*Hydrobiologia* **504:** 251–266, 2003.
*V. Straškrábová, R.H. Kennedy, O.T. Lind, J.G. Tundisi & J. Hejzlar (eds), Reservoir Limnology and Water Quality.*




# Fish migration between a temperate reservoir and its main tributary

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*Key words:* freshwater fish migration, reservoir-tributary ecotone, Czech Republic, spawning

## Abstract

Upstream- and downstream-directed migration between the Římov Reservoir and its only tributary, the Malše River (Czech Republic) was studied using two giant traps, sited at the mouth of the tributary, during the spring and summer periods, 2000–2002. The highest number of fish species was found in the tributary area (26 species and one hybrid). Over 10% of all fish biomass of the reservoir migrated through the tributary zone. The most important migration, in terms of fish numbers and intensity of movement, was the upstream spawning run. The fish species living in the reservoir can be divided into three groups: (1) the obligatory tributary-spawners (asp *Aspius aspius* (L.), bleak *Alburnus alburnus* (L.),chub *Leuciscus cephalus* (L.), and white bream *Blicca bjoerkna* (L.)); (2) generalists — fish spawning both in the tributary and the reservoir (bream *Abramis brama* (L.),roach *Rutilus rutilus* (L.), perch *Perca fluviatilis* L., pike *Esox lucius* L., and ruffe *Gymnocephalus cernuus* (L.)); and (3) fish spawning out of the tributary area (carp *Cyprinus carpio* L., pikeperch *Stizostedion lucioperca* (L.), catfish *Silurus glanis* L. and eel *Anquilla anguilla* (L.)). Tributary spawning is likely to support the strong roach population in the river upstream. Downstream migration from the river by salmonids appeared to be less important, in terms of relative numbers. Asp, roach and perch migrated as single spawners, bleak, bream and chub as multiple spawners. It was possible to define six periods of migration succession during spring and summer, which differed in species dominance, gonadal status and migration rates. The sequence starts with asp spawning and finishes after local movements of resident fish replace the spawning migrations. The most spectacular period during this sequence is the mass spawning of cyprinids when the roach, bleak, chub and bream migrate upstream and spawn nearly synchronically. During this period the daily migration rate exceeded 1000 individuals, which is over 100 times higher than during the feeding migration period.

## Introduction

The fish species living in artificial reservoirs are usually of riverine origin (Fernando & Holčík, 1981). Consequently, many of them cannot complete their whole life cycle in the lacustrine environment of the reservoir and require access to river habitat during crucial periods. Also the river fish may occasionally use the reservoir as a refuge or feeding ground. The inflow zone, the ecotone situated on the boundary between the riverine ecosystem and the reservoir, is likely to be an important migration path. All of the main types of fish migrations as defined by Lucas & Baras (2001) (feeding, refuge seeking, spawning migrations, post-displacement movements, recolonisation and exploratory migration) can be expected to happen in this ecotone.

The last decade has brought a significant increase in knowledge about migrations of freshwater fish especially in rivers (Jungwirth et al., 1998; Lucas & Baras, 2001). Studies of fish migrations and activity in temperate reservoirs, including those in Europe, have a considerable history (Vostradovský, 1968, 1969; Holčík, 1970; Vostradovská, 1974; Gusar et al., 1995; Baruš et al., 1997), but most have been associated with examining loss of and damage to fish moving downstream from reservoirs. None of the above studies were aimed directly at the migration through the river/reservoir ecotone. With respect to the riverine origin of many species, it has been assumed that some species like asp *Aspius aspius* (L.) (Vostradovský, 1974) and roach *Rutilus rutilus* (L.) (L'Abée-Lund and Vollestad, 1985) may exhibit regular migrations between lacustrine and fluvial environments, while others may maintain a restricted home range (Vostradovský 1968; Vostradovská, 1974). The present study aimed to provide a detailed understanding of fish migration events in the river/reservoir ecotone and to estimate the importance of the tributary for the functioning and management of the reservoir fish stock.

## Description of sites studied

The Římov Reservoir was built in 1978 at the Malše River 20 km south of České Budějovice, Czech Republic (dam co-ordinates: 48° 51′ 00″ N, 14° 29′ 29″ E). It is about 12 km long and is a deep valley water supply reservoir, with a mean area of 210 ha, average depth of 16 m and average storage time of about 90 days. The Malše River is a small river with an average discharge of 4.1 $m^3\ s^{-1}$ and it is the only significant river flowing into the Římov Reservoir. The experimental site was located at the point where the depth of impounded water on the former riverbed is 3 m during the very maximum water level of the reservoir (48° 48′ 04″ N, 14° 29′ 51″ E). This point is also usually identical to the location where cooler river-water submerges below the warmer reservoir epilimnion during summer thermal stratification ('plunging point'). At this point, the current of the river is decreased by the impoundment of the reservoir, but the flooded valley still have character of the river (river width 35 m, maximum depth 3 m during maximum reservoir water level). The development of the fish stock in the reservoir has been studied regularly since filling of the reservoir by the method of night shore seining (Kubečka & Bohm, 1991; Sed'a & Kubečka, 1997). The inshore areas had been sampled by the seine nets 50–150 m long, 4 m deep with the mesh size 10 mm. The area swept varied between 3 and 5 hectares every year. In the period of study (2000–2002), the biomass of fish from night shore seining has been levelling to about 100 kg $ha^{-1}$ with the dominant species roach and bream *Abramis brama* (L.) (data available from the Annual Reports of Hydrobiological Institute ASCR were extracted in Table 1). The list of fish species with common and scientific names is given in Table 1.

## Material and methods

Two independent specially constructed traps or fykenets (for detailed description and drawing, see Hladík et al., 2002) captured migrating fish in the tributary zone of the Římov Reservoir. Downstream trap sampled migrants travelling upstream (the wings and entering funnel facing to the reservoir) and an upstream trap sampled migrants travelling downstream (wings and entering funnel facing to the river). Each trap was composed of three chambers with a total length of about 12 m. The entrance frame was square in shape, with dimensions of 3×3 m, while the last chamber was circular with a diameter of 1.5 m. Each trap was equipped with two 3-m high and 25- and 40-m long wings arranged in V shape directing the fish into the chambers. The wings were not symmetrical due to the fact that the place with the maximum depth, where the trap body was located, was not in the centre of the flooded profile valley. The wings were set in a way to prevent any uncontrolled migration of fish. The layout of the wings and chamber on the bottom was checked by a scuba diver several times. The mesh size was 15 mm in all parts of the trap. A construction of tubular scaffolding was erected around each trap for easier installation and manipulation. The optimal depth for proper functioning of the traps was 0.75–2.75 m. If the water column decreased below the 0.75 m (usually in the second half of July) the funnels connecting individual net chambers emerged from the water surface and fish could no longer enter the traps.

The functionality of the traps depended mainly on the flow in the Malše River (Fig. 1). The traps did not function efficiently during periods of high riverflow. The water flowed over and below the wings due to congestion of the wings by drifting material and a substantial proportion of fish could migrate and evade capture. The critical flow rate for efficient capture depended also on the water level in the reservoir. When the water level was maximal, traps were stable during flows of up to 15 $m^3\ s^{-1}$, but when the water level decreased, flows over 5 $m^3\ s^{-1}$ could cause sinking of the wings. The frequent rainfall in 2001 caused increase of permeability of the wings on sev-

*Table 1.* The total numbers and the total biomass (kg) of individual fish species caught by traps during upstream (up) and downstream (do) migration through the tributary zone of the Rimov Reservoir (year 2000–00, 2001–01, 2002–02) and the average abundance and biomass in the Rimov Reservoir

| | | Tributary zone Total number (N) | | | | | | Tributary zone Total biomass (kg) | | | | | | Rimov res. aver. 00–02 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | | up00 | up01 | up02 | do00 | do01 | do02 | up00 | up01 | up02 | do00 | do01 | do 02 | N $ha^{-1}$ | kg $ha^{-1}$ |
| Brown trout | *Salmo trutta* m. *fario* L. | 10 | 4 | 15 | 35 | 45 | 63 | 0.5 | 0.4 | 1.9 | 2.3 | 2.8 | 5.3 | | |
| Rainbow trout | *Oncorhynchus mykiss* (Walbaum 1792) | 25 | 20 | 36 | 89 | 137 | 271 | 3.4 | 2.9 | 4.3 | 15.3 | 26.7 | 27.9 | | |
| Brook trout | *Salvelinus fontinalis* (Mitchell 1815) | 0 | 0 | 2 | 1 | 0 | 2 | 0.0 | 0.0 | 0.5 | 0.1 | 0 | 0.5 | | |
| Grayling | *Thymallus thymallus* (L.) | 0 | 0 | 0 | 4 | 12 | 16 | 0 | 0 | 0 | 0.7 | 0.7 | 1.4 | | |
| Pike | *Esox lucius* L. | 17 | 26 | 22 | 20 | 40 | 31 | 8.5 | 19.1 | 10.6 | 13.0 | 29.4 | 17.1 | 2.7 | 1.5 |
| Roach | *Rutilus rutilus* (L.) | 2301 | 688 | 2024 | 2985 | 1744 | 1297 | 383.9 | 93.6 | 251.1 | 851.4 | 332.4 | 218.4 | 738.0 | 25.8 |
| Dace | *Leuciscus leuciscus* (L.) | 40 | 6 | 11 | 6 | 20 | 35 | 0.5 | 0.1 | 0.3 | 0.3 | 0.4 | 1.3 | 6.5 | 0.1 |
| Chub | *Leuciscus cephalus* (L.) | 199 | 54 | 212 | 86 | 49 | 39 | 89.9 | 30.5 | 116.4 | 63.5 | 28.8 | 12.9 | 0.1 | 0.03 |
| Ide | *Leuciscus idus* (L.) | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0.01 | 0.02 | | |
| Rudd | *Scardinius erythrophthalmus* (L.) | 7 | 11 | 2 | 13 | 16 | 14 | 1.1 | 2.3 | 0.1 | 1.0 | 2.1 | 1.0 | 1.2 | 0.1 |
| Asp | *Aspius aspius* (L.) | 27 | 37 | 30 | 68 | 208 | 207 | 4.6 | 63.2 | 32.4 | 86.0 | 260.0 | 237.9 | 45.0 | 3.5 |
| Tench | *Tinca tinca* (L.) | 3 | 4 | 0 | 2 | 2 | 2 | 0.4 | 0.7 | 0 | 0.1 | 0.5 | 0.3 | | |
| Nase | *Chondrostoma nasus* (L.) | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0.1 | 0 | 0 | 0.5 | | |
| Gudgeon | *Bogio gobio* (L.) | 0 | 5 | 0 | 11 | 11 | 10 | 0.0 | 0.2 | 0.0 | 0.3 | 0.4 | 0.4 | 0.4 | 0.001 |
| Bleak | *Alburnus alburnus* (L.) | 4999 | 3612 | 1559 | 4337 | 2396 | 1184 | 323.9 | 178.6 | 90.8 | 275.2 | 126.2 | 66.4 | 116.4 | 4.5 |
| W. Bream | *Blicca bjoerkna* (L.) | 74 | 54 | 20 | 40 | 61 | 22 | 15.4 | 14.4 | 6.6 | 11.3 | 15.6 | 7.6 | 0.1 | 0.01 |
| Bream | *Abramis brama* (L.) | 591 | 746 | 1748 | 639 | 1206 | 610 | 330.5 | 462.8 | 1087 | 398.9 | 747.0 | 405.2 | 615.1 | 63.4 |
| Ab × Rr | *Abramis* × *Rutilis* (L.) | 21 | 17 | 67 | 71 | 123 | 112 | 5.6 | 5.4 | 22.9 | 25.6 | 39.8 | 38.2 | 8.7 | 0.9 |
| Crucian carp | *Carassius carassius* (L.) | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0.1 | 0.0 | 0.2 | 0.0 | | |
| Prussian carp | *Crassius 'gibelio'* (L.) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1.8 | | |
| Carp | *Cyprinus carpio* (L.) | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 4.0 | 0.1 | 0.5 |
| Catfish | *Silurus glanis* (L.) | 4 | 10 | 3 | 6 | 11 | 1 | 26.0 | 58.1 | 6.0 | 29.8 | 68.4 | 3.4 | | |
| Eel | *Anguilla anguilla* (L.) | 19 | 64 | 9 | 6 | 32 | 11 | 14.5 | 35.4 | 6.2 | 2.4 | 16.5 | 7.5 | 1.0 | 0.3 |
| Perch | *Perca fluviatilis* (L.) | 1495 | 411 | 356 | 684 | 524 | 436 | 95.3 | 43.6 | 48.2 | 65.5 | 90.3 | 56.3 | 64.8 | 4.6 |
| Ruffe | *Gymnocephalus cernuus* (L.) | 105 | 23 | 11 | 129 | 39 | 50 | 1.6 | 0.5 | 0.2 | 2.2 | 0.8 | 1.0 | 35.3 | 0.3 |
| Pikeperch | *Stizostedion lucioperca* (L.) | 44 | 59 | 17 | 43 | 152 | 43 | 11.1 | 24.8 | 9.0 | 10.9 | 46.7 | 17.7 | 14.1 | 3.0 |
| Bullhead | *Cottus gobio* (L.) | 0 | 0 | 1 | 1 | 3 | 4 | 0 | 0 | 0.01 | 0.02 | 0.05 | 0.05 | | |
| Total | | 9929 | 5801 | 6074 | 9127 | 6599 | 4081 | 1304 | 1014 | 1677 | 1825 | 1776 | 1082 | 1650 | 109 |

eral occasions and fish could migrate without being captured during these periods. The drifting trees during a small flood in April 2001 furthermore damaged the net wings and traps were out of full function for 2 weeks. In 2000 and 2002 there were fewer complications caused by high flow during trap operation. Dates of the start and finish of the sampling during particular seasons are given in Figure 1. The traps were installed at the end of March or in early April, as flows declined after elevations due to rainfall and snowmelt. The end of sampling depended on the drop of the water level in the reservoir. During 2000 the traps were installed till August and in 2001 sampling was finished in mid July. In 2002 sampling was finished one month sooner (see Fig. 1) because of an expected flood.

During the periods of intense fish migration, traps were checked and fish catches processed daily, while visits were made every second or third day during periods of less intense migratory activity. Fish were identified, measured, marked (fin clipping and elastomer tags, Northwest Marine Technology, 1995) before release about 100 m beyond the traps in the direction they were originally migrating. Fish received different marks for every migration direction and for every week.

The relative abundance of fish in different categories of reproductive condition in each catch was used as a measure of spawning activity. These categories were: (1) females full of eggs just before the spawning, (2) individuals releasing gonadal products (both sexes) and (3) freshly spent females within a few days after releasing eggs (recognised by the very soft, flaccid abdomen and swollen urogenital papilla). The Vltava River Authority (Povodi Vltavy) and Dr. J. Hejzlar, HBI ASCR, Ceske Budejovice supplied water level and water temperature data.

## Results

### *Fish usage of tributary zone*

The total numbers of migrating fish during individual seasons separated by fish species are given in Table 1. Twenty-six fish species and one distinct hybrid were captured. The dominant fish species in catches were the same as in the reservoir but their proportions varied from those estimated for the reservoir (Table 2). Bleak *Alburnus alburnus* (L.), perch *Perca fluviatilis* L., eel *Anquilla anquilla* (L.), white bream *Blicca bjo-*

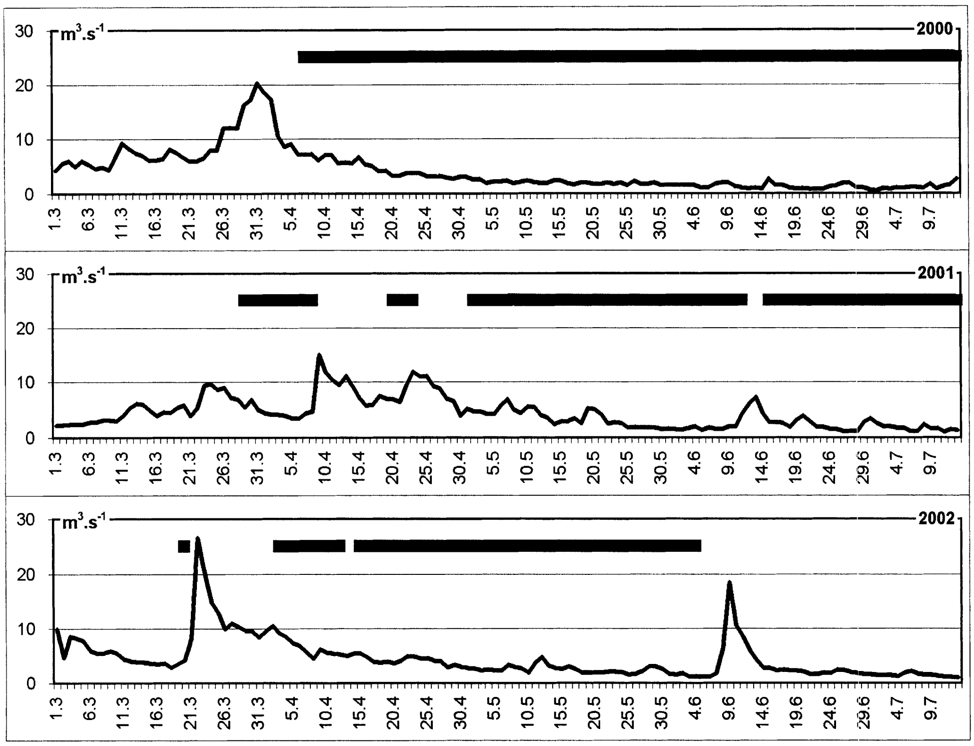


*Figure 1.* Average daily discharges of the Malše River into the Římov Reservoir during three seasons. Thick straight lines on the top of each plot mark the period of the trap operation.

*erkna* (L.) and chub *Leuciscus cephalus* (L.) appeared to prefer the tributary zone by comparison to their proportions in the reservoir, while others including roach, bream, chub, asp, ruffe *Gymnocephalus cernuus* (L.) and pikeperch *Stizostedion lucioperca* (L.) were of similar abundance or more common in the reservoir. Some river species captured in the tributary zone are extremely rarely captured in the reservoir (Table 1). The salmonids, brown trout *Salmo trutta* m. *fario* L., rainbow trout *Oncorhynchus mykiss* (Walbaum 1972), brook trout *Salvelinus fontinalis* (Mitchill 1815) and grayling *Thymallus thymallus* (L.) are regularly stocked in the Malše River above the reservoir by the Czech Fishing Association and fish migrating downstream after stocking were caught during every season. A few exhausted grayling were caught every season drifting downstream after spawning. Invading species Prussian carp *Carassius 'gibelio'*, nase *Chondrostoma nasus* (L.), and ide *Leuciscus idus* (L.) originating certainly from artificial stocking were reported for the first time for both the Římov Reservoir and Malše catchment area.

The total daily numbers of upstream and downstream migrating fish are given in Figure 2. The most intensive migration was the spawning run of cyprinids and perch. The timing of these migrations depended both on the water temperature (Fig. 2) and on the weather. No simple temperature value was found to be a trigger of the migration. It appears that the increase of temperature during nice weather subsequently to cool weather period in the end of April and start of May had the most significant effect irrespective of absolute temperature in any point of the increase. The total biomass of the main fish species caught in the tributary during the season 2000 and the total fish biomass in the Římov Reservoir (210 ha) are compared in Table 2. The fish caught in the tributary could be divided into three groups in accordance to their affinity to the tributary zone. The biomass of bream and pikeperch in the tributary zone was only 4.3 and 2.0% of total fish biomass, respectively, and so these appear to have exhibited low affinity. Moderate affinity was shown by ruffe (8.7% by biomass), pike *Esox lucius* L. (12.0%), perch (13.5%) and roach–bream hybrid (14.4%). Asp (22.7%), roach (24.8%) and bleak (26.6%) displayed rather high affinity. The total biomass of white bream in the reservoir could not be estimated adequately due to extremely low occur-

*Table 2.* The total numbers and biomass of fish caught in the season 2000 in the tributary of the Rimov Reservoir except recaptured fish and the total fish abundance and biomass in the Rimov Reservoir. The proportions of fishes migrating through the tributary zone on the total fish stock of the reservoir are given in the last two columns

| 2000 | Tributary zone | | Rimov Reservoir | | Relative composition (%N) | | Relative composition (%kg) | | Proportion of tributary fish | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Total N | Total kg | Total N | Total kg | Tributary | Reservoir | Tributary | Reservoir | % N | % kg |
| Bream | 918 | 558 | 134148 | 13052 | 5.7 | 31.3 | 21.7 | 57.9 | 0.7 | 4.3 |
| Roach | 5068 | 1167 | 202293 | 4715 | 31.6 | 47.1 | 45.4 | 20.9 | 2.5 | 24.8 |
| Ab×Rr hyb. | 92 | 31 | 2843 | 216 | 0.6 | 0.7 | 1.2 | 1.0 | 3.2 | 14.4 |
| Bleak | 7478 | 480 | 48342 | 1806 | 46.6 | 11.3 | 18.7 | 8.0 | 15.5 | 26.6 |
| Asp | 92 | 91 | 13293 | 399 | 0.6 | 3.1 | 3.5 | 1.8 | 0.7 | 22.7 |
| Perch | 2049 | 149 | 19131 | 1105 | 12.8 | 4.5 | 5.8 | 4.9 | 10.7 | 13.5 |
| Pikeperch | 69 | 15 | 3828 | 725 | 0.4 | 0.9 | 0.6 | 3.2 | 1.8 | 2.0 |
| Pike | 36 | 60 | 273 | 498 | 0.2 | 0.1 | 2.3 | 2.2 | 13.2 | 12.0 |
| Eel | 25 | 17 | 2.1 | 2 | 0.2 | 0.0 | 0.7 | 0.0 | 1190.5 | 801.2 |
| Ruffe | 233 | 4 | 5082 | 44 | 1.5 | 1.2 | 0.1 | 0.2 | 4.6 | 8.7 |
| Total | 16060 | 2571 | 429236 | 22560 | | | | | 3.7 | 11.4 |

rence, but observed spawning runs showed that affinity of adult fish to the tributary during the pre-spawning period was very high. The enormous relative biomass value of eel caught in the tributary to that caught in the lake (800%) suggests that eel lived especially in the tributary zone of the Římov Reservoir. However, this should be viewed with caution, since the numbers caught were low at both sites, and the method of shore seining in the reservoir probably underestimated the abundance of this species in the reservoir. In total, over 11% of the total fish biomass present in the reservoir was captured in the tributary zone.

*Migrations of individual species*

The most abundant fish species migrating to the tributary zone were cyprinids. The first cyprinid migrating to the tributary to spawn each year was asp (Fig. 3). The asp migrated to the tributary so early, that it was difficult to capture the start of the main upstream spawning run due to seasonal constraints on operation of the equipment (see Methods). In all three years we were more successful in capturing asp returning to the reservoir. Table 3 shows that females migrated to the tributary later (in 2001 we sampled the latest upstream migrating females, while males must have been already in the river) and returned immediately after spawning. Males seem to stay at the spawning grounds a few days longer. The average water temperature in the river during asp spawning reached 7–8 °C. The asp has only one spawning and therefore subsequent less distinct migrations (Fig. 3) can probably be classified as local movements of both adult and subadult individuals.

*Table 3.* Catch of asp *Aspius aspius* separated by sex

| 2001 | Upstream | | Downstream | | 2002 | Downstream | |
|---|---|---|---|---|---|---|---|
| Date | Female | Male | Female | Male | date | Female | Male |
| 29/3 | 0 | 0 | 2 | 2 | 3/4 | 43 | 0 |
| 1/4 | 1 | 0 | 3 | 0 | 5/4 | 36 | 20 |
| 3/4 | 4 | 2 | 24 | 4 | 8/4 | 9 | 48 |
| 5/4 | 16 | 0 | 52 | 4 | 10/4 | 2 | 10 |
| 7/4 | 1 | 0 | 41 | 55 | 12/4 | 2 | 12 |
| 9/4 | 0 | 0 | 1 | 0 | | | |

The roach started migrations also very early in the spring; the first migration waves occurred in the first half of April (Fig. 4). Nearly mature fish (females that were not ripe, while males started to release milt) migrated in this period in both directions. The main spawning runs of ripe individuals started on the turn of April and May when the water temperature in the river continuously increased and reached 13–14 °C. Spawning occurred soon after and within a few days the bulk of spawning roach returned downstream. Migration rates during the main spawning run were in the order of hundreds of individuals per day. Only one spawning of roach occurred each year and all subsequent movements may be regarded as local movements.

The most abundant fish species migrating to the tributary to spawn was bleak (Fig. 5). The pre-spawning migration was rather small, the majority of fish were caught during the first migration run when the water temperature in the river reached 13–14 °C.

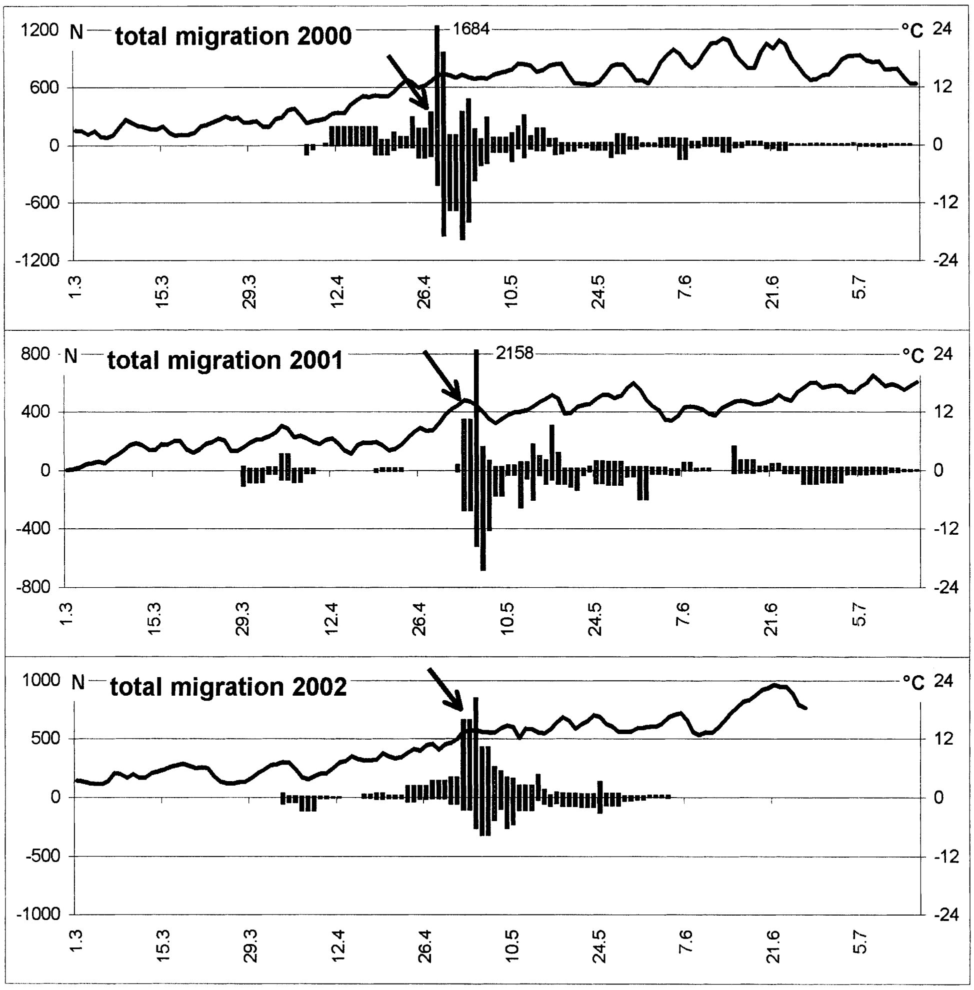


*Figure 2.* Time course of all fish migration through the tributary zone of the Římov Reservoir. Each plot is for 1 year. Upper histogram stands for upstream migrants, lower histogram for downstream migrants (negative sign left for plotting purposes). Continuous line marks the development of temperature. The arrow marks the start of mass spawning of cyprinid fish (third period of fish migration, see Table 5 and text for more details).

*Table 4.* Nuber of bleak in subsequent spawning migration waves

| Season | Total | 1st wave | 2nd wave | 3rd wave | 4th wave | 5th wave | Outside waves |
|---|---|---|---|---|---|---|---|
| 2000 | 4999 | 2254 | 972 | 696 | 186 | 211 | 680 |
| 2001 | 3612 | 2230 | 277 | 380 | 170 | 245 | 310 |
| 2002 | 1559 | 1162 | 131 | 91 | 69 | | 106 |
| | % | % | % | % | % | % | % |
| 2000 | 100 | 45.1 | 19.4 | 13.9 | 3.7 | 4.2 | 13.6 |
| 2001 | 100 | 61.7 | 7.7 | 10.5 | 4.7 | 6.8 | 8.6 |
| 2002 | 100 | 74.5 | 8.4 | 5.8 | 4.4 | 0.0 | 6.8 |

During the first run, according to data from marked fish, the majority of fish stayed in the tributary one day only spawned at once and returned to the reservoir. The bleak behaved like multiple spawners in

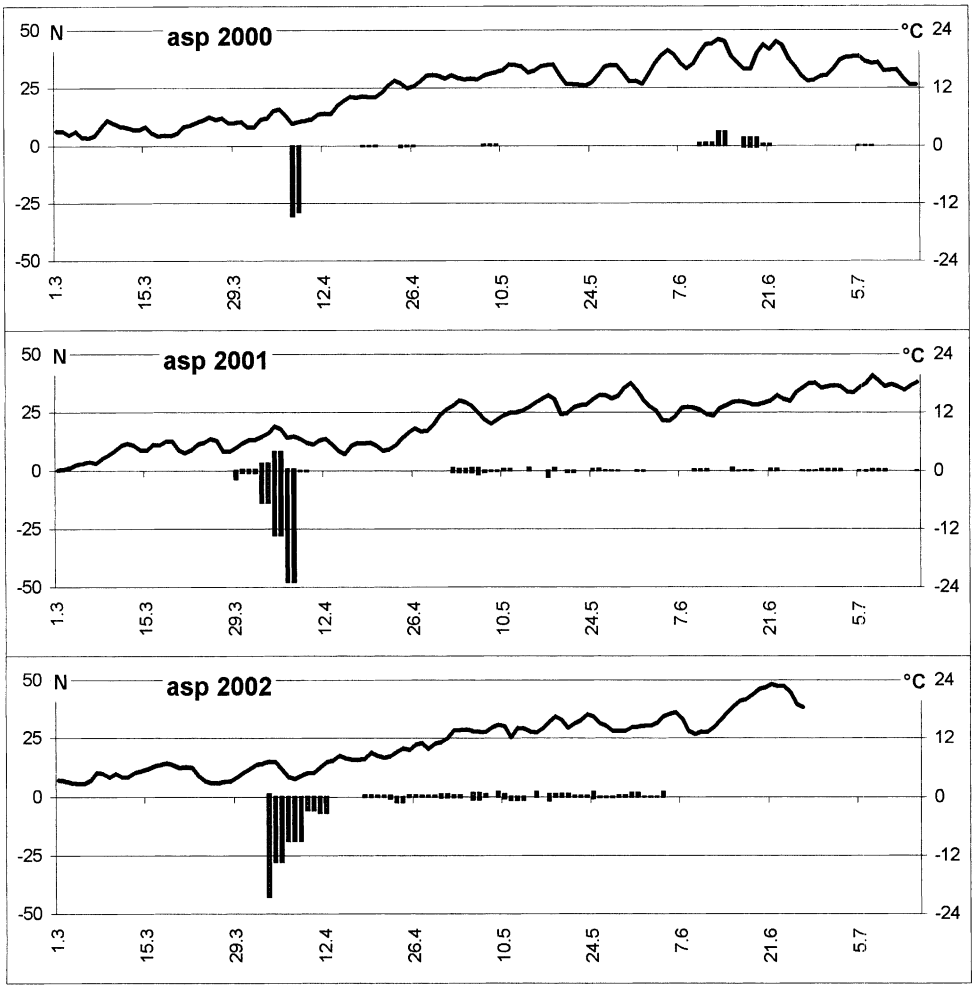


*Figure 3.* Time course of migration of the asp through the tributary zone of the Římov Reservoir. For further explanations see Figure 2.

the tributary of Římov Reservoir. After the main run, several weaker spawning runs occurred, each with decreasing strength (Table 4). Individual fish ripened gradually and every migration wave coincided with warm weather and a rise in water temperature. In 2000 and 2001, daily numbers of migrants exceeded 1000 individuals in the first migration wave and the absolute proportion of this wave on the total bleak upstream activity was 45.1, 61.7 and 74.5%, respectively, in the three seasons. The relative strength of the smallest spawning runs decreased to the level of 3–7% of total seasonal upstream activity; 7–14% of bleak moved outside of the main spawning period. The 2002 bleak migration was weaker due to the disappearance of the previously dominant 1998-year class.

The bream (Fig. 6) exhibited limited pre-spawning activity with a gradual increase of the proportion of ripe individuals and low migration rate. This period was followed by the main spawning run when the daily migration represented hundreds of individuals (13–14 °C). In the same period, massive spawning of bream was recorded in the whole reservoir. Many bream returned back to the reservoir after spawning while another significant part stayed every season in the river pools above the traps for a longer time and returned after subsequent spawning. In the following period, clement weather and increased water temperature stimulated further spawning of this fractionally spawning species. In 2002, the majority of bream remained in the tributary above the traps (MH, JK, personal observation) and it is believed that they returned to the reservoir during the June flood after dismantling the traps.

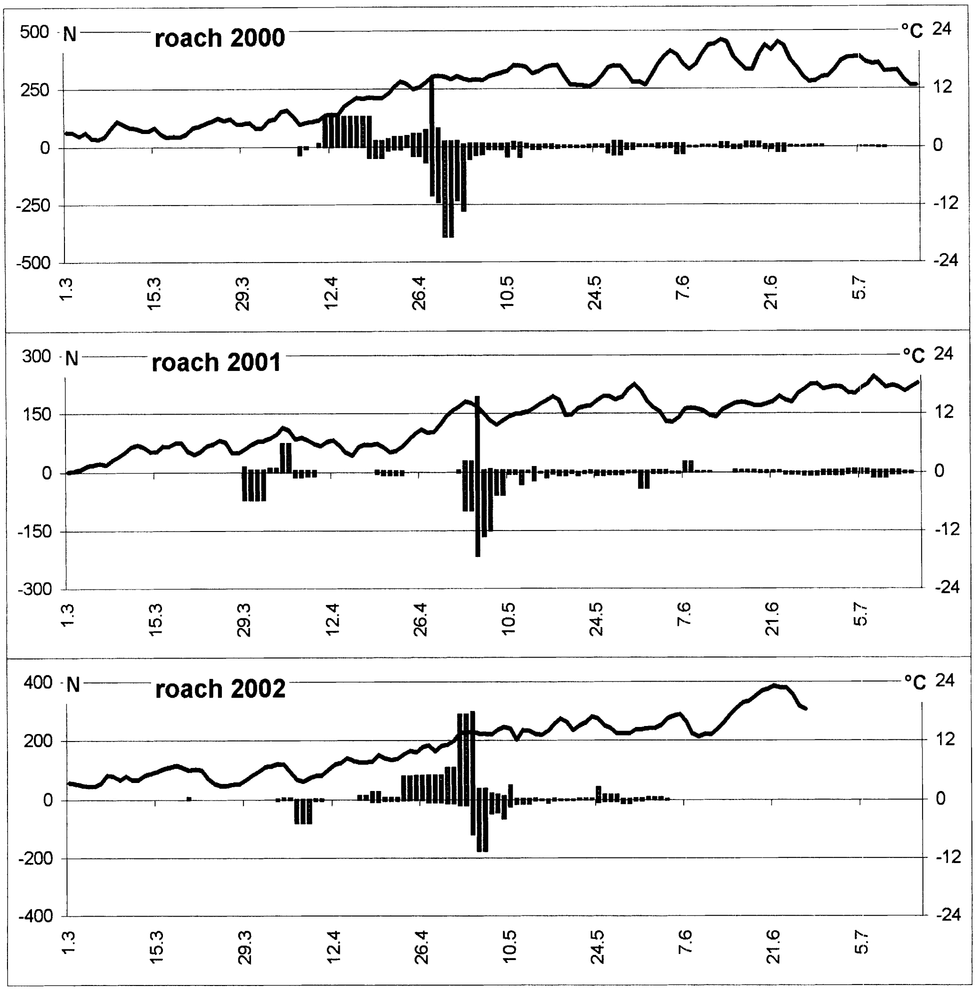


*Figure 4.* Time course of migration of the roach through the tributary zone of the Římov Reservoir. For further explanations see Figure 2.

The main migration of chub was triggered by a similar temperature level of 12–14 °C (Fig. 7). The daily migration rate during the main wave was 10–30 chub, with one to five fish in the remaining period. In all years, the upstream movement prevailed above downstream. This may indicate that this species uses the reservoir as a refuge for overwintering and the river for spawning and feeding during spring and summer. Ripe individuals of the hybrid followed the spawning run of roach and bream. Every season a run of ripe white bream was observed (58, 37 and 13 individuals, respectively) migrating to the tributary to spawn about 2 weeks after the main migration runs of dominant cyprinids (14–16 °C). A few ripe individuals of rudd were also caught in the same period.

The most abundant perciform fish species, perch, started migratory activity very soon in the study period (Fig. 8) and spawning activity culminated when the water temperature reached 8–12 °C. Records for 2001 were interrupted by high flow. Perch spawning migration activity was more prolonged than with cyprinids and gradually changed into feeding migration as especially spent females predate on eggs on cyprinid spawning grounds (MH, JK, personal observation). The peak catches of perch were in the order of 30–90 individuals, but from April onwards some perch were present in nearly all trap liftings. Several individuals of other predatory species (pikeperch, eel, pike and European catfish) were captured nearly every day in the traps. The difference between the period of spawning migration and later period of local movement was less apparent as none of the above species uses the Malše River as preferred spawning ground.

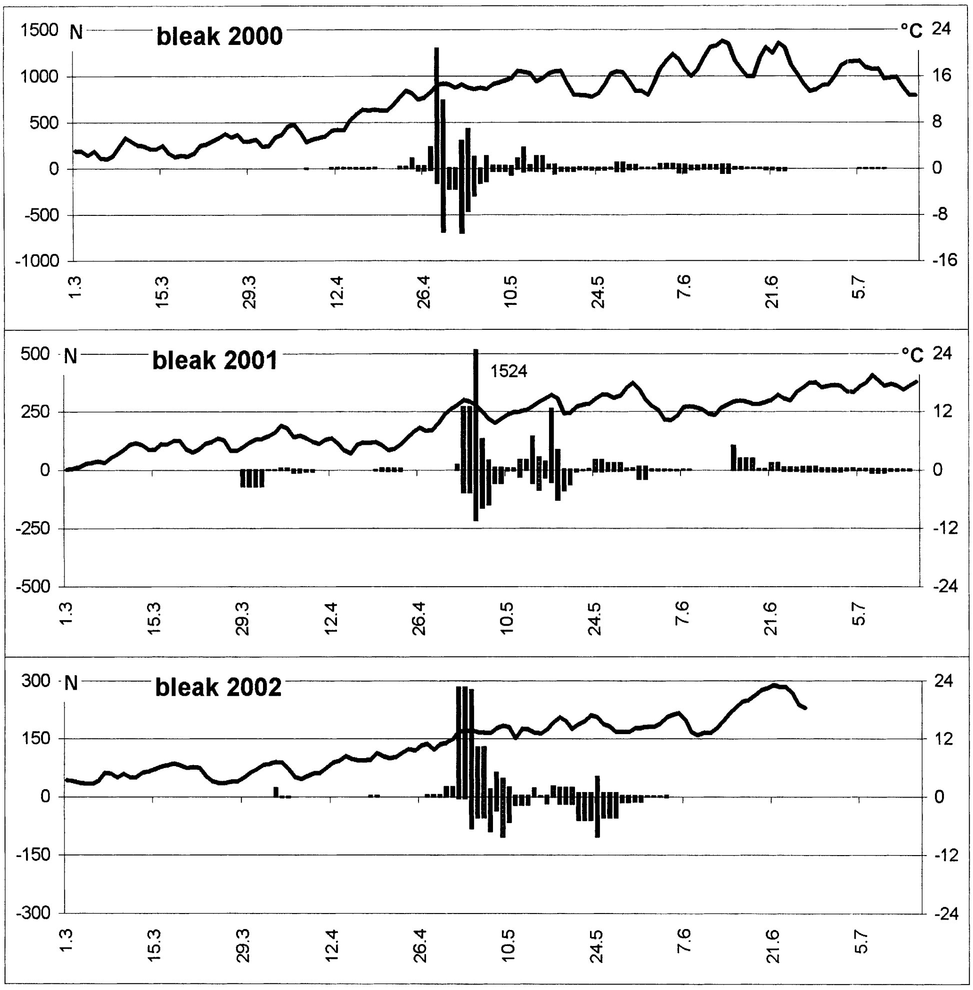


*Figure 5.* Time course of migration of the bleak through the tributary zone of the Římov Reservoir. For further explanations see Figure 2.

*Periods of fish migration*

Three seasons of intensive study revealed several regular periods of spring and summer fish migration events from which it was possible to define characteristic periods of the seasonal succession of migrants (Table 5):

1. Period of asp spawning: 1 March to approximately 10 April, asp dominates in biomass and sometimes in numbers. Prespawning migration of perch, roach and bream is also apparent. Yearly average daily migration rate of all species ranged between 60 and 105 individuals per day.
2. Prespawning phase of the main cyprinid species. Approximately 10 April until 1 May. Phase after finishing of asp spawning (all females spent), but before the main spawning run of cyprinids. The males of roach, bleak, bream and chub may be active and releasing milt, but the females do not release eggs. Perch spawning starts in this period. Yearly average daily migration rate of all species is slightly higher (80–180 fish per day, the data of 2001 were influenced by flood interrupting the sampling — Figure 1)
3. The main spawning run of cyprinids. Last days of April and early May. Females of the roach, bleak, bream and chub start to release eggs nearly simultaneously. These dates are marked by the arrows in Figure 2. The proportion of sexually active individuals reaches its maximum (Fig. 9). Simultaneously, the migration rate increased to over 1000 individuals per day (except 2002 lacking numerous 1998 year classes of bleak, which died during the period 2001/02). Nearly half of fish bio-

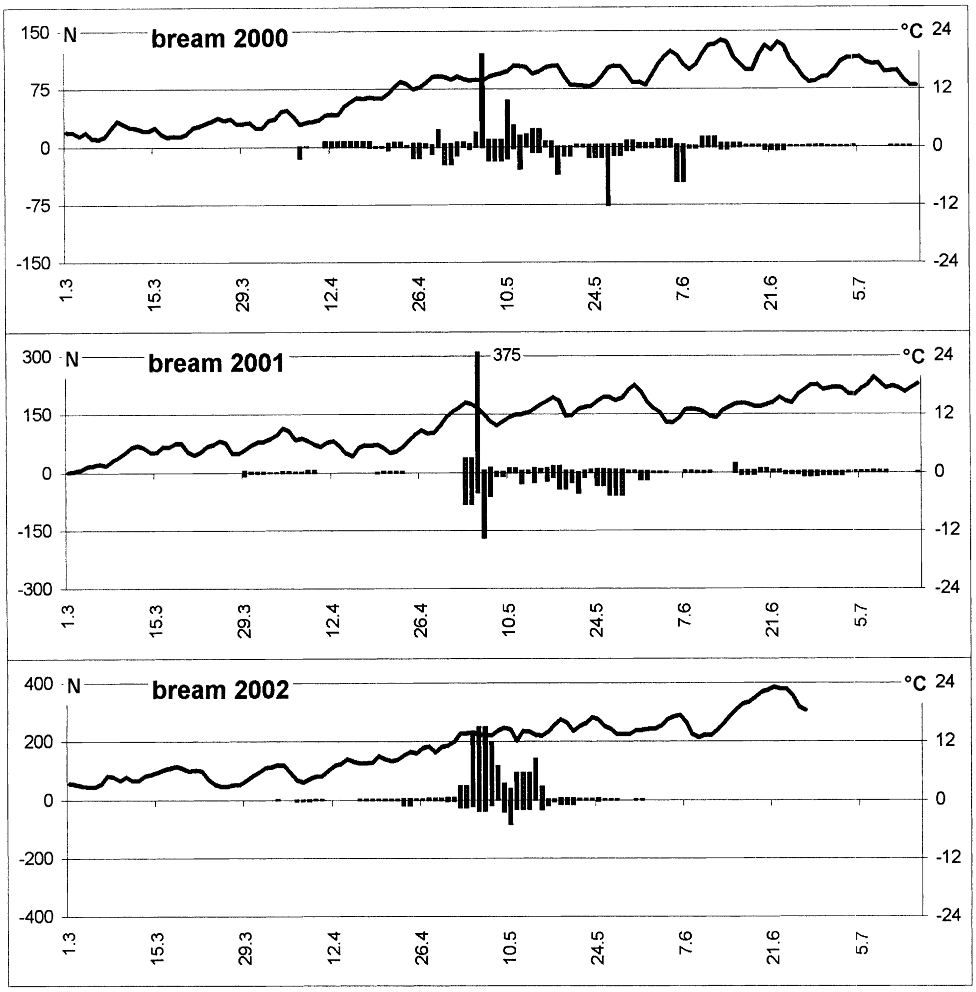


*Figure 6.* Time course of migration of the bream through the tributary zone of the Římov Reservoir. For further explanations see Figure 2.

mass migrates during this period. The end of this period can be defined by the absence of females releasing the eggs. Prolongation of this period depends very much on weather. The usual extent is 3–7 days (Fig. 10), but a drastic cooling can shorten the massive spawning like in 2001. Figure 10 shows that the spawning run of the four species can be completely synchronous as in 2001 or the ripening of bream can be delayed by several days. Figure 10 shows that the first bream run during the main run of roach, chub and bleak was actually not the strongest and the main spawning run of bream happened 10 days later in 2000. The massive spawning of other dominant species was terminated within 8 days and the main bream migration wave fallen into the next period (compare also Table 5 with unusually low bream migration in the period 3 of 2000).

4. The period of multiple spawning migration of multiple spawners, mainly bleak and bream (but also white bream and rudd). Early May–early June. Females of these species release eggs during periods of warm weather, each of which triggers a new wave. Other species carry on mainly local movements, which are much less apparent than spawning migration waves. Migration rate ranged between 100 and 160 individuals per day.
5. Transient period when the local movements takes over the spawning migration of multiple spawners. Early June until mid July. The proportion of ripe individuals decreases (Fig. 9) as well as the migration rate (usually <50 fish per day).

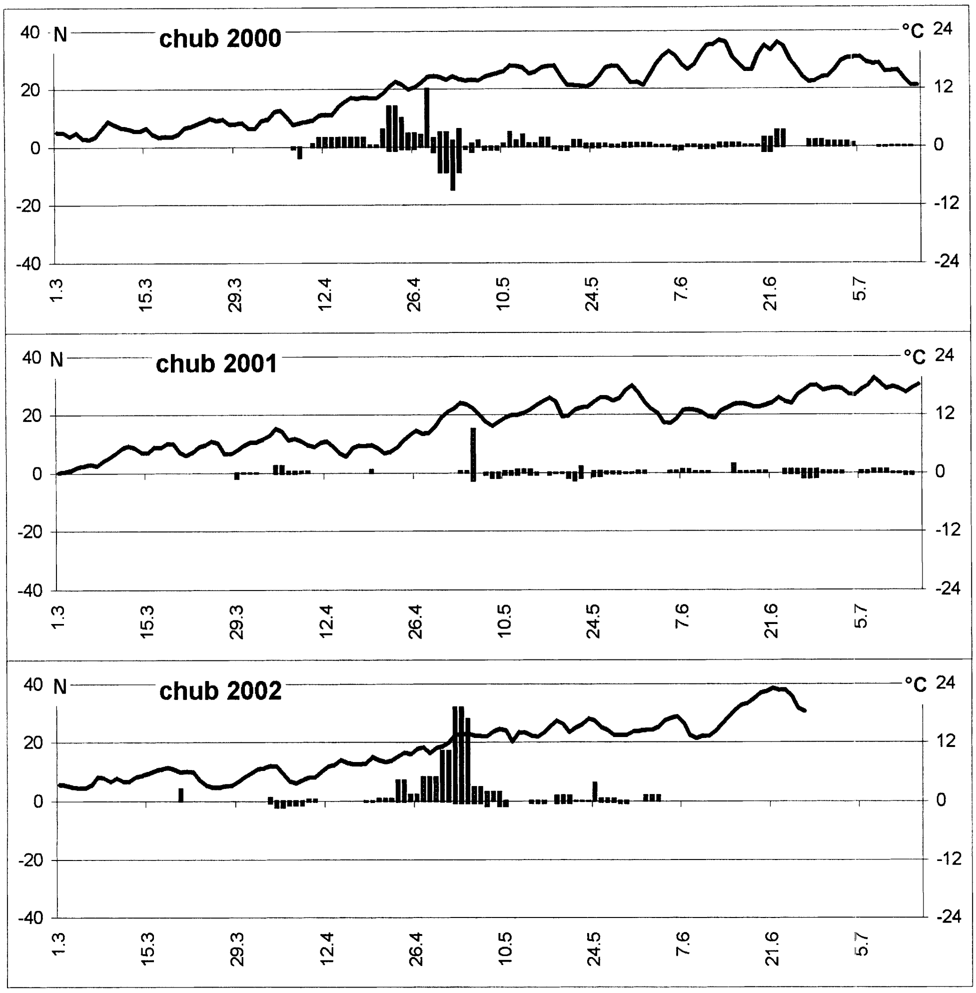


*Figure 7.* Time course of migration of the chub through the tributary zone of the Římov Reservoir. For further explanations see Figure 2.

6. Summer period with highly reduced spawning activity, mid July until August. Ripe individuals are very rare except for bleak (Fig. 9). Most migrating bleak are still ripe for spawning but their numbers are low. The daily migration rate is the lowest of all periods (<10 fish) and most migrations have character of local feeding movements (recaptures of the same individuals were frequent).

## Discussion

The reservoir tributary zone was found to be an extremely important area for fish. A significant proportion of the total fish stock migrated through it. Ecotoneal character predetermined much higher number of fish species recorded here compared both to the reservoir and the river (Kubečka, 1990). Some species seem to be strictly dependent on the tributary zone as they were never observed reproducing in the reservoir (asp, bleak, chub, and white bream), while others are facultative tributary users (roach, bream, pike, perch, rudd). With obligatory tributary spawners, at least 20% of their biomass migrated through the tributary zone. No other spawning activity of these species was recorded in the reservoir. The main source of error of the present study is the fact, that it was extremely difficult to keep giant traps operational during high water discharges. Despite considerable effort of cleaning the wings and additional weighting of the lead line, the traps were out of function for about 10% of the total experimental period. Events during these periods might have been interesting as high discharges might have stimulated both active and passive

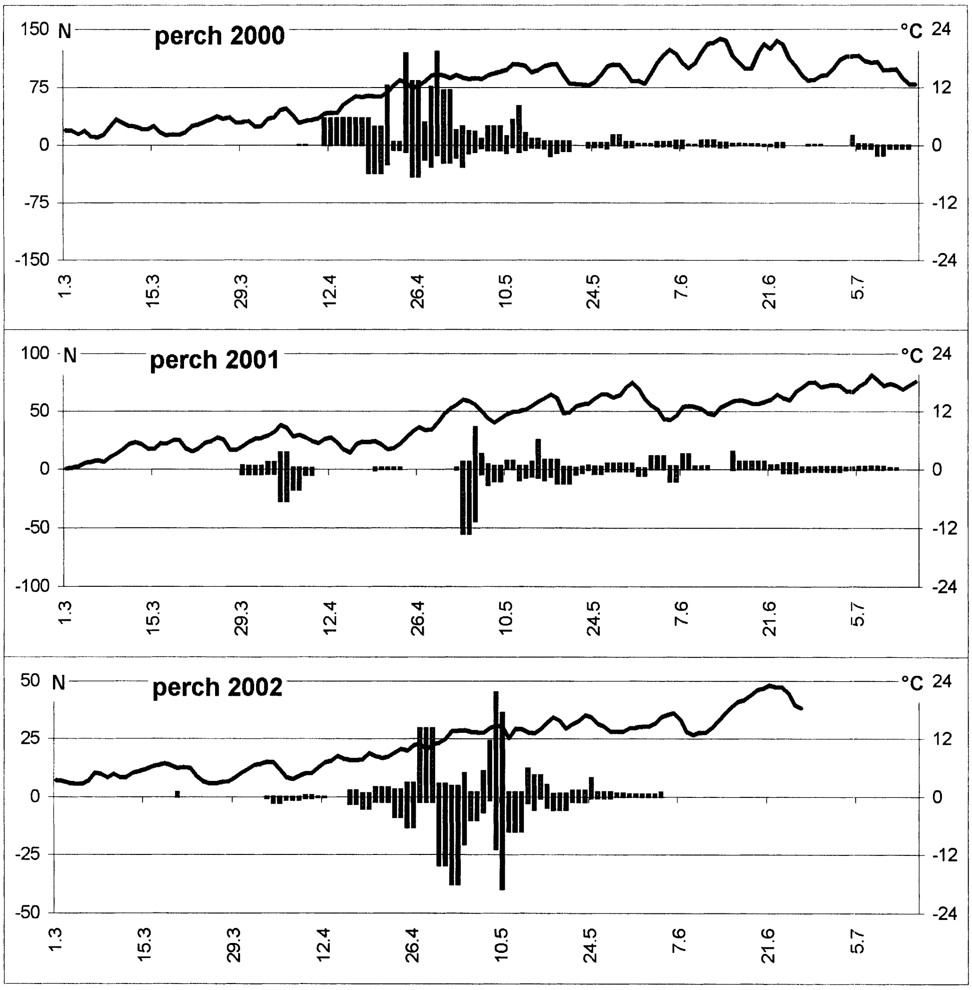


*Figure 8.* Time course of migration of the perch through the tributary zone of the Římov Reservoir. For further explanations see Figure 2.

migrations (Lucas & Baras, 2001). Some fish could also migrate without being sampled during cleaning of the trap wings, when the structure was permeable for about 30 min every second or third day. We do not believe this to have been a major problem because at the same time the cleaning boats created much disturbance around the lifted wing creating a 'disturbance barrier'. In any case we have to consider our catches as the minimum estimates of the total migration activity. Catches of migrating fish were batch marked by elastomer tags (different combinations of colour and tag location) and the ratio of marked and unmarked fish was estimated in both traps, reservoir bellow the traps and the river above the traps. Future analysis of this extensive data set (over 30 000 marked fish) could provide some estimate of the 'permeability' of traps.

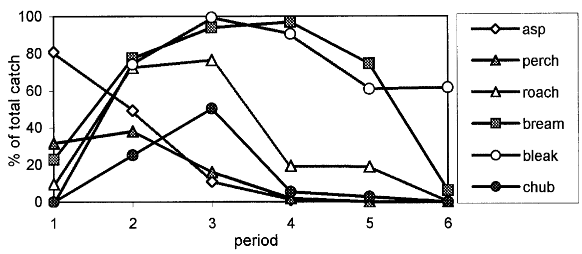


*Figure 9.* The development of the proportion of spawning individuals in particular periods of fish migration as defined in the text and Table 5 (average for the three years compared).

Three replicate years of trapping could help to fill some gaps of knowledge caused by discharge variations. Our attempt to extract more general classification of spring and summer migration events is based on superimposition of the experience of all three years.

*Table 5.* Duration, water temperature. migration rate (ind. per day in both directions) and relative share of individual periods on the total recorded migration of the main fish species (numerical – N, biomass – kg). Question marks stand for periods not sampled. For he definition of the periods see text

| Period | | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | 2000 | ? 7.4– 8.4 | | 9.4 – 26.4 | | 27.4 – 4.5 | | 5.5 – 14.6 | | 15.6 – 14.7 | | 15.7 – 24.8 | |
| | 2001 | 29.3 – 7.4 | | 8.4 – 2.5 | | 3.5 – 7.5 | | 8.5 – 1.6 | | 2.6 – 14.7 | | ? | |
| | 2002 | ? 3.4 – 12.4 | | 13.4 – 1.5 | | 2.5 – 10.5 | | 11.5 – 4.6 | | ? | | ? | |
| W. temp. (°C) | | 7 – 8 | | 8 – 12 | | 12 – 15 | | 14 – 22 | | 16 – 22 | | 14 – 20 | |
| Migration rate | | Aver. | SD | Aver. | SD | Aver. | SD | Aver. | SD | Aver. | SD | Aver. | SD |
| | 2000 | 77 | 27 | 182 | 86 | 1151 | 575 | 153 | 115 | 25 | 23 | 9 | 7 |
| | 2001 | 104 | 42 | 9 | 14 | 1049 | 825 | 160 | 90 | 48 | 39 | ? | ? |
| | 2002 | 61 | 43 | 86 | 72 | 638 | 240 | 104 | 71 | ? | ? | ? | ? |
| % of catch | | N | kg | N | kg | N | kg | N | kg | N | kg | N | kg |
| Asp | 2000 | 60.6 | 82.1 | 4.0 | 6.4 | 0.0 | 0.0 | 16.2 | 4.5 | 15.2 | 1.8 | 4.0 | 5.3 |
| | 2001 | 86.5 | 90.0 | 1.2 | 1.4 | 3.7 | 3.3 | 4.9 | 3.2 | 3.7 | 2.0 | ? | ? |
| | 2002 | 77.2 | 77.6 | 5.5 | 4.8 | 5.5 | 4.1 | 11.8 | 13.5 | ? | ? | ? | ? |
| Perch | 2000 | 0.1 | 0.1 | 38.9 | 38.8 | 27.6 | 26.7 | 24.3 | 23.0 | 5.0 | 4.7 | 4.1 | 6.8 |
| | 2001 | 19.4 | 20.4 | 2.3 | 2.4 | 25.4 | 25.9 | 28.8 | 28.4 | 24.1 | 230 | ? | ? |
| | 2002 | 2.3 | 2.4 | 34.8 | 41.9 | 41.5 | 32.6 | 21.3 | 23.0 | ? | ? | ? | ? |
| Roach | 2000 | 1.0 | 1.0 | 30.9 | 33.2 | 44.9 | 45.0 | 17.6 | 16.2 | 4.5 | 4.0 | 1.1 | 0.5 |
| | 2001 | 21.4 | 22.7 | 3.6 | 3.7 | 40.6 | 41.2 | 18.7 | 17.8 | 15.7 | 14.6 | ? | ? |
| | 2002 | 8.7 | 9.1 | 29.4 | 30.2 | 52.4 | 51.8 | 9.6 | 8.9 | ? | ? | ? | ? |
| Bream | 2000 | 1.3 | 1.4 | 9.1 | 10.1 | 9.4 | 9.9 | 73.6 | 73.9 | 4.0 | 3.0 | 2.5 | 1.6 |
| | 2001 | 1.8 | 2.1 | 1.1 | 1.2 | 49.4 | 56.1 | 40.8 | 35.3 | 7.0 | 5.2 | ? | ? |
| | 2002 | 1.1 | 1.2 | 3.9 | 4.4 | 64.9 | 70.7 | 30.2 | 23.7 | ? | ? | ? | ? |
| Bleak | 2000 | 0.1 | 0.1 | 3.0 | 3.1 | 62.6 | 63.3 | 31.3 | 30.5 | 2.2 | 2.1 | 0.8 | 0.9 |
| | 2001 | 0.3 | 0.3 | 0.7 | 0.7 | 47.7 | 48.5 | 32.3 | 32.0 | 18.9 | 18.5 | ? | ? |
| | 2002 | 1.2 | 1.2 | 2.4 | 2.4 | 63.7 | 64.4 | 32.7 | 32.0 | ? | ? | ? | |
| Chub | 2000 | 1.7 | 1.9 | 29.3 | 31.9 | 30.6 | 29.1 | 21.4 | 18.2 | 13.9 | 13.8 | 3.1 | 5.2 |
| | 2001 | 10.7 | 12.6 | 1.9 | 2.2 | 19.4 | 21.4 | 33.0 | 33.1 | 35.0 | 30.8 | ? | ? |
| | 2002 | 5.7 | 6.5 | 33.3 | 37.0 | 49.2 | 46.9 | 11.8 | 9.5 | ? | ? | ? | ? |

The periods are defined using ecological characteristics (temperature, time, species composition gonadal status, migration rate) and have different extents in time. Therefore formal statistical analysis of the significance of differences between the periods would be difficult. Even without an attempt of rigorous statistic analysis, we are positive that the periods introduced could help understanding migration events in similar river/reservoir systems.

Northcote (1984) and Lucas & Baras (2001) presented schematic models showing how the control of the timing of migration depends on interaction between internal physiological state of the fish and external triggering factors in the environment. These factors are especially water temperature and water discharge. Water temperature in particular has a natural influence on the physiological state of poikilotermic fish. Despite variable weather in the three years, the main spawning events occurred over a very similar period with similar temperatures. When fish are ready to spawn in late April or early May, several warm days function always as a trigger of massive spawning. The same seems to apply to subsequent spawning runs of multiple spawners. It is interesting that many cyprinid fish perform the main spawning at the same time. Synchronous spawning of cyprinids appears to be a

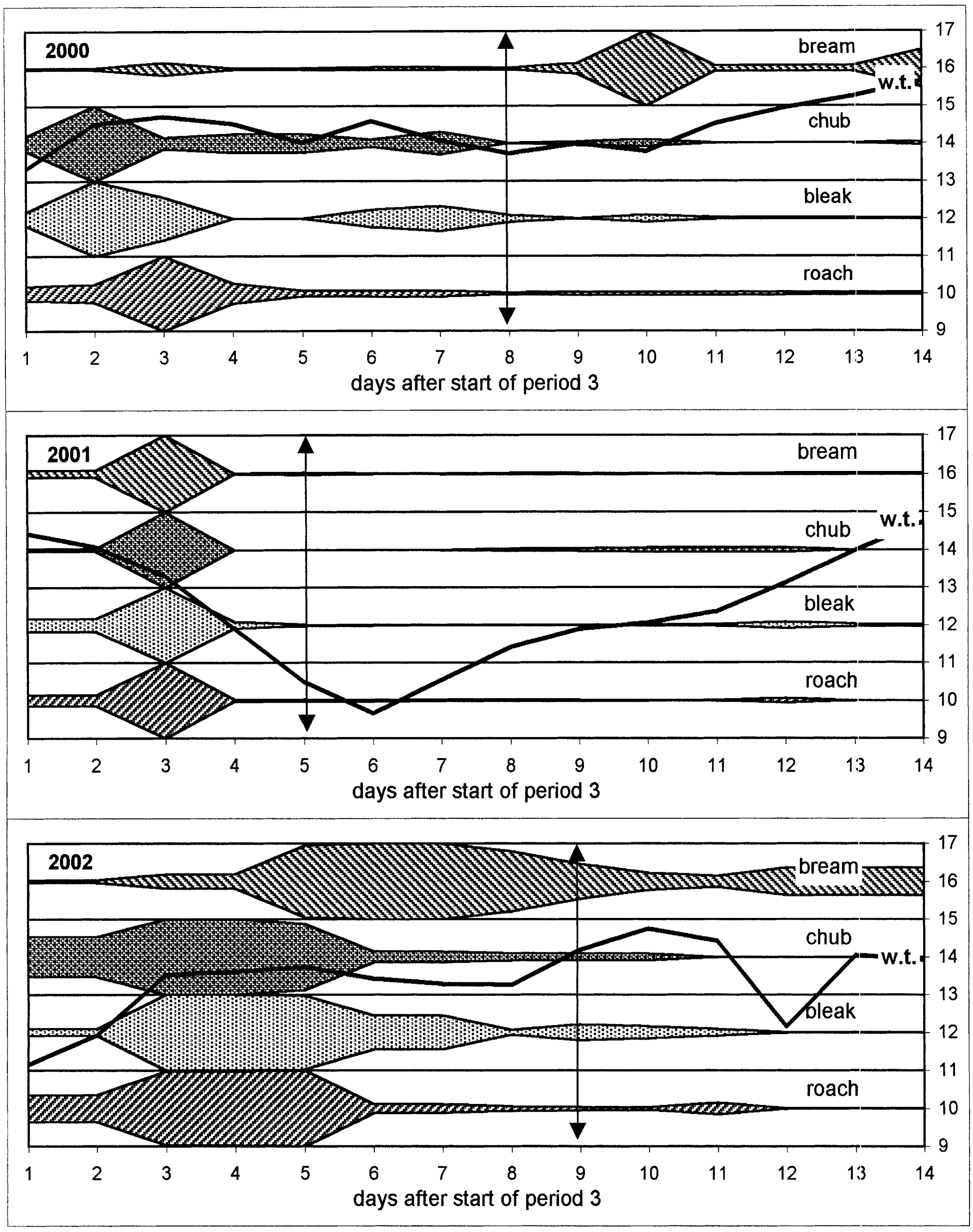


*Figure 10.* Detailed analysis of the upstream migration of four cyprinid species during the period 3 — mass spawning and few subsequent days. Maximum catch of every species fills the whole space between separating horizontal lines. The thickness of shaded area shows every day catch proportionally to the maximum catch. Vertical arrow marks the end of period 3 when no more females releasing eggs were captured. The right axis shows the water temperature (w.t.).

frequent event in Czech reservoirs (Kubečka, 1990; Pivnička & Švátora, 2001). The present study shows that both synchronous and delayed spawning of bream can happen in the tributary. Synchronous spawning may provide a good opportunity for hybridisation. The proportion of roach × bream hybrids to their parent species was usually higher in the tributary zone compared to the main reservoir. Increasing water discharge which usually triggers the migration of anadromous fish (Northcote, 1984) appears to have rather opposite effect in the reservoir tributary as high discharge is usually a consequence of cold rainy weather. In the Malše, cyprinid fish spawn in the river gravel and submerged plants (mostly *Batrachium*), 400–2000 m above the traps, so there is no need for high water level for spawning migration. The fish used high flow rather for the downstream migration or were simple 'flushed' back to the reservoir.

Fishery managers are frequently concerned about upstream influence of reservoir fish stocks especially on salmonid fisheries (Kubečka, 1990). Such influence can be significant especially in early stages of reservoir fish succession dominated by pike or perch (Kubečka, 1993). The fish stock of the Římov Reservoir is a typical example of cyprinid-dominated fish fauna and the results show only limited migratory activity of predatory fish upstream (with the exception of spawning of asp). Asp return quickly to the reservoir and even its juveniles do not stay in the river for long (MH, unpublished observations based on electrofishing of Malše River above the reservoir). Other recorded migrations of predatory fishes tend to be characterised by local movements, as confirmed by marking experiments (the same fish captured many times) and their absence in upstream river reaches (electrofishing). Probably the main upstream effect is a significant input of fish eggs spawned in the river by the reservoir fish during spawning runs. According to electrofishing in the river above the reservoir, roach is the dominant species. Marking revealed that roach from upstream in the Malše River rarely exchange with the reservoir stock, but the upstream population is likely to be supported by high imput of roach eggs. In the 1980s, when the fish stock of the reservoir was perch-dominated (Kubečka, 1990), the perch population in the river was probably supported from the reservoir in a similar way. Two important tributary spawners — bream and bleak seem to behave in a different manner. Adult fish may remain in the river for several weeks or months and participate in multiple spawnings. Later they always return and also their juveniles drift downstream so there are no reservoir-supported populations in the river. Part of the chub stock uses the reservoir as an overwintering refuge. The reservoir's fish stock receives salmonid and cultured fish from upstream river as a result of human activity (stocking, accidental escape from ponds), but this input seems to have little significance.

The significance of the local movements of resident fish seems to be much lower compared with spawning. Many fish utilise as a feeding ground the uppermost part of the reservoir epilimnion (Vašek et al., 2003), which provides the highest primary and secondary production (Macháček, 2001). The traps were installed just above the uppermost point of epilimnion and only relatively poor river water was available upstream of the traps. Reservoir fish (Vostradovský 1968; Vostradovská, 1974) seem to have rather restricted migrations compared to the same species in rivers (Whelan, 1983; Lucas & Baras, 2001). All our results support this notion for facultative tributary spawners (marking revealed that the fish resident not too far from the tributary are the migrants). With obligatory tributary spawners, the fish from the whole reservoir gather for the upstream migration. But even these species seem to be more abundant closer to the tributary (Kubečka et al., 2002).

## Conclusions

The tributary zone of the Římov Reservoir was found to be a very important area for spawning of reservoir fish, and was characterised by spring spawning migrations, especially of cyprinids and perch. Over 10% of all fish biomass of the reservoir migrated through the tributary zone during spring and summer. The highest number of fish species (26 and one hybrid) compared to both river and reservoir inhabited the tributary area. The fish species living in the reservoir can be divided into three groups: (1) the obligatory tributary-spawners (asp, bleak,chub, and white bream), over 20% of estimated total reservoir stock of these fish migrated through the tributary zone; (2) generalists — fish spawning in suitable places both in the tributary and the reservoir (bream,roach, perch, pike, and ruffe); and (3) fish spawning out of the tributary area (carp *Cyprinus carpio* L., pikeperch, catfish *Silurus glanis* L. and eel). Tributary spawning is likely to support a strong roach population in the river upstream. Downstream migration from the river (salmonids) appears to be less important.

Individual species differed in temporal extent of the migration, asp, roach and majority of bream and bleak returned back to the reservoir, while some bream, bleak and especially chub stayed in the river for much longer time. Asp, roach and perch migrated as single spawners, bleak, bream and chub as multiple spawners. It was possible to define six periods of migration succession during spring and summer, which differed in species dominance, gonadal status and migration rates. The sequence starts with asp spawning and finishes after replacing the spawning migrations by the feeding ones. The most spectacular period is the mass spawning of cyprinids when the roach, bleak, chub and bream migrate upstream and spawn nearly synchronically. The daily migration rate exceeds 1000 inds. during this period what is more than 100 times higher than during the feeding migration only.

## Acknowledgements

The study was supported by the project No. 206/02/0520 of the Grant Agency of the Czech Republic and projects No. S6017004 and A6017201 of the Grant Agency of AS CR, programmes No. K6005114 and Z6017912 of the AS CR and the programme MŠM 1231 00004 of Czech Ministry of Education. The help of the members and friends of ichthyological working group of HBI and of Vltava River Authority (Povodí Vltavy) during the extensive fieldwork is greatly appreciated. We thank Dr Martyn Lucas, Dr.Josef Matěna and anonymous referees for constructive comments on the manuscript.

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