure on zooplankton. In Římov Reservoir, both roach and bream were found to be largely zooplanktivorous throughout their whole life span (Vašek *et al.* 2003).

Stocking of piscivorous species into Římov Reservoir resulted in a very slow increase of their proportion in reservoir fish community mainly because of stocking of pikeperch. Several reasons probably account for the lack of response of pike and asp to stocking. Stocking rate of piscivores may have been insufficient to enhance their populations (Seda, Hejzlar & Kubečka 2000) or lack of submerged macrophytes in the reservoir possibly influenced pike reproductive success and population density. Conversely, abundance of asp might be underestimated by the sampling technique of night inshore seining as this species has an affinity to the pelagic zone (Prchalová, Kubečka, Vašek, Peterka, Seda, Jůza, Říha, Jarolím, Tušer, Kratochvíl, Čech, Draštík, Frouzová & Housová 2008). Total share of piscivores in the fish community of Římov Reservoir was relatively low and apparently they did not influence populations of planktivorous cyprinids to any extent. Biomanipulation experiments in other water bodies showed that abundance of piscivorous fish should be substantially higher to suppress planktivorous fish (Drenner & Hambright 1999; Wysujack & Mehner 2005).

The periods of high dominance of perch between 1985 and 1987, and bream and roach between 1991 and 1994 showed low species diversity (Fig. 6a–c). Later, a moderate increase in the densities of other species such as ruffe, *Gymnocephalus cernuus* (L.),

bleak, *Alburnus alburnus* (L.), pikeperch, asp and dace led to an increase in Shannon–Weaver and equitability indexes. Nevertheless, roach and bream were the most abundant species since the late 1980s and their populations appeared to be very stable. Even a major flood event that occurred in Římov Reservoir in 2002 (3 times normal flow volume through the reservoir) did not cause any substantial shift in fish community structure or in abundance of both dominant cyprinids.

Long-term fish stock development in Římov Reservoir is an example of succession toward a cyprinid dominance. After initial boom the fish community passed through a depression and then it reached a very stable cyprinid phase, which can be considered as a final stage in development of fish community in central European reservoirs (Kubečka 1993). The stabilised fish stock level can be approximately defined for the littoral fish community in the Římov Reservoir at an abundance of 2200 ind ha⁻¹ and biomass of 130 kg ha⁻¹.

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