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RESEARCH ARTICLE

Spawning behaviour of Danube huchen from three Austrian rivers

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Abstract. A camera inside an underwater housing was used to record a pair of Danube huchen, *Hucho hucho* (L.) spawning at the Ybbs River, Austria. A description of spawning behaviour is made including observations of two other Danube huchen pairs recorded at the Rivers Mur and Pielach. Results were compared with the spawning behaviour of Siberian taimen, *Hucho taimen* (Pall.), Manchurian trout, *Brachymystax lenok* (Pall.) and Sakhalin taimen, *Parahucho perryi* (Brevoort). Danube huchen females, likewise the Siberian taimen and Manchurian trout females, rest for a variable number of minutes after the spawning act, before covering the eggs with gentle tail beating. This behaviour joins Danube huchen with Siberian taimen intragenerically and *Hucho* with *Brachymystax* intergenerically, distinguishing it from *Parahucho* and strengthening our current conception of the Salmoninae subfamily.

Keywords: phylogeny of behaviour, underwater video, postspawning behaviour, male digging

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Introduction

The Danube huchen, *Hucho hucho* (L.) referred to further as "huchen", is a freshwater salmonid inhabiting the Danube River system in the European Black Sea watershed. It lives in well-oxygenated waters and can grow to sizes ranging from 1500 to 1800 mm in length and 40 to 70 kg in weight (Holčik 1990, Kottelat and Freyhof 2007). As top predator, huchen is a key species that regulates the ecology of the montane and submontane water systems it inhabits (Holčik et al. 1988). As the most-westerly distributed species of its genus, huchen is a key species in the evolutionary history of the *Hucho* group (Holčik 1982). Finally, as a member of the genus *Hucho*, considered to be basal in the Salmoninae subfamily (Crespi and Fulton 2004, Wilson and Williams 2010), it is an important link in the understanding of the evolution of all the salmonids. Unfortunately, its current status in Europe is critical as it has disappeared from most of its original range, and only a few self-sustaining populations survive. The loss of habitat space and quality from water regulation and pollution from industrial and agricultural development is responsible for this dramatic decline (Holčik 1990). Today, most of the remaining populations are thought to be largely dependent on stocking (Holčik 1995), with the consequent loss of genetic variability and other problems associated with hatchery fish

propagation (Fleming and Petersson 2001, Álvarez and Nicieza 2003, Araki et al. 2007, Fraser 2008).

Since huchen is an endemic species to the Danube catchment area, Austria lies in the center of its natural distribution range. Before human interference, huchen inhabited the Austrian Danube and its larger tributaries in the barbel and grayling zones totalling over 2,500 km in length (Schmutz et al. 2002). Stocks had already declined dramatically by the late nineteenth century (Jungwirth 1984) mainly due to fragmented migration routes between the Danube and tributaries as a result of hydropower development and river channelization (Schmutz et al. 2002). According to IUCN criteria (IUCN 2013) and the Bern Convention (Appendix III), huchen is listed as an endangered species. In Austria today the largest population of approximately 1,500 adult huchen inhabits a 270-km segment of the Mur River; however, the Mur population has declined by 80% over the last twenty years (Schmutz et al. 2011). Small, self-sustaining populations are currently also found in the Pielach, Drau, and Gail rivers. Huchen occurs at very low densities in the approximately forty rivers of its historic natural distribution in Austria (Schmutz et al. 2002). The Danube itself functions mainly as habitat for sub-adults and adults, while reproduction and early development happen in the tributaries. The River Ybbs is one of the most promising areas for huchen restoration in the nearest future since habitat enhancement measures are being carried out in it, and fish passes are being constructed to reopen migration barriers. In its lower reaches, a small population of > 50 adult individuals has been established (Guttmann 2006, Unfer et al. 2012), and huchen occurs in small numbers up to the village of Göstling.

Despite its status as one of the largest, only surpassed by the co-generic Siberian taimen, and most emblematic members of the entire Salmoninae subfamily, a complete description of the huchen spawning ritual has not been compiled to date. Holčik et al. (1988), in an impressive monograph provide a consensus review of huchen spawning ecology and behaviour referencing the written work of several authors who published in languages other than English. However, this manuscript lacks details about the spawning act itself or the female behaviour immediately after spawning. Witkowski (1988) presented a study of the spawning ecology of a huchen population in Poland. These observations, together with the works referred to by Holčik et al. (1988) and later corroborated by Esteve et al. (2009a) with Siberian taimen, identified a spawning behavioural singularity with respect to the other salmonines; namely that pair formation in huchen and Siberian taimen occurs days or weeks before spawning starts (Esteve et al. 2009a). Interestingly, Holčik et al. (1988) reported another exceptional behaviour: huchen males, like females, contribute to digging the nests in which eggs are deposited. Reports of huchen as well as Siberian taimen male digging behaviour were later reported by other authors, although none of these were based on their own observations (Mateyev et al. 1998, Kottelat and Freyhof 2007, Freyhof and Kottelat 2008). This is a remarkable fact as male digging among the salmonids is only present in the *Oncorhynchus* genus, and it is thought to be the result of displacement reactions (McCart 1969, Esteve 2007).

The validity of behaviour as a phylogenetic signal has been demonstrated repeatedly (Brooks and McLennan 2002 and references therein). Salmonines are categorized into three groups according the female post-spawning behaviour from egg deposition to egg covering (Esteve et al. 2011): 1. *Brachymystax* + *Hucho*: the female rests for a number of minutes and then digs to cover the eggs; 2. *Salvelinus*: the female undulates her body over the deposited eggs and then digs; 3. *Salmo* + *Parahucho* + *Oncorhynchus*: female digs to cover the eggs immediately after spawning. This classification was made before there was any knowledge of female huchen post-spawning behaviour. In the present paper, the validity of this behaviour as a phylogenetic tool is assumed to predict, firstly, that after having spawned the female will rest for a number of minutes before covering the eggs, and, secondly, that the male will not dig. These predictions were tested using an underwater video recording system that permitted monitoring huchen spawning in the wild without

disrupting natural behaviour. The aim of this study was to describe huchen spawning behaviour and to compare these results with the spawning behaviours of other salmonids.

Material and methods

Study area

Underwater recordings were made during the 2011 spring spawning season on the Pielach (April 1), Ybbs (April 8), and Mur (April 10) rivers in Austria (Fig. 1). The Pielach is a fourth order stream that drains into the Danube. At 74 km long, its source is located in the foothills of the northern limestone pre-Alps. Huchen were recorded in the lower course of the river (48°12'33.26"N, 15°24'05.84"E) close to

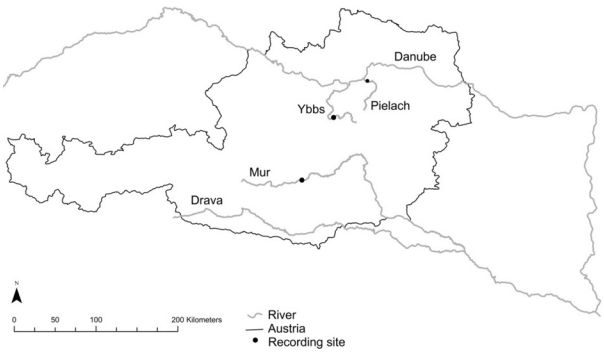

Figure 1. Map showing the three spawning sites in this study.

the mouth of the Danube. The average river width at the spawning site was about 20 m. The river section is inhabited by a variety of Danube species, but the main species noted are barbell, *Barbus barbus* (L.), chub, *Squalius cephalus* (L.), and common nase, *Chondrostoma nasus* (L.).

The Ybbs drains over a total length of 133 km from the northern limestone Alps into the Danube. The river width at the spawning site (47°48'10.68"N; 14°47'1.03"E) was about 25 m. Huchen were recorded in the middle reaches where the Ybbs is a fifth order stream. At this site, huchen shares its habitat primarily with grayling, *Thymallus thymallus* (L.), brown trout, *Salmo trutta* L., and rainbow trout, *Oncorhynchus mykiss* (Walbaum).

The River Mur is located in central Austria and is 460 km long. Its source is in the eastern Alps, and its main runoff direction is south-east through Slovenia, Croatia, and Hungary before it discharges into the River Drava, a tributary of the Danube. At the spawning site (47°7'42.85"N; 14°14'40.83"E), the river is a sixth order stream with an average width of 35 m. The dominant species in this section of the river is grayling, accompanied by brown trout and rainbow trout.

Underwater video

A Sony HDR-HC7 color digital video camera mounted inside an underwater housing was used to record the fish. The video signal from the camera was transmitted via cable to a digital recorder located on land. The camera was positioned approximately 0.75 m from the nest in which a female had been observed previously. Redds, which are disturbed areas of gravel containing nests, were located in tail pool areas with decreased water depths ranging from 1 to 0.5 m and increased flow velocity. Males and females presented with very little sexual dimorphism (Fig. 2), and in each of the rivers where recordings were made the male was slightly darker and redder in comparison to the female. Sex was confirmed by the behaviours exhibited. The fish were positioned one slightly behind the other; the male was identified as the fish intermittently performing quiverings, which is

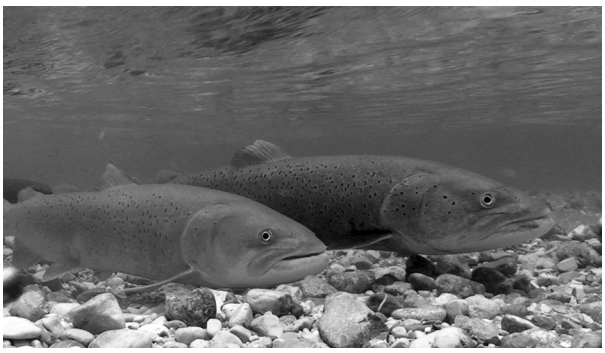

Figure 2. A pair of huchen (*H. hucho*) over a redd a few minutes before spawning. Female is on the left, and male on the right.

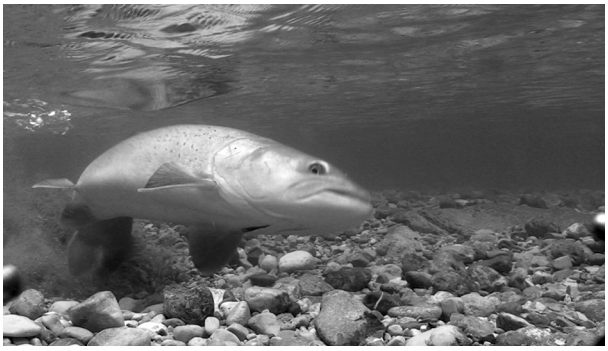

Figure 3. A huchen (*H. hucho*) female digging her nest in the Ybbs River.

a courtship behaviour consisting of low amplitude, high frequency body vibrations from head to tail, while the female was the fish that regularly performed nest digging by turning on her side and excavating a depression in the gravel by beating her tail (Fig. 3). It is important to note that in all the pairs recorded, quiverings and digs were always performed by a single fish, and no fish performed both quivering and digging.

Spawning behaviour

From previous descriptions with Siberian taimen the following behaviours were identified (Esteve et al. 2009b): probing: the female lie on the nest with her tail raised and presses her anal fin into the gravel; displacement quivering: the male quivers his body away from the female, which differs from normal quivering in its greater amplitude and shorter frequency; false spawning: the female assumes the spawning position, with her mouth gaping and trembling, but she does not release eggs; the spawning act: the pair, remaining in an horizontal position, releases gametes while their bodies tremble and their jaws gape partially (Fig. 4).

Figure 4. A huchen (*H. hucho*) pair spawning in the Ybbs River.

Female digging was divided into three types according to the progress of nest building: nest starting digs: a high number of tail beats (7-14) per digging episode, female progresses upstream while digging (approximately 1-2 m), high tail beat intensity, visually judged according to the velocity with which the female repetitively flexed her tail and by the amount of gravel moved; nest finishing digs: low number of tail beats (3-6) per digging episode, female concentrates digging in one location, medium tail beat intensity; egg covering digs: low number of tail beats (2-5) per digging episode, female progresses while digging (approximately 0.5-1 m), low intensity tail beating.

Evolution

Female behaviour immediately after spawning and the presence or absence of male digging was studied, and then both characters were optimized (Farris 1970, Maddison et al. 1984) onto a Salmoninae supertree based on 34 different molecular, morphological, and behavioural studies (Wilson and Williams 2010).

Results

The details of the fish pairs in each of the rivers follow (Tables 1 and 2).

The Pielach

A pair of huchen was found at 11:20 in a river stretch located in the tail of a pool. Their approximate size, judged visually by two independent observers, was estimated to be between 90-100 cm for the female and 75-85 cm for the male. The camera was deployed at 11:36 and both fish left the area. The male returned after 33 minutes and stayed there until we removed the camera at 16:29 because of battery

Table 1
Video recording history of huchen (*H. hucho*) spawning in three Austrian Rivers. The number of female digs and male quiverings is included

River	Time period	Cumulative time (min)	Female digs	Male quiverings
Ybbs	15:39 -19:29	230	161	103
Pielach	12:09-16:29	260	0	0
Mur	13:09-17:20	251	32	154
Total		741	193	257

Table 2
Video recording history of a huchen (*H. huchen*) pair spawning in the Ybbs Rivers. The number of digs (d), quiverings (q), displacement quiverings (dq), false spawnings (fs), and male attacks (ma) is included

Time period	Cumulative time (min)	d	q	dq	fs	ma
15:39-16:21	42	20	18	1	2	2
16:21	19 s	Spawning				
16:22-19:29	187	141	85	1	0	9
Total	229	161	103	2	2	11

failure. The female returned at 13:23, stayed only for six minutes, and never returned, presumably because the area had been invaded by common nases. The fact that the area in which the pair was found was much clearer than its surroundings indicated that the female had previously dug intensively and that most probably at least one nest containing one egg pocket was already there.

The Ybbs

A pair of huchen was found at 14:45 in a redd located approximately 3 meters from the left river bank. The female was slightly larger than the male at 90-100 cm and 80-90 cm, respectively. When they were first seen, the female was actively involved in nest building, and two digging episodes were observed before deploying the camera. The camera was submerged at 15:18, and both fish left the area. The pair returned together at 15:39 and stayed there until 19:29 when the natural light was too low to permit recording. At 15:58 and at 16:09 the male left the area to attack another male of about the same size that approached the female. On both occasions he returned to the nest after only a few seconds (9 and 23 s, respectively). A noticeable change in colouration (darker) was noticeable just before the attacks. During most of the time, different species such as graylings, brown trout, rainbow trout, and brook trout, *Salvelinus fontinalis* (Mitchill), were seen crossing over or hiding in the redd gravel presumably waiting for spawning and an opportunity to feed on the eggs. Neither one of the pair seemed to pay much attention to these fish. As spawning drew near, changes were visible in both the male and the female. The male became visibly darker and increased his quivering frequency, while the female increased her respiratory and probing frequencies. In the last minutes before spawning, she emitted bubbles frequently. At 16:02 and 16:20, the female performed two false spawnings. At 16:21 the pair performed the spawning act that lasted 19 s. In the final seconds she moved upward, while the male moved forward. After spawning the female remained slowly moving above the nest. During this time several fish, mainly graylings and trout, were seen feeding on the eggs, but the huchen pair played little attention to them. The female performed her first covering dig five minutes and 43 s after spawning. The digs observed before spawning were all of the nest finishing type with an average number of tail beats per dig of 3.6, n = 20. The first digs after spawning were nest covering (3.2,

n=12). From this point, the female increased the number and intensity of tail beats until she reached a plateau one hour and 20 minutes after spawning of 10-11 tail beats per dig for 39 minutes. After that, the digs were performed with gradually fewer tail beats, and they were concentrated on a single point (nest finishing digs).On three occasions after spawning, the male left the area to attack another approaching male. On one occasion, one hour and 20 minutes after spawning, he allowed a second male to come within about two meters of the nesting female. During the 3 hours and 50 minutes of recording time, the female performed 161 digs and the male 103 quiverings. Additionally, the male performed 2 displacement quiverings before spawning.

The Mur

A pair of huchen was found at 12:50 in a redd located approximately 1.5 meters from the left river bank. The female was larger than the male at 80-90 cm and 50-60 cm, respectively. At the time they were first seen, the female was actively involved in nest building. The camera was submerged at 12:55 and both fish left the area. The pair returned together at 13:09 and stayed there until 17:20 when the camera was removed from the water. During the 4 hours and 11 minutes of recording time, the female performed 32 digs and the male 154 quiverings. Additionally, the male performed 10 displacement quiverings. A second, very large male approximately 110-120 cm made three short visits to the nest area, and each time forced the original male to move away without even fighting. The first visit was made at 13:23, and he only stayed for 29 s. The second visit was at 16:29 and lasted for 2 minutes and 25 s. The last visit was at 17:09 and lasted 3 minutes and 6 s. A few minutes after each of these three visits, the original male returned to the nest and continued courting the female.

Evolution

The Ybbs River huchen female rested for 5 minutes and 43 s before covering her eggs with gentle tail beats. Female post-spawning behaviour in huchen was classified as resting then digging. All of the 193 digs recorded during this study were performed by the two digging females observed in the Ybbs and Mur rivers. None of the males observed performed a single dig. Thus, male digging was classified as

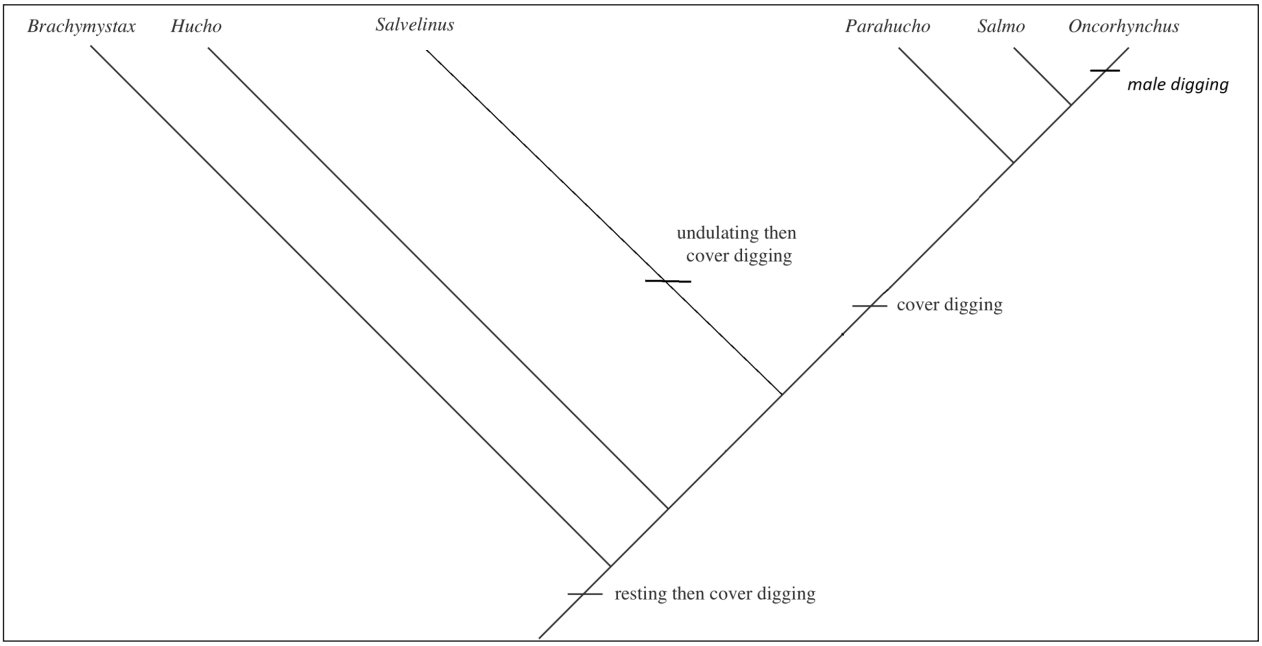

Figure 5. Female post spawning and male digging characters states optimized onto a supertree for the Salmoninae based on a compilation of studies using morphological, molecular and behavioural data (Wilson and Williams 2010).

absent among huchen. A hypothesis for the evolution of female post-spawning and male digging behaviours in the salmonines is presented in Fig. 5.

Discussion

Danube huchen spawning behaviour was generally observed to be similar to that of other salmonids and remarkably similar to that of Siberian taimen (Schroder 1981, Groot 1996, Esteve et al. 2009a). The female employed her time building the nest, while the male courted the female and guarded her from other males. Recording in the Ybbs began only 43 minutes before the pair spawned, so we were not able to observe the complete sequence from nest initiation, nest completion, spawning, and egg covering. However, using the hours recorded after spawning and the observations of the Mur pair, we have a complete representation of the spawning sequence. Several changes were noted regarding the nest building stage; namely, the female varied her digging behaviour in its intensity, the number of tail beats, and the distance travelled while digging, while the male varied his courting frequency. This is consistent with observations of other salmonids (Groot 1996, Gaudemar et al. 1999). As with Siberian taimen, huchen spawning is probably a single pair event. The typical hierarchy ranking that is commonly noted among other salmonids, in which there is a dominant male close to the female and then various subdominant males downstream, was not observed in huchen. On several occasions during recording in the Ybbs, a second male tried to approach the nesting female, but the mating male repelled him powerfully by chasing him more than 30 meters away from the nest. Only once during the 741 minutes recorded were two males recorded on the monitor without fighting. Furthermore, if single pair spawning in huchen is the norm, sperm competition would not be as great as it is for other salmonids like *Salmo, Salvelinus* and *Oncorhynchus*, among which multi-male spawnings are common (Esteve 2005). In fact, the sperm cloud observed during spawning was barely visible.

Other details link huchen with Siberian taimen. For instance, male quiverings in huchen, like in Siberian taimen, were exceptionally long (7-20 s). During spawning, the pair remained in a horizontal position; but among other species, the fish typically raise their caudal fins to arch the superior part of their bodies. As with Siberian taimen, huchen spawning, lasts longer (19 s in the present study) than it does among other salmonids studied (Esteve 2005). Finally, huchen only partially gape their jaws while spawning. Our observations indicate that differences between huchen and Siberian taimen are rather quantitative. Huchen exhibited a higher tolerance to other fish in the nest vicinity. In fact, the pair allowed the presence of other fish species in the nest, and on one occasion the mating male even permitted another huchen male to approach. Given the limited number of females in this study, more observations are needed to confirm this trend, but if huchen is indeed more tolerant this possibly reflects differences in species diversity and density between Alpine and Siberian rivers. Since we found fish already paired at nests in each of the three rivers of this study, we cannot confirm if pair bonding in huchen occurs before reaching the spawning areas as is stated by Witkowski (1988). However, whether or not pairs form before reaching spawning grounds or in them, our observations in the Mur indicate that pairing can be broken easily. In fact, one huchen male in the Mur adopted a strategy similar to the one described for Sakhalin taimen (Esteve et al 2009b). Instead of courting and guarding the female permanently, he approached her from time to time forcing the guarding male to flee.

Throughout all of our observations in both the Ybbs and Mur rivers, only one of the two fish on screen performed nest digs while the other only performed quivering. The continuous monitoring of the complete spawning act allows us to state confidently that the female was the one that dug and the male was the one that quivered. Reports of males digging by Holčik et al. (1988) were very possibly the result of river bank observations. Throughout spawning the

two fish shift positions, and if they are of similar sizes, it is extremely difficult to distinguish between them. Overall, our observations reinforce the previous hypothesis about the evolution of female post-spawning behaviour in salmonids (Esteve et al. 2011, Fig. 5). The difference in the post-spawning behaviour among the three groups very possibly reflects the progressive colonization of new habitat types as salmonid groups became larger and expand their original ranges.

Conclusions and future research

Our results present remarkable similarities between two species that live thousands of kilometers apart in very different habitats. This is confirmation that behaviour carries a strong phylogenic signal. Both the absence of male digging and female post-spawning behaviour, throughout maximum parsimony, confirm the most complete Salmoninae phylogeny hypothesis we have to date (Wilson and Wilson 2010). However, given that we have only recorded the spawning act of one female, our study should be replicated with more females, preferably in different rivers of the huchen natural range. The behavioural and ecological habits of two of the *Hucho* members remain a complete mystery. In fact it is not known for certain if Korean taimen, *Hucho ishikawae* Mori, which inhabits the Yalu River on the North Korea – Chinese border and some of its tributaries, is extinct. The status of Sichuan taimen, *Hucho bleekeri* Kimura, is similar having already disappeared from most rivers of its original range in Sichuan, Qinghai, and Shaanxi provinces in China. The salmonid scientific community should join efforts to launch projects to learn more about the status of these two species. Specimens should be collected for morphological and molecular analysis; their behavioural and ecological characteristics should be investigated, preferably in the wild, and, if we are not too late, critical management measures should be undertaken. Meanwhile, here in Europe, we are responsible for providing advice to governments, local environmental agencies, and angling associations, and we emphasize that habitat restoration and preservation are the best techniques to conserve the formidable huchen in our rivers.

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Author contributions. M.E. analyzed the underwater tapes and wrote the paper. G.U. planned and coordinated all the field work, wrote part of the Introduction, and provided comments to improve the other sections. K.P. wrote part of the Material and Methods and the Figures sections, and provided comments to improve the other sections. I.D. provided comments to improve the entire paper. The underwater recordings were performed by G.U., K.P., and M.E.

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