# River fragmentation and barrier impacts on fishes have been greatly underestimated in the upper Mekong River

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**Highlights**

- 50.5% of sub-catchments in the Upper Mekong are impacted by river barriers.
- Small barriers are the main causes of river fragmentation in the Upper Mekong.
- The Middle region of the Upper Mekong is the most fragmented region.
- Barrier construction has reduced habitat for both migratory and locally-resident fish species.

**Abstract**

River barriers reduce river connectivity and lead to fragmentation of fish habitats, which can result in decline or even extinction of aquatic biota, including fish populations. In the Mekong basin, previous studies have mainly focused on the impacts of large dams but ignored the impacts of small-scale barriers, or drew conclusions from incomplete barrier databases, potentially leading to research biases. To test the completeness of existing databases and to evaluate the catchment-scale fragmentation level, a detailed investigation of river barriers for the whole Upper Mekong (Lancang catchment) was performed, by conducting visual interpretation of high-resolution remote sensing images. Then, a complete catchment-scale barrier database was created for the first time. By comparing our barrier database with existing databases, this study indicates that 93.7% of river barriers were absent from the existing database, including 75% of dams and 99.5% of small barriers. Barrier density and dendritic connectivity index ($DCI_D$ and $DCI_P$) were used to measure channel fragmentation within the catchment. Overall, 50.5% of sub-catchments contained river barriers. The Middle region is the most fragmented area within the Lancang catchment, with a median barrier density of 5.34 [0.70-9.67] per 100 km, $DCI_P$ value of 49.50 [21.50-90.00] and $DCI_D$ value of 38.50 [9.00-92.25]. Furthermore, since 2010, distribution ranges of two representative fish species *Schizothorax lissolabiatus* (a rheophilic cyprinid) and *Bagarius yarrelli* (a large catfish) have reduced by 19.2% and 32.8% respectively, probably due in part to the construction of river barriers. Our findings indicate that small-scale barriers, including weirs and bridge aprons are the main reason for habitat fragmentation in the Lancang and must be considered alongside large dams in water management and biodiversity conservation within the Mekong.

**Keywords:** hydrological connectivity, river barrier, habitat restoration, river management, fish passage, Lancang River

## 1. Introduction

River infrastructure, including hydropower facilities and reservoir dams, has been increasingly constructed in many rivers globally, to meet peoples' needs for water supply, energy, and flood control (Grill et al., 2019; Lehner et al., 2011). Other small river structures such as weirs, bridge aprons and sluices are built to facilitate irrigation, water supply, flood control, water level measurement or to facilitate navigation. However, these human-engineered structures, large and small, also cause negative effects on aquatic ecosystems, leading to changes in aquatic environment and biodiversity loss (Baumgartner et al., 2022; Birnie-Gauvin et al., 2017). The impacts of large dams (typically those more than 10-15 m high) on aquatic ecosystems have been relatively well studied. Large hydropower facilities and reservoir dams interrupt the natural flow regime, causing widespread physical, chemical, and biological changes (Nilsson et al., 2005; Reid et al., 2019). They also break river ecosystem continuity, affecting the movement of aquatic organisms, and can lead to a shift in biological communities in some cases (Barbarossa et al., 2020; Zhang et al., 2018). On the other hand, small-scale river infrastructures such as small hydropower facilities, weirs, fords, and bridge aprons, tend to be built in much large numbers globally (Couto & Olden, 2018; Belletti et al., 2020; Jumani et al., 2020). Unlike large-scale hydropower facilities, small barriers are usually constructed in small rivers or headwater tributaries (Sun et al., 2020). The impacts of individual small barriers on fish movement, river fragmentation and flow alteration might be low compared to those for large barriers. However, due to fewer regulations, numerous small barriers are often commissioned along a single river, resulting in considerable cumulative effects (Januchowski-Hartley et al., 2013; Jones et al., 2019; Jumani et al., 2020).

For migratory fish species, river barriers can obstruct migration paths, isolate populations, and reduce the availability of spawning grounds and other key habitats (Lucas & Baras, 2001; Rodeles et al., 2019; Wilkes et al., 2019). It has been demonstrated that barrier construction is one of the leading causes of population decline and local extinction for many migratory species including *Acipenser sturio*, *Salmo trutta* and *Anguilla anguilla* (Birnie-Gauvin et al., 2018; Miqueleiz et al., 2021; Sun et al., 2021). River barriers also have negative effects on populations of river-resident species with restricted dispersal capabilities (Jones et al., 2021; Rodeles et al., 2021; Sun et al., 2022), impacting metapopulation processes (Wilkes et al., 2019).

With increased urgency for fish conservation and river basin management, a clear understanding of the impacts of river barriers across large scale (e.g. the catchment-scale) on river connectivity is needed. To do that, a complete river barrier inventory is required, incorporating the specific location and nature of each barrier should first be obtained (Januchowski-Hartley et al., 2013). Although several global dam databases are publicly available, these are mainly for large barriers, and small barriers are normally poorly documented (Grill et al., 2019). Since small-scale barriers are often easily missed by surveys, they are under-represented in most, but not all, barrier inventories (Atkinson et al., 2018; Januchowski-Hartley et al., 2013; Sun et al., 2020).

The Mekong River, the largest river in Southeast Asia, is widely recognised for its diverse aquatic biodiversity and fisheries production (Dugan et al., 2010; Kang and Huang, 2021; Soukhaphon et al., 2021). As one of the world's 35 biodiversity hotspots, it ranks third for fish diversity with 1148 species, after the Amazon and Congo River basins (Chea et al., 2017; MRC, 2018; Nuon et al., 2020). There are also major concerns about loss of ecosystem services within the Mekong due to damming and hydropower, although the main emphasis of this to date has been in the Middle and Lower Mekong (Dugan et al., 2010; Ziv et al., 2012). The Upper Mekong, known as the River Lancang in China, supports many endemic fishes, including within the subfamilies Schizothoracinae (finescale carp) and Glyptosterninae (torrent catfishes) (Zhang et al., 2021). It also provides habitat for several migratory fishes, including the families Pangasiidae, Sisoridae and Anguillidae (Zheng et al., 2013). In 2021, the Chinese Government promulgated the “Tibetan Plateau ecological protection and restoration project (2021-2035)”, which aims to protect the region’s biodiversity, conserve wildlife habitat, restore and maintain good connectivity, and safeguard migration routes for migratory species (National Development and Reform Commission, 2021). As part of the plan, conservation of river connectivity and fish biodiversity of the Lancang catchment has become a major goal that has to be achieved.

Due to its high-gradient geographic landform and rich water resources, rivers in southwest China, including the Lancang catchment, have experienced a massive explosion in the construction of small-scale river barriers over recent decades (Wang et al., 2013), to meet the need in growing irrigation and energy requirements. However, these barriers may not have been recorded in existing barrier inventories. For the Mekong catchment, several barrier inventories exist, including the Global Reservoir and Dam Database (GRanD, Lehner et al., 2011), and have been used to assess the connectivity of the Mekong River in previous studies (Barbarossa et al., 2020; Grill et al., 2014; Winemiller et al., 2016). It was concluded that the impacts of small dams on river connectivity were still rather small in the Mekong catchment, and the catchment is still considered as moderately free-flowing (Grill et al., 2014; Barbarossa et al., 2020), although numerous large, planned dams risk the Mekong ecosystem's integrity (Zarfl et al., 2019). However, the completeness of the barrier databases used by previous studies are less clear. Using an incomplete barrier database to assess river connectivity can result in inefficient evaluation and can directly affect connectivity restoration planning (Atkinson et al. 2020). To test the degree to which current Mekong barrier databases may be fit for river connectivity assessment purposes, an intensive desk study was carried out to identify all potential river barriers in the Upper Mekong (hereinafter referred to as the Lancang River) catchment by using high resolution satellite images. After that, indices calculated from the desk study were used to assess the fragmentation level of the Lancang catchment and the spatial distribution pattern of river connectivity across regions. After that, indices calculated from the desk study were compared against results calculated from existing databases, to test the completeness of existing databases. Furthermore, two representative fish species were selected to test the impacts of river barriers on the habitat of both migratory and locally resident fish species.

## 2. Methods

### 2.1 Study area

The Lancang River (Upper Mekong) originates from the Tibetan Plateau at an altitude of 5244 m, and flows into the southwest mountainous region of China (Zhou & Guan, 2001). The catchment covers an area of 167 487 km$^2$, and mainstream length is 2161 km (Zhou & Guan, 2001). The river and its tributaries are confined by narrow, deep gorges, with aquatic habitat primarily consisting of fast-flowing mountain spate rivers (Chen et al., 2016). The upper Lancang is characterized by high altitude and low temperature environment, and its fish assemblages mainly consist of cold-water, rheophilic species (Chen, 2013; Zhang et al., 2019). The lower Lancang is characterized by a lower altitude (522-1894 m) and warmer environment, with higher species richness (Chen, 2013; Liu et al., 2013). Due to its abundant hydropower resources, a total of 21 hydropower dams are planned for the main channel of the Lancang River, ten of which (Manwan, Dachaoshan, Jinhong, Xiaowan, Gongguoqiao, Nuozhadu, Dahuaqiao, Huangdeng, Lidi, and Wunonglong dams) are currently commissioned (Fan et al., 2015; Zhang et al., 2019). Although large hydropower facilities have been well documented in the Langcang River, several existing databases (GRanD, GOODD, Greater Mekong Subregion hydropower dams, Mekong Dams Observatory) (Lehner et al., 2011; Open Development Mekong, 2016; Mulligan et al., 2020; WLE Greater Mekong, 2021) have barely recorded any small river barriers such as weirs and bridge aprons, and their impacts on river connectivity and fish habitat in the Lancang is currently unclear.

As river management units are often delineated at the sub-catchment scale (Hermoso et al., 2011; Sun et al., 2020), in order to generate a detailed river barrier inventory the Lancang catchment was firstly split into four regions: Source, Upper, Middle and Lower regions based on its geographic, topographic and hydrodynamic characteristics (Figure 1; Kang et al., 2009). Then, a total of 198 sub-catchments (Hydrobasin level 8) were identified according to the HydroBASINS spatial layer within the HydroSHEDS database (https://www.hydrosheds.org/), as Hydrobasin level 8 is the recommended hydrobasin level for sub-catchment scale environmental impact assessment (Couto et al., 2021; Zarfl et al., 2019). The Source region is located on the Qinghai-Tibetan Plateau, from the headwater to Chamdo (Kang et al., 2009). This region has the highest gradient within the whole catchment, and contains a total of 102 sub-catchments. The Upper region occurs between Chamdo and Gongguoqiao, which is the narrowest section of the catchment (Kang et al., 2009), with a river width from 30 m to 150 m and a gradient of ~0.004, and contains 22 sub-catchments. The main river channel in this region is contained within a V-type valley along the fault line. The Middle region is located within the transition area from the Qinghai-Tibet plateau to the Yunnan-Guizhou Plateau, between Gongguoqiao and the Lancang-Mengjia confluence, and contains 36 sub-catchments. The main river channel in this region is also a V-type valley, but with wider river width (50-150 m). The Lower region is located between the Lancang-Mengjia confluence and the Lancang-Nanla confluence, and contains 38 sub-catchments. The main river channel in this region is wider (80-300 m), with the lowest gradient of ~0.002 in the Lancang catchment (Kang et al., 2009; Liu et al., 2013) (Figure 1).

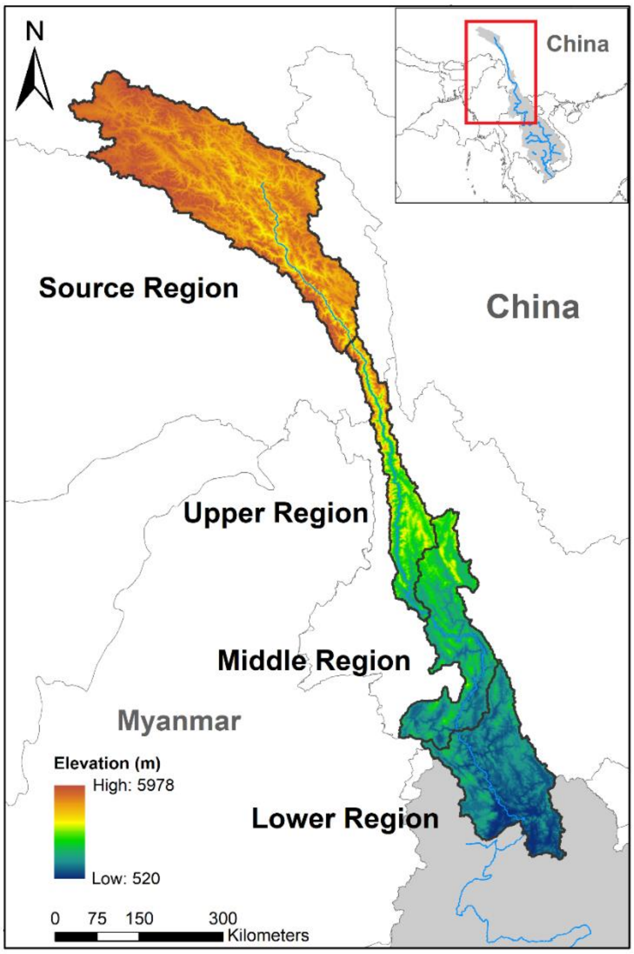


Figure 1. The Lancang (Upper Mekong) catchment and the four regions (boundaries of these four areas are shown by black lines) into which it was split for the purposes of this study.

### 2.2 Desk study barrier database

To perform a detailed desk survey for all river segments in the Langcang catchment, the main river and tributary networks of the catchment were gathered from the HydroRIVERS database (https://www.hydrosheds.org/), then the shapefile layer was plotted on high-resolution images (shot between year 2018 and 2021) from Google Earth. Each river segment was visually examined from the source to confluence at the highest resolution (0.5 m), and all potential barriers (i.e. dams, weirs, aprons, etc.) were marked as a point, which was placed at the center of the barrier, then the coordinates (latitude and longitude) of all points were saved as a shapefile (Atkinson et al., 2018). For each barrier, a unique identification code was given, then sub-catchment identity, coordinate (latitude and longitude), stream order (Strahler stream order) and altitude (m above sea level) were recorded. Identified barriers were categorized into four types, based on their physical features: large dam (hydropower facilities or reservoir dam ≥ 15 m height, with impounded area clearly evident immediately upstream of dam), small dam (hydropower facilities or reservoir dam < 15 m height, with impounded area clearly evident immediately upstream of dam), weir (run-of-river flow-regulating structure, normally with water flowing over the top) and bridge apron (concrete or rock riprap step structures that are constructed under bridges), to form the Lancang River Barrier Database (LRBD). Height information of dams, particularly large dams was gathered from documented dam engineering descriptions or online information or by contacting local government. No attempt was made to measure the height of weirs and bridge aprons, but they were typically in the range of 1-3 m. Field survey checks at a sample (n = 50) of barriers identified in the desk study confirmed that the barriers identified existed in the form and location identified.

### 2.3 Existing barrier database

To build an integrated barrier database for the Lancang catchment, combining data from existing databases with those gathered from the high-resolution image desk study, data were collected from three open access Mekong barrier databases: the Greater Mekong Subregion hydropower dams 2016 database (Barbarossa et al., 2020; Open Development Mekong, 2016), Mekong Dams Observatory database (WLE Greater Mekong, 2021), and Winemiller Mekong dam database (extracted from GRanD database; Winemiller et al., 2016). The geographic coordinate (latitude and longitude) of each barrier was recorded, then plotted on Google Earth and manually checked, to remove duplicates. Only existing barriers and barriers that are under construction were recorded. Planned dams were excluded from further analysis.

### 2.4 River fragmentation assessment

Two river fragmentation metrics, barrier density, and dendritic connectivity index (DCI, Cote et al., 2009), were used to assess the fragmentation level at each region (Atkinson et al., 2020). For each sub-catchment, the river length was calculated according to the HydroRIVERS database, and the Strahler stream order of each river segment was recorded. Then, barrier density was calculated for each sub-catchment, using the total number of barriers divided by total river length (km) in that sub-catchment (Jones et al., 2019; Sun et al., 2020), and the median barrier density (n/100 km) and quartiles was calculated for each region.

To evaluate impacts of river barriers on longitude connectivity, the DCIs were calculated for each sub-catchment. The DCI is calculated based on the number, location and passability of barriers within a given catchment (Cote et al., 2009). The resulting DCI is a value ranging between 0 and 100, where a free-flowing river with no barriers obstruction would receive a value of 100. The $DCI_P$ (potamodromous index) quantifies the ability of fish to make regular migratory movements between two randomly chosen segments of the river network in both upstream and downstream directions (Cote et al., 2009). The $DCI_D$ (diadromous index) quantifies the ability of fish to move from the furthest downstream point of the river (e.g. river mouth, confluence) to a randomly chosen segment in both upstream and downstream directions (Cote et al., 2009). Since diadromous fish species were rarely present in the Lancang catchment, in this case the $DCI_D$ was used to assess if fish could freely enter from one sub-catchment to another, and to a randomly chosen river segment within the sub-catchment (Baumgartner et al., 2022). This metric was used to measure the potential for (meta)population level dispersal.

To calculate the $DCI_D$ and $DCI_P$, a numerical value for the overall passability ($p_m$ = upstream passability x downstream passability) of each barrier is needed, with the value of passability ranging between 0 and 1, where 0 represents an impassable barrier, and 1 represents a fully passable structure. In this study, dams were assumed to be impassable due to their physical dimensions and form, so the passability of 0 was given to both large and small dams (Grill et al., 2014; Baumgartner et al., 2022). Few Chinese dams, in the Lancang, have fishways, further supporting that passability allocation value (Shi et al., 2015). For weirs and bridge aprons, three passability values (i.e. 0.1, 0.5 and 0.8) were assigned to calculate DCI to represent low, moderate and high passage efficiency (Shaw et al., 2016; Shaad et al., 2018).

$$DCI_P = \sum_{i=1}^{n} \sum_{j=1}^{n} \frac{l_i}{L} \frac{l_j}{L} \left(\prod_{m=1}^{M} p_m\right) \times 100 \quad (1)$$

$$DCI_D = \sum_{i=1}^{n} \frac{l_i}{L} \left(\prod_{m=1}^{M} p_m\right) \times 100 \quad (2)$$

Where $l_i$, $l_j$ are the lengths of the river section i and j; L is the total length of the river network; M is the total number of obstacles between segments; $p_m$ is the overall upstream and downstream passability of the $m^{th}$ barrier.

**2.5 Fish distribution range assessment**

To assess the impacts of barrier construction on fish distribution, two native fish species with different migration behavior and habitat preference,smoothlip finescale carp (*Schizothorax lissolabiatus*) and goonch catfish (*Bagarius yarrelli*) were chosen. Smoothlip finescale carp is one of most abundant fish in the Lancang catchment. It is a schizothoracine cyprinid, with an adhesive organ under the head, and is adapted to the fast-flowing, stony-bottomed upper catchment. Historically, it was widely distributed between the Source and Middle regions, and it inhabits both main river and small tributaries across all stream orders. Although it may undertake short facultative movements for spawning, it is generally regarded as a locally resident species. In comparison, within the Lancang, the goonch catfish is mostly distributed in the Middle and Lower regions, where it inhabits the main river and major tributaries (stream order ≥ 3). This predatory species is also widespread throughout much of the middle and lower Mekong in rocky habitats (Poulsen et al., 2004). It is a potamodromous species, and carries out medium-distance (~10-100 km) feeding and spawning migrations between March and August (Poulsen et al., 2004). Due to barrier construction and increased fishing pressure, the population of this species is decreasing, and it is listed as vulnerable by the International Union for Nature Conservation (IUCN) (Ng, 2020). However, there is very limited information on this species from the Lancang drainage (Ng, 2020).

To construct the historical (1978-2010) and recent (2011-2021) distribution range of these two species, an extensive literature review on records of both species was undertaken by scrutinizing books, peer-reviewed articles, grey literature, and online databases. In addition, field sampling data between the Upper and Lower Lancang from 2003 to 2021 gathered by Yunnan University on a yearly basis, were included (Ding, unpublished data). For capture records checked and regarded as valid, in terms of confirmed fish identification, the coordinates of those sampling records were extracted (Appendix I), then saved as an SHP file. Although smoothlip finescale carp has been recorded in the Source region of the Lancang, the very low sampling efforts (n = 9, by all institutions between 1978 and 2021) in the Source region may not reflect the true distribution range of this species. So, distribution points within this region were not considered in the following analysis.

The dispersal ability of both species was estimated using the 'fishmove' R package (Radinger & Wolter, 2014). Total fish length, aspect ratio of the caudal fin, stream size (stream order), and time were employed in this model (Radinger et al., 2017). Based on expert judgement, common lengths of 250 mm were applied to smoothlip finescale carp and 700 mm to goonch catfish. Mean species-specific aspect ratios of the caudal fin for both species were calculated based on field measurement and FishBase data (Appendix II, Table S1). A time parameter of 10 years was used, as appropriate to long-term population level dispersal (Radinger et al., 2017; Herrera-R et al., 2020). Predicted dispersal movement distance was calculated across stream orders where the species historically occurred, then a mean dispersal movement distance was calculated from those values. This generated dispersal movement distances of 15 km and 66 km for finescale carp and goonch catfish respectively, which were used to generate buffer zones of 15 and 66 km radius for positive records of the respective species and hence, to generate distribution maps for these species.

The distribution ranges of both species were split into three categories based on the sampling time: historical distribution range (1978-2010), distribution range after 2010 (2011-2021), and apparent reduction in distribution range. To assess the impacts of river barriers on access to fish habitat, barrier densities and DCIs were calculated. For finescale carp, because the spatial scale of its dispersal was estimated to be less than the size of sub-catchments, barrier densities and DCIs were calculated separately for each sub-catchment within its distribution range, then a median value for its whole distribution range was generated. For goonch catfish, due to its larger-scale seasonal migratory behavior, we assumed that this species could move across its whole historical distribution range when the Lancang was in its original free-flowing state, so barrier density and DCIs were calculated for its whole distribution range within the study area rather than calculated separately for each sub-catchment.

### 2.6 Data analysis

Dendritic Connectivity Indexes (DCIs) were calculated using the Freshwater Health Index tool (Vollmer et al., 2018). All statistical analysis were conducted in SPSS v25. Spearman's Rank Order Correlation was used to determine whether there was any correlation between barrier density and both DCI indices. Kruskal-Wallis *H* tests were used to compare the barrier densities and DCI values across the four regions of the Lancang. Mann-Whitney *U* tests were used to compare densities of different types of barriers and DCI values between the LRBD database and existing database. In addition, Mann-Whitney *U* tests were used to compare the barrier densities and DCI values between fishes' current distribution ranges (after 2010) and the range from which they have been lost.

## 3. Results

### 3.1 Abundance and spatial distribution of river barriers

A total of 1052 river barriers belonging to 100 sub-catchments were identified during the desk survey (Appendix III), including 126 large dams (≥ 15 m high), 122 small dams (< 15 m high), 753 weirs and 51 bridge aprons (Figure 2). By comparison, the existing database contained 66 river barriers including 60 large dams, two small dams and four weirs, indicating that 93.7% of barriers (i.e. 52.4% of large dams, 98.4% of small dams, 99.5% of weirs and 100% of bridge aprons) were missing from the existing database. For the new LRBD database, combining our desk study with previously generated databases, the Source region contains fewest barriers (n = 99); the Upper region contains a total of 120 barriers; the Middle region contains most barriers (n = 633), including 515 weirs; and the Lower region contains 200 barriers (Figure 3). Across all altitudes, barriers were mainly located at altitudes between 1000 and 3000 m (n = 832), and only eight barriers were constructed above 4000 m. Across all stream orders, second order streams had the highest barrier numbers (n = 442) including 373 weirs (84.4% of weirs), followed by third order streams (n = 308 barriers) and first order streams (n = 182 barriers). Surprisingly, it was noticed that large dams were mostly located within first order streams (n = 52), rather than in other larger tributaries.

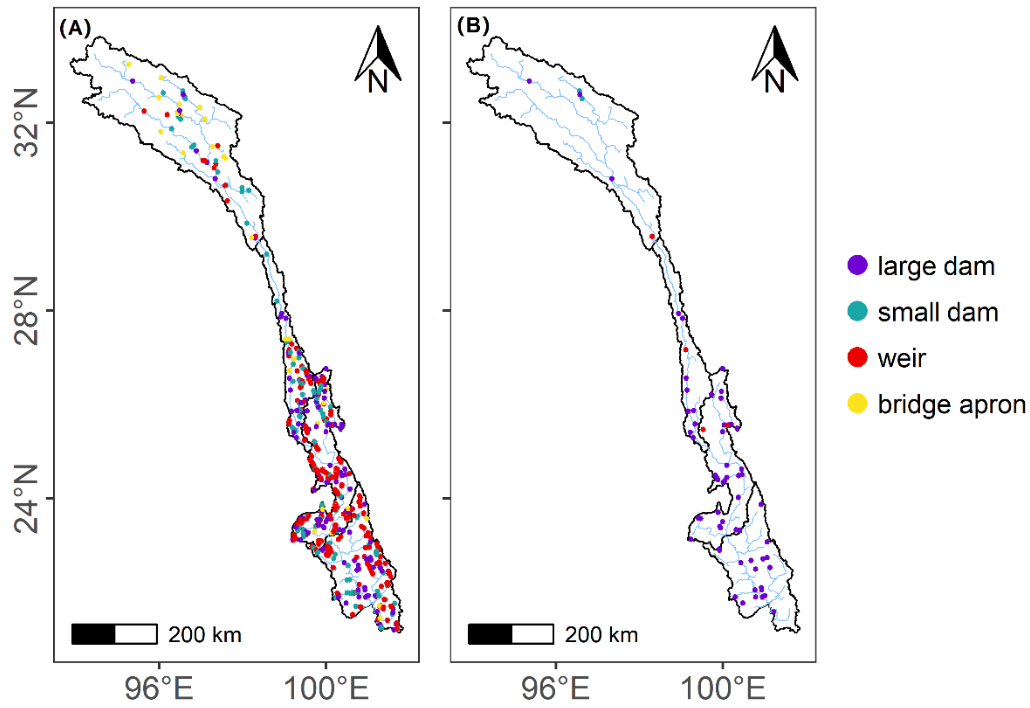


Figure 2. Locations of four types of barriers in the Lancang (Upper Mekong) River recorded in (A) LRBD database and (B) existing database. Large dams are those ≥ 15 m high.

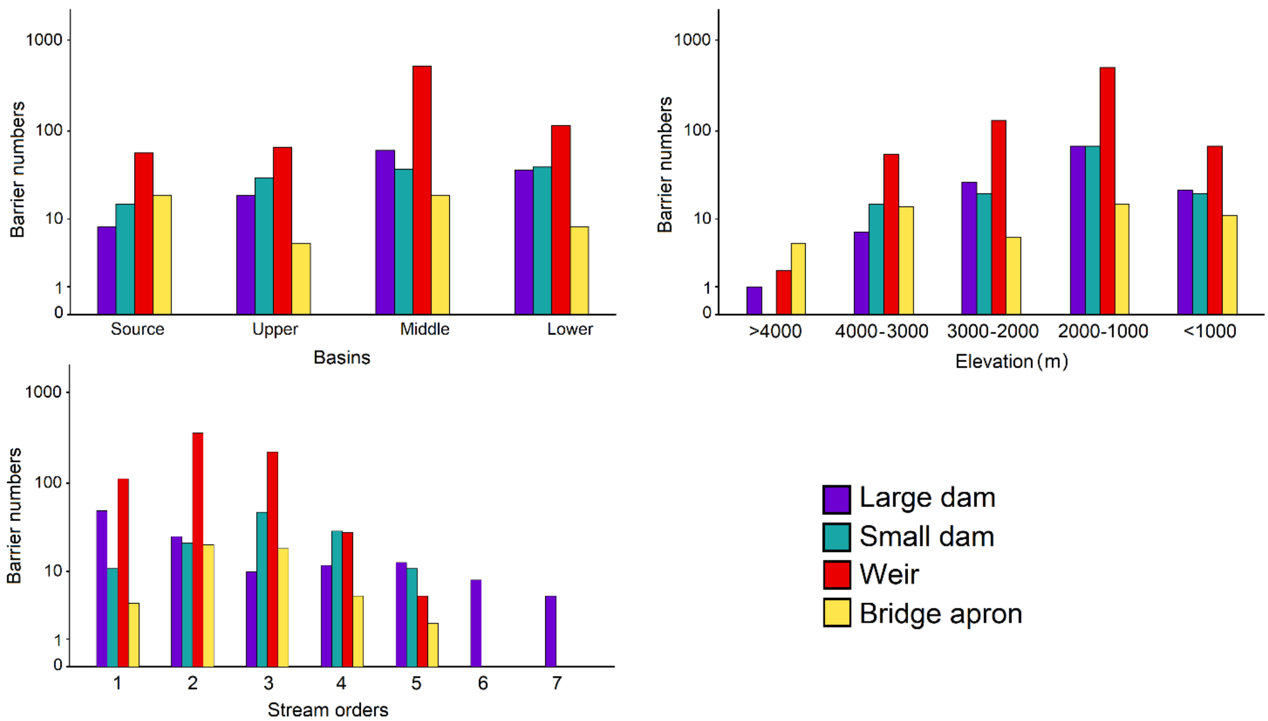


Figure 3. Distribution of four types of barriers in basins, and by elevation and stream orders on the Lancang (Upper Mekong) catchment. Note the log scale. Large dams are those ≥ 15 m high.

### 3.2 Barrier density and Dendritic Connectivity Index

Based on the LRBD database, the overall barrier density (median and quartiles) across the whole Lancang catchment was 0.18 [Q1-Q3: 0.00-1.83] per 100 km, which is significantly higher compared with barrier densities (0.00 [0.00-0.00] per 100 km) calculated from the existing database (Figure 4, Mann-Whitney *U* test, $U$ = 26 843, $P < 0.001$). Similarly, for river connectivity, the $DCI_P$ (98.5 [51.0-1000]) and $DCI_D$ (99.5 [38.5-100.0]) calculated based on the LRBD database (passability of small barriers = 0.1) were significantly lower compared with those ($DCI_P$ 100.0 [100.0-100.0], $DCI_D$ 100.0 [100.0-100.0]) calculated from the existing database (Figure 5; Mann-Whitney *U* test, $P < 0.001$ in both cases).

For the LRBD database, a significant negative correlation was found between the barrier density and both DCI indices (Spearman's Correlation, $r_s(196) = -0.947$, $P < 0.001$; $r_s(196) = -0.905$, $P < 0.001$, respectively). Significant differences in overall barrier densities (Kruskal-Wallis *H* test, $\chi^2(3) = 66.6$, $P < 0.001$), $DCI_P$ (Kruskal-Wallis *H* test, $\chi^2(3) = 59$, $P < 0.001$), and $DCI_D$ (Kruskal-Wallis *H* test, $\chi^2(3) = 48.4$, $P < 0.001$) occurred across the four regions, with the Middle region having the highest median barrier densities (5.34 [0.70-9.67] per 100 km) and lowest median DCI indices ($DCI_P$ 49.50 [21.50-90.00], $DCI_D$ 38.50 [9.00-92.25]) (Figures 5 and 6; Appendix II, Figures S1 and S2, Table S2). In comparison, the Source region had the lowest barrier densities (0.00 [0.00-0.26] per 100 km) and highest median DCI indices ($DCI_P$ 100 [97.25-100], $DCI_D$ 100 [98.50-100]) (Table S2). Significant differences occurred in median densities of all four types of barriers across the regions (Kruskal-Wallis *H* test, $P < 0.05$ in all cases; Figure 6). For large dams (pairwise post hoc, $P \leq 0.005$ in all cases) and small dams (pairwise post hoc, $P < 0.05$), densities in the Source region were lower compared with other regions (Figure 6). Weir density in the Middle region was higher compared with the Source and Upper regions (pairwise post hoc, $P < 0.01$ in both cases), and reduced density occurred in the Source region compared with the Lower region (pairwise post hoc, $P < 0.001$).

Across all barrier affected sub-catchments (n = 100), significant differences occurred between the frequencies of types of barriers (Kruskal-Wallis *H* test, $\chi^2(3) = 31.9$, $P < 0.001$), with weirs having the highest densities (0.59 [0.00-3.17] per 100km), followed by large dams (0.30 [0.00-0.81] per 100 km), small dams (0.15 [0.00-0.80] per 100 km) and bridge aprons (0.00 [0.00-0.25]; Figure S1, Table S2). Weir densities were higher compared with densities of bridge aprons and small dams (pairwise post hoc, $P < 0.01$), large dam densities were higher compared with densities of bridge aprons (pairwise post hoc, $P < 0.01$), no difference was found between the densities of other types of barriers (pairwise post hoc, $P > 0.05$ in all cases). Within all barrier affected sub-catchments, the $DCI_P$ significantly decreased when the passability of small barriers decreased from high (67.0 [45.5-83.8]) to low (51.0 [29.0-72.8]) (Appendix II, Table S3, Kruskal-Wallis *H* test, $\chi^2(2) = 12.1$, $P = 0.002$). Although $DCI_D$ values also decreased along with reduced passability (Table S3), not significant differences were found between three conditions (Kruskal-Wallis *H* test, $P > 0.05$).

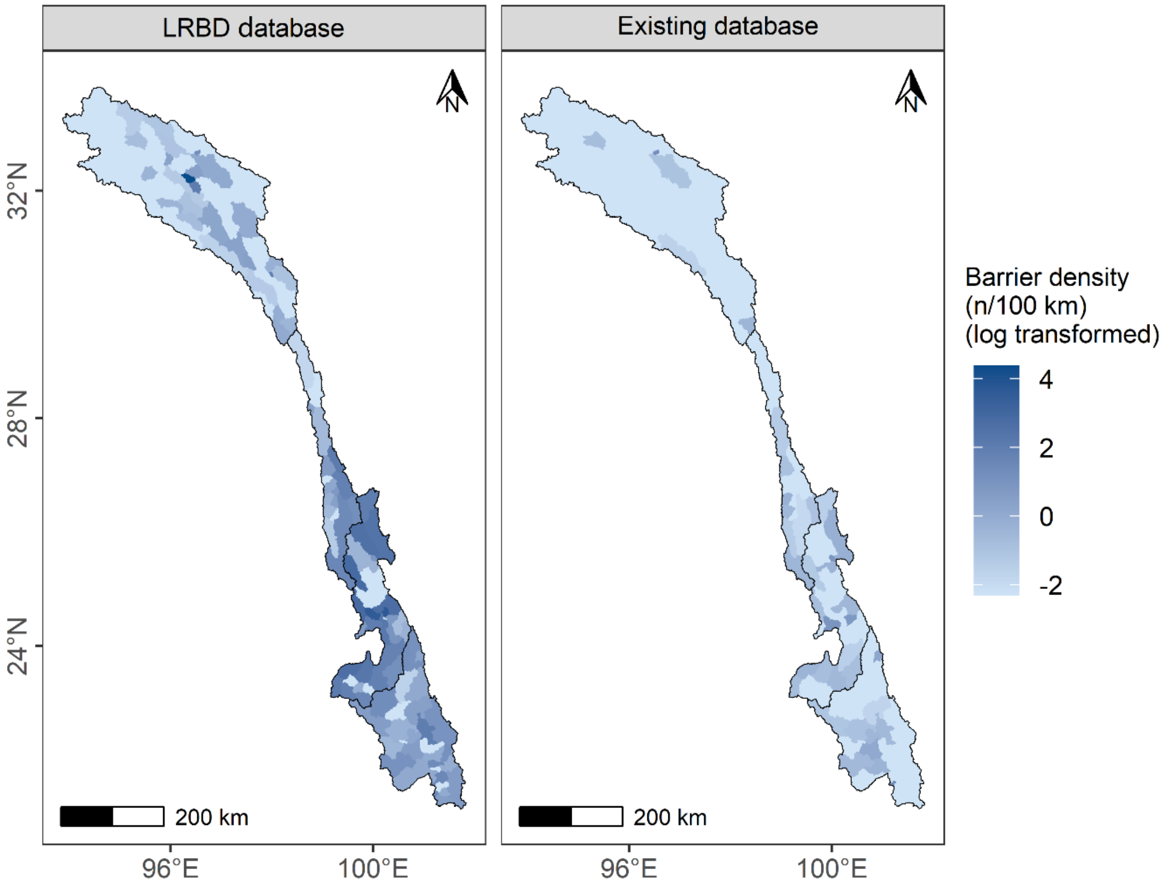


Figure 4. Overview of the barrier density in the Lancang (Upper Mekong) catchment based on the LRBD database (left panel) and existing database (right panel). Barrier density was natural log transformed when creating the figure.

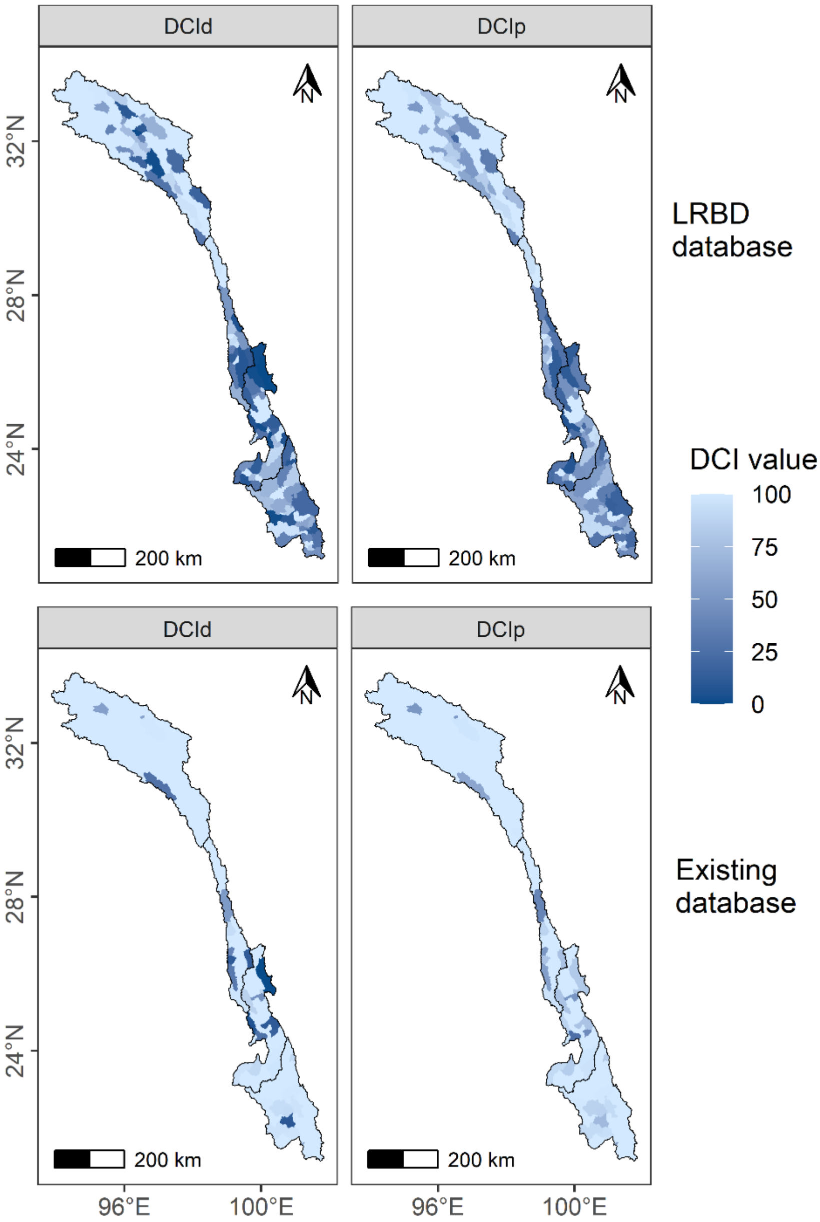


Figure 5. Dendritic Connectivity Index (DCI) values in the Lancang (Upper Mekong) catchment based on the LRBD database (upper panel) and existing database (lower panel). DCId refers to diadromous fish DCI and DCIp refers to potamodromous fish DCI. High connectivity is indicated by high DCI (light shading), while poor connectivity, associated with high barrier density, is indicated by low DCI (dark shading). Passability of 0.1 was assigned to weirs and bridge aprons when calculating DCI values here.

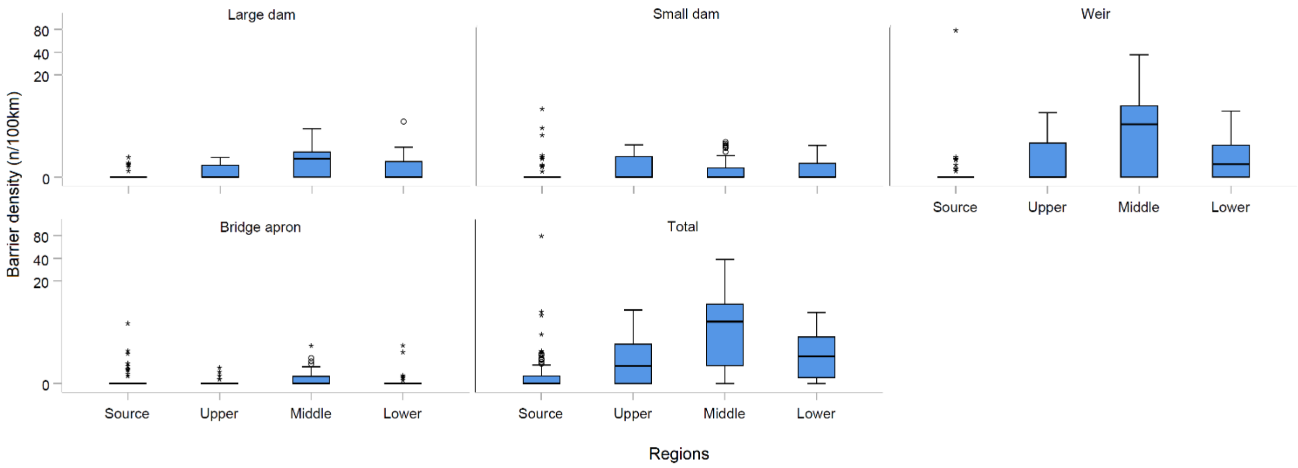


Figure 6. Box plots showing median (with quartiles, ranges, and outliers) barrier densities (n/100 km) at each region in the Lancang (Upper Mekong) catchment. Note the log scale.

### 3.3 Impacts of river barriers on fish habitat

The overall distribution range of smoothlip finescale carp covered 51 sub-catchments with a total river length of 11 956 km within the Upper, Middle and Lower regions. This species has completely disappeared from 12 sub-catchments since 2010, with a total length of 2294 km, a 19.2% reduction. The distribution of this species has also greatly reduced within another eight sub-catchments, mostly located in the downstream part of the historical range (Figure 7). A total of 525 river barriers including 420 small-scale barriers (i.e. weirs and bridge aprons) were identified within the current distribution range, and 151 river barriers, including 127 small-scale barriers, were identified in the range from which smoothlip finescale carp have disappeared.

The median barrier density of the distribution range from which smoothlip finescale carp has been lost or reduced (2.86 [0.73-9.33] per 100 km) was slightly higher compared to the distribution range where they remained (0.94 [0.00-7.37] per 100 km; Mann-Whitney *U* test, $P > 0.05$). $DCI_P$ (62 [34-100], passability of small barriers = 0.1) of the distribution range from which smoothlip finescale carp have been lost or reduced was also similar to the distribution range over which they remain ($DCI_P$ 48.5 [20.3-88.0]; Mann-Whitney *U* test, $P > 0.05$ at three passability scenarios). However, the $DCI_D$ of the distribution range from which they have been eliminated (15 [6.5-84.3]; passability = 0.1) was significantly lower compared with the remaining distribution range (68 [27-100]), when the passability was low and moderate for small barriers (Mann-Whitney *U* test, $P < 0.05$ in both cases). In the context of the $DCI_D$ analysis, this suggests movement between subcatchments (and potential metapopulations) was reduced in the localities from which smoothlip finescale carp have been lost.

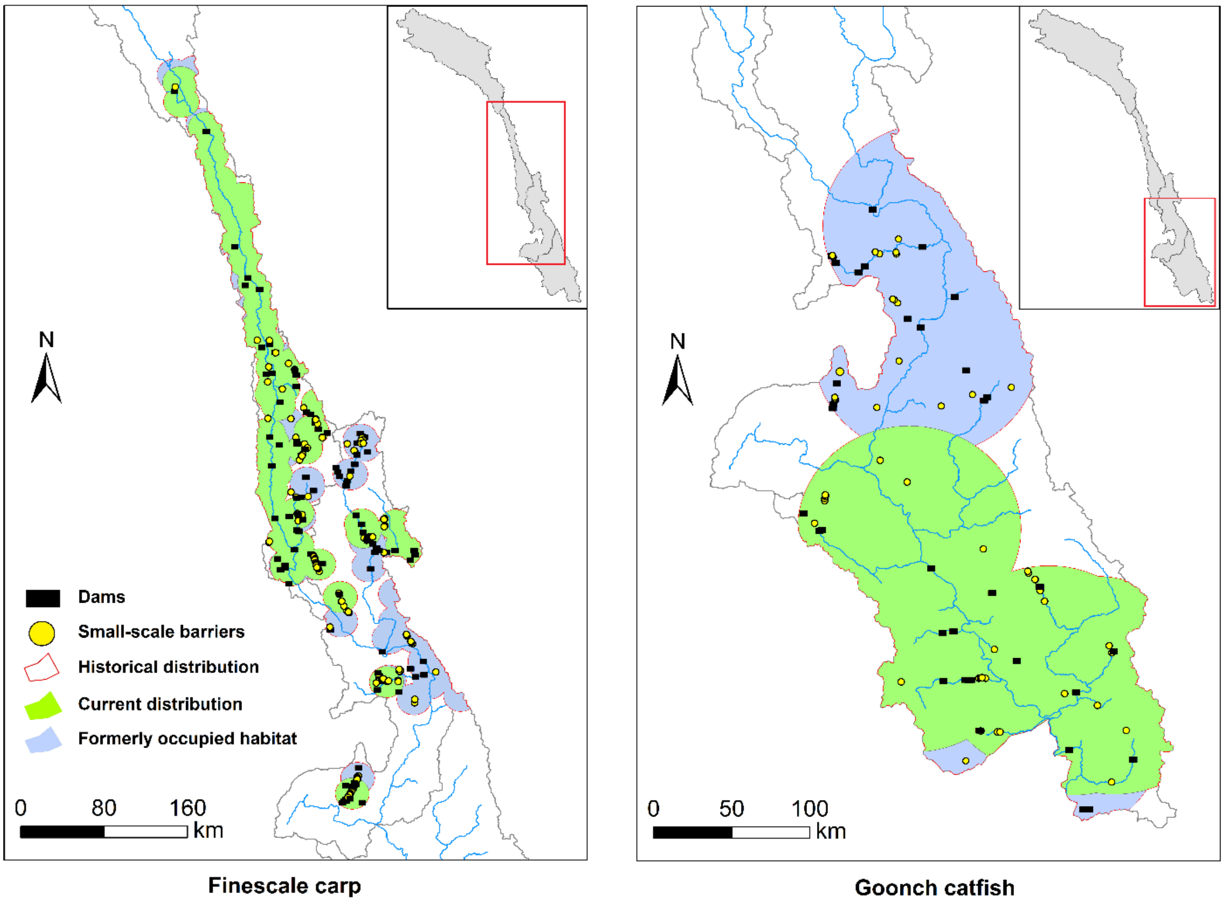


Figure 7. Current and historical distribution of the smoothlip finescale carp (left panel) and goonch catfish (right panel), and the location of river barriers within the Lancang (Upper Mekong) catchment. Weirs and bridge aprons were categorized as small-scale barriers. Distribution data from the Source region are not included due to insufficient sampling (see text for more information).

Goonch catfish were, historically, distributed across 61 sub-catchments of the Lancang, with a total length of 3 143 km (stream order ≥ 3). The current distribution range in the Lancang has shrunk to 39 sub-catchments with a total length of 2 113 km, a reduction of 32.8%, mostly in the upstream part of its historical range (Figure 7). A total of 51 river barriers including 21 dams and 30 small-scale barriers were identified within the current distribution range, and a total of 45 river barriers including 17 dams and 28 small-scale barriers were identified within the area from which goonch catfish have been lost. The barrier density of the current distribution range (2.41 per 100 km) was lower compared with the distribution range from which goonch catfish have been lost (4.37 per 100 km). In addition, DCI values of the range ($DCI_P$ = 11, $DCI_D$ = 21, at three passability scenarios) from which goonch catfish have been lost were lower compared with current distribution range ($DCI_P$ = 25, 28, 31; $DCI_D$ = 39, 41, 42, at three passability scenarios). Since these are calculated over single zones (see Methods) statistical comparison is not possible.

## 4. Discussion

This study generates the first desk-based complete river barrier inventory for the Lancang catchment (Upper Mekong), and provides a test of the completeness of the former existing database. We find that 93.7% of river barriers were absent from the existing database, including 75% of dams and 99.5% of small-scale barriers. The desk-surveyed barrier densities were significantly higher compared with barrier densities calculated from the existing database, and previous assessment of river connectivity largely underestimated the true level of river fragmentation. Considering the DCI values, our study indicates that river connectivity in the Middle Lancang region was most impacted, due to the construction of many small-scale river barriers including weirs and small dams. Evident recent decreases in distribution range of two native fish species, may be linked to habitat fragmentation for migratory indicator species, but there is limited evidence of such an effect, on resident rheophilic indicator species such as smoothlip finescale carp.

Our findings disagree with the statement made by Barbarossa et al. (2020) that impacts of small-scale river barriers on river connectivity are still small in the Mekong catchment, at least not for the Lancang region. This is probably because existing databases used in previous studies are highly incomplete, resulting in underestimation of true fragmentation levels of the catchment, a pattern evident in Europe too (Belletti et al., 2020). Recent research in two Lower Mekong sub-catchments supports our view that most small-scale barriers were missing from existing barrier inventories, and among all identified barriers 90.5% are small-scale structures (Baumgartner et al., 2022). Small barriers can potentially have a much greater fragmentation impact than large dams in the Mekong catchment (Baumgartner et al., 2022), particularly outside the main channel. Our results show that small-scale barriers are the major fraction of all river barriers, and similar results have been observed elsewhere. A detailed walkover survey at two English catchments found that 95.2% river barriers are less than 10 m high (Sun et al., 2020). Large-scale river barrier surveys conducted in 36 European countries, found that 91% of identified river barriers are less than 5 m high (Belletti et al., 2020). Numbers of small-scale barriers (i.e. road crossings) are 38 times greater than dams in the Great Lakes basin of North America (Januchowski-Hartley et al., 2013).

Across all sub-catchments of the Lancang River, only 49.5% of sub-catchments are unfragmented by river barriers, and the majority of these unfragmented sub-catchments are located within the Source region. Due to its high altitude, thin air, and large permafrost area, the human population density in the Lancang Source region is markedly lower compared with the three downstream regions, resulting in less human influence on the river and surrounding habitat (Li et al., 2018). So, the majority (73.5%) of sub-catchments within the Source region of the Lancang were free from human interference. However, with increased human population density and anthropogenic activities further southeast (Li et al., 2018), the Upper, Middle and Lower Lancang regions suffered more intensive human pressures, including greater river barrier construction. River barriers in the Lancang are mostly constructed within the city and rural areas, which may relate to increased urban power demand and agricultural irrigation demand (Bhattacharyya & Ohiare, 2012; Gu et al., 2010). The rapid rural electrification in China led to a significant increase in construction of small hydropower infrastructures such as small dams (Bhattacharyya & Ohiare, 2012), and this is particularly the case for the Lancang catchment. On the other hand, rice and sweetcorn production along the Lancang had an area of 4132 $km^2$ by 2008, and these crop fields were mainly located within the Middle and Lower regions, along with other crops (e.g. wheat, potato, tea) resulting in a large demand for irrigation water (Gu et al., 2010), leading to increased construction of small irrigation infrastructures (i.e. weirs). All these small barriers lead to a significant decrease of river connectivity from the Upper to Lower Lancang regions, and contribute to extensive fragmentation of the catchment.

The distribution range in the Lancang of two widespread native fish species, smoothlip finescale carp and goonch catfish, is shown to have declined since 2010. Our results provide some support that the cause for this is due to reduced connectivity, as $DCI_D$, here indicative of connectivity between subcatchments, was significantly lower in subcatchments from which smoothlip finescale carp have been lost. However, barrier densities and $DCI_P$ were similar between the historical distribution range and that from which finescale carp has been lost. Subcatchment connectivity is important for the persistence of fish metapopulations (Radinger & Wolter, 2014; Wilkes et al., 2018) and we postulate this as contributing to the decline in smoothlip finescale carp, although further study of the impacts of barriers on the habitat use, recruitment and dispersal of this species is necessary to confirm this. The high barrier density and low DCI values in the Middle Lancang catchment are a severe cause for concern for conserving the native fish communities and other aquatic biota. For rheophilic lithophiles like smoothlip finescale carp, that require coarse riverbed substrates for habitat, particularly to spawn, the ponding effects and siltation associated with river barriers could be another reason for their disappearance (Sun et al., 2021, 2022). Recent studies in Europe indicate that small-scale barriers can limit the dispersal and persistence of river-resident species (Jones et al., 2021; Tummers et al., 2016), change the aquatic habitat immediately upstream and downstream of the barrier (Sun et al 2021, 2022), and lower survival rates of fish eggs and inhibit the emergence of fry (Louhi et al., 2008).

For goonch catfish, it is assumed that the reduced distribution range is mainly caused by the construction of large dams in the main river. The Nuozhadu Dam is suggested to be main cause of habitat loss, as it has blocked upstream passage completely, while also reducing the rocky, lotic habitat that goonch catfish favour. We suggest that, in future, habitat of the goonch catfish will shrink further downstream due to the construction of another large dam, the Jinghong Dam, which is located 100 km downstream of the Nuozhadu Dam. Apart from passage obstruction, changes in chemical and physical characteristics due to dam construction would also cause negative effects on fish. For example, in July 2014 during the water-retaining stage of the Jinghong Dam, high temperatures associated with reduced dissolved oxygen immediately downstream of the dam led to hypoxia exposure and resulted in a massive kill of the goonch catfish population (Du, 2022). Currently, among 192 Lancang fish species, 18 has been evaluated as near threatened or threatened species by the IUCN Red List (Appendix II, Table S4; IUCN, 2022), and dam construction was suggested to be one of the main reasons for population decline in more than half of them. This is potentially the case for many potamodromous species that require free access to critical habitats on both sides of the barrier, as well as for locally resident species (Wilkes et al., 2019), will be impacted by the proliferation of barriers there.

As a necessary component for effective river management, a complete barrier database makes it possible to estimate the true impacts of barriers on river connectivity (Jones et al., 2019). Creation of a complete river barrier database will help river managers and policy makers to better understand the true extent of barrier abundance and distribution. Then, barrier removal or mitigation approaches could be applied on prioritized barriers to improve river connectivity (Atkinson et al., 2018). By using visual interpretation of high-resolution remote sensing images, we have managed to build the first complete barrier inventory for the Lancang catchment. However, the intensive desk work is extremely time consuming even with a pre-trained team. We assume that it may take years to visually examine all remote sensing images for the Lower Mekong, in order to build the Lower Mekong barrier database. In this case, some alternative approaches with faster barrier detection efficiency should be considered. For example, in recent years, with the rapid development of deep learning algorithm, convolutional neural networks (CNNs) have been widely employed for objective detecting from remote sensing images (Liu et al., 2019). This approach has been successfully used to identify reservoirs and dams from satellite images (Fang et al., 2019, 2021; Jing et al., 2021), and could potentially be applied to identify small-scale barriers in the Lower Mekong, as the first priority to fill in the gaps in existing barrier databases for all Middle and Lower Mekong sub-catchments.

Currently, the mean barrier density of the Lancang catchment (0.02 per km) is much lower than the mean barrier density (0.74 per km) of many European rivers (Belletti et al., 2020). However, concerns should be raised as connectivity restoration and mitigation approaches are still lacking for Lancang catchment barriers. So far, among all 1052 barriers, only two large dams (i.e. Huangdeng and Dahuaqiao Dam) have been installed with fish lifts, and their efficiency has not been evaluated. None of the small-scale barriers are fitted with fish passage facilities. In addition, only one small dam has been intentionally removed for river connectivity restoration purposes (Ding et al., 2018). This demonstrates that more effort should be put into river conservation by the government As an efficient measure to propose, the next step would be select prioritized barriers to plan their removal. It is our intention that the barrier database created in this study (Appendix III) can provide baseline data for the Tibetan Plateau ecological protection and restoration project, and support management plans for future Lancang river connectivity restoration and habitat conservation work.

## 5. Conclusions and recommendations

This study suggests that more than 90% of river barriers, including the majority of small-scale river barriers were absent from existing Upper Mekong barrier databases, and previous research has underestimated true fragmentation levels of the catchment. In future we anticipate that when evaluating the impacts of rive barriers on hydrological connectivity and fish habitat, all barriers including those small-scale ones, should be considered. Construction of river barriers in the Lancang appears to have led to distribution range shrinkage of two native fish species by blocking fish passage and causing habitat change. Given that only two representative fish species were assessed in this study, we encourage future studies to more fully evaluate the effects of barrier construction on the habitat availability and population status of the whole fish fauna in the Lancang catchment. Our study findings have important implications for river barrier management and river restoration works across the Mekong basin by extending the emphasis beyond just the largest dams to a more integrated consideration of catchment connectivity impacts.

**CRediT authorship contribution statement**

Jingrui Sun: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – original draft, Visualization, Writing - review & editing. Weilong Du: Investigation, Data curation, Formal analysis, Writing – review & editing. Martyn C. Lucas: Methodology, Formal analysis, Writing – review & editing. Chengzhi Ding: Conceptualization, Methodology, Supervision, Writing – review & editing. Jinnan Cheng: Visualization, Writing - review & editing. Juan Tao: Writing - review & editing. Daming He: Supervision, Writing – review & editing.

**Declaration of competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**Appendix A. Supplementary data**

Supplementary data to this article can be found online at https://doi. org/10.1016/j.jenvman.2022.116817

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