

Past and present of and perspectives for the Danube huchen, *Hucho hucho* (L.), in the Danube basin

Andrzej Witkowski, Aleksandar Bajić, Tomislav Treer, Aleksandar Hegediš, Saša Marić, Nikica Šprem, Marina Piria, Andrzej Kapusta

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Abstract. Huchen, *Hucho hucho* (L.), also known as Danube salmon, is an iconic, endemic species inhabiting the Danube basin of Central Europe. Historically, the Danube huchen inhabited a significant portion of the Danube drainage basin stretching to the Iron Gate and the majority of large and

medium-sized tributaries. Larger populations in the natural zoogeographical distribution of Danube huchen were once found in Austria, Bavaria, the former Yugoslavia, Slovakia, and western Ukraine. Currently, the species is severely fragmented within the Danube drainage, where most populations exclusively depend on stocking and natural reproduction is very limited due to habitat alterations and flow regime changes. In the Czech Republic and Poland, Danube huchen occurrence is the result of introducing the species to several rivers in the Baltic Sea and North Sea drainage basins. Danube huchen is a threatened species throughout its range of occurrence, and, according to IUCN criteria, it is classified as endangered (EN). Habitat degradation is the most serious negative factor impacting huchen populations. Dam construction, pollution, and river regulation have led to loss and degradation of spawning sites. Detailed research on population abundance and structure is greatly needed to help identify the populations which are most threatened and to help to develop the best protection systems.

Keywords: conservation, distribution, habitat loss, *Hucho*, population status, salmonids

A. Witkowski [✉]
Museum of Natural History
University of Wrocław
ul. Sienkiewicza 21, 50-335 Wrocław, Poland
Tel.: +48 71 375 41 53, e-mail: a.witkowski@biol.uni.wroc.pl

T. Treer, N. Šprem, M. Piria
Department of Fisheries, Beekeeping
Game Management and Special Zoology
Faculty of Agriculture, University of Zagreb
Svetošimunska 25, 10000 Zagreb, Croatia

A. Bajić
Department of Biology and Ecology
Faculty of Science, University of Novi Sad
Trg D. Obradovića 2, Novi Sad, Serbia

A. Hegediš
Institute for Multidisciplinary Studies of the University of Belgrade
Kneza Višeslava 1, 11030 Belgrade, Serbia

S. Marić
Institute of Zoology, Faculty of Biology
University of Belgrade
Studentski Trg 16, 11000 Belgrade, Serbia

A. Kapusta
Department of Ichthyology
Inland Fisheries Institute in Olsztyn, Poland

Introduction

Over the past century, human activities in the Danube River basin and its tributaries have led to substantial environmental changes, including in this region's fauna and flora. The river continuum has

become fragmented, and the biodiversity in discrete sections of modified streams has changed. Fishes are among the animals most affected (Holčík et al. 2006). Huchen, *Hucho hucho* (L.), also known as Danube salmon, is an iconic, endemic species inhabiting the Danube basin of Central Europe (Geist et al. 2009, Witkowski et al. 2013). As Danube huchen is such a valuable species, it is difficult to obtain enough specimens to investigate its biology and ecology. Recent papers on this subject are few, the official data is fragmentary, and some information is obtained directly from anglers. Danube huchen is one of the world's largest salmonid species attaining sizes of up to 1.8 m in length and 70 kg in weight (Holčík 1990). This species is long lived with many data indicating that it can reach ages of thirty years or more (Prawochensky and Kolder 1968, Kottelat and Freyhof 2007, Andreji and Stráňai 2013). Danube huchen grows quickly, which is the result of the dietary shift to a predatory life strategy. Huchen hatchling and fry food includes aquatic invertebrates, primarily insect larvae (Witkowski et al. 1994, Augustyn et al. 1998). By the time it attains lengths of 50-98 mm, it begins to feed on fish (Holčík et al. 1988). Adult huchen are selective predators which, above all else, consume the most readily available prey (Witkowski and Kowalewski 1984, Holčík 1990, Šubjak 2013).

Danube huchen has long been of great interest to recreational fishers, fish farmers, and scientists (Holčík et al. 1988, Witkowski et al. 2003). However, interest in huchen has never paralleled that of other salmonid species. This species occurs rather rarely, so it has never been targeted by commercial fisheries, has been caught primarily by anglers (Holčík 1990), and has been cultured at low intensity (Andreji and Stráňai 2013, Witkowski et al. 2013). The first information regarding huchen culture dates to 1876 (Stráňai 2012). Significant culture success was not achieved until the implementation of artificial reproduction procedures and juvenile rearing techniques based on replacing natural feeds (Grudniewska et al. 2013) with commercial starters (Kowalewska-Hryc et al. 2005).

The aim of this paper is to present data on the distribution and trends of several huchen populations from different areas in its range of distribution. Specifically, historical and contemporary data regarding huchen distribution are compared, the factors that have been most instrumental in its declining abundance and range are discussed, and measures that could help to conserve this species are presented.

Distribution and population structure

Historically, the Danube huchen inhabited a significant portion of the Danube drainage basin stretching to the Iron Gate and the majority of large and medium-sized tributaries. Larger populations in the natural zoogeographical distribution of huchen were once found in Austria, German Bavaria, the former Yugoslavia, Slovakia, and western Ukraine (Holčík et al. 1988). The shrinking range of this species was observed as early as in the late nineteenth and early twentieth centuries, and the rate at which it disappeared from subsequent rivers increased following the Second World War. Holčík (1990) estimates the huchen inhabits just 33% of its original distribution range. Currently, the range of huchen is subject to discussion; isolated populations occur in areas of Austria, Germany, Slovenia, Croatia, Bosnia and Herzegovina, Serbia, Montenegro, Romania, Hungary, Ukraine, Slovakia, the Czech Republic, and Poland (Fig. 1; Freyhof and Kottelat 2008). In the last two countries, Danube huchen occurrence is the result of introducing the species to several rivers in the Baltic Sea and North Sea drainage basins (Hanel et al. 2013, Witkowski et al. 2013). Danube huchen has also been introduced to waters in France, Belgium, Germany (North Sea drainage basin), Sweden, Spain, Morocco, and North America. However, nowhere other than in the Danube River and the Poprad River in Poland have self-sustaining populations established themselves (Prawochensky and Kolder 1968, Holčík 1984, Elvira and Almodóvar 2001, Freyhof and Kottelat 2008). Knowledge regarding



Figure 1. Recent distribution of Danube huchen (*H. hucho*) in Europe (from Freyhof and Kottelat 2008, changed).

huchen distribution varies among countries (Holčík 1990, Schmutz et al. 2002, Muhamedagić and Habibović 2013, Witkowski et al. 2013).

Changes in huchen range of occurrence in Austria are well documented. Historically, Austria was at the center of the range of this species, and huchen occurred in 16 primary rivers and their tributaries inhabiting grayling and barbel zones totaling over 2,500 km in length (Schmutz et al. 2002). In various areas of Austria, the river segments that huchen inhabited historically are described as being from five to 10 m in width with waters of flow rates ranging from 0.5 to 2 m³ s⁻¹ (Ratschan 2012). The largest huchen population occurred in the Danube River, but declines in its abundance were noted as early as in the nineteenth century. Currently, self-sustaining populations of Danube huchen inhabit only approximately 10% of its former range, and in many smaller rivers huchen occurs only thanks to stocking programs (Ratschan and Zauner 2012). The largest population numbering about 2,000 adult individuals inhabits a 110 km segment of the River Mur between the towns of Murau and Leoben (Schmutz et al.

2002). The most reproductively viable population is in the River Pielach, and smaller populations still exist in the upper River Drau and the lower River Gail. The density of huchen in other Austrian rivers is very low and is dependent on stocking programs. Relatively high huchen density has been re-established in the Danube River through continuous stocking, but access to former spawning areas in the tributaries is almost completely blocked (Schmutz et al. 2002). The size structure of Danube huchen populations is largely dependent on river size, and, in rivers with higher water flow rates, this species attains a greater maximum body size (Ratschan 2012).

Until about thirty years ago, excellent habitat conditions for Danube huchen still existed in many rivers in Romania. The historical range of this species included the majority of the Carpathian river systems (Bănărescu 1964), but hydropower development, river pollution, and overfishing and poaching led to drastic declines in the area inhabited by huchen (Bănăduc 2008, Virban and Ionescu 2011), and the species is now extinct in the Mures, Times, Cerna, Olt, Arges, and Ialomita river systems. Data on the

current area of huchen occurrence in Romania are fragmentary, and the species only occurs in a few rivers, including, among others, the Tisa River and its tributaries of the Vişeu, Ruscova, Crasna, Bistra, Vaser Somesul, and Crisul rivers and in the Siret River.

In Ukraine before the Second World War, Danube huchen occurred in the Tisa River from the confluence of the White Tisa and the Black Tisa in nearly all tributaries and in the the Prut and Cheremosh rivers (Staff 1950). In this period, huchen occurrence in the Prut River had become rare, but the primary, permanent site of huchen occurrence was the Cheremosh along with its tributaries (Kulmatycki 1931). In the late 1920s and early 1930s, pioneering studies of huchen were undertaken in the Cheremosh and data regarding population structure, biology, and ecology were collected (Kulmatycki 1930). These historic data indicate that the Danube huchen occurred abundantly in the Cheremosh, and that this population was, at the time, a attractive fish to anglers. The current distribution and abundance of huchen in the Cheremosh and Prut are not known (A. Didenko, personal communication), but, according to reports from anglers, several Danube huchen were caught by poachers in the White Cheremosh in spring 2013, and several fish are usually caught annually in this river during the spawning migration. Two huchen, a female of 5 kg and a male of 3 kg, were caught in the Prut River in the winter of 2007 near Chernovtsy. Currently, this species probably only occurs in the Tisa River catchment area in Ukraine (Velykopolsky 2012); nevertheless, huchen occurrence in the Prut basin is likely (Mateleshko and Potish 2011). Huchen occurs in the Tisa River along a segment approximately 170 km long, and it also inhabits several tributaries including the Teresva, Rika, and Terebla. Huchen spawning grounds are found in the Tisa, Black Tisa, and Shopurka rivers, but the primary spawning grounds are located in the Teresva River and its tributaries the Luzhanka, Krasna, Mokryanka, and Brusturyanka rivers (Velykopolskiy and Mruk 2012). Some of the huchen spawning grounds have been designated as special conservation areas. Unfortunately, despite

long-term conservation efforts, both the abundance and area of occurrence of huchen in Ukraine is significantly lower than the historical data indicate. Not until the most recent measures were implemented were the first positive results noted. For example, the number of Danube huchen spawning nests in the Teresva River increased from 14 to 25 in the 2010-2012 period (Velykopolskiy and Mruk 2012). Information on the structure and abundance of huchen populations inhabiting rivers flowing through Ukraine remain scant and fragmentary; nevertheless, recent signals indicate that interest in this species is growing (Krazhan et al. 2012, Mruk and Velykopolskiy 2012).

The distribution of huchen in Slovenia has declined drastically in the Mura-Drava river basin (Ivanc 2012). In the past, huchen inhabited the Mura River, but it had disappeared there by the 1960s. Huchen only occurs in some of the rivers of the Sava River drainage basin, which is the most important river system in Slovenia (Ivanc 2012). It is estimated that huchen currently inhabits 39% of the length of rivers in which it previously inhabited (Zabriz et al. 2003 in Bertok 2010), and, currently, the Danube huchen inhabits the Sava Bohinjka, Sava, Ljubljanka, Sora, Mirna, Drava, Krka, and Kolpa rivers and their tributaries.

The main Serbian river inhabited by huchen is the Drina and its tributaries. This river is 346 km long, 220 km of it flows through Serbia, and the average discharge is $395 \text{ m}^3 \text{ s}^{-1}$ (Mijović-Magdić 2007). The section that flows through Serbia is the border with Bosnia and Herzegovina, and it can be divided in two segments. The first is between the Perućac and Zvornik dams, which is the salmonid section of the river, while the second stretches from the Zvornik Dam to the Sava River mouth and is dominated by cyprinids. The River Lim, at a length of 220 km, is one of the largest tributaries of the Drina River, and 110 km of it flows through Serbia at an average discharge at the mouth of $113 \text{ m}^3 \text{ s}^{-1}$. The Uvac River is a 119-km-long tributary of the River Lim that has an average discharge of $13.2 \text{ m}^3 \text{ s}^{-1}$. The Vapa River is the most significant tributary of the River Uvac, while Pobraćnica River is one of smallest tributaries of the

Lim, and it flows partially through Bosnia and Herzegovina and Montenegro, but it is also a significant huchen breeding area. All of these rivers lie in the Drina River drainage basin. Huchen also inhabit some rivers in the Velika Morava drainage basin. The Moravica and Đetinja form the Zapadna Morava River, and they are 87 and 75 km long, respectively, and Danube huchen from the Drina River has been reintroduced to these two rivers (Hegediš et al. 2005). Ibar, at 272 km in length, is the largest Zapadna Morava tributary and has an average discharge of 65.7 s^{-1} . While few data exist concerning the historical distribution of huchen, it is generally agreed that it probably did not far exceed its present range. This species is considered to be common in the Drina River between the Perućac and Zvornik dams, while it is rarely reported downstream from Zvornik Dam. In the Lim River and its tributaries, Danube huchen is considered common, while in the Đetinja, Moravica, and Ibar rivers it is reported only in their upper courses (Fig. 2).

Danube huchen inhabits direct or indirect tributaries of the Danube River in northwestern Croatia, namely, the Drava and Sava rivers in their upper courses, as well as the Kupa, Mrežnica, Dobra, and Una rivers (Mrakovčić et al. 2006). Although huchen inhabited these rivers in the past, in some of them, the Drava and Dobra in particular, abundance has

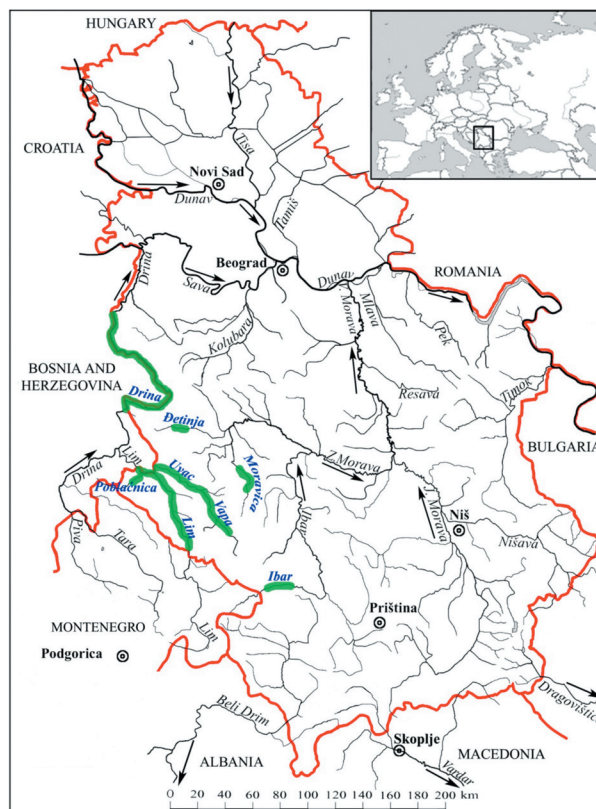


Figure 2. Map of the recent distribution of Danube huchen (*H. hucho*) in Serbia.

declined dramatically primarily because of habitat degradation. Data from the 2004-2010 period indicates catches of only one to three specimens annually from the Kupa River and only two from the Drava River. However, the accuracy of these data is not reliable since there have been reports of unregistered catches. The most comprehensive data on huchen catches comes from the Kupa, Dobra, and Una rivers in the 1970s and 1980s (Sabioncello et al. 1970, Pažur et al. 1982), and these permit calculating growth in length (Fig. 3). It was not possible to perform calculations with the von Bertalanffy growth curve because of the similarly high growth patterns in all three rivers that was noted even for older specimens. However, the

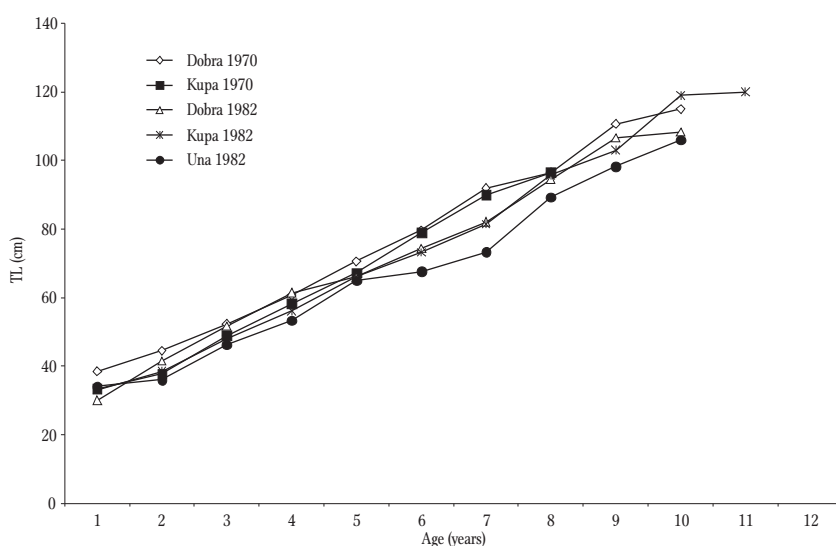


Figure 3. Danube huchen (*H. hucho*) growth (cm TL) in the Dobra, Kupa, and Una rivers (Sabioncello et al. 1970, Pažur et al. 1982).

cubic regression between age and length was good, and according to these data huchen from these rivers attained average total lengths of 33.76 cm in the first year, 67.01 cm in the fifth year, and 113.45 cm in the tenth year of life. The most recent data regarding the population from the Kupa River indicate that the huchen length-weight growth relationship and maximum specimen size is unique in comparison to other species as it depends on the size of the river the fish inhabit (Treer et al. 2014).

Although data on the structure of Serbian huchen populations are scant and incomplete, indications are strong that population size has decreased significantly and population structure has been disrupted (Marić et al. 2009). However, it was possible to set a minimum landing size for adult Danube huchen from the Drina River based on its growth characteristics (Simonović et al. 2000, 2011).

The huchen area of occurrence in Slovakia has changed significantly (Holčík 1990, Koščo 2012). Huchen naturally inhabited the Váh and Hron rivers and their tributaries, and it was introduced through stocking to several dam reservoirs, the Hornád and Nitra rivers in the Danube basin, and the Poprad and Dunajec rivers (Vistula basin, Baltic Sea; Koščo 2012, Andreji and Stráňai 2013). Although the population of this species inhabiting Slovakian rivers is

relatively well understood (Ivaška 1951, Bastl et al. 1975, Nagy 1976, Holčík 1990, Andreji and Stráňai 2013, Šubjak 2013), it appears that Danube huchen has recently fallen slightly out of favor with local researchers. The average quantities of this fish caught by recreational fishers in recent years has been about 100 individuals annually (Krajč et al. 2012), which is a figure that is slightly higher than that in the 1979-1989 period (Holčík 1990). This suggests that there has been a slight increase in the population or that abundance has remained at the same level.

In Poland, the Danube huchen's natural area of occurrence includes the Czadecznka River, a tributary of the Kysuca River, and the Czarna Orawa and its tributaries (Witkowski et al. 2013). Widespread poaching in the Czarna Orawa drainage basin and industrial pollution in the Kysucy system led to progressively lower numbers of huchen in subsequent years. The long-term impact of these factors was the disappearance of autochthonous populations in the early 1950s (Witkowski et al. 2003, Witkowski et al. 2013). Current environmental conditions, constructions on rivers, and water pollution do not permit assuming that huchen inhabits the waters of the Czadecznka or Czarna Orawa rivers (Kotusz et al. 2010). Before huchen disappeared from these rivers, it was decided to translocate this species outside of its natural area of

occurrence and to introduce it into rivers of the Baltic Sea drainage basin (Witkowski et al. 2013). In the 1950s, huchen was introduced to the Vistula basin beginning with stocking the Poprad and Dunajec rivers followed by the San, Raba, Skawa, and Soła rivers. Huchen was also introduced to the Nysa Kłodzka, Bóbr, and Gwda rivers in the Oder basin. The results of these measures are numerous self-sustaining populations in the Poprad, Dunajec, and San rivers.

Populations of Danube huchen occurring outside of its natural range have been the subject of many studies. The fastest growth rates were noted in the Dunajec River in the first

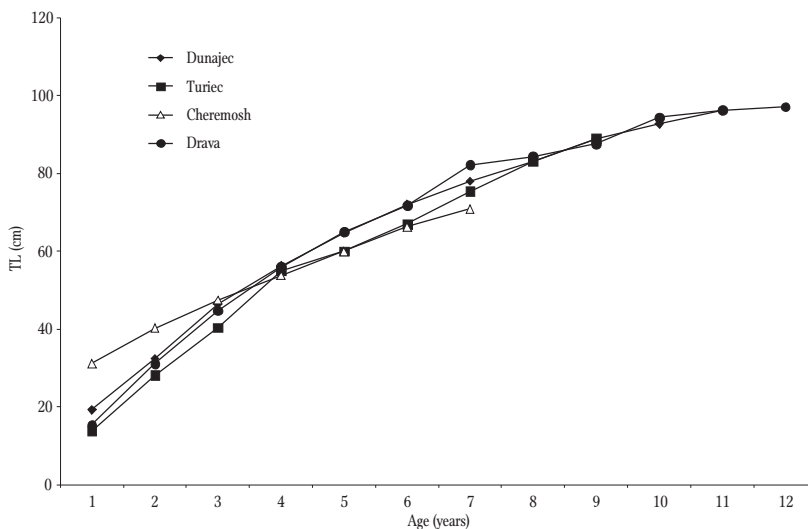


Figure 4. Example of growth (cm TL) of Danube huchen (*H. hucho*) in its natural range of distribution (Turiec, Cheremosh, and Drava rivers) and outside of it (Dunajec River) (data from Kulmatycki 1931, Witkowski et al. 1984, Holčík et al. 1988).

year of life (Witkowski et al. 1984), which was similar to that of populations inhabiting this species's natural range of occurrence (Fig. 4). Increases in body length were similar for both males and females in subsequent years, but were slightly larger among females. The sex ratio of Danube huchen spawning in Niedziczanka Stream, which is where the largest spawning stock from the Dunajec was noted annually, was not proportional (Witkowski 1988). Females usually dominated catches at a ratio of 1.4-2.3:1, and only in one year was the same number of fish from both sexes noted. The age of the fish at the spawning grounds ranged from four to 12 years. The youngest spawning males were aged four, while the females matured one year later (Witkowski 1988).

Conservation

Danube huchen is a threatened species throughout its range of occurrence, and, according to IUCN criteria,

it is classified as endangered (EN). In most countries, huchen has been assigned the same status (Mrakovčić et al. 2006, Wolfram and Mikschi 2007), but in the Czech Republic and Poland this species is categorized as extinct in the wild (EW; Witkowski et al. 2009, Lusk et al. 2011). The northern border of the huchen's natural distribution range is in these two countries, and, currently, the species only occurs in them because of introductions into rivers in the Baltic Sea (Witkowski et al. 2013) and North Sea (Hanel et al. 2013) catchment basins. In the Carpathians, this species is categorized as critically endangered (CR) (Witkowski et al. 2003), while according to the Red Book of the Ukrainian Carpathians, the Danube huchen is classified as near threatened (NT) (Mateleshko and Potish 2011).

Danube huchen is protected by limits on the number of fish that anglers can catch in given periods, minimum size limits, and closed fishing seasons, during which fishing for this species is banned (Table 1). The smallest minimum size is in the Czech Republic (65 cm), and the largest is in Serbia (100

Table 1
Huchen (*H. hucho*) fishing regulations in some European countries

Fishing regulations	Closed season	Minimum legal size (cm TL)	Fishing regulations	Barbel hooks	Night fishing	Others
Austria	1 Feb/1Mar - 15 May/30 Jun	75-85	none	Yes	Yes	very strict rules in some beats
Bavaria (Germany)	15 Feb - 31 May	70				
Bosnia & Herzegovina	1 Jan - 31 May	70	three huchen limit per season	Yes	Yes	only artificial bait permitted
Croatia	16 Feb - 30 Sep	80	one huchen limit per day*	Yes	No	only artificial bait permitted
Czech Republic	1 Jan - 30 Sep	65				
Poland	1 Mar - 31 May	70	one huchen limit per week	Yes	No	only artificial bait permitted
Serbia	1 Mar - 31 Aug	100 to caudal fin base	three huchen limit per season	Yes	No	only artificial bait permitted
Slovakia	1 Jan - 31 Oct	70	special license purchase, one huchen limit per year	Yes	No	
Slovenia	15 Feb - 30 Sep	70		Yes	No	

*catches are unlimited for angling club members who pay a daily license fee

cm). The most common minimum size is 70 cm, but this can be increased at different fishing grounds. For example in Austria each province where Danube huchen actually occurs has its own regional rules for season and minimum catch size of all fish species. The provincial rules differ from 75 to 85 cm size limit and closed season beginning between earliest 1st February and latest 1st March and ending between 15th May earliest and 30th June latest. (C. Ratschan personal communication). Additionally, each fishing club or river owner limits the number of specimens that can be caught per angler during a given season. Additionally, the catch and release system is quite widespread among huchen anglers.

Active protection measures for Danube huchen in most countries are limited to stocking programs or placing the fish under protection during spawning. Measures such as restoring key habitats and rendering rivers passable (Schmutz et al. 2002, Zitek et al. 2008) are rarely undertaken. The number of hatcheries artificially reproducing huchen is small, which makes it difficult to maintain the genetic diversity of the various populations (Geist et al. 2009, Weiss et al. 2011). In many countries, most frequently one enterprise (Romania) cultures Danube huchen, and interest in producing this species is declining; for example, in Poland the number of hatchery facilities producing huchen has shrunk from nine to just one currently (Witkowski et al. 2013). Danube huchen stocking is usually performed by local angling associations or NGOs. Huchen hatcheries are in operation in the Kupa (Slovenia) and Una (in Bosnia and Herzegovina) rivers. Since these are both border rivers, stocking has been done successfully in co-operation with Croatian fishing clubs. These types of hatcheries could also assist with population translocation. Habitat protection is crucial, and there are many conscientious people who are willing to help. Naturally, dam removal would help the huchen cause considerably, but the likelihood of this happening anywhere is unrealistic.

In an effort to develop adequate huchen management, two action plans have been realized: “Action Plan for the Fisheries Management of Huchen Stocks in Republic of Serbia Catchments” (Hegediš et al.

2005) and “Research of the Life History and Population Traits of Huchen in Serbia” (Marić et al. 2009). Two successful artificial reproduction projects have also been conducted in the past twenty years: the first was implemented in 2000 with the release of approximately 10,000 fish in the Drina, Vapa, Uvac, Lim, Moravica and Ibar rivers, and the second project, which began in 2011, is known as the “Artificial reproduction of huchen to supplement the natural population in the Drina River” and is currently ongoing. In the past two years, under the auspices of this program, 33300 0+ and 7200 1+ Danube huchen were released into the Drina River. Further plans focus on building a broodstock of a known genetic profile, and increasing the numbers of fish released annually. In addition to the Drina population, more attention should be focused on other segments of the Serbian huchen population, the most vulnerable of which could be supplemented by stocking with material from fish farms. Protecting breeding grounds is crucial, and water flow fluctuation and gravel exploitation should be adjusted according to breeding seasons and grounds. Hydropower plant management should be required to act with increased awareness of the environment, especially during maintenance work.

Threats

Danube huchen is faced with many threats throughout its distribution range, and these were identified by many authors as early as at the beginning of twentieth century (Holčík 1990). River regulation, overfishing, and water pollution are the most important factors impacting huchen. The degree of threat and intensity differs in the various areas of huchen occurrence.

Habitat changes

Habitat degradation is the most serious negative factor impacting huchen populations. River waters in Europe

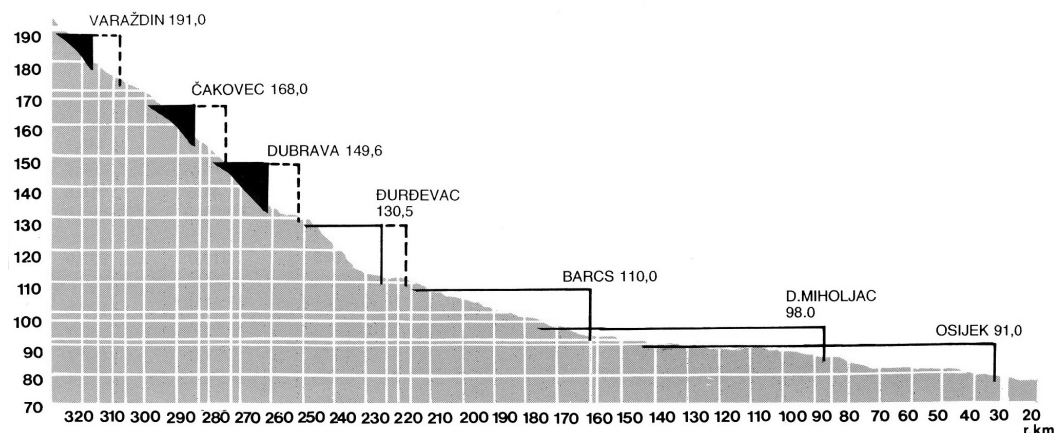


Figure 5. Dams on the Drava River in Croatia (existing – solid triangles, planned – hollow triangles), (from Bolić 1991).

are susceptible to a variety of anthropogenic factors that usually manifest as changes in water quality, hydrological phenomena, and river morphology and continuity (Schinegger et al. 2012). River valley industrialization includes dam construction, riverbed regulation, and changes in the structure of land exploitation. Dams often divide rivers up into segments, which limits huchen areas of occurrence and blocks access to historical spawning grounds. Hydropower dams are the most serious causes of habitat degradation, and examples of their negative impact as reflected in decreased abundance or the disappearance of Danube huchen are many throughout its range of occurrence (Holčík 1990, Kotusz et al. 2010). One such series of dams is located on the Drava River (Fig. 5), and it has led to the near extinction of huchen in the Croatian part of this river. Prior to the Second World War, huchen exceeding 30 to 40 kg were common catch, whereas, today even catches of small fish are rare (Mateš 2005).

Many Danube huchen habitats in Serbia have been irrevocably altered by dam construction. For example, the three dams constructed on the Drina River changed the ecosystem drastically by creating deep lakes with habitats that are unsuitable for huchen. The high water fluctuations that occur several times daily because of the dams have rendered the main riverbed of the Drina River almost entirely unsuitable for huchen spawning. A dam on the Lim River has led to the formation of a lake about 20 km in length, and the last of the three dams on the Uvac River leaves the riverbed completely dry for a length

of 10 km. Both the Ibar and Đetinja rivers have dams. Only the Zvornik Dam was constructed with a fish ladder, but this is only in operation for a few months annually. The result is that the huchen population in Serbia is heavily fragmented by these impassable barriers.

Dams also cause many other ecological changes that impact river ecosystems, and this can affect Danube huchen either directly or indirectly. These include blocked migration routes, changes in ichthyological assemblages, micro-evolution of isolated populations, changes in water thermal regimes in upper river courses and in segments downstream from dams, blocked transport of organic and inorganic materials, and sediment accumulation. Hydroelectric power plants cause fish mortality directly and can also radically alter water flow rates. The scale of environmental changes caused by dam and weir construction varies by country. River channelization and the construction of hydroelectric facilities on rivers was done much earlier in Austria and German Bavaria than in Romania and Ukraine. Currently, in Austria alone more than 300 dams and weirs limit or block fish movements. In recent years, however, some positive changes have been observed with regard to this issue (Schmutz et al. 2002). In Austria and Germany much activity has been noted in the design and construction of fish passes over the last twenty years, and fish pass design tends to take into consideration many potamodromous species (Parasiewicz et al. 1998).

Overfishing

Overfishing is one of the main causes of the declining abundance of Danube huchen (Holčík 1990), although currently it seems that this factor is not as significant as it once was, and is much less significant in the case of taimen, *Hucho taimen* (Pall.) (Jensen et al. 2009, Rand 2013). This species has always been attractive to recreational fishers because of its size. However, increasing levels of consciousness among anglers has led to the increasing popularity of catch and release (C&R) fishing, and this permits concluding that the impact anglers have on declining Danube huchen abundance is much smaller than it has been in the past. Huchen draws anglers from the world over to Slovenia, Montenegro, and Slovakia, and businesses have been established to cater to the needs of these fishers by offering guided fishing tours.

Poaching has a terribly negative impact on huchen, and that these fish are often caught during spawning compounds the consequences of this illegal activity. The overall scale of poaching is difficult to estimate since the scale of it and the variety of techniques employed in it vary widely by region; however, Danube huchen is usually not the main target of poaching (Didenko et al. 2011). Poaching in Croatia was very widespread in the past, and Kišpatić (1893) reported in his book that it was easy to catch huchen with harpoons during spawning. Catch regulations have not always been strict, and in the past it was permitted to catch many fish at once (Fig. 6). Poaching

has been a great problem over the last twenty years in Serbia, and while the distribution range of huchen has not been drastically reduced, the size of its populations has been. Currently, even in its typical habitats huchen is a rare species, and its range of occurrence has been limited to small stream and rivers where it spawns. Poaching in Romania poses a serious threat to Danube huchen, and many spots where illegal catches are made have been known for generations (Vîrban and Ionescu 2011). Poachers use various techniques, including potentially dangerous poisons and explosives.

Pollution

Pollution is one of the most frequent anthropogenic factors impacting river ecosystems (Schinegger et al. 2012), and Danube huchen is not resistant to river pollution. The raw or partially processed sewage released into many river systems was the reason huchen disappeared; for example, industrial pollution caused the disappearance of this species from the upper course of the Kysuča (Kotusz et al. 2010, Witkowski et al. 2013). Many small streams and brooks which were previously spawning grounds are now abandoned because of pollution, which is caused mainly by fish farms and surrounding agricultural lands. In the past two decades, Drina River has suffered two massive pollution crises caused by the Perućac hydropower plant – one in 1993 and the second in 2010.

The development of sewage systems and the modernization of sewage treatment facilities has meant that this factor has a much lesser impact on huchen abundance and distribution; however, the impact of river valley industrialization and industrial development on huchen is still notable (Muhamedagić and Habibović 2013). The situation differs in various huchen ranges of occurrence, and except in the vicinity of large cities, pollution in the Drava and Sava rivers is no longer a significant issue. However, in certain regions of Romania and Ukraine, Danube huchen is threatened significantly by



Figure 6. One-day catch from the Kupa River in 1940 (from Mateš, 2005).

pollution from metal mining (Vîrban and Ionescu 2011, Velykopolsky 2012).

Other threats

While no in-depth analyses of the impact climate change has on Danube huchen were performed, it is likely that the huchen, just like other cryophilic species (Heino et al. 2009, Woodward et al. 2010), is threatened by it. Climate warming can lead to hydrological changes that affect water flow rates and thermal regimes in rivers (Markovic et al. 2013), and these could effect phenological changes exhibited as spawning earlier and larval fish leaving nests earlier (Hari et al. 2006). Riverine fish are adapted to continual changes in temperature and water flow rates, but in contrast to eurythermal species that spawn in spring and can benefit from increased water temperatures in this period (Wolter 2007), stenothermal, cryophilic species are threatened by even the slightest changes in water temperature. The consequences of accelerated spawning in huchen are not known, but disturbances of ecological rhythms can disturb relationships within and among species in different stages of development. Extremely high water temperatures persisting over longer periods of time pose deadly consequences for cryophilic fish species (Markovic et al. 2013).

Final remarks and recommendations

Since data on huchen are scarce and the species is endangered, conducting further research on its distribution, abundance, growth, condition, conservation, and other parameters is of critical importance. Detailed research on population abundance and structure is greatly needed to help identify the populations which are most threatened and to help to develop the best protection systems. Detailed distribution mapping, especially of breeding areas, is necessary to protect the species during this most critical period of its life cycle. Preliminary information

on the genetic structure of Danube huchen populations in Serbia indicate that the populations analyzed require conservation measures (Marić et al. 2009, 2012). However, to acquire a more comprehensive picture of the genetic structure of populations, extensive research must be conducted in the near future that analyzes a large number of individuals using a broad set of genetic markers. Genetic structure research should also determine whether the physical fragmentation of this population has caused genetic fragmentation, and such data will permit reducing or even preventing possible inbreeding depression. Lastly, special attention must be paid to preventing the translocation of individuals among different basins, and genotyping brood stock individuals must be obligatory (Weiss et al. 2011).

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References

- Andreji J., Stráňai I. 2013 – Growth parameters of huchen, *Hucho hucho* (L.), in the wild and under culture conditions – Arch. Pol. Fish. 21: 179-188.
- Augustyn L., Witkowski A., Błachuta J. 1998 – Ecology of the young (0⁺) Huchen, *Hucho hucho* (L.) (Salmonidae), planted in a mountain streams – Arch. Pol. Fish. 6: 5-18.
- Bastl I., Holčík J., Kirka A. 1975 – Ichthyological investigation of the protected habitat of the Danubian salmon (*Hucho hucho* L.) on the river Turiec (Czechoslovakia) and suggestions for its management – Ac. Rer. Natur. Mus. Nat. Slov., Bratislava, 21: 191-224 (in Slovak with English summary).
- Bănăduc D. 2008 – The *Hucho hucho* (Linnaeus, 1758), (Salmoniformes, Salmonidae), species monitoring in the Vișeu River (Maramureș, Romania) – Transylv. Rev. Syst. Ecol. Res. 5: 183-188.
- Bănărescu P. 1964 – Pisces – Osteichthyes. Fauna Republicii Populare Romîne, 13th editura – Academiei Republicii Populare Romîne, Bucuresti, 962 p. (in Romanian).
- Bertok M. 2010 – Plan for implementation of the fisheries management in the Sava River in the period 2011-2016 – Zavod Za Ribištvo Slovenije Spodnje Gameljne 61 A, 1211 Ljubljana-Šmartno, 85 p. (in Slovenian).
- Bolić J. 1991 – Croatian waters – Ministry of Water Management and Hrvatska vodoprivreda, Zagreb, 216 p (in Croatian with English summary).
- Didenko A., Velykopol'sky I., Buzevich, I. 2011 – Illegal fishing in the Tisza River drainage within Ukraine: a threat for local fish stocks? – Arch. Pol. Fish. 19: 249-257.
- Elvira B., Almodóvar A. 2001 – Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century – J. Fish Biol. 59: 323-331.
- Freyhof J., Kottelat M. 2008 – *Hucho hucho* – In: IUCN 2013. IUCN Red List of Threatened Species. Version 2013.1. <www.iucnredlist.org>. Downloaded on 12 September 2013.
- Geist J., Kolahsa M., Gum B., Kuehn R. 2009 – The importance of genetic cluster recognition for the conservation of migratory fish species: the example of the endangered European huchen *Hucho hucho* (L.) – J. Fish Biol. 75: 1063-1078.
- Grudniewska J., Przybył A., Goryczko K., Andrzejewski W. 2013 – Preliminary attempts to start feed huchen (*Hucho hucho*) – Arch. Pol. Fish. 21: 225-227.
- Hanel L., Lusk S., Andreska J. 2013 – Huchen in the Czech Republic: A review – Arch. Pol. Fish. 21: 143-154.
- Hari R.E., Livingstone D.M., Siber R., Burkhardt-Holm P., Güttinger H. 2006 – Consequences of climatic change for water temperature and brown trout populations in Alpine rivers and streams – Glob. Chang. Biol. 12:10-26.
- Hegediš A., Mićković B., Cvijanović G. 2005 – Action Plan for Fisheries Management with Huchen Stocks in Catchments of Republic of Serbia – University of Belgrade, Center for Multidisciplinary studies, Belgrade, 52 p (in Serbian).
- Heino J., Virkkala R., Toivonen H. 2009 – Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions – Biol. Rev. Camb. Philos. Soc. 84: 39-54.
- Holčík J. 1984 – Review of experiments with introduction and acclimatization of the huchen, *Hucho hucho* (Linnaeus, 1758) (Salmonidae) – Food and Agriculture Organization of the United Nations, Rome, 42(2): 290-298.
- Holčík J. 1990 – Conservation of the huchen, *Hucho hucho* (L.), (Salmonidae) with special reference to Slovakian rivers – J. Fish Biol. 37 (Suppl. A): 113-121.
- Holčík J., Hensel K., Nieslanik J., Skácel L. 1988 – The Eurasian huchen, *Hucho hucho*, largest salmon of the world – Dr W. Junk Publisher, Dordrecht-Boston-Lancaster, 239 p.
- Holčík J., Klindov, A., Masár J., Mészáros J. 2006 – Sturgeons in the Slovakian rivers of the Danube River basin: an overview of their current status and proposal for their conservation and restoration – J. Appl. Ichthyol. 22: 17-22.
- Ivanc M. 2012 – The Danube Salmon - *Hucho hucho* (Linnaeus, 1758) in Slovenia: distribution, threats, conservation – In: Book of Abstracts II International Hucho Symposium (Eds) A. Witkowski, J. Kotusz, K. Goryczko, B.M. Pokryszko, J. Kuszniierz, Mus. Nat. Hist., Univ. Wrocl., Wroclaw: 30.
- Ivaška S. 1951 – Danube salmon – its catch and farming – Tatran, Bratislava, 87 p (in Slovak).
- Jensen O.P., Gilroy D.J., Hogan Z., Allen B.C., Hrabik T.R., Weidel B.C., Chandra S., Vander Zanden M.J. 2009 – Evaluating recreational fisheries for an endangered species: a case study of taimen, *Hucho taimen*, in Mongolia – Can. J. Fish. Aqua. Sci. 66: 1707-1718.
- Kišpaćić M. 1893 – Fish – Matica Hrvatska, Zagreb, 455 p. (in Croatian).
- Košćo J. 2012 – God save the Queen – In: Book of Abstracts II International Hucho Symposium (Eds) A. Witkowski, J. Kotusz, K. Goryczko, B.M. Pokryszko, J. Kuszniierz, Mus. Nat. Hist., Univ. Wrocl., Wroclaw: 30-31.
- Kottelat M., Freyhof J. 2007 – Handbook of European freshwater fishes – Kottelat, Cornol, Switzerland and Freyhof, Berlin, Germany, 646 p.
- Kotusz J., Witkowski A., Kuszniierz J., Popiółek M. 2010 – Does huchen, *Hucho hucho* (L.), have a chance to return to Czadeczká Stream? – Chrońmy Przyr. Ojcz. 66: 169-174 (in Polish).
- Kowalewska-Hryc I., Hryc M., Epler P. 2005 – Impact of feeding different feeds on the growth and survival of larval

- huchen (*Hucho hucho* L.) – Komun. Ryb. 5(88): 5-7. (in Polish).
- Krajč T., Štencl R., Hurčala P. 2012 – The Danube salmon – *Hucho hucho* (Linnaeus, 1758) in Slovakia (protection, breeding and fishing) – In: Book of Abstracts II International Hucho Symposium (Eds) A. Witkowski, J. Kotusz, K. Goryczko, B.M. Pokryszko, J. Kuszniarz, Mus. Nat. Hist., Univ. Wrocl., Wroclaw: 32.
- Krazhan S.A., Mruk A.I., Koba S.A., Handozhivska H.I. 2012 – Features feeding Danube salmon (*Hucho hucho*, L.) in autumn in River Teresva, Tisa – In: Contemporary theoretical and practical problems of ichthyology (Eds) M.M. Marchenko, O.Y. Khudyi, L.V. Khuda, Yuriy Fedkovych Chernivtsi National University Press: 118-120 (in Ukrainian).
- Kulmatycki W.J. 1930 – On alleged locations of huchen occurrence – Prz. Ryb. 21: 696-697 (in Polish).
- Kulmatycki, W.J. 1931 – Über das Vorkommen und die Biologie des Huchens im Czeremosz-Fluss – Verh. Inst. Ver. Limnol. 7: 313-320.
- Lusk S., Lusková V., Hanel L., Lojkásek B., Hartvich P. 2011 – Red List of lampreys and fishes of the Czech Republic – Biodiverzita ichtyofauny ČR 8: 68-78 (in Czech).
- Marić S., Nikolić V., Paunović M., Simonović P. 2009 – Investigation of life cycle and population features of huchen in Serbia – Faculty of Biology and Ministry of Environment Protection and Spatial Planning, University of Belgrade, 79 p. (in Serbian).
- Marić, S., Razpet, A., Nikolić, V., Snoj, A., Simonović, P. 2012 – Genetic diversity of the Huchen (*Hucho hucho*) in Serbia – In: Book of Abstracts II International Hucho Symposium (Eds) A. Witkowski, J. Kotusz, K. Goryczko, B.M. Pokryszko, J. Kuszniarz, Mus. Nat. Hist., Univ. Wrocl., Wroclaw: 35-36
- Markovic D., Scharfenberger U., Schmutz S., Pletterbauer F., Wolter C. 2013 – Variability and alterations of water temperatures across the Elbe and Danube River Basins – Clim. Change 119: 375-389.
- Mateleshko O.Y., Potish L.A. 2011 – Red Book of Ukrainian Carpathians. Wildlife – Uzhorod, Karpaty, 366 p. (in Ukrainian).
- Mateš A. 2005 – Huchen and grayling – J&B, Zagreb, 216 p. (in Croatian).
- Mijović-Magdić J. 2007 – The current status of the huchen, *Hucho hucho* (Linnaeus, 1758), in Serbian waters and possibilities for its controlled spawning and rearing of juveniles – Doctoral dissertation, Faculty of Agriculture, University of Novi Sad, Novi Sad, Serbia, 175 p. (in Serbian).
- Mrakovčić M., Brigić A., Buj I., Čaleta M., Mustafić P., Zanella D. 2006 – Red book of freshwater fish of Croatia – Ministry of Culture, State Institute for Nature Protection, Zagreb, 253 p. (in Croatian with English introduction).
- Mruk A., Velykopolskiy I. 2012 – Artificial reproduction of Danube salmon *Hucho hucho* (Linnaeus, 1758) in Ukraine – In: Book of Abstracts II International Hucho Symposium (Eds) A. Witkowski, J. Kotusz, K. Goryczko, B.M. Pokryszko, J. Kuszniarz, Mus. Nat. Hist., Univ. Wrocl., Wroclaw: 36-37.
- Muhamedagić S., Habibović E. 2013 – The State and Perspective of Danube Salmon (*Hucho hucho*) in Bosnia and Herzegovina – Arch. Pol. Fish. 21: 155-160.
- Nagy S. 1976 – Contribution to the knowledge of the food of the Huchen (*Hucho hucho*) (Teleostei: Salmonidae) – Zool. Listy 25: 183-191.
- Parasiewicz P., Eberstaller J., Weiss S., Schmutz S. 1998 – Conceptual guidelines for natural-like bypass channels – In: Fish migration and fish bypasses (Eds) M. Jungwirth, S. Schmutz, S. Weiss, Fishing News Books, Oxford, UK: Blackwell Science Ltd Publisher.
- Pažur K., Habeković D., Popović J. 1982 – River charr (*Hucho hucho* L. 1758) growth dynamics in the waters of the SR of Croatia – Ichthyologia, 14: 161-169 (in Croatian with English summary).
- Prawochensky R., Kolder W. 1968 – Synopsis of biological data on *Hucho hucho* (Linnaeus, 1758) – Food and Agriculture Organization on the United Nations Rome, 32 p.
- Rand P.S. 2013 – Current global status of taimen and the need to implement aggressive conservation measures to avoid population and species-level extinction – Arch. Pol. Fish. 21: 119-128.
- Ratschan C. 2012 – Maximum size and distribution limits of Danube salmon (*Hucho hucho*) as a function of river size and geology in Austria and Bavaria – Österreichs Fischerei 65: 296-311 (in German).
- Ratschan C., Zauner G. 2012 – Past and present situation of huchen, or Danube salmon, in Upper Austria, future prospects – Österreichs Fischerei 65: 250-258 (in German).
- Sabioncello I., Marko S., Pažur K. 1970 – Bio-Ecological Research on Salmonids in Croatia – Ribarstvo Jugoslavije 25: 29-37 (in Croatian with English summary).
- Schinegger R., Trautwein C., Melcher A., Schmutz S. 2012 – Multiple human pressures and their spatial patterns in European running waters – Water Environ. J. 26: 261-273.
- Schmutz S., Zitek A., Zobel S., Jungwirth M., Knopf N., Kraus E., Bauer T., Kaufmann T. 2002 – Integrated approach for the conservation and restoration of Danube salmon (*Hucho hucho* L.) populations in Austria – In: Freshwater Fish Conservation - Options for the Future (Eds) M.J. Collares-Pereira, I.G. Cowx and M.M. Coelho, Fishing News Books, Blackwell Science, Oxford: 157-173.
- Simonović P., Marić S., Nikolić V. 2000 – Growth characteristics of huchen *Hucho hucho* (L.) from Rivers Drina, Una and Sana – Acta Biol. Iugosl. – Ekologija Belgrade, 35: 123-26.

- Simonović P., Nikolić V., Tošić A., Marić S. 2011 – Length-weight relationship in adult huchen *Hucho hucho* (L., 1758) from Drina River, Serbia – *Biologia*, Bratislava, 66: 156-159.
- Staff F. 1950 – Freshwater fish in Poland and neighboring countries – Wydawnictwo Trzaska, Evert and Michalski, Warszawa, 286 p. (in Polish).
- Stráňai I. 2012 – Samuel Ivaška – the pioneer in the Danube Salmon farming – In: Book of Abstracts II International Hucho Symposium (Eds) A. Witkowski, J. Kotusz, K. Goryczko, B.M. Pokryszko, J. Kuszniere, Mus. Nat. Hist., Univ. Wrocl., Wroclaw: 45-46.
- Šubjak J. 2013 – Observations of food and feeding of angler-caught huchen, *Hucho hucho* (L.), in Slovak rivers in winter – *Arch. Pol. Fish.* 21: 219-225.
- Treer T., Šprem N., Piria M. 2013 – Condition of huchen (*Hucho hucho* Linnaeus, 1758) from the Croatian-Slovenian Kupa River – *J. Appl. Ichthyol.* doi: 10.1111/jai.12309.
- Velykopolskyy I. 2012 – Huchen in Zakarpattya – *Sztuka Łowienia* 1(12): 35-37 (in Polish).
- Velykopolskiy I., Mruk A. 2012 – The Danube Salmon in the Zakarpate Region of Ukraine: current state and perspectives – In: Book of Abstracts II International Hucho Symposium (Eds) A. Witkowski, J. Kotusz, K. Goryczko, B.M. Pokryszko, J. Kuszniere, Mus. Nat. Hist., Univ. Wrocl., Wroclaw: 52-53.
- Vîrban I., Ionescu O. 2011 – Study on Danube salmon populations (*Hucho hucho* L.) of Romania – In: Proc. Biennial International Symposium, Forest and Sustainable Development, 15-16th October 2010, Braşov, Romania: 373-380.
- Weiss S., Marić S., Snoj A. 2011 – Regional structure despite limited mtDNA sequence diversity found in the endangered Huchen, *Hucho hucho* (Linnaeus, 1758) – *Hydrobiologia*, 658: 103-110.
- Witkowski A. 1988 – The spawning run of the huchen *Hucho hucho* (L.) and its analysis – *Acta Ichthyol. Piscat.* 18: 23-31.
- Witkowski A. 2003 – The Huchen *Hucho hucho* (L.) – saved for the Polish ichthyofauna – *Suppl. Acta Hydrobiol.* 6: 109-113.
- Witkowski A., Kowalewski M. 1984 – Food of the Danube salmon *Hucho hucho* (L.) introduced into the River Dunajec – *Acta Hydrobiol.* 25/26(2): 205-214.
- Witkowski A., Błatucha J., Kowalewski M. 1984 – Growth rate of huchen introduced into the Dunajec River – *Gosp. Ryb.* 34: 15-16 (in Polish).
- Witkowski A., Błachuta J., Kowalewski M. 1994 – Food interaction between 0+ Huchen *Hucho hucho* (L.) (*Salmonidae*) and native fish species in a mountain stream – *Arch. Pol. Fish.* 2: 95-101.
- Witkowski A., Kotusz J., Przybylski M. 2009 – Degree of threats to the freshwater ichthyofauna of Poland. Red list of fishes and lampreys in 2009 – *Chrońmy Przyr. Ojcz.* 65: 33-52 (in Polish).
- Witkowski Z., Król W., Solarz W. 2003 – Carpathian list of endangered species – WWF and Institute of Nature Conservation, Polish Academy of Sciences, Vienna-Krakow, 64 p.
- Witkowski A., Goryczko K., Kowalewski M. 2013 – The history of huchen, *Hucho hucho* (L.), in Poland – distribution, restoration, and conservation – *Arch. Pol. Fish.* 21: 161-168.
- Wolfram G., Miksch E. 2007 – Rote Liste der Fische (Pisces) Österreichs – In: Rote Listen gefährdeter Tiere Österreichs (Ed.) K.P. Zulka, Wien, Böhlau: 61-198.
- Wolter C. 2007 – Temperature influence on the fish assemblage structure in a large lowland river, the lower Oder River, Germany – *Ecol. Freshw. Fish.* 16: 493-503.
- Woodward G., Perkin D.M., Brown L.E. 2010 – Climate change and freshwater ecosystems: impacts across multiple levels of organization – *Philos. Trans. R. Soc. B-Biol. Sci.* 365(1549): 2093-2106.
- Zitek A., Schmutz S., Jungwirth M. 2008 – Assessing the efficiency of connectivity measures with regard to the EU-Water Framework Directive in a Danube-tributary system – *Hydrobiologia* 609: 139-161.