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Seasonal migration and habitat use of adult barbel (*Barbus barbus*) and nase (*Chondrostoma nasus*) along a river stretch of the Austrian Danube River

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Abstract Migration patterns and habitat use of adult barbel (*Barbus barbus*) and nase (*Chondrostoma nasus*) were monitored by radio telemetry over a period of 13 months along a 58-km-long section of the Austrian part of the Danube River. The study site is confined upstream and downstream by two hydropower plants, and contains a larger tributary, the Pielach River. Telemetry transmitters were implanted into fish caught in this tributary after spawning in June (25 individuals per species). The results show that both species use the entire available width and depth spectrum of the Danube along the full migratable river length. Nase had an average home range of 22.4 km, while that of barbel was 34.4 km. The habitat use of the two species differs significantly. While the nase was primarily encountered in the free-flowing section, barbel mainly used deep areas of the impoundment during the year. Nase showed a distinct site fidelity to certain areas in the free-flowing reach which were periodically revisited. During the spawning season, distinct homing behavior was observed in both species. All seven nase that could still be detected during the spawning season returned to the tributary (homing rate 100%). Six homing nase migrated up to the first migration barrier in the tributary but did not pass the existing fish passage facility. In contrast, only nine barbel returned to spawn in the tributary (homing rate 50%), while nine barbel were most likely using a spawning location in the head of impoundment section. Homing fish entered the tributary during darkness.

Keywords Large river · Homing behavior · Site fidelity · Rheophilic cyprinids · Connectivity

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Introduction

Most riverine fish migrate during their lifetime as a central component to complete their life cycle. Fish migrate from one type of habitat to another to spawn, to forage, or to avoid unfavorable conditions (Lucas and Baras 2001; Brönmark et al. 2014). Migration patterns depend on specific spatio-temporal traits and environmental factors encountered during the life cycle of each species (De Leeuw and Winter 2008; Brönmark et al. 2014; Alexandre et al. 2016; Benitez and Ovidio 2018; Capra et al. 2018). During the past 150 years, habitat conditions for fish have deteriorated dramatically (Hohensinner et al. 2013; Grill et al. 2015; Haidvogl 2018). The loss of suitable habitats and the disruption of migratory routes have led to a general decline in riverine fish populations (Lucas and Baras 2001; Nilsson et al. 2005; Binder et al. 2011; Grizzetti et al. 2017; Gutmann et al. 2019; Pavlov et al. 2019; Belletti et al. 2020).

While the migratory behavior of highly migratory salmonid species is comparatively well researched (Northcote 1997; Winter and Van Densen 2001; Ovidio et al. 2007; Brönmark et al. 2014), much less is known about migrations of potamodromous fish species, in particular that of cyprinids. However, over the past 15 years, the number of related studies has increased substantially, the majority of which have focused on small and medium-sized rivers. For instance, the migration behavior of barbel (*Barbus barbus*) was investigated in English rivers (Lucas and Batley 1996; Gutmann et al. 2019), the River Ourthe in Belgium (Baras and Cherry 1990; Baras 1997; Ovidio et al. 2007), and the River Jihlava (Czech Republic) (Penáz et al. 2002). The migration and spawning behavior of nase (*Chondrostoma nasus*) was examined along Swiss, Belgian, and Austrian rivers (Huber and Kirchhofer 1998; Ovidio and Philippart 2008; Melcher and Schmutz 2010). Large rivers, however, are often the habitat of core populations within population networks and are therefore of central importance for the respective metapopulations (Schmutz and Jungwirth 1999; Dettmers et al. 2001; Wilkes et al. 2018). Interestingly, large-scale tagging studies on the migratory behavior of river fishes on large European rivers such as the Danube, Rhine, Main, and Neckar rivers were conducted as early as the 1920s and 1930s (Steinmann et al. 1937). Although Steinmann et al. (1937) documented migration distances of single individuals of several hundred kilometers, major research projects on the migratory behavior of fishes in large European rivers are pending since then. Only few studies documented spawning migrations over longer as well as site fidelity and homing behavior to previously used spawning sites (Baras and Cherry 1990; Ahnelt and Keckeis 1994; Lucas and Batley 1996; Ovidio et al. 2007; Capra et al. 2018). Waidbacher and Haidvogl (1998) provide a generalized view of characteristic migration distances for potamodromous species of the Danube catchment such as barbel or nase with "medium distance migrations" between 30 and 300 km in one direction within 1 year. The extent of migrations depends on the size of the rivers, and populations in small to medium-sized rivers often perform shorter migrations because suitable breeding habitats, nurseries, shelter, and foraging sites are often spatially closer to each other (Baras 1997; Huber and Kirchhofer 1998; Vilizzi et al. 2006; Rakowitz et al. 2008; Berger 2009; Benitez et al. 2015; Ovidio et al. 2016). Apart from limited insights into the migratory behavior, it must be emphasized that most larger European rivers are highly fragmented (Grill et al. 2019; Belletti et al. 2020). Therefore, the natural migratory behavior of nase and barbel can only be observed to a limited extent or only on individual rivers without extensive barriers. Comprehensive knowledge, however, concerning the migratory behavior of the various species and populations inhabiting large rivers is a basic prerequisite for developing suitable measures and strategies to sustainably improve river habitats and the corresponding fish populations (Cooke et al. 2013; Alexandre et al. 2016).

A main reason for the large gaps in knowledge regarding the migratory behavior of potamodromous fishes in large rivers is that the studies are methodologically much more complex due to the dimensions of the rivers compared to medium and small streams (Zajicek and Wolter 2018). Due to the partial great water depths and the extensive dimensions of water bodies, fish ecological studies on large rivers, such as the Danube, pose considerable methodological difficulties (reviewed by Radinger et al. 2019).

Within the frame of this study, the migration behavior of nase and barbel, two key fish species of the Austrian Danube River, was observed over a period of 1 year. The central objectives of the present study were as follows: (i) to describe species-specific habitat use, whereby we hypothesized that nase and barbel primarily colonize shallower gravel bars with average maximum water depths of 3 to 4 m and only move to deeper habitats during the winter months; (ii) to record seasonal migration behavior, hypothesizing that tagged individuals colonize stretches of the Danube only a few kilometers away from the tributary (their spawning site) throughout the year; and (iii) describing potential homing behavior to specific habitats and/or to specific spawning sites based on the telemetry data.

Materials and methods

Study area

The study was undertaken between June 2002 and June 2003 along a 58-km-long reach of the Austrian Danube situated between river kilometers 1980 and 2038 from the Black Sea. The study reach is physically bounded by the run-of-river hydropower plants (HHP) Melk at the upstream end and the HPP Altenwörth confining the study reach downstream (Fig. 1). Both HPPs were not equipped with fish migration facilities at the time the study took place. The reach comprises two main river sections of different habitat quality: (1) the 34-km-long free-flowing section called "Wachau" (channel width: 250–300 m, cross-sectional maximum water depths: 6–9 m) below the HPP Melk, and (2) the 22-km-long impoundment upstream the HPP Altenwörth (channel width: 350 m, cross-sectional maximum water depths: 10–15 m). These two main sections are connected by the head of the reservoir section of the HPP Altenwörth situated near the city of Krems, depending on the water level, approximately between the Danube River kilometers 2004 and 2002. This 2-km-long part in-between the free-flowing and the impounded sections will hereafter be named as the "transition zone" (Fig. 1). In the upper section, the free-flowing Wachau, morphological habitat development, such as the formation of islands, side arms, and gravel banks, is restricted by the narrow valley bottom. Also, the natural morphology was altered by diverse river regulation measures (e.g., groynes, bank stabilization/riprap). The natural morphological character of the Danube changes in

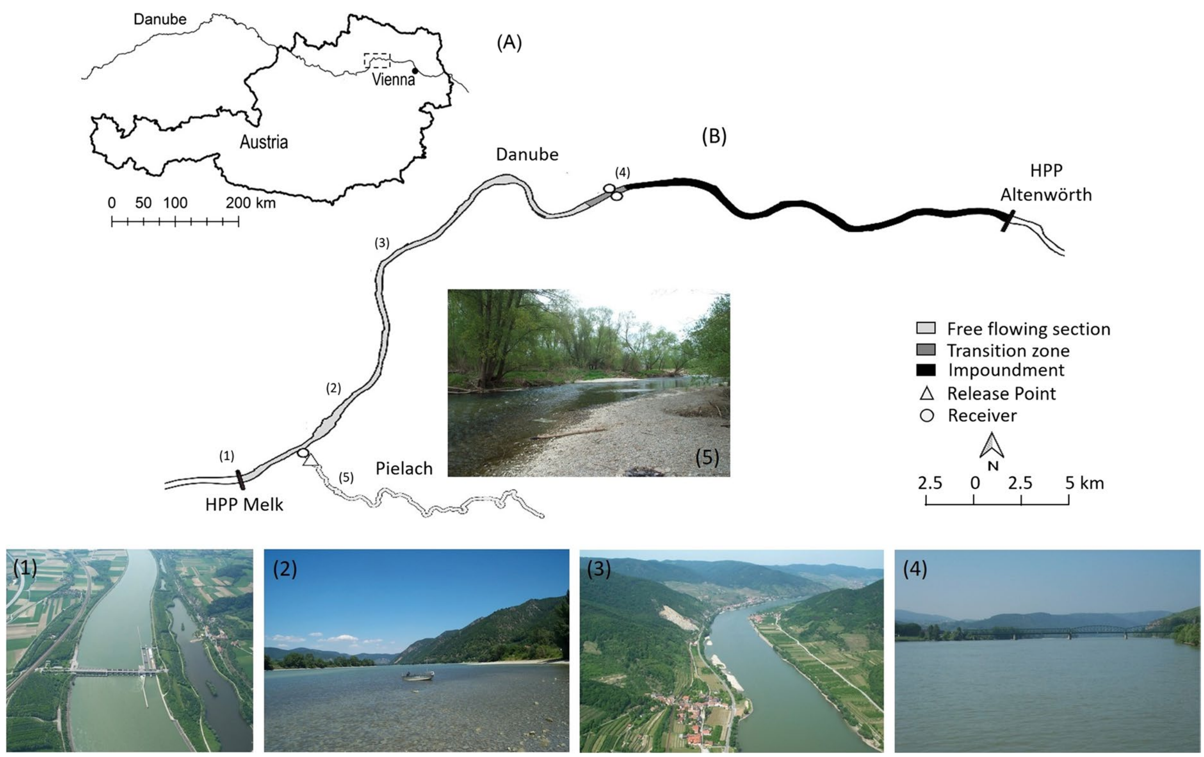

Fig. 1 Study reach: **A** general map showing the location of the study area west of Vienna. Map (**B**) provides a schematic view of the study reach with the Danube between the HPPs Melk (1) and Altenwörth, and the River Pielach. In the Danube, the free-flowing Sect. (2, 3), the transition zone (4), and the impoundment at Altenwörth are displayed by different colors. Circles indicate the position of fixed receivers in the lower section of the River Pielach (5) and the road bridge (4) in the transition zone

the transition zone as the valley bottom also becomes wider. While the free-flowing Wachau area still offers predominately lotic habitats and a near natural river morphology, stagnant habitats dominate the impounded lower section.

A major tributary, the Pielach River, joins the Danube River 3.7 km below the HPP Melk at kilometer 2034. The lower reaches of the Pielach provide suitable spawning grounds for lithophilic fishes along a stretch of 1.6 km below the first migration barrier (Zitek et al. 2008). The Pielach River drains a mean annual flow of 6.5 $m^3 \cdot s^{-1}$ and has an average channel width of 25 m and mean maximum water depths of 1.5 m.

Water temperature and discharge data of the Danube were continuously recorded during the study period at a gauging station centrally located in the study area and operated by the Lower Austrian provincial government. The Danube's daily temperature ranged from 1 to 21 °C with an average of 11 °C. The daily mean flow during the study period ranged from 1161 to 11,072 $m^3 \cdot s^{-1}$. The mean water discharge during the study period was 2207 $m^3 \cdot s^{-1}$. During the study period, an extreme high flow event (discharge over 11,000 $m^3 \cdot s^{-1}$) occurred in August 2002 (see Online Resource 1).

Fish tagging

Eighteen female and seven male barbel with a length of 460–610 mm, weight 854–2015 g, as well as 25 female nase with a length of 410–510 mm, weight 712–1548 g, were caught by electrofishing during their post-spawning downstream migration in the Pielach River (Tables 1 and 2). After the catch, the fish were immediately placed in a caged receptacle set up on the riverside and rested for approximately half an hour. Each fish was then transferred to an anesthetic tank containing clove oil at 24 $ml \cdot l^{-1}$ for 5 to 10 min until their operculum rate slowed significantly. After length and weight measurement, each fish was placed on a V-shaped surgical cradle and supplied with continuous flow of water for gill irrigation. Fish were tagged with coded radio transmitters on five different transmission frequencies (Lotek MCFT-3EM, 11 × 49 mm) and 399 days of operational life. Transmitter weight did not exceed 2% of fish body weight on air nor 1.25% of their weight in water (Jepsen et al. 2005).

The transmitter was implanted into the body cavity via a 2-cm mid-ventral incision posterior to the pelvic girdle, and the incision was closed with two separate monofilament absorbable sutures (Serasynth) and tied with a double surgeon's knot. The same expert performed all surgeries. Tagging equipment and all other surgical accessories were cleaned by alcohol. Duration of each tagging procedure was approximately 5 min. After transmitter implantation, tagged fish were allowed to recover in another cage for 20–30 min until they regained full equilibrium. Only female nase were tagged as males have been found to be physically weakened after spawning and may therefore show an increased mortality rate (Luskova et al. 1995; Huber and Kirchhofer 1998; Ovidio and Philippart 2008), which may affect detection rates over the entire study period. After the tagging procedure and checking the functionality of the transmitters, all fish were released back into the Pielach River next to the capture site on June 10th and June 18th in 2002 (Tables 1 and 2).

Fish tracking

Fish tracking started the day after tagging and release. Tagged barbel and nase were primarily monitored by manual tracking along the study reach. Tracking surveys at the Danube River were carried out by boat using a Lotek SRX-400 receiver additionally equipped with an antenna amplifier (Triax TA 4135). Fish locations were logged using a hand-held Global Positioning System (GPS) unit (Garmin Map 76S). When a fish was located, we successively reduced the receiver gain and switched from a Yagi antenna to an antenna with a weaker reception (rod antenna).

The actual location of the fish—the place where the signal could just be received—could thus be narrowed down to about 10 m^2. At each fish's positions, water depth was determined using an echo-sounder (Lowrance X-71), and distance to the nearest riverbank was measured using a Riegl Lasertape FG21-HA. Fish positions were recorded during 43 days within the 13 months study period. Sampling intensity during June to December 2002 ranged from 1 to 5 days per month (see Online Resource 2). No tracking surveys by boat were performed between January and February 2003.

Additionally, three permanent data logging stations were installed. One at the mouth of the Pielach River,

Table 1 Characteristics of radio-tracked barbel during 2002–2003

Code	Tagging date (dd/mm/yy)	Sex	Length (mm)	Weight (g)	Emigration date after release (dd/mm/yy)	Last detection (mm/yy)	Detection period (month)	Freq. records		Home range (km)	Main habitat (month present)	Homing	Chronology at the Pielach River				
								By boat	Days in transition zone				Arrival date	Immigration date	Immigration time	Emigration date	Emigration time
B01	10/06/02	F	580	1093	10/06/02	03/03	10	2	–	41.5	IM (7)	–	–		–	–	–
B02	10/06/02	F	515	1212	10/06/02	06/02	1	2	–	–	–	–	–	–	–	–	–
B03	10/06/02	M	525	1166	11/06/02	05/03	12	11	–	17.9	FF (11)	No	–	–	–	–	–
B04	10/06/02	F	505	1155	11/06/02	06/03	13	–	1/1	34	IM (11)	Yes	27/05/03	03/06/03	22.32	RP	–
B05	10/06/02	M	525	1217	10/06/02	06/03	13	2	16/8	34	IM (9)	No	–	–	–	–	–
B06	10/06/02	M	460	864	10/09/02	06/03	13	2	8/0	34	IM (6)	Yes	16/03/03	17/03/03	03.55	RP	–
B07	10/06/02	F	485	1030	21/06/02	06/03	13	2	19/10	34	IM (11)	No	–	–	–	–	–
B08	10/06/02	F	490	990	13/06/02	06/03	13	1	11/3	34	IM (9)	No	–	–	–	–	–
B09	10/06/02	F	565	1342	13/06/02	06/03	13	3	6/1	34	IM (9)	Yes	10/04/03	15/04/03	21:23	31/05/03	15:28
B10	10/06/02	F	570	1571	10/06/02	06/02	1	1	–	–	–	–	–	–	–	–	–
B11	10/06/02	F	465	1000	13/06/02	06/03	13	–	43/33	34	IM (9)	Yes	16/06/03	16/06/03	02:48	RP	–
B12	18/06/02	F	485	879	18/06/02	06/03	13	8	30/21	34	IM (9)	No	–	–	–	–	–
B13	10/06/02	F	520	1105	18/06/02	06/03	13	7	19/12	35.7	IM (9)	Yes	29/04/03	02/05/03	–	26/05/03	08.13
B14	10/06/02	F	530	1335	10/06/02	05/03	12	1	16/7	34	IM (9)	Yes	06/05/03	06/05/03	10:17	8/05/03	22.38
B15	10/06/02	F	585	1670	11/06/02	03/03	10	–	6/0	34	IM (9)	–	–	–	–	–	–
B16	10/06/02	F	500	1000	13/06/02	03/03	10	1	2/0	42.3	IM (9)	–	–	–	–	–	–
B17	10/06/02	F	495	965	10/06/02	06/03	13	2	5/2	34	IM (9)	Yes	29/04/03	02/05/03	–	05/06/03	03.22
B18	10/06/02	F	605	2015	11/06/02	05/03	12	12	6/2	20.1	FF (11)	No	–	–	–	–	–
B19	10/06/02	F	480	920	10/06/02	08/02	3	1	–	47	IM (2)	–	–	–	–	–	–
B20	10/06/02	M	535	1275	18/06/02	04/03	11	2	6/4	42.4	IM (9)	No	–	–	–	–	–
B21	18/06/02	F	610	1534	18/06/02	06/03	13	1	22/12	34	IM (10)	No	–	–	–	–	–
B22	18/06/02	M	565	1343	18/06/02	06/03	13	1	25/15	34	IM (9)	No	–	–	–	–	–
B23	18/06/02	M	465	854	18/06/02	05/03	12	5	10/2	34	IM (9)	Yes	21/04/03	26/04/03	21:41	12/5/03	02.06
B24	18/06/02	M	515	957	18/06/02	06/03	13	2	8/1	34	IM (9)	Yes	14/04/03	15/04/03	22:05	31/05/03	14.19
B25	18/06/02	F	570	1650	–	–	0		–	–	–	–	–	–	–	–	–

The two numbers in column “days in transition zone” refer to the number of days the fish was localized there across the whole study period and days during mid of April and mid of June, respectively. IM, FF, and PR are the abbreviation of fish whereabouts in the impoundment section, the free-flowing section, and the Pielach River, respectively. RP indicates fish remained in the Pielach River after spawning

Table 2 Characteristics of radio-tracked nase during 2002–2003

Code	Tagging date (dd/mm/yy)	Sex	Length (mm)	Weight (g)	Emigration date after release (dd/mm/yy)	Last detection (mm/yy)	Detection period (month)	Freq. records		Home range (km)	Main habitat (month present)	Homing	Chronology at the Pielach River				
								By boat	Days in transition zone				Arrival date	Immigration date	Immigration time	Emigration date	Emigration time
N01	10/06/02	F	475	1260	11/06/02	06/03	13	17	–	21.3	FF (10)	Yes	15/04/03	15/04/03	20:08	RP	–
N02	10/06/02	F	450	929	05/03/03	05/03	12	4	–	0.4	PR (11)	Yes	13/04/03	13/04/03	21:35	RP	–
N03	10/06/02	F	470	981	13/06/02	05/03	12	13	–	5.6	FF (10)	Yes	10/04/03	14/04/03	21:49	RP	–
N04	10/06/02	F	445	987	11/06/02	06/02	1	3	–	–	–	–	–	–	–	–	–
N05	10/06/02	F	505	1389	31/07/02	08/02	3	1	–	–	–	–	–	–	–	–	–
N06	10/06/02	F	490	1183	13/06/02	11/02	6	9	–	15.6	FF (5)	–	–	–	–	–	–
N07	10/06/02	F	475	1194	11/06/02	05/03	12	18	–	20.3	FF (9)	Yes	10/04/03	16/04/03	20:48	24/04/03	19:06
N08	10/06/02	F	495	1548	10/06/02	03/03	10	13	–	21.4	FF (9)	–	–	–	–	–	–
N09	10/06/02	F	425	786	–	07/02	2	–	–	–	–	–	–	–	–	–	–
N10	10/06/02	F	510	1300	11/06/02	06/02	1	2	–	–	–	–	–	–	–	–	–
N11	10/06/02	F	500	1220	–	06/02	1	–	–	–	–	–	–	–	–	–	–
N12	10/06/02	F	455	935	11/06/02	06/02	1	1	–	–	–	–	–	–	–	–	–
N13	10/06/02	F	495	1360	–	–	0	–	–	–	–	–	–	–	–	–	–
N14	10/06/02	F	470	1077	10/06/02	06/02	1	2	–	–	–	–	–	–	–	–	–
N15	10/06/02	F	450	985	10/06/02	06/03	13	11	–	43.3	FF (9)	Yes	31/03/03	31/03/03	22:50	RP	–
N16	10/06/02	F	465	960	10/06/02	06/02	1	4	–	–	–	–	–	–	–	–	–
N17	10/06/02	F	445	830	18/06/02	03/03	10	6	–	18.1	FF (9)	–	–	–	–	–	–
N18	10/06/02	F	475	1060	–	08/02	3	–	–	–	–	–	–	–	–	–	–
N19	10/06/02	F	410	712	11/06/02	07/02	2	1	–	–	–	–	–	–	–	–	–
N20	10/06/02	F	455	1015	–	07/02	2	–	–	–	–	–	–	–	–	–	–
N21	18/06/02	F	510	1473	31/07/02	05/03	12	6	4/0	38.6	IM (8)	Yes	31/03/03	31/03/03	23:47	RP	–
N22	18/06/02	F	485	1380	18/06/02	06/03	13	12	13/6	34.8	IM (9)	Yes	14/04/03	17/04/03	21:40	21/4/03	16.30
N23	18/06/02	F	465	1029	18/06/02	03/03	10	2	4/0	34.2	IM (9)	–	–	–	–	–	–
N24	18/06/02	F	500	1324	08/07/02	08/02	3	1	–	–	–	–	–	–	–	–	–
N25	18/06/02	F	495	1345	01/07/02	10/02	5	5	–	15.7	FF (3)	–	–	–	–	–	–

The two numbers in column "days in transition zone" refer to the number of days the fish was localized there across the whole study period and days during mid of April and mid of June, respectively. IM, FF, and PR are the abbreviation of fish whereabouts in the impoundment section, the free-flowing section, and the Pielach River, respectively. RP indicates fish remained in the Pielach River after spawning which covered the entire course of the river on the lowest approx. 200 m, and two more on a bridge located in the transition zone (Danube km 2002.5, Fig. 1). Each of the two stations at the transition zone was equipped with three directional antennas to cover the Danube's full channel width and to differentiate up- and downstream migrating fish. The antennas were mounted on the bridge piers about 10 m above the water surface. The stations operated between March 04th and June 30th in 2003. The station at the entrance of the Pielach River observed fish that immigrated into the tributary and emigrating out of the system; recording started on March 16th and operated until June 23rd.

Data analyses

A nonparametric median test was used to compare home range (HR; km), depth position (DP; m), and horizontal position (HP; m) differences between the two species. Home range (HR; km) was defined as the distance between farthest upstream and downstream recorded fish position from their release point throughout the tracking period (Baras and Cherry 1990; Peter 1998; Gilroy et al. 2010; Capra et al. 2018). Home range was calculated only for individuals which could be followed at least until autumn 2002 (12 nase, 22 barbel, Tables 1 and 2). Horizontal position (HP; m) was considered by measuring the distance of a fish's position to the nearest riverbank. After testing for normality, Spearman rank correlation was used to assess the DP and HP of both fish species related to temperature and discharge. Homing in this study refers to the return of tagged fish to the Pielach River for spawning (Lucas and Baras 2001).

Results

Emigration behavior after tagging

Apart from undetectable fish after release (B25 and N13), the majority of fish (20 barbel and 14 nase) emigrated within 3 days to the Danube River. The remaining barbel and nase stayed in the tributary for a longer period of time before emigration, 8 days to 3 months for barbel and 8 days to 8 months for nase (see Online Resource 3). Thereafter, 4 nase were no longer tracked till the end of study period.

Migration patterns and habitat use during the off-spawning-season (July 2002–March 2003)

Throughout the study period, signal detection of barbel ranged from 0 to 66 signals per fish (see Online Resource 3). Four barbel (B13, B16, B19, B20), which could be detected in the impounded section on single survey days only, were resident in the impoundment for the entire year outside the spawning period (Fig. 2). Two further barbel (B12, B23), which were found in the free-flowing section until December and October, respectively, also moved to the impoundment for overwintering. In total, 21 barbel (84%) moved to the impounded section during summer/fall and spent the most time of the year outside the spawning period there (Table 1).

For nase, between 0 and 48 signals per fish were detected throughout the study period. The majority of nase were detected in the free-flowing section. The impounded section was hardly used as habitat by nase. However, four nase (N15, N21, N22, N23) were detected in shallower habitats of the impoundment. Three of them (N21, N22, N23) also spent the winter in this area and were redetected in March at the transition zone (Table 2; Fig. 3).

While 21 barbel could irregularly be detected over a period of at least 10 months, nine nase in the Danube could not be detected between June and November together with the five individuals that were lost during the first month of the study, 15 nase were no longer detected during the study before wintering (Table 2; Fig. 3; Online Resource 3).

The patterns of habitat use reveal that barbel were found in slightly deeper locations (mean 4.8 m, SD 1.3) than nase (mean 4.2 m, SD 1.5) (Fig. 4a). The species-specific differences in depth-use are statistically significant ($p = 0.01$). The depth-usage of barbel ranged from 2.5 to 8.0 m, while nase occupied a range of 1.0–9.0 m.

The localization of whereabouts concerning the distance to the nearest bank (Fig. 4b) shows that barbel occupy spots with a mean distance of 38.4 m from the nearest bank; for nase this was 66.2 m. Maximum distances where recorded at 172 m (nase) and 120 m (barbel) from the nearest bank; these distances underline that the concerned specimens were detected in the middle of the Danube River. In general, barbel were found closer to the bank than nase ($p = 0.0000$) but both species occupied the entire river profile (Fig. 4b).

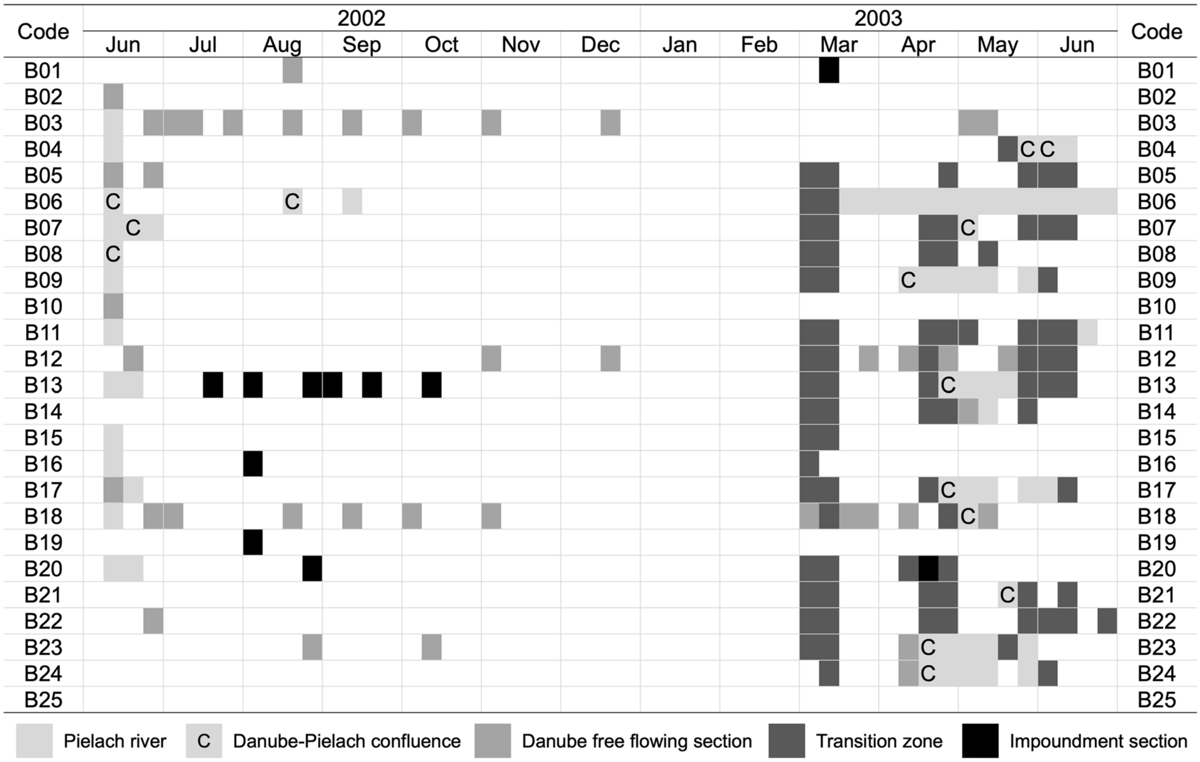

Fig. 2 Detections of barbel throughout the study period: Pielach River (light gray), free-flowing section (gray), transition zone (dark gray), and impoundment section (black). Empty cells indicate missing evidence of barbel locations. See Online Resource 3 for more detailed descriptions

Migration patterns and habitat use during early spring (March) and the spawning-season (April–May)

Pre-spawning period (early spring)

Only ten nase were present in the study area after winter to observe their further migration behavior, while 21 barbel could be tracked at least until March.

After winter, between March 04th and March 07th, 18 barbel were first registered at the data logging station on the bridge in the transition zone (Fig. 2). Since these fish already occupied the head of impoundment section, their movement into this area is unknown. Similarly, the three nase (N21, N22, N23) that overwintered in the impoundment were recorded at the data loggers in the transition zone between March 05th and March 11th (see Online Resource 3). This accumulation of both species in the transition zone was observed until March 13th, after which the animals left the area again.

Spawning migration of nase

For three of ten nase, the spawning migration to the Pielach River could not be further documented. Their signals were lost after a last detection in the free-flowing section (N08, N17) respectively in the impoundment (N23). The remaining seven specimens (N01, N02, N03, N07, N15, N21, N22) showed a 100% homing rate and approached the estuary of the River Pielach between March 31st and April 15th. All homing nase entered the Pielach between March 31st and April 17th. Six nase (N1, N2, N3, N7, N15, N21) migrated upstream to the first migration barrier (2 km) during the following days (for details see Online Resource 3) but did not pass the fish migration facility there. Spawning was not observed during this study. The first nase left the tributary on April 21st (Table 2). Based on the immigration and emigration data, it is very likely that spawning did occur in April.

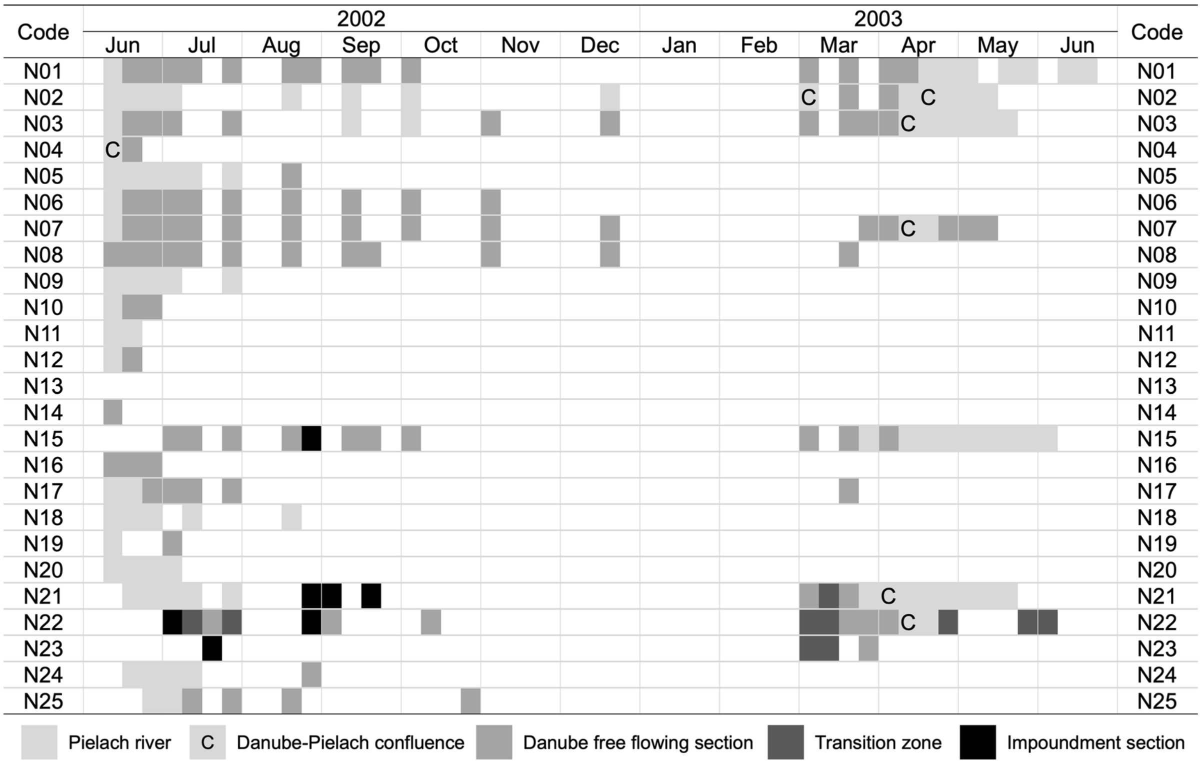

Fig. 3 Detections of nase throughout the study period: Pielach River (light gray), free-flowing section (gray), transition zone (dark gray), and impoundment section (black). Empty cells indicate missing evidence of nase locations. See Online Resource 3 for more detailed descriptions

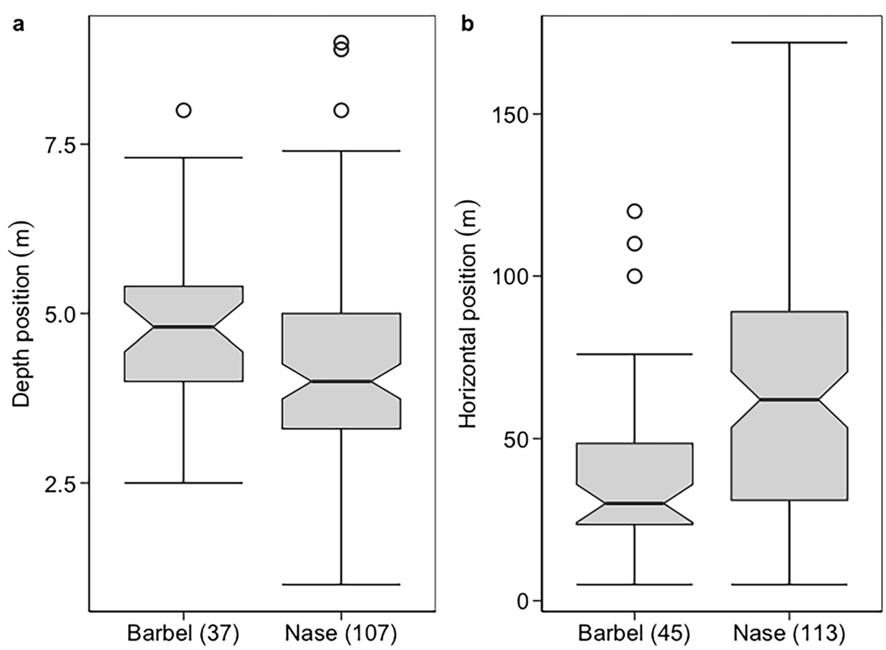

Fig. 4 Habitat use of both species in the free-flowing section of the Danube River: **a** water depth, **b** horizontal position, distance from the nearest bank. The number in parentheses for each species indicates the number of detected locations

Spawning migration of barbel

The movement patterns of barbel during the spawning period are more diverse and, for some individuals, markedly more complex than those of nase (Figs. 2 and 5b, c). For the barbel registered in the transition zone in early March (Figs. 2 and 5b, c), two general patterns can be observed during the spawning period: (1) five individuals (B05, B08, B11, B20, B22) are again recorded in the transition zone between mid-April and mid-June and spent the spawning period there. Only one individual out of these (B11) migrated to the Pielach River as late as June 16th. The second pattern (2) refers to seven individuals (B06, B07, B13, B14, B17, B18, B21) which migrated to the River Pielach. One of these (B6) returned already in March, while six barbel where first registered during April/May at the permanent loggers at the transition zone and subsequently migrated towards the Pielach. Of these, again three fish (B13, B14, B17) migrated into the tributary, while the other three fish (B07, B18, B21) were recorded only at the confluence of the Pielach and Danube Rivers. The four remaining barbel (B03, B04, B12, B15) did not follow either pattern (for details see Online Resource 3).

Like the nase, homing barbel gathered at the Pielach-Danube confluence. A total of eight barbel were recorded there. Five of these (B09, B13, B17, B23, B24) immigrated a few days later (between 1 and 5 days). Three of the barbel that returned to the Pielach River (B06, B09, B24) also migrated up to the first weir without passing it (see Online Resource 3), as observed for nase.

Timing of immigration and emigration

The majority of nase and barbel (13 out of a total of 16 homing fish) migrated from the Danube River into the Pielach River during darkness, between 20:08 and 03:55. The only exception was barbel B14 which immigrated during daytime at 10:17 (Table 1). The immigration of two barbel (B13, B17) was not registered by the fixed station.

There is no time pattern concerning emigration, neither for nase nor for barbel. Out of the seven homing nase only two individuals (N7, N22) emigrated to the Danube River right after spawning. All others remained in the lower Pielach River till the end of the study (June 23rd) or till the transmitters expired (for the last records of each individual see Online Resource 3). Out of nine barbel returning to the Pielach River, six fish (B09, B13, B14, B17, B23, B24) left the tributary at different times of the day, and three fish (B04, B06, B11) were still in the Pielach River at the end of the study. Five out of the six barbel were registered in the transition zone moving downstream towards the impoundment section between 1 and 14 days after emigration from the River Pielach River.

Discussion

As telemetry studies observe a limited number of individuals, uncertainties remain as to whether the full portfolio of movement patterns and behaviors within the studied population could be captured, and the general validity of the results thus remains limited (Lucas and Baras 2000; Cooke et al. 2013). Over the course of the study, which lasted more than a year, contact was lost with four barbel but with 15 nase. The reasons for these losses can be manifold, and in most cases remain speculative. The only evidence is the taking of one barbel by an angler and the predation of one fish by the cormorant. Also, whether the markedly higher loss rates for nase are due to increased natural mortality, increased removals, movements out of the study site, or because nase are more sensitive to transmitter application (Bauer et al. 2005) remains an open question. The optimal range of use for radio telemetry is waterbodies with water depths up to 5 m (Marsden et al. 2021) because the probability of detection decreases sharply with increasing water depth (Watkins et al. 2019). Although the methodology used in the deeper Danube River does not meet current methodological standards and the number of boat surveys was limited, the study proved that both species migrated along the full continuous river length. Due to water depths of up to 9 m in some areas of the free-flowing Danube section, not every fish could be detected during every boat survey, which is a shortcoming of the present study. However, the elaborate search and the precise localization of the individuals found provided new insights into the habitat use of both species on a very large river like the Danube.

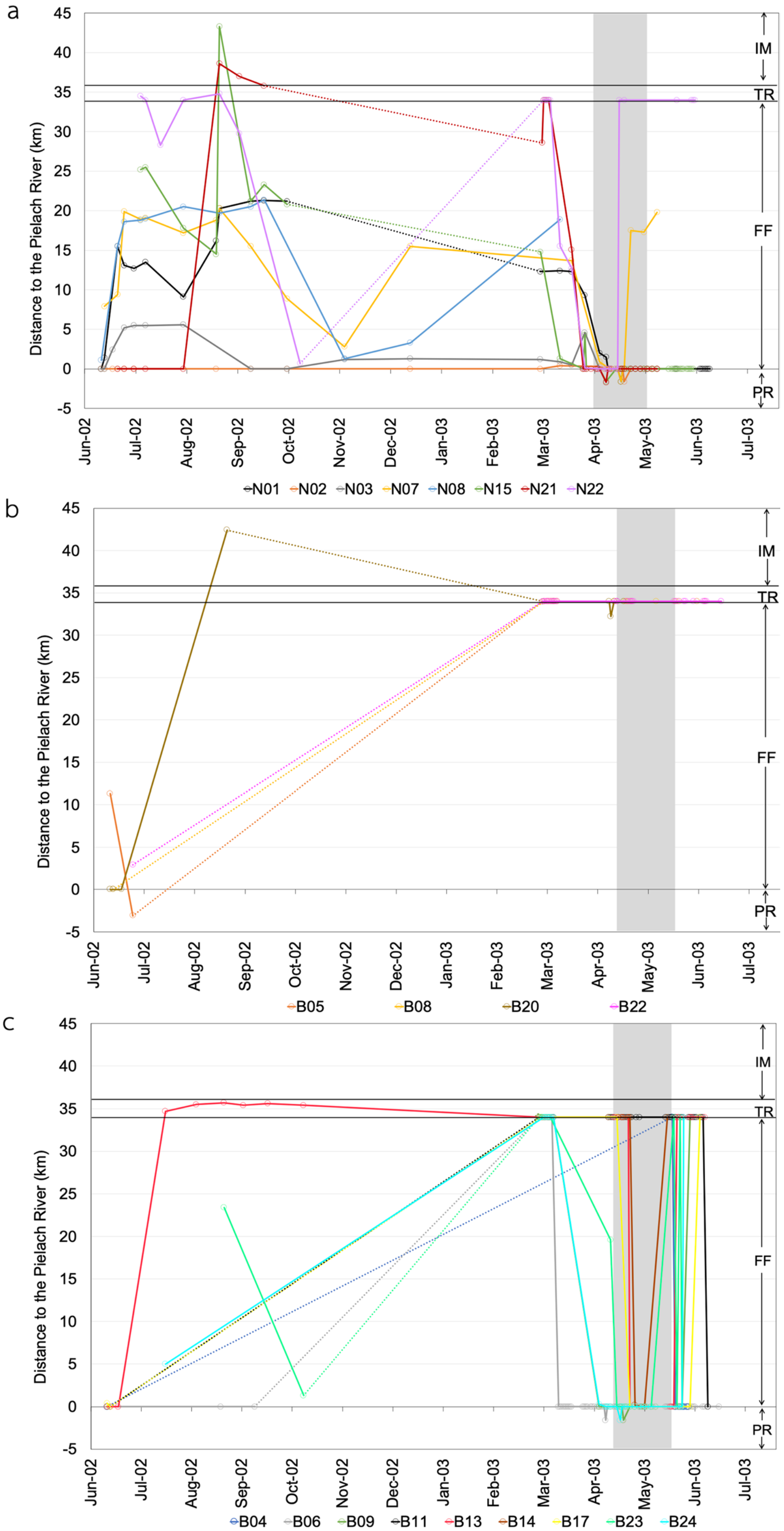

Fig. 5 Individual migration patterns of 8 nase (**a**) and 13 barbel (**b** and **c**) during the study period. Dashed lines indicate fish that moved to the impoundment section and were therefore undetectable until they were redetected in the transition zone after winter. Gray shadings scheme the spawning seasons. IM, TR, FF, and PR are the abbreviation of fish whereabouts in the impoundment section, the transition zone, the free-flowing section, and the Pielach River, respectively

Habitat use and movements during off-spawning periods

The results revealed clear differences in the temporal and spatial movement behavior of the two observed species, as well as divergent intraspecific patterns. One of the key observations regarding habitat use is that nase were almost exclusively detected in the free-flowing section (Figs. 3 and 5a). Therefore, the nase can be characterized as a species that clearly prefers and most likely depends on lotic habitats. The habitat use of barbel over the course of the year in the investigated Danube section, on the other hand, is clearly concentrated in the 10–15-m-deep areas of the impoundment. Barbel reappeared in early spring after spending the year within the impounded section where the water was too deep to detect them (Figs. 2 and 5b, c). The barbel's movements to the impoundment in the off-spawning-season likely could be related to food availability in the flowing river sections or the impoundment, respectively. However, it remains questionable to what extent the observed preference of the barbel for the impounded area would correspond to the natural habitat selection in an unregulated Danube River. It remains to be elucidated why the tagged barbel did not colonize the deep areas in the free-flowing section but chose to migrate to the artificially created reservoir. In any case, this result can be interpreted as an indication of opportunistic habitat selection (Baras and Nindaba 1999). On the other hand, the avoidance of the impounded section by the nase clearly indicates that nase exhibit high habitat losses in dammed rivers in any case.

Certainly, the habitat use patterns of both species gained by boat surveys in the free-flowing section were surprising, as the tagged fish were encountered, on average, in areas of more than 4-m water depth (Fig. 4). However, it should be emphasized that the habitat use of barbel in the free-flowing Danube essentially characterizes habitat use during migrations between the Pielach River and the reservoir, where the vast majority of barbel congregate by autumn at the latest. However, also nase, most of which are resident to the free-flowing section year round, use habitats that are on average very deep and very far from the bank (Fig. 4). In some cases, nase as well as barbel were localized directly in the navigation channel and were not restricted to gravel banks as described by other authors (Huber and Kirchhofer 1998; Hirzinger et al. 2004). It is also notable that testing for possible correlations between habitat selection (depth/horizontal location) and discharge and temperature did not yield significant results (data not shown). However, diurnal movements were not tracked in this study, though interdaily habitat selection of both species in the Danube River are a necessary future research aspect to further increase the knowledge on habitat use and movement behavior as a basis for sound and targeted environmental management.

The movement patterns of nase during the non-reproductive period provide evidence of site fidelity of certain individuals to very specific locations in the free-flowing section (Fig. 5a). Although the movements or locations of these fish between the respective localizations are unknown, the examples depicted returned, sometimes several times, to specific sites that had been abandoned for several months (e.g., N1, N7, N8, N22; Fig. 5a). Between these visits to the same section of the river, they carried out movements of several tens of kilometers. How the fish orientate themselves in the mostly very turbid Danube River is not clear, but the site fidelity to certain places within their home range and that the movements between these spots are clearly not random (Crook 2004; Huntingford et al. 2012).

A generally much larger home range of the Danube's populations compared to well-studied populations from smaller waters (e.g., Baras 1997; Huber and Kirchhofer 1998; Benitez et al. 2015; Ovidio et al. 2016) outside the reproductive period is evident. The calculated average home ranges were 22.4 km (nase) and 34.4 km (barbel), with maximum values exceeding 40 km for both species. However, both species were able to spread and to move over much longer distances in the formerly unobstructed and free-flowing Danube. How far the range of migration of the Danube populations formerly was within 1 year can of course no longer be answered for the Austrian Danube. This certainly applies to the habitat utilization during the year as well as to spawning migrations. Currently, the two hydropower plants that have delimited the study area are already equipped with fishways. Ongoing and planned monitoring studies of the migration activity at the Danube's fish migration facilities (especially PIT-tag studies) will show to what extent reestablished or extended migration activity of Danube fishes will be found.

Spawning migrations

Since all test animals were marked after spawning in the Pielach River and homing behavior in fish, especially in salmon, has been known for a long time (e.g., Hasler and Wisby 1951), it was also to be assumed that nase and barbel show a certain site fidelity with regard to the spawning site. In addition, Baras (1997), Ovidio et al. (2007), and Zięba et al. (2014) have shown spawning site fidelity for the observed species in smaller rivers. In any case, the observed homing rates as well as the periods of immigration into the Pielach River differed significantly between nase and barbel.

In barbel, two general patterns of behavior were seen during the spawning period: half of the fish (9 individuals) returned to the Pielach River and the other nine remained in the Danube River. Since out of the latter group five barbel have been registered between mid-April and mid-June for up to 33 days in the transition zone, we assume that a spawning ground was also located there. The gravel transported by the Danube is known to deposit in the head impoundment of the power plant and has to be regularly dredged for flood protection purposes and to keep the navigation channel open (personal communication, hydropower operator—Verbund company). Consequently, it is known that suitable spawning substrate (Melcher and Schmutz 2010) accumulates in this section. However, due to rip-rap stabilized banks and the artificially confined channel, no shallow gravel banks—known as preferred spawning sites for the barbel for smaller rivers (Melcher and Schmutz 2010)—are established within the transition zone. We are not aware of any other river described as having barbel spawning in water depths of 4–5 m. In any case, the area very likely offers suitable conditions in terms of flow velocity and substrate. Therefore, we deduce that in this case the water depth might only be of subordinate importance for spawning site selection. The existence of spawning sites in the Danube River itself was suspected beforehand, as it could not be assumed that the entire barbel population spawns exclusively in the Pielach River. However, until now, spawning sites have not yet been documented in the main channel of the Danube River. The fact that three barbel were recorded only in the confluence area, without ascending into the Pielach, could indicate the presence of another spawning site at the Danube gravel bar just downstream of the Pielach confluence.

The second behavioral pattern is the pronounced migration to the Pielach River. The homing barbel entered the tributary between March 17th and June 16th, mainly in April and May (Table 1). In addition, the main activity in the transition zone was also recorded between mid-April and early May (Fig. 2). Therefore, we assume that the main spawning season of the barbel fell into this period.

Seven nase returned to the Pielach River, i.e., all that could still be detected at that time, suggesting a spawning site homing rate of 100% for nase. Nase show synchronized and concentrated migration compared to barbel. Similar patterns were observed in Meulenbroek et al. (2018), where Danube nase reached spawning sites very concentrated in April and barbel showed a much more dispersed arrival until July. It is also remarkable that the returnees to the Pielach gather in the area of the confluence with the Danube and, with the exception of one barbel, migrate during darkness. During further upstream migration within the Pielach River, limitations due to the first barrier were evident. Although the weir is equipped with the fish migration facility, it was either not accepted or was impassable. However, the high proportion of blocked nase in particular gives a clear indication of how central the connectivity of the main river and tributaries is for the Danube populations. This also underlines that functioning fishways are an important prerequisite for restoring passage, which, after all, aim to reconnect suitable spawning and juvenile habitats.

Conclusion

The studied nase and barbel occupied the full length of the accessible habitat of the Danube and the tributary. Habitat use in the free-flowing section of the study area showed that not only gravel bank areas with moderate depths, but also the middle of the river respectively the navigation channel are colonized. The nase remained in the free-flowing section throughout the year and showed site fidelity to specific habitats that were used for longer periods of time, then abandoned and later revisited. The pattern of habitat use underlines that nase are tied to flowing habitats year-round. In contrast, the lifestyle of the studied barbel can be characterized as opportunistic. The barbel spent most of the year in the impounded section and did not visit lotic areas in the Danube or in the tributary again until the spawning season. The study could also reveal how difficult it is to study natural long-distance migrations, especially since migration routes on most major rivers in Europe and beyond are now fragmented. The potential home range of the tagged fish was restricted to the area bounded by the two run-of-river power plants. Whether habitat use would be more extensive with an open continuum remains an open question, albeit it is very likely that this would be the case. However, further key questions concerning the population ecology as whether long-distance migratory behavior is a common pattern of barbel or nase in large rivers, or whether it is rather up to individual strayers that travel particularly long distances while the majority of populations occupy their life-cycle habitats within a few river kilometers (sensu Gerking 1959), remain open. In any case, the portfolio of natural behaviors has shrunk due to the construction of hydropower plants and the alterations in the natural morphology. The results of the study clearly indicate that the focus of restoration and management measures aimed at maintaining or improving habitat conditions for potamodromous fish species in large rivers such as the Danube River should in any case address the opening of migration routes. Secondly, the rheophilic fish species of the Danube, such as the nase, need flowing rivers that provide the full set of suitable habitats for all age stages and especially suitable spawning habitat.

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Author contribution Conceived and designed the investigation: Günther Unfer, Stefan Schmutz. Performed field and/or laboratory work: Ruamruedee Panchan, Günther Unfer, Kurt Pinter. Analyzed the data: Ruamruedee Panchan, Günther Unfer. Wrote the paper: Ruamruedee Panchan, Günther Unfer, Kurt Pinter, Stefan Schmutz.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval All procedures performed in the study were conducted under animal use and care procedure number GZ 66.016/5Pr/4/2002 according to Austrian law.

Consent for publication All authors consent for publication of this work.

Conflict of interest The authors declare no competing interests.

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