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Japoshvili , Bella; Couto, Thiago B.A. ; Mumladze, Levan ; Epitashvili, Giorgi ; McClain, Michael E.; Jenkins, Clinton N. ; Anderson, Elizabeth P.

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Authors: Bella Japoshvili,[1] Thiago B.A. Couto,[2] Levan Mumladze,[1] Giorgi Epitashvili,[1] Michael E. McClain,[3,4] Clinton N. Jenkins,[2,5] and Elizabeth P. Anderson[2]

[1]Institute of Zoology, Ilia State University, 3/5 Cholokashvili ave, 0169, Tbilisi, Georgia

[2]Department of Earth & Environment and Institute of Environment, Florida International University, Miami, FL 33199 USA

[3]Department of Water Resources and Ecosystems, IHE Delft Institute for Water Education, Delft, The Netherlands

[4]Faculty of Civil Engineering and Geosciences, Delft University of Technology, Delft, The Netherlands

[5]Kimberly Green Latin American and Caribbean Center, Florida International University, Miami, FL 33199 USA

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Hydropower development in the Republic of Georgia and implications for freshwater biodiversity conservation

Abstract: The Caucasus region is a meeting point for culture and nature, lying at the nexus of Europe, the Middle East, Central Asia, and Africa, and identified as one of 36 global biodiversity hotspots. The Republic of Georgia, the center of the Caucasus biodiversity hotspot, encompasses a geographically diverse landscape inhabited by a remarkable, endemic, and understudied flora and fauna under increasing threat from human activities. A wave of new and proposed dams for hydropower presents one of the most pressing challenges for freshwater biodiversity conservation in Georgia, a country where hydropower accounts for >90% of electricity. However, this situation remains largely unknown to the international scientific community and there is limited scientific information available about Georgia in the internationally indexed peer-reviewed literature. In this article, we describe the geography, politics, and freshwater biodiversity of rivers of Georgia, with a focus on fishes. We examine trends in hydropower development over the past century and identify four distinct periods: the pre-Soviet period (until 1921), the Soviet period (1922-1991), the 1990s immediately following Georgia's declaration of independence, and the 21st century. We explore the effects of existing and proposed dams on the connectivity of rivers of western Georgia and their potential consequences for conservation of diadromous, potamodromous, and resident fish. Using the Dendritic Connectivity Index (DCI) as an analytical lens, we found serial decreases in DCI values following different periods of hydropower development in the country. Finally, we offer four considerations for future research and conservation in light of ongoing hydropower development: i) expand biodiversity research and environmental monitoring, ii) assess and implement environmental flows for Georgian rivers, iii) implement strategic planning for new hydropower development, and iv) establish strict conservation areas for protection of endangered sturgeons.

Introduction

Few issues have defined the challenges for conservation of the world's freshwater fish fauna in the first part of the 21st century as significantly as the unprecedented boom in hydropower dam development currently underway in many countries. Whereas an earlier wave of hydropower dam building in the mid-20th century resulted in extensive river modification throughout North America and Western Europe, the current proliferation of hydropower dams has targeted rivers in countries with emerging economies (Zarfl et al. 2015; Couto and Olden 2018). Geographically, this modern wave of hydropower development overlaps with places that harbor extraordinary freshwater fish species richness and endemism, including numerous migratory species, and extensive inland river fisheries that provide a major source of protein and income to riparian human populations (Winemiller et al. 2016; Anderson et al. 2018; Barbarossa et al. 2020). Indeed, the conservation challenge of the 21st century's rapid hydropower development for freshwater biodiversity has received substantial coverage in the scientific literature and popular media over the past decade. Nevertheless, most articles have documented the hydropower trends and related conservation challenges for tropical river basins such as the Amazon and Mekong (Ziv et al. 2012; Winemiller et al. 2016; Anderson et al. 2018).

This paper aims to increase knowledge of modern hydropower trends and their consequences for freshwater biodiversity beyond these already documented areas by offering a case study from a lesser-known area: the Republic of Georgia. Georgia, an important part of the Caucasus biodiversity hotspot (Myers et al. 2000), encompasses a geographically diverse landscape inhabited by a remarkable, endemic, and understudied flora and fauna under increasing threat from human activities, including hydropower development. In the past two decades, Georgia has experienced a proliferation of hydropower dams (most <100 MW) that have added ~1000 MW in installed generation capacity. More than 100 proposed projects are in various stages of planning or licensing as of 2020. The same rivers in Georgia that are subjected to hydropower development harbor several fish species classified as critically endangered (CR) by the International Union for the Conservation of Nature (IUCN), including seven species of sturgeon. However, to our knowledge, no published studies to date have examined the effects of hydropower dams on these and other freshwater fishes in Georgia, and the conservation status of Georgia's freshwater fauna currently is not well understood.

Here, we examine trends in hydropower development in Georgia and their implications for rivers and their biodiversity. For context, we provide an overview of river geography, relevant political history, and freshwater biodiversity in Georgia, as many readers may be unfamiliar with this region given the paucity of published studies about Georgia in the natural resource conservation literature, particularly in English. We then examine historical and modern trends in hydropower development, highlighting their consequences for river connectivity and freshwater fish diversity in Georgia. Finally, we articulate a list of research needs for freshwater science and conservation in light of current hydropower development and its future trajectory.

Geography, politics, and rivers of Georgia

The Caucasus region has long been a meeting point for culture and nature, lying at the nexus of Europe, the Middle East, Central Asia, and Northern Africa. Within the larger Caucasus region, the Republic of Georgia covers an area of roughly 70,000 km^2 and is home to approximately 3.7 million people (Figure 1). Within this relatively small geographic area, Georgia is rich in freshwater resources, including an estimated 59,000 km of rivers. Most Georgian rivers flow either westward into the Black Sea or eastward through Azerbaijan and into the Caspian Sea; the Likhi ridge divides these two drainages. Major rivers of eastern Georgia include the Kura, Alazani, and Iori, all of which drain transnational basins shared with either Turkey or Azerbaijan, or both. Of these, the Kura River is the largest and longest fluvial system of the Caucasus ecoregion, flowing for ~1515 km over Turkey, Georgia, and Azerbaijan, with a substantial portion of its headwaters in Georgia and an estimated annual discharge of 18.1 km^3 (579 m^3/s). The Rioni River (estimated annual discharge of 12.7 km^3 (403 m^3/s), flowing ~327 km, is the principal system of western Georgia, with its 13,500 km^2 basin entirely within national territory and spanning from the Caucasus mountains to the Black Sea. Although its basin is less than 10% of the Kura in land area, the Rioni's average annual discharge is nearly 70% that of the Kura River, (Gigineishvili, 2000). In its upper drainage, the glacier-fed Rioni River flows through mountainous regions (Figure 2a, 2b). Its lowland region is characterized by extensive swamps, marshes, and floodplain areas as it approaches the Black Sea coastline (Figure 2c). Also draining western Georgia into the Black Sea are the Kodori, Enguri, Supsa and numerous smaller rivers. Given the country's mountainous topography, most rivers in Georgia are short (< 25 km long), high gradient, turbulent systems.

Rivers in present-day Georgia reflect the country's complex history over the past century. From 1922-1991, Georgia was part of the Soviet Union. This period, referred to as the 'Soviet period' was marked by large scale industrial projects in Georgia and other former-Soviet republics of the southern Caucasus region, like Azerbaijan and Armenia (Kuljanishvili et al. 2020). For example, the Mingachevir Dam, built in Azerbaijan between 1945-1954, fragmented the Kura River and disconnected upstream areas of the Kura and Alazani basins within Georgia from the Caspian Sea. Other noteworthy industrial projects were the Vartsikhe Dam for hydropower, built between 1971-78 on the Rioni River, and the construction of an irrigation/high water protective dam and the largest hydropower dam on the Enguri River in the 1970-80. This dam resulted in the disconnection of the Rioni and Enguri basins into isolated parts.

Introduction of non-native species to Georgian freshwaters, both accidentally and intentionally for aquaculture, also occurred during the Soviet period, especially between 1960-70 (Kuljanishvili et al., In prep). For example, the most problematic invasive species, such as *Carassius gibelio* (Prussian carp), *Pseudorasbora parva* (topmouth gudgeon or stone moroko), and *Gambusia holbrooki* (mosquitofish), were all introduced in the 20th century and are now very widespread in the region. The Soviet period in Georgia was also a time of substantial research on freshwater systems and their fauna, particularly fishes, largely motivated by interest in aquaculture (Barach 1941; Demetrashvili 1977; Sharvashidze 1982; Elanidze 1983).

Georgia declared itself independent from the Soviet Union in 1991. In Georgia and throughout the Caucasus, the dissolution of the Soviet Union reportedly marked a shift in management of freshwater resources, such as fisheries, as fishing rights and regulations were suddenly divided among new independent states. In the Caspian Sea, for example, an increase in illegal harvest and trade of fish, particularly sturgeons, occurred immediately after Soviet disintegration, and continued throughout much of the 1990s (Pikitch et al. 2005).

Freshwater fishes of Georgia

Presently available information on freshwater biota in Georgia is fragmented and incomplete. A recent analysis of Georgia's freshwater biodiversity reviewed 300 published works between 1930-2012 that contained data on fishes and other freshwater species in Georgia and identified a few trends (Japoshvili 2012). First, most published works are in Russian or Georgian, without English translations, and therefore not readily accessible to an international scientific audience. Second, ichthyological research in general peaked in the 1960s and was focused primarily on rivers during that time. It gradually declined over the remainder of the 20th century but has started to see a slight rise since the early 2000s. These trends are similar across countries of the southern Caucasus (Armenia, Azerbaijan, Georgia) (Kuljanishvili et al. 2020), but run contrary to those seen in other parts of the world, particularly the tropics, where ichthyological research, both in terms of alpha taxonomy and ecological studies, has increased markedly since the 1970s (Reis et al. 2016). Ichthyological research has also lagged behind other biodiversity studies in Georgia (Mumladze et al. 2020). Indeed, the first checklist of fishes of Georgia from the post-Soviet period was compiled by Ninua and Japoshvili (2008) only just over a decade ago and based mainly on literature review. Third, nearly all publications on freshwater fishes and other freshwater biota in Georgian waters report results of taxonomic, ecological, or fisheries-related studies. While there has been an uptick in application of molecular methods that has improved ichthyological knowledge since 2000, there have been only very limited attempts at any kind of ecological monitoring or long-term research. Finally, of all freshwater animals, fishes are the best studied taxa in Georgia. No other freshwater species other than fishes are listed in the Georgian Red List, part of the Georgian Biodiversity Database, which is freely available online (Georgian Biodiversity Database 2021).

Acknowledging these limitations, current estimates report 96 freshwater fish species from Georgian freshwater bodies (Kuljanishvili et al. 2020). Within a larger biogeographic context, Georgian freshwater fishes represent an important vertebrate faunal component of the Caucasus biodiversity hotspot, from which 162 species of freshwater fishes and four species of lamprey—scaleless, jawless fishes that emerged roughly 280 million years ago—have been documented to date (Freyhof et al. 2020; Kuljanishvili et al. 2020). Of these, 51 fish species and one lamprey are endemic to the Caucasus (Freyhof et al. 2020). Abell et al. (2008) recognize three main freshwater eco-regions in the Caucasus: the Western Transcaucasian, Kura-South Caspian, and Western Caspian. Similar to other biodiversity hotspots in their original designations (Myers et al. 2000), freshwater fish diversity was not considered among the criteria used to assign the Caucasus (and Georgia as a part) as a biodiversity hotspot. However, recent studies have shown that the freshwater biota is very diverse in the Caucasus, potentially exceeding terrestrial ecosystems in rate of endemicity (including small range endemics) in many animal groups (Gabelashvili et al., 2018; Grego et al., 2020; Oláh et al., 2020).

Georgia and the larger Caucasus region once harbored a remarkable diversity of sturgeons (Order Acipenseriformes: Family Acipenseridae), but the current status of their populations in the region is unclear (Freyhof et al. 2020). Sturgeons are native to subtropical, temperate, and sub-Arctic freshwaters and coastal areas of Eurasia and North America. Of the four extant genera of sturgeons, two have been documented in the Caucasus region and in Georgia (*Huso* and *Acipenser*). Of the 26 sturgeon species recognized worldwide, seven are native to Georgia: Russian sturgeon (*A. gueldenstaedtii*), Persian sturgeon (*A. persicus*), Colchic sturgeon (*A. colchicus*), Fringebarbel or Ship sturgeon (*A. nudiventris*), Star sturgeon (*A. stellatus*), Atlantic (Baltic) sturgeon (*A. sturio*), and Beluga sturgeon (*Huso huso*) (CEPF 2003; Pikitch et al. 2005; Ninua and Japoshvili 2012; Fricke et al. 2020). However, there remain many ambiguities about the taxonomy of Black Sea sturgeons. All Caucasian sturgeon species, and nearly all sturgeons worldwide, are considered threatened or endangered (Table 1). Several characteristics of sturgeon's natural history make them especially vulnerable to hydropower development and to overfishing. Sturgeons are generally long-lived fishes, slow to grow and mature; female Fringebarbel sturgeon (*A. nudiventris*), for example, reach maturity at about 17 years and spawn once every three years (Vecsei et al. 2002). Ages of >100 years have been reported for Beluga sturgeon (*Huso huso*; Helfman et al. 1997). Commercial sturgeon species can reach lengths of several meters and weigh >100 kg. Life history and catch statistics for Caucasian species report large sizes for *A. gueldenstaedtii* (2.3 m max length; 100 kg max weight). *A. persicus* (2.4 m; 70 kg), *A. stellatus* (2.2 m; 80 kg). *Huso huso* is considered the world's largest freshwater fish (>6 m; 1300 kg; Pikitch et al. 2005). Finally, sturgeon spawn in freshwaters and most are diadromous; therefore, they depend on longitudinally connected riverine pathways that are unimpeded by dams to complete their life cycle. The Rioni River in Georgia is considered critical to global sturgeon conservation: it is thought to still harbor surviving populations of *A. persicus, A. stellatus, A. gueldenstaedtii,* and *H. huso* (Freyhof et al. 2020).

The Caucasian fish fauna includes other anadromous species, represented by shads (Clupeidae), trout (Salmonidae), and barbels (*Luciobarbus*) that are also at risk from hydropower development and from commercial and recreational fisheries (Freyhof et al. 2020; Kuljanishvili et al. 2020). Bulatmai barbell (*Luciobarbus capito*) for instance, is one of the largest (semi) anadromous fish that are restricted to Caspian Sea drainage. The Kura River basin is still the largest part of its distribution area. However, within the Kura River, the population of this species is strongly fragmented as a consequence of barriers presented by dams and local extinction in the near future is a major concern. Other species with migratory life history traits (such as for instance potamodromous species; see Table 1) that are not globally threatened and have never been evaluated locally are subjected to the same threats of habitat fragmentation and impeded movement because of existing and future dams on Georgian rivers.

Methods

We used a mixed methods approach to gather information about hydropower development and its implications for river connectivity and freshwater fish species persistence in Georgia. To understand historical and modern trends in hydropower development, we reviewed information on dams constructed, planned, or proposed in Georgia over the past century. Information on hydropower development from the Soviet period (1922-1991) and before was gathered from publicly available information on the web page of the Ministry of Economy and Sustainable Development of Georgia (http://energy.gov.ge) and technical reports (Kochladze, 2013). For information on hydropower development in Georgia since 1991, we requested and retrieved the most updated dataset of existing and proposed hydropower facilities from the United States Agency for International Development's (USAID) Energy Program of Georgia (https://ge.usembassy.gov). We used this dataset to classify dams as existing, planned, or proposed, and to plot the locations of all dams according to the most updated data available.

We used available data on dam locations and reported fish distributions to examine the consequences of dams for longitudinal river connectivity and freshwater fishes in western Georgia as revealed by a commonly-applied metric, the Dendritic Connectivity Index (described below; Cote et al. 2009). Longitudinal connectivity refers to the connectedness of upstream and downstream habitats in a riverscape, and has been identified as a critical ecological component for the dispersal and migration of freshwater organisms (Ward 1989; Haxton and Cano 2016). Our analysis of connectivity focused on the rivers of western Georgia that drain into the Black Sea whose basins fall entirely or nearly entirely within the country. Distributional data on fish species occupying basins of western Georgia were assembled based on the most up to date faunistic literature (Epitashvili et al., 2020; Kuljanishvili et al., 2020; 2021). Life history traits were based on Kottelat and Freyhof (2007) and Froese and Pauli (2020).

We used HydroSHEDS and HydroBASINS global hydrographic mapping products (Lehner et al. 2008; Lehner et al. 2013) to delimit rivers and their basins across western Georgia (55 basins in total, each one containing a fully connected network that drains to the Black Sea), and to plot the locations of existing, planned, and proposed hydropower dams. To improve reliability of results, we performed spatial edits on the dataset of hydropower dams to accurately match it to the river network, which included removal of duplicate points (e.g., from sequences of powerhouses over canals that share the same impoundment) and automatic snapping of dams within 300 m to the nearest river reach. We manually repositioned points for dams >300 m from the river network using visual reference to Google Earth imagery and the reservoir polygons from HydroLAKES dataset (Messager et al. 2016). Additionally, all dams larger than 50 MW were inspected manually to ensure their location in the river network followed visual references. These steps reduced our dataset from an initial 105 datapoints to 91 for the purpose of the analyses described below.

To examine losses in longitudinal riverine connectivity over space and time as a consequence of hydropower dam development, we applied the Dendritic Connectivity Index (DCI). The DCI is a widely-used metric of longitudinal river connectivity that estimates the probability that a fish can move between two randomly selected points in a river network (see Cote et al. 2009 for detailed methods and equations). Based on a review by Jumani et al. (2020), we identified the DCI as the most appropriate metric for our analysis due to its flexibility and adjustability to different fish life histories. The DCI ranges from 100 to 0, with the larger number indicating a completely connected river network with no barriers. We adopted two DCI equations in our analyses to approximate the connectivity estimates to the migratory behavior of the different fish species present in the region (Cote et al. 2009; Table 1). The DCIp provides connectivity estimates for potamodromous fish, referring to those migratory species that perform movements entirely within freshwaters. The DCId adjusts the index to be more suitable for diadromous fish, referring to those migratory species that move between fresh and saline water to complete their life cycle. Whereas the DCIp considers the connectivity of any combination of random locations across the entire river network, the DCId focuses on the connectivity between random locations of the network and the mainstem river mouth (i.e., where every diadromous fish should pass to access the saline waters of the Black Sea). Considering the reported inefficiency or total absence of fish passages in the region, we adopted 0.1 (10%) as a conservative estimate of barrier permeability in upstream and downstream directions for all dams. This estimate was made on the basis of professional judgement and following similar analysis in the literature that assume dams to be fully impassible or to have low permeabilities (Barbarossa et al. 2020; Couto et al. 2021). This barrier permeability parameter (p) reflects a two-way possibility for both DCI equations of this study. The spatial steps of the analyses were conducted in a GIS environment using the Barrier Analysis Tool (BAT), an extension to ArcMap (version 10.7) that takes barrier datasets and cuts up a river network into connected segments with unique fragment IDs (BAT 2010). The spatial data was then imported into the software R (version 4.0.2), where DCI functions were applied to the spatial data following the codes provided by Couto et al. (2021).

Based on the start of operations of each existing hydropower dam in the dataset, we were able to calculate DCId and DCIp values for various scenarios during the period 1900 to 2021. An additional projected future scenario was created to accommodate planned and proposed dams.

Basin-level estimates of river connectivity were assigned to each fish species according to their occurrence records and migratory behavior, with DCId being adjusted for diadromous species, and DCIp for potamodromous and residents. Although resident fish do not migrate, connectivity loss by dam building has been reported to limit dispersal, promote local extinctions, and affect genetic diversity in resident species, with DCIp being the most suitable metric to track changes in connectivity in this case (Perkin & Gido et al. 2012; Barbarossa et al. 2020). Based on the occurrence records of each species (see the Supplementary Information), basin-level estimates of species richness and average river connectivity at the species' range were estimated. To assess how improvements in dam permeability could affect DCI estimates, we ran a sensitivity analysis that simulated DCId and DCIp estimates for permeability values ranging from 0 (i.e., fully impassible) to 0.9 (i.e., 90% passible). All of these analyses were run with the software R (version 4.0.2).

Results

Trends in hydropower development in Georgia

Hydropower development trends in Georgia reveal four distinct periods: pre-Soviet (until 1922), Soviet (1922-1990), post-independence Georgia (1991-present), and modern Georgia (2010-present). In the pre-Soviet period, the first small hydropower dam (0.1 MW) was built in 1898 on the Borjomula River by German engineers, followed by a number of small hydropower projects in different regions by 1922. This year, 1922, marked the starting date of construction of the first large hydropower project on the Kura River near Tbilisi, the Zahes Dam (36.8 MW), completed in 1927. Until the 1960s, construction of small hydropower projects (<1 MW capacity) was the priority, with an estimated 300 small projects constructed unsystematically around Georgia, mainly for providing electricity to local populations. However, centralization of electricity production and distribution in the 1960s triggered a wave of construction of much larger dams. Perhaps the most notable hydropower project of this time period was the Enguri Dam (1,300 MW) on the Enguri River in western Georgia, whose construction began in 1961 and spanned nearly two decades. At the time and up until 2012, Enguri Dam was the world's largest concrete arch dam (272 meters high), and it remains the largest industrial project in the Caucasus region. By the end of the Soviet period in 1991, there were approximately 30 medium and large hydropower dams in Georgia and an unknown number of smaller projects, with a total installed generation capacity of 2,800 MW (Kochladze, 2013).

Since Georgia declared its independence in 1991, hydropower development has been on a varied trajectory. Post-independence, an economic recession halted growth in the hydropower sector during the 1990s; Georgia struggled to maintain existing infrastructure projects from the Soviet period and was unable to pursue new projects. Hydropower dams and other infrastructure in Georgia in the 1990s deteriorated significantly or was plagued by theft at many levels, from theft of power to breaking and stealing of metal and other materials associated with infrastructure projects. Most of the country experienced chronic electricity blackouts during this period, receiving access to no or only a few hours of power a day. A series of economic and energy sector reforms established the Georgian National Energy and Water Supply Regulatory Commission (GNERC) in 1997 and resulted in deregulation and privatization, allowing for energy generators, distributors, customers, and exporters to enter into direct contracts (IHA 2016). Practical outcomes of these reforms in the electricity sector appeared in the early 20th century, following the Rose Revolution in 2003, with increased international and private sector interest in the investment environment of Georgia.

In modern Georgia (2010 – present), international and private investments have helped catalyze a proliferation of new hydropower development. During the last decade, several large hydropower projects were completed including Paravani Dam in 2014 (86 MW), Dariali Dam in 2016 (108 MW), and Shuakhevi Dam in 2018 (178 MW) along with a high number of small to medium size projects. Presently, hydropower accounts for >90% of installed electricity generation capacity in Georgia, making it the dominant source of electricity. In the most recent Hydropower Status Report (IHA 2020), Georgia's total hydropower capacity was 3,271 MW based on 27 large HPPs (installed capacity over 13 MW) and 62 small HPPs (below 13 MW capacity); it added 50 MW that same year. Further development of the hydropower sector in Georgia has been considered a key aspect of energy security and decreased reliance on imported fossil fuels (IHA 2016). Hydropower in Georgia is increasingly influenced by international support from other European (e.g., Turkey, Norway) and Asian (India, Korea) countries. During summer months, Georgia exports electricity generated by hydropower facilities to neighboring countries, particularly Turkey and Russia. The recently commissioned Paravani Hydropower Project (87 MW) located near the Georgia-Turkey border, for example, is connected to the Georgian and Turkish power grids and was completed with international financing (IHA 2016). Many other new or planned projects in Georgia are energized by international support, including the Shuakhevi Dam (187 MW), which includes Indian and Norwegian partners. Interconnected hydropower development schemes—such as cascades of multiple dams on one river—have emerged for some Georgian rivers in the past decade, such as the Adjaristskali, Rioni, and Enguri rivers. These interconnected schemes, still largely in planning, are considered important for energy independence in Georgia, especially during winter seasons that correspond with dry periods for river flows.

Implications of hydropower development to river connectivity and fish conservation

Temporal trends in losses in longitudinal river connectivity in western Georgia, as revealed by our analyses, aligned with distinct periods of hydropower development: pre-Soviet, Soviet, post-independence, and modern Georgia (Figure 3). Hydropower development during the Soviet period (1922-1991) fragmented the lower portions of the largest river basins, such as the Rioni and Enguri, but rivers in many of the smaller, coastal basins remained longitudinally intact. More recent hydropower development (post-2010) has increased losses in river connectivity in these remaining smaller basins. Considering existing, planned and proposed dams, 10 of 55 basins in western Georgia already have or will have at least one hydropower dam in the future (Figure 3).

Depending on their position in the river network, hydropower dams have caused major losses in longitudinal riverine connectivity for several western Georgian rivers. For example, the completion of the Enguri Dam in 1978, Georgia's largest hydropower dam (1300 MW), disconnected the lower and montane sections of the Enguri River (Fig. 3). However, small projects have also had big consequences for basin-level connectivity losses. An example is the Kintrishi Dam (6 MW), constructed in 2017, which alone reduced the longitudinal connectivity of the Kintrishi River by 50% for both DCId and DCIp. The recent wave of new hydropower development has exacerbated decreases in river connectivity for diadromous species with new construction near the mouth of some rivers and has fragmented upper portions of some basins. For instance, the Khelvachauri dam (47 MW) was built in 2019 just 13 km from the mouth of the Chorokhi River (also known as Çoruh River, its Turkish name) and is the most downstream dam of the whole basin. In addition, many of the new planned and proposed dams are small and located in parts of river basins relatively distant from the coast, such as the 16 new projects proposed for the uppermost portion of the Enguri Basin – 15 of them below 10 MW. This new wave of small projects is promoting considerable decreases in DCIp in some basins like Enguri, Chorokhi, and Supsa (Fig 3).

The most species-rich basins in western Georgia are also those most heavily affected by hydropower development (Figure 4). We documented 36 fish species from western Georgia, of which 15 are diadromous, 8 potamodromous, and 13 resident species (Table 1). During the Soviet period (1921-91), the Enguri (31 fish spp.) and Rioni (32 fish spp.) basins were the most heavily fragmented by hydropower development. In the modern period (2010-present), hydropower development has intensified river fragmentation in the Enguri and the Rioni and affected several other large and mid-size river basins, such as the Khobistskali, Supsa, Natanebi, Kintrishi and Chorokhi, which harbor many resident fish species. In contrast, basins located in northwestern Georgia have been less subjected to hydropower development. Whereas they may harbor fewer species than larger basins, some free-flowing rivers, such as the Kodori and Mzipi, may still support populations of migratory species, including sturgeons (*A. gueldenstaedtii, A. stellatus* and *H. huso*) and the European eel (*Anguilla anguilla*) – all these species are classified as critically endangered (CR) according to IUCN criteria.

Both resident and migratory species are vulnerable to hydropower development in Georgia. Our analysis indicated that four species (*A. gueldenstaedtii, A. sturio, Capoeta banarascui*, and *Oxynoemacheilus cemali*) presently have average DCIs below 70 at the level of their geographic range in western Georgia, meaning that connectivity losses exceed 30% of their range. Connectivity losses are expected to increase substantially for these four species and exceed 30% for 10 more species if all the planned and proposed hydropower projects are constructed (Table 1). Species potentially affected include five out of six sturgeon species, four species of diadromous Gobiids, two species of potamodromous Leuciscids (*Abramis brama* and *Alburnus alburnus*), and resident species of the genus *Capoeta* and *Oxynoemacheilus*.

As expected, increasing barrier permeability increases river connectivity estimates for western Georgia basins for both DCId and DCIp metrics (Figure 5). However, our estimates reveal that significant improvements in basin-level connectivity can only be reached with major improvements in dam permeability. For instance, in all the scenarios very little gain in connectivity occurs with any levels of permeability ranging from zero to 0.2. Although this is a simulation exercise based on key assumptions (e.g., all dams have the same permeability value), these results highlight that fish passages must have much higher efficacy than currently reported to serve as efficient mitigation action that restore basin-level river connectivity.

Discussion

In this paper, we have provided an overview of hydropower development in Georgia, an area with interesting political and natural history for which limited studies have been published in the international conservation biology literature. We have offered a window into the challenges for freshwater biodiversity science and conservation in modern Georgia. Using longitudinal river connectivity as an analytical lens, we illustrated how historical and modern hydropower development has fragmented Georgian rivers and constrained freshwater fish habitat along riverine corridors, especially for migratory species.

Our examination of the trends in hydropower development over time revealed two major periods of intensive dam construction: the Soviet period of the past century and right now (2010-present). Our analysis showed significant losses in longitudinal river connectivity in basins of western Georgia during both of these periods as linked to construction of existing dams, for which reliable information exists. We projected further losses of longitudinal river connectivity under future hydropower development scenarios, considering planned and proposed dams, although the likelihood that all of these dam projects will be completed is uncertain, especially for proposed dams. Many dams listed as proposed today have plans that date back to the Soviet period but were discarded or postponed then because of high risk of environmental damage, threats to human populations, or limited investment capital. It remains to be seen whether those projects will eventually be constructed and, if they do proceed, what kind of mitigation plans for environmental and social impacts will be incorporated. Finally, our exploration of the implications of hydropower development for freshwater fishes was completed using the best available data for freshwater fauna in Georgia. Future improvements of species-level estimates of impacts of dams can be incorporated as more refined data becomes available on fish species distributions, migratory paths, and critical habitats.

Our efforts underscore the fact that the ecological impacts of hydropower development in Georgia remain highly understudied. In our review, we did not encounter targeted studies post-operation of hydropower dams in Georgia on freshwater fauna. However, anecdotal evidence and data from other biodiversity studies can be used to deduce some of their consequences. For example, historically, the Rioni River contained the most important spawning areas for 5 to 6 Black Sea sturgeon species. The construction and operation of the Vartsikhe Dam in the 1970s resulted in the loss of most of their spawning areas. This situation was exacerbated by the construction of additional hydropower dams and by illegal or unsustainable fishing. As a consequence, all sturgeons in the eastern Black Sea are now considered critically endangered (Guchmanidze, 2009). Hydropower facilities outside of Georgia's national borders, such as the Mingachevir Dam on the Kura River in Azerbaijan, also have affected freshwater fauna. The original dam at this site was constructed during the Soviet period and began operation in 1953, with a height of 80 meters and a flooded reservoir area of 605 km^2 (15.7 km^3 volume). The dam was recommissioned early this century and its installed generation capacity increased to 420 MW. The Mingachevir Dam's closure effectively split the Kura River Basin into an upper and lower portion and disconnected its headwater region within Georgia from the Caspian Sea. This split was followed by the subsequent extinction of Caspian lamprey and sturgeons in the upper Kura Basin (Demetrashvili, 1963).

In the past decade, the paucity of information on the ecological impacts of dams and concern for their effects on Georgian rivers has helped to catalyze efforts to apply internationally accepted approaches to understanding or mitigating effects of hydropower dams. For example, in response to concerns over the multiple dams that are existing or proposed for the Rioni River, a pilot study of environmental impact assessment for cumulative impacts of hydropower projects was realized and completed in 2016 (Vogel et al. 2016). This effort focused on practical aspects of environmental impact assessment and was intended to support the Ministry of Environment and Natural Resource Protection (MENRP) and the National Environmental Agency (NEA) in their evaluation of hydropower projects. The pilot project tried to align with the European Union's Water Framework Directive's principles for both environmental impact assessment (EIA) and for cumulative impact assessment (CIA), though the CIA was based on existing EIA report's expert judgement and only considered impacts of hydropower projects. The project also included a 5-day training component for Georgian environmental authorities (Vogel et al. 2016). Overall, the CIA of the Rioni River found that the studied segment of the river and its tributaries are at risk for several reasons, for example: a large amount of the river flows will be used by hydropower plants; planned and existing hydropower plants are large in size relative to rivers;

and mitigation measures for environmental impacts of hydropower were lacking. Until today, the Rioni CIA pilot project remains the only example, albeit with limited success, of more advanced EIA and impact mitigation planning in Georgia.

Further, rapid hydropower development in Georgia has encouraged several efforts to advance the science and practice of environmental flows—defined as the quantity, timing, and quality of freshwater flows and levels necessary to sustain aquatic ecosystems which, in turn, support human cultures, economies, sustainable livelihoods, and well-being (Arthington et al. 2018a). These efforts have linked Georgia with a larger scientific community of practice on environmental flows and drawn on experiences from similar geographies. Beginning in 2012-13, the Georgian Ministry of Environment and Natural Resources Protection requested support from the United States Agency for International Development (USAID) to develop a methodology for estimation of environmental flows for Georgian rivers. This request occurred around the same time that Georgia signed an association agreement with the European Union and therefore emphasis was given to developing a methodology that would be compatible with the European Water Framework Directive. Experiences from Austria—with its well-established methods and ordinances for environmental flows—and from the U.S. state of Connecticut—with similar migratory fish species assemblages—were considered in the development of a specific framework and step-by-step methodology for environmental flows in Georgia, which took place between 2014-17 and involved an international team of environmental flow experts and close collaboration with Georgia's National Environmental Agency, under the Ministry of Environment and Natural Resources Protection of Georgia. Additionally, development of the environmental flows framework and methodology engaged numerous Georgian stakeholders, involved consultation with other government ministries (Energy and Agriculture), and included a detailed piloting of the proposed approach on the Supsa River, where a cascade of hydropower projects are under development. Three of the authors on this paper participated in leadership or supporting roles in these efforts (USAID 2017).

Considerations for future research and conservation

In light of current and anticipated future trends in hydropower development in Georgia, we articulate four specific research needs for freshwater biodiversity and its conservation.

Expansion of biodiversity research and environmental monitoring

Among the obstacles facing freshwater diversity protection and conservation in Georgia is a lack of relevant expertise and long-term data (i.e., time series); this kind of information is critical for understanding and mitigating the impacts of hydropower development on rivers, including how losses in river connectivity affect freshwater fauna. As a consequence of frequent political and social-economic transitions, Georgia does not yet have a functional, unified infrastructure for collecting and maintaining biodiversity and environmental data. Except for sparse and fragmented historical information, no reference collection or comparable data for evaluating temporal changes in biodiversity exists. An attempt to establish a unified national system for biodiversity evaluation and monitoring has been unsuccessful (NBISAP, 2014), but could be revived with additional support and increased involvement from universities. Indeed, the best source of reliable information on any aspect of biodiversity or biodiversity-related issues is internationally published research papers that are produced by scientists at Georgian universities, but these too are relatively scarce (Mumladze et al. 2020). This particularly concerns freshwater biodiversity, increasingly affected by various anthropogenic activities—

such as hydropower, mining, water withdrawals, pollution, and illegal fishing. Additionally, taxonomic expertise on freshwater biota is extremely limited within Georgia, for fishes and especially for invertebrates.

The situation with the Red List of threatened species of Georgia illustrates the kind of challenges facing biodiversity-related research. In 2006, Georgia adopted a Red List of species based on Soviet-era data published in 1982, with a commitment to update the list every decade. However, in 2021, the Red List of species of Georgia remains the same as it was in 2006 and still based on the 1982 publication. Few attempts have been made to advance the understanding of the conservation status of individual species. There is thus an immediate need to encourage biodiversity research and environmental monitoring in Georgia in a nationally coordinated effort.

To address this need, we recommend the development of an infrastructure and system for biodiversity monitoring, which could start with freshwater biota given the current conservation challenges for rivers in light of hydropower development. An example of the kind of infrastructure and system for biodiversity monitoring that could serve Georgia is the Biodiversity Information System of Colombia (SiB Colombia), which is a national-level effort developed over the past two decades to create an open network of biodiversity data for the country. An effort in Georgia should unite government, non-governmental organizations, and academic institutions within Georgia. However, this effort could also benefit from international partnerships, provided that these partnerships include—in a compulsory way—opportunities for leadership or co-leadership by Georgian scientists and opportunities for training students and early career researchers in Georgia. Also important is to make sure that international standards for biodiversity data are followed in Georgia to improve access and limit duplication of data, and to allow corrections to propagate throughout databases.

Maintenance or restoration of hydrologic connectivity in Georgian rivers.

As many hydropower dams already exist across Georgian rivers, the implementation of efficient fish passage facilities and appropriate flow management are among the only remaining alternatives to restore longitudinal river connectivity in dammed basins in the country. Currently, fish passages are not mandated for hydropower projects in Georgia, even in basins that harbor nationally protected migratory fish species. Therefore, building, maintaining, and monitoring fish passage structures are uncommon practices in Georgia. With the growing development of hydropower dams and other environmental threats in the country, fish passages are an important issue that must be better integrated into policies and regulations related to hydropower. For instance, redesigning and rebuilding fish passages on the Vartsikhe and Gumati dams could be the most efficient measure to conserve sturgeon populations in the lower Rioni River, where most sturgeon species of western Georgia still reproduce.

It is important to highlight that planning and maintaining fish passage structures are not trivial and cheap tasks, and that sturgeons' special needs must be considered in design of fish passages for them to be successful (Jager et al. 2016). Although the efficiency of fish passages has much to improve worldwide (Pelicice and Agostinho 2007; Olden 2016; Cooke et al. 2020), some well-designed experiences can provide sufficient outcomes to be considered an actual mitigation action. From North American rivers, we know that fish passages for sturgeons must consider things beyond flow and connectivity, such as water quality, and must be designed to facilitate both upstream and downstream movement (Jager et al. 2016). This bidirectionality is often ignored, even though downstream migrations are equally important for the completion of the life cycle of sturgeons and other migratory fish (Pelicice and Agostinho 2007; Cooke et al.

2020). Georgia has an opportunity to learn from decades of study of fish passages for sturgeons and implement recommendations for such structures that increase the likelihood of positive outcomes for sturgeon conservation in rivers with dams (Jager et al. 2016).

In addition to fish passage at hydropower dams, the protection of environmental flows will also be important to the conservation of freshwater fishes in Georgia, as in other parts of the world (Arthington et al. 2018b). Environmental flows are typically assessed for rivers during environmental impact studies and then implemented during hydropower operations to maintain a recommended compensation flow downstream from a dam. Environmental flows can help reduce losses in connectivity associated with river de-watering and can be combined with fish passage structures to improve possibilities for fish movement through dammed sections of river. At present, Georgia does not have a clear legal framework for integrated water resources management with explicit requirements for assessment and protection of environmental flows. Conventional practice in environmental impact assessments in Georgia has been to set aside 10% of river flow for environmental purposes, calculated as 10% of annual or monthly average flows, depending on the circumstance. This 10% value dates from the Soviet period and was until recently referred to as a "sanitary flow," suggesting its origins may be more related to public health than to environmental concerns.

An earlier project, described in previous sections here, developed a framework and methodology for estimating environmental flows in Georgia with input from Georgian scientists, government authorities, and international cooperation. This methodology drew upon experiences in other places where sturgeons are present, such as North America and Europe. Since the pilot study of the methodology in the Supsa River in 2016, to our knowledge, not much more has advanced on environmental flows in practice in Georgia. We recommend that this framework and methodology for estimating environmental flows be adopted immediately for all new hydropower developments in Georgia. For existing dams, restoration of environmental flows will be needed, but the same framework and methodology could be applied to determine ecological needs as a starting point for discussions on flow restorations. The framework and methodology for environmental flows should be reviewed periodically and adapted as needed as more information becomes available about Georgian rivers and according to global advances in the science and practice of environmental flows.

Strategic planning of new hydropower development

Multi-objective optimization approaches have been employed in different parts of the world to balance the trade-offs between hydropower benefits and the socioecological costs that different dams may have (Tickner et al. 2017). For instance, it is possible to assess the performance of sets of prospective dams on the trade-offs between energy generation and losses in longitudinal river connectivity, which affect migratory fish (Ziv et al. 2012; Couto et al. 2021). To date, hydropower development in Georgia has not proceeded according to comprehensive basin-level strategic planning. Hydropower dams are rarely, if ever, considered in terms of their cumulative or synergistic effects on a river basin and its connectivity. For example, the first and only pilot project to consider the cumulative impacts of multiple hydropower projects on the Rioni River basin was realized in 2016 (Vogel et al. 2016). An interesting output of the Rioni pilot project was the finding that river size was inappropriate for the energy production demand of existing and planned hydropower development. In other basins with multiple dams, flow regimes have been strongly affected by hydropower operations, sometimes experiencing near or complete drying of river channels during dry seasons, as occurred in the

Chorokhi River during 2010-11 or the Tergi (Terek) River in 2019. Monitoring of the impacts of hydropower development post-operation also rarely takes place.

We recommend the implementation of strategic planning of hydropower development at a basin level, including intergovernmental planning and biodiversity monitoring in the case of transboundary river basins. Maintaining longitudinal river connectivity could be a central theme of strategic planning. Two of the largest river basins in the southern Caucasus region—the Kura and Chorokhi—are shared by multiple countries and have intensive hydropower development, often conducted unilaterally. Strategic planning for hydropower at a basin level should consider both existing and future hydropower developments and could draw on experiences and approaches of other areas also experiencing a proliferation of new hydropower developments for optimization, biodiversity monitoring, and impact assessment and mitigation. We also recommend that strategic planning involve a broad swath of interested parties and stakeholders.

Strict conservation areas for protection of sturgeons

Sturgeons are widely accepted internationally as a highly threatened species in need of protection (Pikitch et al. 2005). In Georgia, sturgeons are indeed among the species most affected by hydropower development in the 20th century, especially losses in river connectivity. An examination of the historical (based on Barach 1941; Sharvashidze 1982; and Elanidze 1983) and recent records (Guchmanidze 2012 and reports from Fauna and Flora International's Georgian sturgeon team) of sturgeon in the eastern Black Sea region revealed that their distribution ranges are now restricted to just one-sixth of the reported original extent. Surely, there are other factors that have affected sturgeon populations, such as illegal fishing or poorly controlled bycatch in Georgia's coastal areas of the Black Sea, water pollution from mining, and other small but potentially significant river barriers (Belletti et al. 2020). However, hydropower development likely outweighs all of these other threats. The lower reaches of the Rioni River are considered the only remaining spawning habitats for sturgeons of the eastern Black Sea region, so the Rioni and other rivers of western Georgia are therefore critical pieces of the global puzzle of sturgeon conservation and their habitats must remain intact to avoid species' extinctions.

To this end, we recommend that Georgia begin a process of identifying and assessing the feasibility of the establishment of strict conservation areas along some Georgian rivers, designating them as off limits to new hydropower development. This idea follows similar recommendations as those made by Freyhof et al. (2015) and fit in with global trends towards designation of freshwater protected areas. Potential areas for such protection include the lower reaches of the Rioni and Enguri, as well as other medium to large rivers such as the Bzyb, Kodori, Khobi, and Supsa. All of these rivers (and some others) were historically known to harbor many endangered species such as the European eel (*A. Anguilla*) and sturgeon species (Ninua et al. 2013; Table 1). The lack of occurrence data from the last few decades does not mean that sturgeon species are extinct in these basins, as just a few studies have been done to assess their status. Further, segments of other rivers, such as the Kura and Alazani in eastern Georgia, should also be considered for protected status. Although no sturgeon or other diadromous species currently inhabit these rivers since the closure of Mingachevir dam in 1954, the resident ichthyofauna still harbors remarkable diversity.

Conclusions

Conservation of Georgia's freshwater biodiversity depends on better understanding of the current status of freshwater species and the environmental conditions in the rivers they inhabit, and careful consideration of the impacts of existing and future hydropower development, particularly its effects on river connectivity. Our aim in this manuscript was to tell the story of Georgian rivers and their freshwater biota to a broader audience, engaging colleagues that may have been previously unaware of this region's biological richness, political history, and conservation challenges. It is our hope that others may find the case of Georgia insightful for understanding global trends in hydropower development, its effects on river connectivity, and its consequences for freshwater biodiversity. It is also our hope that this manuscript helps catalyze more interest from the international scientific and conservation community in the country and contribute to an upward trajectory of freshwater biodiversity research across the Caucasus region in the future.

Literature Cited

Abell, R. et al., 2008. Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. BioScience 58, 403-414.

Anderson, E.P., Jenkins, C.N., Heilpern, S., Maldonado-Ocampo, J.A., Carvajal-Vallejos, F.M., Encalada, A.C., Rivadeneira, J.F., Hidalgo, M., Cañas, C.M., Ortega, H., Salcedo, N., Maldonado, M., Tedesco, P.A., 2018. Fragmentation of Andes-to-Amazon connectivity by hydropower dams. Sci. Adv. 4, 1–8. https://doi.org/10.1126/sciadv.aao1642

Arthington, A.H., Kennen, J.G., Stein, E.D., Webb, J.A., 2018a. Recent advances in environmental flows science and water management—Innovation in the Anthropocene. Freshw. Biol. 63, 1022–1034. https://doi.org/10.1111/fwb.13108

Arthington, A.H., Bhaduri, A., Bunn, S.E., Jackson, S.E., Tharme, R.E., Tickner, D., Young, B., Acreman, M., Baker, N., Capon, S., Horne, A.C., Kendy, E., McClain, M.E., Poff, N.L., Richter, B.D., Ward, S., 2018b. The Brisbane Declaration and Global Action Agenda on Environmental Flows (2018). Frontiers in Environmental Science 6, 45. https://doi.org/10.3389/fenvs.2018.00045

Barach, G., 1941. Freshwater fishes. In Fauna of Georgia (Volume 1). Tbilisi, Georgia: Izdatelstvo Akademii Nauk Gruzinskoj SSR, pp 1-287 (in Russian).

Barbarossa, V., Schmitt, R.J.P., Huijbregts, M.A.J., Zarfl, C., King, H., Schipper, A.M., 2020. Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. Proc. Natl. Acad. Sci. U. S. A. 117, 3648–3655. https://doi.org/10.1073/pnas.1912776117

Barrier Analysis Tool (BAT), 2010. www.geodata.soton.ac.uk/geodata/gis/project173

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., Fernandez Garrido, P., Garcia-Vazquez, E., Garrido, S., Giannico, G., Gough, P., Jepsen, N., Jones, P.E., Kemp, P., Kerr, J., King, J., Łapińska, M., Lázaro, G., Lucas, M.C., Marcello, L., Martin, P., McGinnity, P., O'Hanley, J., Olivo del Amo, R., Parasiewicz, P., Pusch, M., Rincon, G., Rodriguez, C., Royte, J., Schneider, C.T., Tummers, J.S., Vallesi, S., Vowles, A., Verspoor, E., Wanningen, H., Wantzen, K.M., Wildman, L., Zalewski, M., 2020. More than one million barriers fragment Europe's rivers. Nature 588, 436–441. https://doi.org/10.1038/s41586-020-3005-2

CEPF (Critical Ecosystem Partnership Fund), 2003. Ecosystem Profile: Caucasus Biodiversity Hotspot.

Cooke, S.J., Cech, J.J., Glassman, D.M., Simard, J., Louttit, S., Lennox, R.J., Cruz-Font, L., O'Connor, C.M., 2020. Water resource development and sturgeon (Acipenseridae): state of the science and research gaps related to fish passage, entrainment, impingement and behavioural guidance. Rev. Fish Biol. Fish. 30, 219–244. https://doi.org/10.1007/s11160-020-09596-x

Cote, D., Kehler, D.G., Bourne, C., Wiersma, Y.F., 2009. A new measure of longitudinal connectivity for stream networks. Landsc. Ecol. 24, 101–113. https://doi.org/10.1007/s10980-008-9283-y

Couto, T.B.A., Messager, M.L., Olden, J.D., 2021. Safeguarding migratory fish via strategic planning of future small hydropower in Brazil. Nat. Sustain. https://doi.org/10.1038/s41893-020-00665-4

Couto, T.B.A., Olden, J.D., 2018. Global proliferation of small hydropower plants – science and policy. Front. Ecol. Environ. 16, 91–100. https://doi.org/10.1002/fee.1746

Demetrashvili, M, 1963. Trade freshwater fishes of Georgia. Academy of Science of Georgia, 95pp. (in Georgian).

Demetrashvili M.G., Elanidze R.P., Kokhia A.B., 1977. Systematics and some other data of acclimatized coregonids in high mountain lakes of Georgia. Materials of II conference. Study of reservoirs of Georgia and their importance for fishery. 90-100.

Elanidze, R., 1983. Ichthyofauna of the rivers and lakes of Georgia. Tbilisi, Georgia: Metsniereba (in Russian).

Epitashvili, G., Geiger, M.F., Astrin, J.J., Herder, F., Japoshvili, B., Mumladze, L., 2020. Towards retrieving the Promethean treasure: a first molecular assessment of the freshwater fish diversity of Georgia. Biodiversity Data Journal, e57862.

Freyhof, J., Khorozyan, I., Sadigov, F., Japoshvili, B., Batsatsashvili, K., Fayvush, G., Shukurov, E., 2015. Towards sustainable dam and hydropower in the south Caucasus. WWF.

Freyhof, J., Pipoyan, S., Mustafayev, N., Ibrahimov, S., Japoshvili, B., Sedighi, O., Levin, B., Pashkov, A., Turan, D., 2020. Freshwater fish and lampreys of the Caucasus. Ecoregional Conservation Plan.

Fricke, R., Eschmeyer, W. N. & R. van der Laan (eds) 2020. Eschmeyer's Catalog of Fishes: Genera, Species, References. (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). Electronic version accessed December 2020.

Froese, R., Pauly D. (editors), 2021. FishBase. World Wide Web electronic publication. www.fishbase.org, version (06/2020).

Georgian Biodiversity Database. 2021. Georgian Red List. Available at: http://biodiversity-georgia.net/index.php?redlist=1. Accessed January 11, 2021.

Gabelashvili, S., Mumladze, L., Bikashvili, A., Sroka, P., Godunko, R.J., Japoshvili, B., 2018. The first annotated checklist of mayflies (Ephemeroptera: Insecta) of Georgia with new distribution data and a new record for the Country. Turkish J. Zool. 42, 252–262. https://doi.org/10.3906/zoo-1709-4

Gigineishvili, G., 2000. Inland waters. In: Tatashidze, Z., Kharadze, K., Kekelia, J., Khazaradze, R. (eds.), Geography of Georgia, Part I – Physical geography. Published by "Metsniereba", Tbilisi, Georgia. Pp: 116-133 (TSBN99928-835-4-5)

Grego, J., Mumladze, L., Falniowski, A., Osikowski, A., Rysiewska, A., Palatov, D.M., Hofman, S., 2020. Revealing the stygobiotic and crenobiotic molluscan biodiversity hotspot in caucasus: Part i. the phylogeny of stygobiotic sadlerianinae szarowska, 2006 (mollusca, gastropoda, hydrobiidae) from georgia with descriptions of five new genera and twenty-one new species. Zookeys 2020, 1–77. https://doi.org/10.3897/zookeys.955.51983

Guchmanidze, A. 2009. Current and Historical Status of Sturgeon (Acipenseridae, Osteichthyes) in Georgia. in Zazanashvili, N. and Mallon, D. (Eds.) Status and Protection of Globally Threatened Species in the Caucasus. Tbilisi: CEPF, WWF. Contour Ltd., 232 pp.

Guchmanidze A., 2012. Sturgeons of Georgian Black Sea Coast, Genesis, Taxonomic Consistence, Bio-ecology, Structure of Otoliths and Conservation of them. Batumi Shota Rustaveli State University. (In Georgian).

Haxton, T.J., Cano, T.M., 2016. A global perspective of fragmentation on a declining taxon-the sturgeon (Acipenseriformes). Endanger. Species Res. 31, 203–210. https://doi.org/10.3354/esr00767

Helfman, G., Collette, B., Facey, D., 1997. The Diversity of Fishes. Blackwell Science, Malden, MA. 528 p.

IHA, 2020. Hydropower Status Report 2020. Int. Hydropower Assoc. 1–83.

IHA, 2016. Country profile: Georgia [WWW Document]. URL https://www.hydropower.org/country-profiles/georgia

Jager, H.I., Parsley, M.J., Cech, J.J., Jr., McLaughlin, R.L., Forsythe, P.S., Elliott, R.F. and Pracheil, B.M. (2016), Reconnecting Fragmented Sturgeon Populations in North American Rivers. Fisheries, 41: 140-148.

Japoshvili B. 2012. Biodiversity of Internal waters, Situation Analysis. Report. Project: Sustainable Management of Biodiversity, South Caucasus. Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) GmbH, unpublished.

Jumani, S., Deitch, M.J., Kaplan, D., Anderson, E.P., Krishnaswamy, J., Lecours, V., Whiles, M.R., 2020. River fragmentation and flow alteration metrics: a review of methods and directions for future research. Environ. Res. Lett. 15, 1-52.

Kochladze, M. 2013. Off balance. The Georgian energy sector and the contradictions in EU policy and practice. CEE bankwatch network. Available at: https://bankwatch.org/publication/off-balance-the-georgian-energy-sector-and-the-contradictions-in-eu-policy-and-practice. Accessed: Jan 10, 2021

Kottelat, M., Freyhof, J., 2007. Handbook of European freshwater fishes. Imprimeria du Democrate SA, Dlemont, 646 pp.

Kuljanishvili, T., Epitashvili, G., Freyhof, J., Japoshvili, B., Kalous, L., Levin, B., Mustafayev, N., Ibrahimov, S., Pipoyan, S., Mumladze, L., 2020. Checklist of the freshwater fishes of Armenia, Azerbaijan and Georgia. J. Appl. Ichthyol. 36, 501–514. https://doi.org/10.1111/jai.14038

Kuljanishvili, T., Japoshvili, B., Mumladze, L., Mustafayev, N., Ibrahimov, S., Patoka, J., Pipoyan, S., Kalous, L., 2021. The first unified inventory of non-native fishes of the South Caucasian countries, Armenia, Azerbaijan, and Georgia. Knowledge & Management of Aquatic Ecosystems, In Press.

Lehner, B., Grill, G., 2013. Global river hydrography and network routing: baseline data and new approaches to study the world’s large river systems. Hydrol. Process. 27, 2171–2186. https://doi.org/10.1002/hyp.9740

Lehner, B., Verdin, K., Jarvis, A., 2008. New global hydrography derived from spaceborne elevation data. Eos, Transactions, American Geophysical Union. EOS Trans. 89, 93–94.

Messager, M.L., Lehner, B., Grill, G., Nedeva, I., Schmitt, O., 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. Nat. Commun. 7, 1–11. https://doi.org/10.1038/ncomms13603

Mumladze, L., Japoshvili, B., Anderson, E.P., 2020. Faunal biodiversity research in the Republic of Georgia: a short review of trends, gaps, and needs in the Caucasus biodiversity hotspot. Biologia (Bratisl). 75, 1385–1397. https://doi.org/10.2478/s11756-019-00398-6

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501

NBSAP, 2014. National Biodiversity Strategy and Action Plan of Georgia 2014-2020 1–105.

Ninua, N.S., Japoshvili, B.O., 2008. Check list of fishes of Georgia. Proc. Inst. Zool. 23, 163–176.

Oláh, J., Vinçon, G., Kerimova, I., Kovács, T., Manko, P., 2020. On the Trichoptera of the Caucasus with western and eastern relatives. Opusc. Zool. 51, 3–174. https://doi.org/10.18348/opzool.2020.s3.3

Olden J.D., 2016. Challenges and opportunities for fish conservation in dam-impacted waters. In: Closs GP, Krkosek M, and Olden JD (Eds). Conservation of freshwater fishes. Cambridge, UK: Cambridge University Press.

Pelicice, F.M., Agostinho, A.A., 2008. Fish passage facilities as ecological traps in large Neotropical rivers. Cons. Biol. 22, 180-188.

Perkin, J.S., Gido, K.B, 2012. Fragmentation alters stream fish community structure in dendritic ecological networks. Ecol. Appl. 22, 2176–2187.

Pikitch, E.K., Doukakis, P., Lauck, L., Chakrabarty, P., Erickson, D.L., 2005. Status, trends and management of sturgeon and paddlefish fisheries. Fish Fish. 6, 233–265. https://doi.org/10.1111/j.1467-2979.2005.00190.x

REC Caucasus (The Regional Environmental Centre for the Caucasus), 2019. Developing guideline and checklist to include Biodiversity into Environmental Impact Assessment for Hydro Power Plants. Unpublished report.

Reis, R.E., Albert, J.S., Di Dario, F., Mincarone, M.M., Petry, P., Rocha, L.A., 2016. Fish biodiversity and conservation in South America. J. Fish Biol. 89, 12–47. https://doi.org/10.1111/jfb.13016

Sharvashidze V., 1982. Fishes of Georgia, Publ. “Ganatleba”, Tbilisi, 307pp. [Georgian]

Scheumann, W., Tigrek, S., 2015. Regional energy trading—a new avenue for resolving a regional water dispute. Int. J. Water Govern, 1, 49-70.

Tickner, D., Parker, H., Moncrieff, C.R., Oates, N.E.M., Ludi, E., Acreman, M., 2017. Managing rivers for multiple benefits-A coherent approach to research, policy and planning. Front. Environ. Sci. 5, 1–8. https://doi.org/10.3389/fenvs.2017.00004

USAID, 2017. The assessment of environmental flows for the rivers and streams of Georgia - Methodology. http://geo.org.ge/wp-content/uploads/2019/02/THE-ASSESSMENT-OF-ENVIRONMENTAL-FLOWS-FOR-THE-RIVERS-AND-STREAMS-OF-GEORGIA-1.pdf

Vogel B, Schmutz S, Gugushvili T, Bakradze E, Burjanadze K, Bzhalava G, Dolidze A, Egiazarova D, Japoshvili B, Kaplanishvili G, Kordzakhia M, Kordzaia I, Makarova M, Nasuashvili T, Phirtskalaishvili I, Sharashidze T, Tsiklauri K, Tsuladze A., 2016. Pilot Testing in the Rioni River Basin Regarding Impacts from Hydropower including the Methodology, Risk Assessment Results and a Check---List to Review EIA Documents, Final Report. Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) GmbH, Berlin, Germany.

Ward, J. V., 1989. The four-dimensional nature of lotic ecosystems. J. North Am. Benthol. Soc. 8, 2–8.

Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., Baird, I.G., Darwall, W., Lujan, N.K., Harrison, I., Stiassny, M.L.J., Silvano, R.A.M., Fitzgerald, D.B., Pelicice, F.M., Agostinho, A.A., Gomes, L.C., Albert, J.S., Baran, E., Petrere, M., Zarfl, C., Mulligan, M., Sullivan, J.P., Arantes, C.C., Sousa, L.M., Koning, A.A., Hoeinghaus, D.J., Sabaj, M., Lundberg, J.G., Armbruster, J., Thieme, M.L., Petry, P., Zuanon, J., Torrente Vilara, G., Snoeks, J., Ou, C., Rainboth, W., Pavanelli, C.S., Akama, A., Van Soesbergen, A., Sáenz, L., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. Science 351, 128–129. https://doi.org/10.1126/science.aac7082

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., Tockner, K., 2015. A global boom in hydropower dam construction. Aquat. Sci. 77, 161–170. https://doi.org/10.1007/s00027-014-0377-0

Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I., Levin, S.A., 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. Proc. Natl. Acad. Sci. U. S. A. 109, 5609–5614. https://doi.org/10.1073/pnas.1201423109

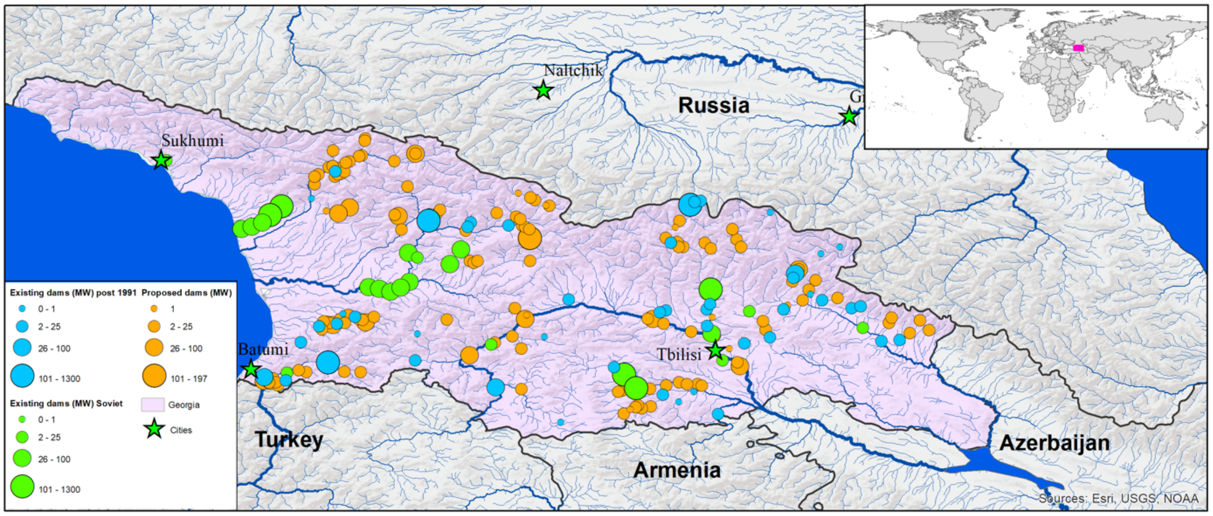


Figure 1. The Republic of Georgia is located in the south Caucasus region. Existing hydropower dams are marked in green (built before 1991) and blue (built post 1992) to distinguish dams built during the Soviet period. Proposed dams are in orange.

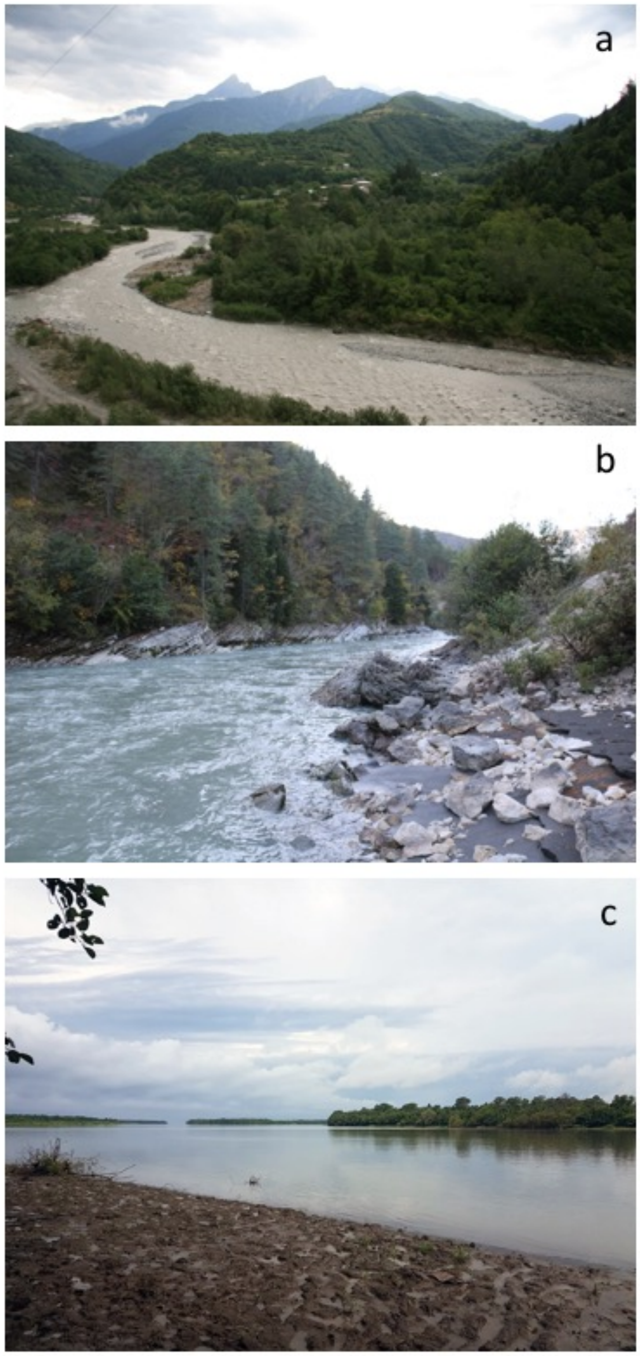


Figure 2. The Rioni River is the largest fluvial system draining western Georgia, with its discharge into the Black Sea. Here shown are the (a) upper Rioni, near Glola village; (b) middle Rioni, 9 km upstream from Namokhvani village, near an area of ongoing construction of the Namokhvani hydropower plant; and (c) lower reaches of the Rioni River, near the city of Poti.

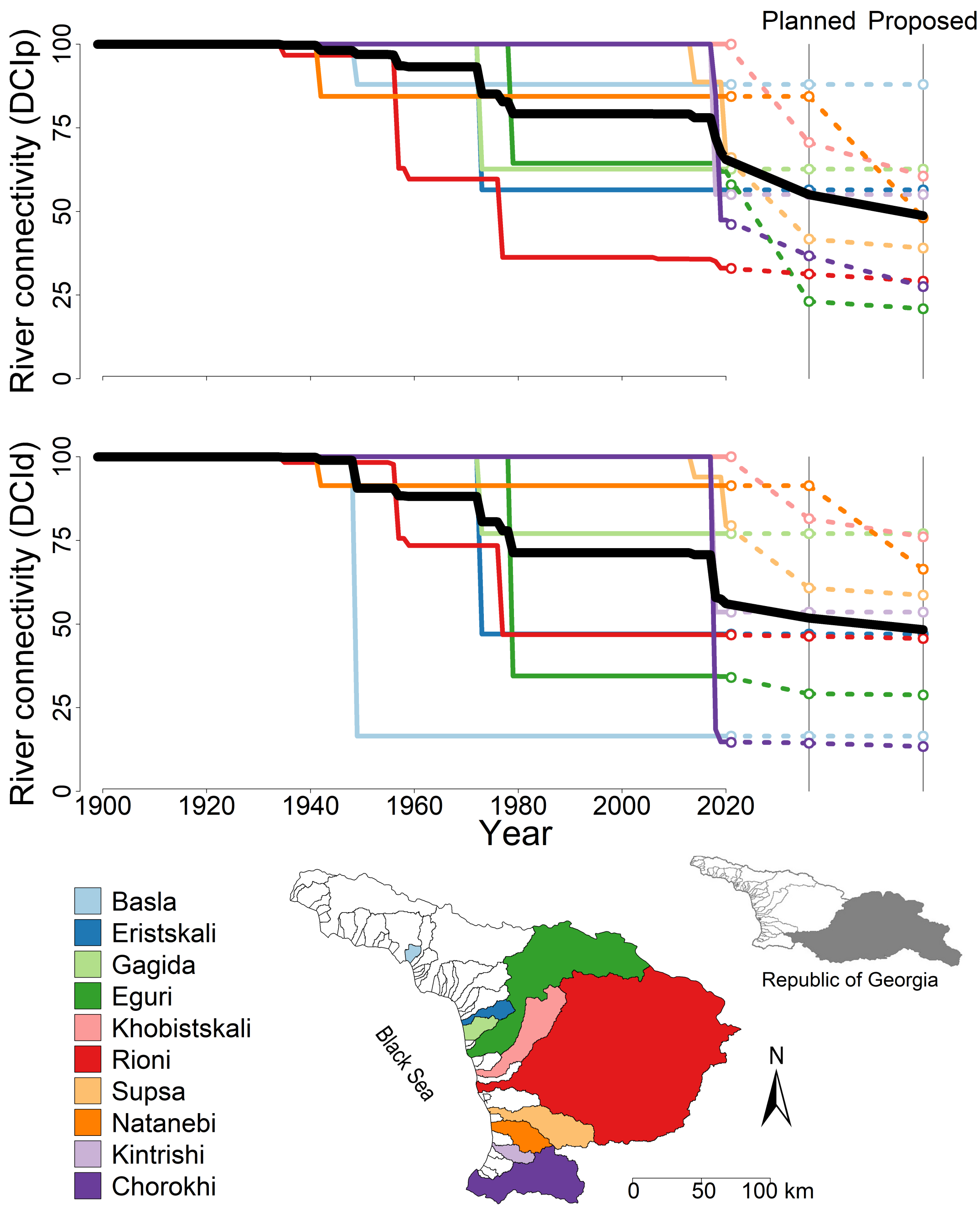


Figure 3. Trends over time in river connectivity for Black Sea drainages of western Georgia according to calculated DCI_p and DCI_d values, with 100 being a fully connected, free-flowing river network. Colored lines on graph correspond to color coded dammed river basins in the map; undammed basins are represented in white. Trends are shown for hydropower dams already built (continuous lines) and for prospective dams (dashed line). Prospective dams include those under construction and in various licensing stages (planned), and those under feasibility studies (proposed). Averages of dammed basins are summarized by black lines.

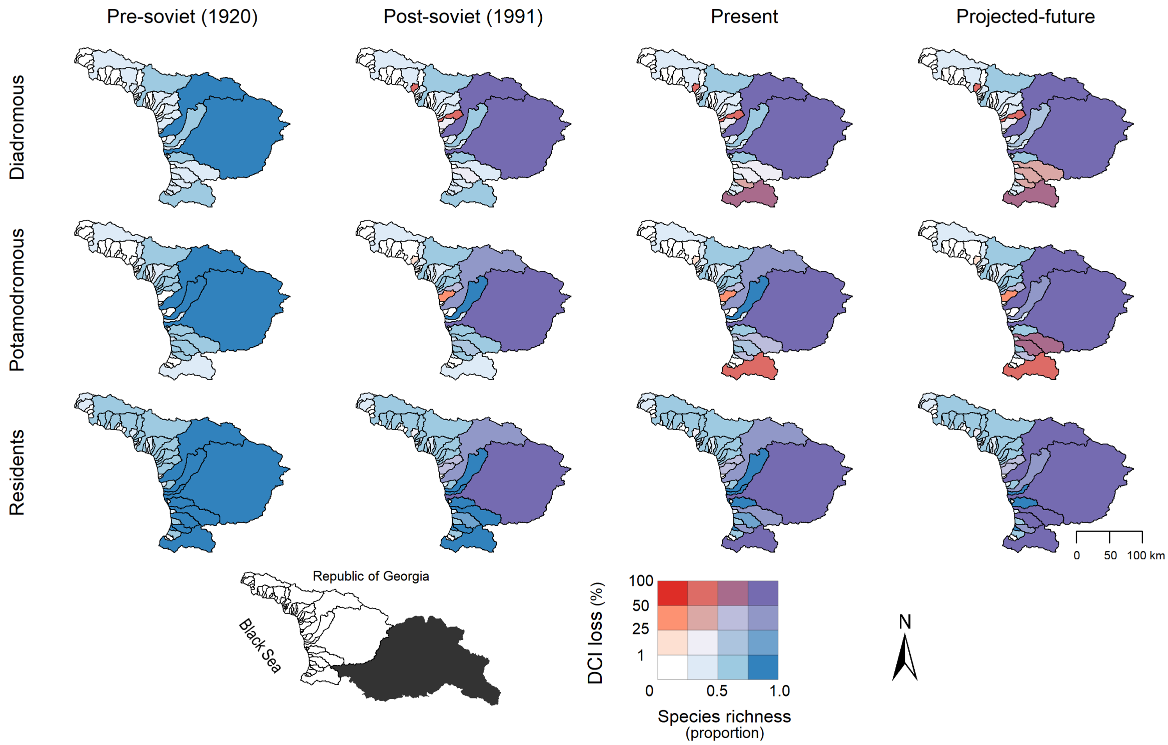


Figure 4. Set of maps depicting historical and projected-future loss in river connectivity, and fish species richness for all the 55 Black Sea drainages of western Georgia. The four critical periods of hydropower development in Georgia are represented as the pre-soviet (year 1921), post-soviet (year 1991), present-day (2021) and projected-future scenarios (all planned and proposed dams built). Percentage of connectivity loss estimates (i.e., 100 - DCI estimates) are presented for three sets of migratory fish life histories: Diadromous, potamodromous and residents. Fish species richness for these three life histories are represented as proportions calculated based on the pool of species registered in these 55 basins. Full species list, summary statistics and records per basin are presented in Table 1 and Supplementary information.

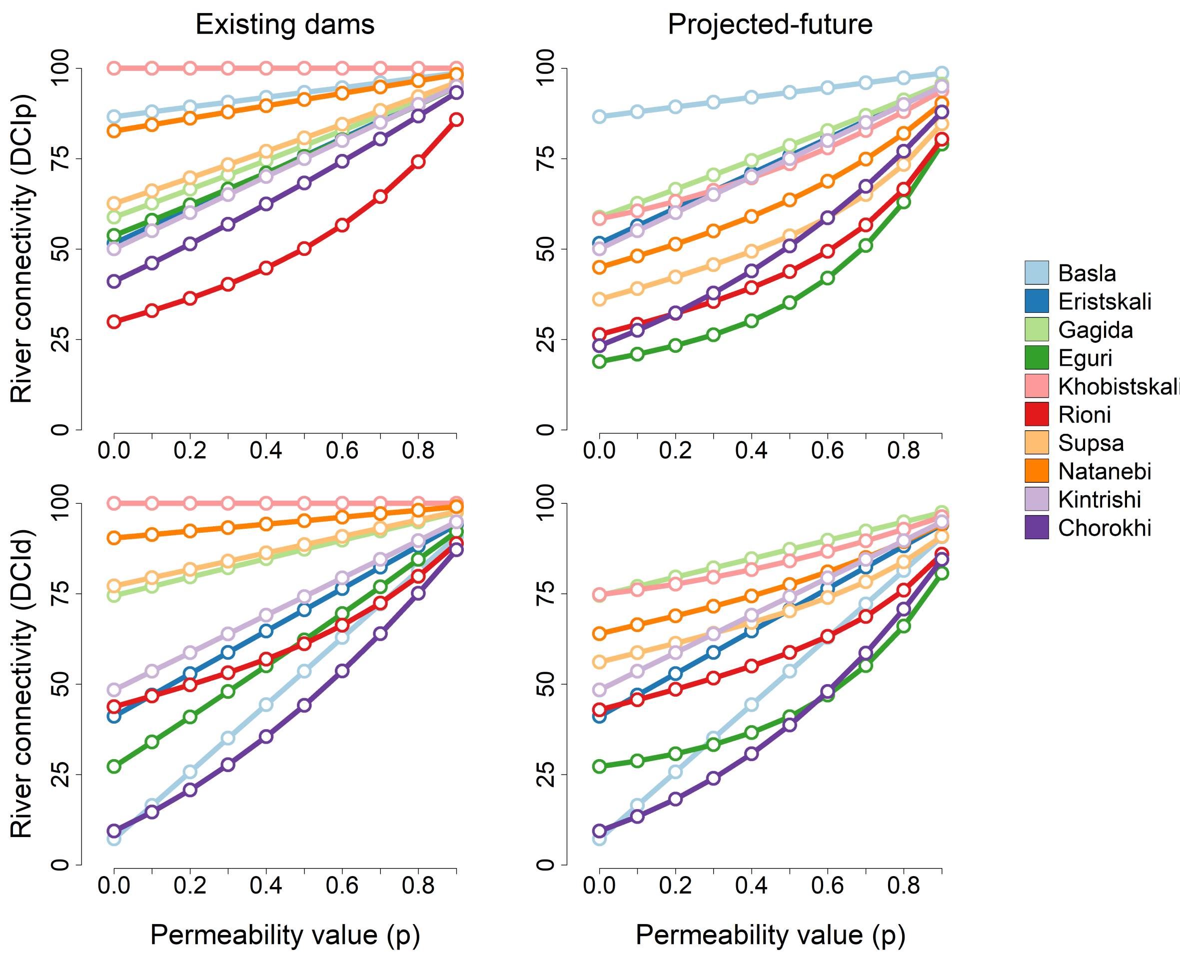


Figure 5. Sensitivity analysis depicting the relationship between dam permeability parameter (p) and river connectivity estimates for the western Georgia basins. Both equations, DCIp (upper panels) and DCId (lower panels), were fit with permeability values ranging for 0 (i.e., fully impassible) to 0.9 (i.e., 90% passible) for current and projected-future scenarios. The current scenarios include all the existing hydropower dams in 2021 (left panels), and projected-future scenarios include all the planned and proposed dams. Colored lines on graph correspond to color coded dammed river basins.

Table 1. Fish species recorded in western Georgia (Black Sea drainages). Conservation status follows IUCN criteria – Critically Endangered (CR), Near Threatened (NT), Least Concern (LC), and Not Evaluated (NE) – and species that are endemic to the Caucasus region are marked with an asterisk (*). Average DCI estimates across the species' range (i.e., all basins occupied by the species) are provided for the present-day (existing dams by 2021) and projected-future scenarios (all planned and proposed dams). DCI estimates were adjusted according to the species migratory behavior: Diadromous (DCId) and potamodromous/residents (DCIp). Lower and upper ranges of DCI estimates are presented inside parenthesis, and average range-wide connectivity losses that exceed 30% are highlighted in bold (i.e., DCI < 70).

Species	Family	Common name	Conservation status	Migratory behavior	DCI present	DCI future
Rhodeus colchicus Bogutskaya & Komlev, 2001	Acheilognathidae	Georgian bitterling	LC*	Resident	93.4 (33-100)	90.2 (21-100)
Acipenser gueldenstaedtii Brandt & Ratzeburg, 1833	Acipenseridae	Danube sturgeon	CR	Diadromous	79.6 (33-100)	**67.3** (21-100)
Acipenser nudiventris Lovetsky, 1828	Acipenseridae	Ship sturgeon	CR	Diadromous	**48.9** (15-100)	**47**.0 (13-100)
Acipenser persicus Borodin, 1897	Acipenseridae	Persian sturgeon	CR	Diadromous	75.1 (33-100)	**51.8** (21-100)
Acipenser stellatus Pallas, 1771	Acipenseridae	Starry sturgeon	CR	Diadromous	76.7 (33-100)	**68.2** (21-100)
Acipenser sturio Linnaeus, 1758	Acipenseridae	Atlantic sturgeon	CR	Diadromous	**45.5** (33-58)	**25.1** (21-29)
Huso huso (Linnaeus, 1758)	Acipenseridae	Beluga sturgeon	CR	Diadromous	81.4 (15-100)	78.5 (13-100)
Anguilla anguilla (Linnaeus, 1758)	Anguillidae	European eel	CR	Diadromous	88.5 (15-100)	86 (13-100)
Cobitis satunini Gladkov, 1935	Cobitidae	Colchic spined loach	LC*	Resident	92.5 (33-100)	88.9 (21-100)
Barbus rionicus Kamensky, 1899	Cyprinidae	Rioni barbel	NE*	Resident	92.5 (33-100)	89.1 (21-100)
Capoeta banarescui Turan, Kottelat, Ekmekçi & Imamoglu, 2006	Cyprinidae	Banarescu's barb	LC*	Resident	**14.6** (15-15)	**13.4** (13-13)
Capoeta sieboldii (Steindachner, 1864)	Cyprinidae	Colchic khramulya	LC	Potamodromous	90.2 (34-100)	86.9 (29-100)
Esox lucius Linnaeus, 1758	Esocidae	Northern pike	LC	Resident	93.1 (33-100)	90 (21-100)
Babka gymnotrachelus (Kessler, 1857)	Gobiidae	Racer goby	LC	Diadromous	76.2 (33-100)	**64.9** (21-100)
Knipowitschia longecaudata (Kessler, 1877)	Gobiidae	Longtail dwarf goby	LC	Diadromous	73.1 (46-100)	**63.8** (28-100)
Neogobius fluviatilis (Pallas, 1814)	Gobiidae	Monkey goby	LC	Diadromous	78.4 (33-100)	**64.1** (21-100)
Ponticola constructor (Nordmann, 1840)	Gobiidae	Caucasian goby	LC	Potamodromous	87.5 (33-100)	80.7 (21-100)
Ponticola syrman (Nordmann, 1840)	Gobiidae	Syrman goby	LC	Diadromous	73.5 (58-100)	**61.2** (21-100)
Gobio artvinicus Turan, Japoshvili, Aksu & Bektaş, 2016	Gobionidae	Gudgeon	NE*	Resident	86.5 (46-100)	79.1 (28-100)
Gobio caucasicus Kamensky, 1901	Gobionidae	Colchic gudgeon	LC*	Resident	90.8 (33-100)	86.5 (21-100)
Abramis brama (Linnaeus, 1758)	Leuciscidae	Freshwater bream	LC	Potamodromous	76.2 (33-100)	**64.9** (21-100)

Alburnoides fasciatus (Nordmann, 1840)	Leuciscidae	Transcaucasian spirlin	LC*	Potamodromous	88.7 (33-100)	83.5 (21-100)
Alburnus alburnus (Linnaeus, 1758)	Leuciscidae	Common bleak	LC	Potamodromous	79.7 (33-100)	**67.4** (21-100)
Alburnus derjugini Berg, 1923	Leuciscidae	Georgian shemaya	LC	Resident	86.3 (15-100)	83.8 (13-100)
Petroleuciscus borysthenicus (Kessler, 1859)	Leuciscidae	Dnieper chub	LC	Resident	86.1 (33-100)	79.6 (21-100)
Phoxinus colchicus Berg, 1910	Leuciscidae	Minnow	LC*	Resident	88.5 (15-100)	86.0 (13-100)
Squalius orientalis Heckel, 1847	Leuciscidae	Oriental Chub	NE*	Potamodromous	87.0 (33-100)	79.4 (21-100)
Vimba vimba (Linnaeus, 1758)	Leuciscidae	Vimba bream	LC	Diadromous	79.8 (15-100)	75.5 (13-100)
Oxynoemacheilus cemali Turan, Kaya, Kalayci, Bayçelebi & Aksu, 2019	Nemacheilidae	Stone loach	NE	Resident	**67.1 (46-100)**	**60.9** (28-100)
Oxynoemacheilus veyselorum Cicek, Eagderi & Sungur, 2018	Nemacheilidae	Stone loach	NE*	Resident	80.4 (33-100)	**66.1** (21-100)
Perca fluviatilis Linnaeus, 1758	Percidae	European perch	LC	Diadromous	90.0 (15-100)	88.3 (13-100)
Sander lucioperca (Linnaeus, 1758)	Percidae	Pike-perch	LC	Potamodromous	84.4 (33-100)	73.0 (21-100)
Lampetra ninae Naseka, Tuniyev & Renaud, 2009*	Petromyzontidae	Western transcaucasian lamprey	NT*	Diadromous	92.9 (33-100)	89.5 (21-100)
Salmo labrax Pallas, 1814	Salmonidae	Black Sea salmon	LC	Diadromous	90.8 (33-100)	86 .0(21-100)
Salmo rizeensis Turan, Kottelat & Engin, 2010	Salmonidae	Rize trout	LC	Potamodromous	87.7 (15-100)	85.5 (13-100)
Silurus glanis Linnaeus, 1758	Siluridae	Wels catfish	LC	Resident	89.3 (15-100)	87.4 (13-100)

Supplementary material

Supplementary Table 1. Fish species recorded in western Georgia (Black Sea drainages), the respective average DCI estimates (range inside parenthesis) inside their distribution range, and the basin IDs where they were recorded. A map linking all these basins IDs with their names and locations is provided in the Supplementary Figure 1.

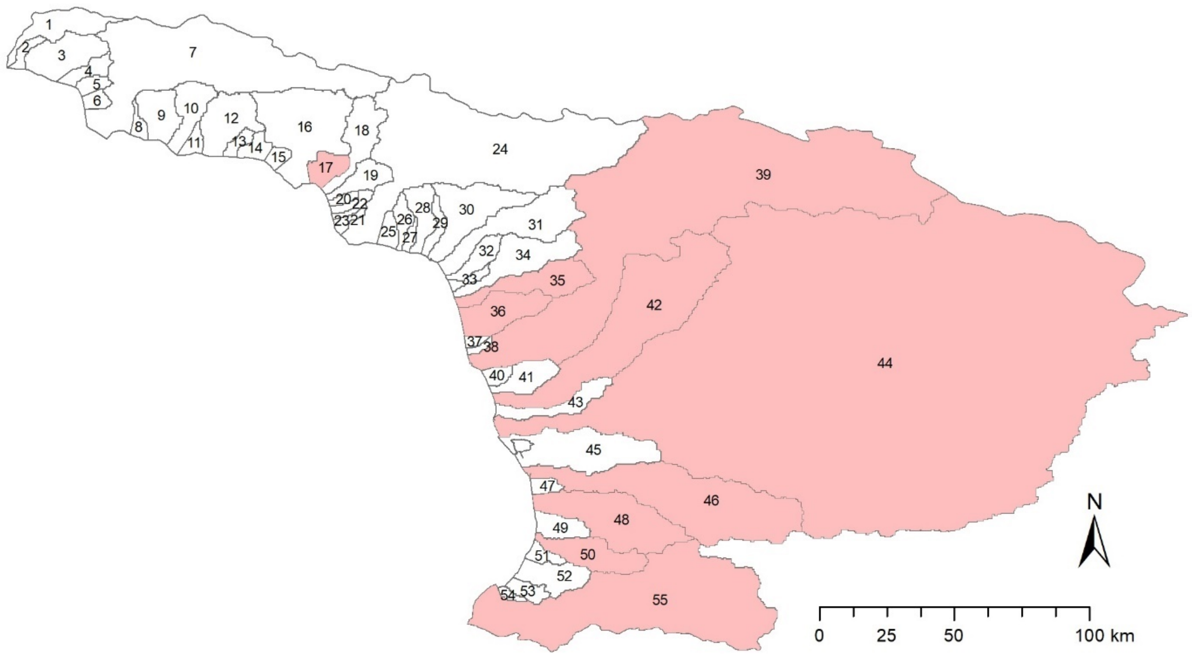
Species	DCI present	DCI future	Basins IDs
Abramis brama	76.2 (33-100)	64.9 (21-100)	32, 33, 34, 39, 44, 46
Acipenser gueldenstaedtii	79.6 (33-100)	67.3 (21-100)	7, 24, 26, 39, 42, 43, 44, 55
Acipenser nudiventris	48.9 (15-100)	47 (13-100)	39, 44, 45, 55
Acipenser persicus	75.1 (33-100)	51.8 (21-100)	39, 42, 44, 45, 48
Acipenser stellatus	76.7 (33-100)	68.2 (21-100)	16, 24, 25, 39, 44, 45, 55
Acipenser sturio	45.5 (33-58)	25.1 (21-29)	39, 44
Alburnoides fasciatus	88.7 (33-100)	83.5 (21-100)	1, 2, 7, 9, 16, 17, 18, 19, 24, 25, 26, 28, 30, 31, 32, 33, 34, 35, 36, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 55
Alburnus alburnus	79.7 (33-100)	67.4 (21-100)	39, 40, 42, 43, 44, 45, 48, 49, 50, 51, 55
Alburnus derjugini	86.3 (15-100)	83.8 (13-100)	1, 2, 3, 7, 9, 10, 12, 16, 17, 18, 19, 23, 24, 25, 30, 31, 32, 33, 34, 35, 36, 39, 41, 42, 43, 44, 45, 46, 48, 50, 52, 55
Anguilla anguilla	88.5 (15-100)	86 (13-100)	19, 23, 24, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55
Babka gymnotrachelus	76.2 (33-100)	64.9 (21-100)	38, 39, 43, 44, 45, 46
Barbus rionicus	92.5 (33-100)	89.1 (21-100)	1, 2, 3, 4, 5, 6, 7, 9, 12, 13, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 38, 39, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55
Capoeta banarescui	14.6 (15-15)	13.4 (13-13)	55

Capoeta sieboldii	90.2 (34-100)	86.9 (29-100)	23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 39, 41, 42, 43, 44, 45, 46, 48, 49
Cobitis satunini	92.5 (33-100)	88.9 (21-100)	1, 2, 3, 4, 5, 6, 7, 9, 10, 12, 16, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 55
Esox lucius	93.1 (33-100)	90 (21-100)	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 55
Gobio artvinicus	86.5 (46-100)	79.1 (28-100)	45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55
Gobio caucasicus	90.8 (33-100)	86.5 (21-100)	1, 2, 3, 7, 9, 10, 11, 12, 16, 17, 18, 19, 20, 24, 25, 27, 28, 29, 30, 31, 32, 34, 35, 36, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 55
Huso huso	81.4 (15-100)	78.5 (13-100)	7, 22, 23, 24, 25, 39, 42, 43, 44, 45, 55
Knipowitschia longecaudata	73.1 (46-100)	63.8 (28-100)	24, 55
Lampetra ninae	92.9 (33-100)	89.5 (21-100)	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 28, 29, 30, 31, 32, 33, 34, 35, 36, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 55
Neogobius fluviatilis	78.4 (33-100)	64.1 (21-100)	17, 39, 42, 44, 45, 46, 48, 49, 50, 51
Oxynoemacheilus cemali	67.1 (46-100)	60.9 (28-100)	50, 51, 55
Oxynoemacheilus veyselorum	80.4 (33-100)	66.1 (21-100)	36, 39, 42, 43, 44, 45, 46, 47, 48, 49

Perca fluviatilis	90 (15-100)	88.3 (13-100)	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20, 21, 22, 23, 24, 30, 31, 32, 33, 34, 35, 36, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 55
Petroleuciscus borystenicus	86.1 (33-100)	79.6 (21-100)	7, 9, 24, 33, 34, 39, 40, 41, 42, 43, 44, 45, 50, 51, 55
Phoxinus colchicus	88.5 (15-100)	86 (13-100)	1, 2, 3, 9, 10, 19, 20, 24, 25, 29, 30, 31, 32, 33, 34, 35, 36, 39, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 54, 55
Ponticola constructor	87.5 (33-100)	80.7 (21-100)	18, 19, 24, 25, 26, 28, 30, 31, 32, 33, 34, 35, 39, 42, 43, 44, 45, 46, 48, 49, 50, 51, 54, 55
Ponticola syrman	73.5 (58-100)	61.2 (21-100)	36, 39, 41
Rhodeus colchicus	93.4 (33-100)	90.2 (21-100)	7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51
Salmo labrax	90.8 (33-100)	86 (21-100)	1, 2, 3, 4, 5, 6, 7, 9, 10, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 30, 31, 34, 35, 39, 42, 44, 46, 47, 48, 49, 50, 51, 52, 55
Salmo rizeensis	87.7 (15-100)	85.5 (13-100)	1, 2, 3, 4, 5, 6, 7, 9, 10, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 30, 31, 34, 35, 39, 42, 44, 46, 47, 48, 49, 50, 51, 52, 55
Sander lucioperca	84.4 (33-100)	73 (21-100)	6, 7, 39, 40, 42, 44, 45
Silurus glanis	89.3 (15-100)	87.4 (13-100)	9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 39, 40, 41, 42, 43, 44, 45, 46, 48, 49, 50, 51, 55

Squalius orientalis	87 (33-100)	79.4 (21-100)	6, 7, 24, 25, 31, 32, 33, 34, 35, 39, 42, 44, 45, 46, 47, 48, 49, 50, 51
Vimba vimba	79.8 (15-100)	75.5 (13-100)	7, 16, 17, 24, 39, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 54, 55

Supplementary Figure 1. Map to of the western Georgia basins with their respective basin IDs. The basins with existing, planned and/or proposed hydropower dams are displayed in pink. The remaining ones are in white.



1. Psou-Pkhista
2. Lapsta
3. Khashupse
4. Zhvaviakvara
5. Gagripshi
6. Kolkhida
7. Bzipi
8. Miusera
9. Mchishta
10. Khipsta
11. Gudau
12. Aapsta
13. Tskvara
14. Psirtskha
15. Shitskvara
16. Gumista
17. Basla
18. Kelasuri
19. Machara
20. Agudzera
21. Bogapsta
22. Pshapi
23. Skurcha
24. Kodori
25. Tabaghuri
26. Chasha
27. Toumishi
28. Dghamishi
29. Tskhenistskali
30. Mokva
31. Ghalidzga
32. Anaria
33. Okhurei
34. Okhumi
35. Ersitskali
36. Gagida
37. Kvadiash-Gali
38. Ghele-Burgazi
39. Enguri
40. Bui
41. Churia
42. Khobistskali
43. Tsivi
44. Rioni
45. Pichori-Tkhorina
46. Supsa
47. Sepa
48. Natanebi
49. Choloki
50. Kintrishi
51. Dekhva
52. Chakvi-Korolostskali
53. Kuba-tskali
54. Bartskhana
55. Chorokhi

Supplementary Table 2. Fish species richness and DCI estimates for the 10 basins that have existing, planned and proposed hydropower dams. Species richness is presented for all species together and separated by species' migratory behavior – diadromous (Diadro), potamodromous (Potamo) and residents. Both DCId and DCIp estimates are provided for five different scenarios: Pre-soviet (1920), post-soviet (1991), current with all existing dams (by 2021), and two future projections that include all the planned dams and all the proposed dams.

Basin ID	Basin Name	Fish species richness				DCId					DCIp				
		All	Diadro	Potamo	Residents	Pre-soviet	Post-soviet	Existing	Planned	Proposed	Pre-soviet	Post-soviet	Existing	Planned	Proposed
17	Basla	13	5	2	6	100.0	16.5	16.5	16.5	16.5	100.0	88.0	88.0	88.0	88.0
35	Eristskali	17	4	5	8	100.0	47.0	47.0	47.0	47.0	100.0	56.4	56.4	56.4	56.4
36	Galidzga	15	4	2	9	100.0	77.1	77.1	77.1	77.1	100.0	62.6	62.6	62.6	62.6
39	Enguri	32	14	8	10	100.0	34.5	34.0	29.2	28.8	100.0	64.4	58.0	23.1	20.9
42	Khobistskali	26	9	7	10	100.0	100.0	100.0	81.5	76.1	100.0	100.0	100.0	70.6	60.6
44	Rioni	31	13	8	10	99.9	46.8	46.7	46.3	45.7	99.8	36.3	33.0	31.3	29.3
46	Supsa	23	7	6	10	100.0	100.0	79.4	60.8	58.7	100.0	100.0	66.1	41.8	39.1
48	Natanebi	23	7	6	10	100.0	91.4	91.4	91.4	66.4	100.0	84.4	84.4	84.4	48.1
50	Kintrishi	22	6	5	11	100.0	100.0	53.6	53.6	53.6	100.0	100.0	55.0	55.0	55.0
55	Chorokhi	25	10	4	11	100.0	100.0	14.6	14.4	13.4	100.0	100.0	46.1	36.7	27.5