Conservation status assessment and a new method for establishing conservation priorities for freshwater mussels (Bivalvia: Unionida) in the middle and lower reaches of the Yangtze River drainage

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Abstract:

1. The freshwater mussel (Unionida) fauna of the Yangtze River is among the most diverse on Earth. In recent decades, human activities have caused habitat degradation in the river, and previous studies estimated that up to 80% of the Yangtze River's mussel species are threatened or Near Threatened with extinction. However, a comprehensive and systematic evaluation of the conservation status of this fauna has yet to be completed.
2. This study evaluated the conservation status of the 69 recognized freshwater mussel species in the middle and lower reaches of the Yangtze River, using the criteria by the International Union for the Conservation of Nature (IUCN). We then developed and applied a new method for prioritizing species for conservation termed Quantitative Assessment of Species for Conservation Prioritization (QASCP), which prioritizes species according to quantifiable data on their distribution and population status, life history, and recovery importance and potential.
3. IUCN assessments revealed that 35 (51%) species in the study region are threatened or Near Threatened (i.e. 11 Endangered, 20 Vulnerable, 4 Near Threatened). In addition, 16 species (23%) could not be assessed due to data deficiency. Key threats to the freshwater mussel biodiversity of the Yangtze River include pollution, habitat loss and fragmentation, loss of access to host fish, and overharvesting of mussels and their host fish. The genera *Aculamprotula*, *Gibbosula*, *Lamprotula*, *Pseudodon*, *Ptychorhynchus* and *Solenaia* were identified as particularly threatened.
4. Data availability allowed for QASCP assessment of 44 species. Only *Solenaia*

carinata, regionally Endangered under IUCN criteria, achieved the highest QASCP rank, i.e. First Priority. The five species assessed as Second Priority were considered either regionally Endangered (1), Vulnerable (3) or Data deficient (1) under IUCN criteria. The 23 Third Priority species were assessed as regionally Endangered (2), Vulnerable (15), Near Threatened (2) or Least Concern (4).

Keywords: China; conservation prioritization; endangered species; freshwater mussels; Unionida; Yangtze River;

INTRODUCTION

Freshwater mussels (Bivalvia: Unionida) are among the most important faunas in freshwater ecosystems in terms of biodiversity and ecosystem functioning (Vaughn & Hakenkamp, 2001; Graf & Cummings, 2007; Bogan, 2008; Vaughn, 2018), and can constitute >90% of the benthic biomass of rivers (Negus, 1966; Wu, 1998). At the same time, freshwater mussels are considered to be among the most vulnerable groups of organisms as many species are declining precipitously worldwide (Lydeard et al., 2004; Strayer, 2008; Haag & Williams, 2013; Zieritz et al., 2018a). Despite their diversity, ecological and commercial values and endangered status, relatively little is known about the biology of many freshwater mussel species (Zieritz et al., 2018a; Lopes-Lima et al., 2018b). This is especially true for species outside of Europe and North America (Zieritz et al., 2018a).

The International Union for Conservation of Nature (IUCN) Red List of Threatened Species is the most comprehensive and widely recognized inventory of the conservation status of species. To date, the global conservation status of 511 out of 859 currently recognized freshwater mussels has been assessed through the IUCN (Graf, 2013; IUCN, 2019). IUCN assessments, as most of the currently used evaluation processes of extinction risk, are essentially based on trends in distribution area, habitat area and/or population sizes of the species in question (IUCN Standards and Petitions Subcommittee, 2014). IUCN assessment criteria give no or little importance to underlying ecological interactions, which may have critical importance to extinction processes. For example, freshwater mussels have unique life history traits that are related to their dispersal abilities and that ultimately determine their distribution and abundance (Vaughn, 2012). As adult mussels are mostly sedentary, dispersal is mostly dependent on their larval stage (glochidia), which attach to vertebrate (usually fish) hosts (Wächtler, Mansur, & Richter, 2001). However, mussel species vary in the type and number of fish hosts used, the mechanism employed in infecting the host(s), and the timing of glochidial development and release (Barnhart, Haag, & Roston, 2008). This variation has consequences for dispersal ability and population dynamics of mussels, and their distribution and abundance can be strongly influenced by the composition of the co-occurring fish assemblage (Rashleigh, 2008; Schwalb, Cottenie, Poos, & Ackerman, 2011). Furthermore, the IUCN assessment method is solely focused on assessing a species' risk of extinction; it does not consider differences in the economic value of species (e.g. as a source of food or pearls; Hua & Gu, 2002) and is therefore unsuitable as a basis to prioritize species in that respect for conservation.

In contrast to North American and Europe, where the conservation status of most freshwater mussel species has been assessed at various spatial scales and jurisdictional levels (Williams, Warren, Cummings, Harris, & Neves, 1993; FMCS, 2016; Lopes-Lima et al., 2017), the conservation status of most freshwater mussels in Australia, South America, and Asia is not known (Lopes-Lima et al., 2018b). Of the 99 freshwater mussels currently known from China (Zieritz et al., 2018a), the global conservation status has been formally assessed using IUCN criteria only for 41 species, which are currently listed as following: 2 Critically Endangered (CR), 5 Vulnerable (VU), 1 Near Threatened (NT), 21 Least Concern (LC), and 12 Data Deficient (DD). Within China, the Yangtze River basin is of particular conservation interest, as it features the most diverse freshwater mussel fauna in China (Wu, Liang, Wang, Xie, & Ouyang, 2000; Xiong, Ouyang, & Wu, 2012) and one of the most diverse assemblages on Earth (Zieritz et al., 2018a). Since the 1950s, a wide variety of studies have been published on freshwater mussels from the Yangtze River basin, but most of this work has been confined to local areas and lacked quantitative data, resulting in a general lack of knowledge on the current status of Yangtze mussel species (Wu et al., 2000; Shu, Wang, Pan, Liu, & Wang, 2009; Xiong et al., 2012). That said, populations are known to be declining. In 2009, Shu et al. (2009) assessed the regional conservation status of 33 of the 69 known species of the middle and lower reaches of the basin, and 41% of the assessed species were considered threatened with extinction (i.e. conservation status CR, EN or VU) or NT. Wu et al. (2000) estimated that about 80% of the freshwater mussel species in this region are threatened or NT as a result of habitat degradation over the last decades.

Considering the prevalence of threats to freshwater mussels and their habitats, it is critical that the conservation status of species and populations should be assessed and monitored closely, particularly in Asia (Lydeard et al., 2004; Vorosmarty et al., 2010; Haag & Rypel, 2011; Zieritz et al., 2018a). However, as outlined above, the latest conservation status assessments of the freshwater mussels of the Yangtze River date back ten years and did not include >50% of the species known from this area. A comprehensive and updated evaluation of the conservation status of this fauna is urgently needed as a basis for developing conservation measures for this important fauna. In order to maximize the impact of the developed tools specifically in a Chinese context, the conservation assessments should not only be based on quantifiable data on population status, distribution, biology and ecological interactions, but also prioritize species in terms of their value for people.

This study aims to: 1) assess the regional conservation status of the freshwater mussels of the middle and lower reaches of the Yangtze River using IUCN criteria; 2) develop a new, comprehensive and quantitative method for prioritizing species for conservation; 3) apply this method to the freshwater mussels of the Yangtze River in order to rationally justify the utilization of resources for conservation and restoration; 4) compare results achieved by IUCN criteria and the newly developed method to prioritize species for conservation; and 5) provide direction for critical conservation research needs.

METHODS

Study area and data collection

With a length of 6300 km and a total area of 1.8×10^6 km^2, the Yangtze River is the third longest river in the world and the largest river in China, forming a complex system with more than 3000 tributaries and 4000 lakes (Fu, Wu, Chen, Wu, & Lei, 2003; Wu et al., 2004; Xie, 2017). It originates from alpine springs on the slopes of the Geladandong Mountains on the Tibetan Plateau, and follows a sinuous west to east route before emptying into the East China Sea (Figure 1). The drainage basin receives an average annual precipitation of 1100 mm which is concentrated in the April to October wet season (Fu et al., 2003; Wu et al., 2004). The upper reach spans from the Tibetan Plateau to Yichang (length of main branch = 4504 km), the middle reach from Yichang to Hukou (length of main branch = 955 km), and the lower reach from Hukou to Shanghai (length of main branch = 938 km) (Fu et al., 2003; Wu et al., 2004; Figure 1). Due to its sheer scale and position in central Asia, the Yangtze River drainage is of great importance for biodiversity and economy both nationally and at global scales.

Data were collected for all freshwater mussels reported from the middle and lower reaches of the Yangtze River (Figure 1, Appendices 1 and 2). We focused on the middle and lower reaches rather than the upper reach of the basin as this is where historical data availability is best and anthropogenic threats, including deforestation, pollution and dams, are most prevalent (Wu et al., 2000; Shu et al., 2009). Presence/absence data on freshwater mussels species in each of the 14 major lake and 14 major river drainages of the study area were collected from the literature (Heude, 1874-1885; Simpson, 1900; Lin, 1962; Tchang, Li, & Liu, 1965; Tchang & Li, 1965; Haas, 1969; Liu & Wang, 1976; Liu, Zhang, & Wang, 1979; Liu, Zhang, Wang, & Wang, 1979; Liu, Zhang, & Wang, 1980; Zeng & Liu, 1989; Liu, Wang, & Zhang, 1991; Chen & Wu, 1990; Wu, 1993; Wei et al., 1990; Wei et al., 1993; Liu, Zhang, Wang, & Duan, 1994; Li & Huang, 1994; Huang & Liu, 1995; Wu, Ouyang, & Hu, 1994; Wu, 1998; Huang, Li, Liu, Zhang, & Wang, 1999; Wu et al., 2000; Hu, Yang, & Hu, 2004, Hu, 2005; Prozorova, Sayenko, Bogatov, Wu, & Liu, 2005; Hu, Liu, Fu, & Yan, 2007; Liu, Ouyang, & Wu, 2008; Shu et al., 2009; Xiong et al., 2012; He & Zhuang, 2013; Xu, 2013), MUSSELp Database (http://mussel-project.uwsp.edu/), NSII (National Specimen Information Infrastructure, http://www.nsii.org.cn/2017/home.php) and museum collections (i.e., Nanchang University; Institute of Zoology, Chinese Academy of Sciences; Institute of Hydrobiology, Chinese Academy of Sciences).

Data analysis

Conservation status assessment

The conservation status of all freshwater mussel species present in the middle and lower reaches of the Yangtze River were assessed using the Guidelines for Application of IUCN

Red List criteria at regional and national levels (IUCN, 2012). Although a considerable amount of distributional data for freshwater mussels in the middle and lower reaches of the Yangtze River Basin is available, evaluating changes in spatial distribution over time is difficult due to the lack of comprehensive, long-term surveys. In addition, data are largely restricted to a limited number of genera, specifically *Aculamprotula*, *Acuticosta*, *Anemina*, *Cristaria*, *Cuneopsis*, *Lamprotula*, *Lanceolaria*, *Lepidodesma*, *Nodularia*, *Schistodesmus*, *Sinanodonta*, *Sinohyriopsis* and *Solenaia*, whilst relatively little information is available for other genera.

A new method for species conservation prioritization

A new framework for Quantitative Assessment of Species for Conservation Prioritization (QASCP) was then developed to provide a tool for a comprehensive and structured assessment of the conservation status of the freshwater mussels recorded from the middle and lower reaches of the Yangtze River. Our aim was for QASCP to correctly reflect the ecological and biological characteristics of freshwater mussel species, their importance to humans and potential for recovery.

Step 1. Structuring the decision problem into nine quantifiable elements

As a first step, we structured the complex problem of prioritizing conservation of freshwater mussel species into nine elements (=criteria), which can be grouped into three general aspects of a species: (A1) distribution and population status; (A2) life history limitations; and (A3) recovery importance and potential. For each species, A1 was based on three quantifiable criteria, i.e. (C1) distribution frequency, (C2) population status and trends, and (C3) endemism on a national and regional scale; A2 was based on the four criteria (C4) fecundity, (C5) timing of reproduction period, (C6) habitat/substrate preference, and (C7) drought resistance ability; A3 was based on the two criteria (C8) economic value of the species and (C9) whether propagation has been achieved or research into propagation is ongoing or not (Table 1).

Step 2. Scoring indicator layers

For each species a score from 1 to 3 was given for each of the nine criteria (C1-9) based on available data and applying evaluation standards detailed in the Appendix (Table 1; see Appendix 2-12 for detailed information and data sources). Scores for some species and criteria for which available data were limited were estimated using a precautionary approach that would result in a conservatively high score and thus conservation priority.

Step 3. Determination of conservation priority coefficients and classes

In the final step, the conservation priority index (CPI) was calculated for those species for which data availability was sufficient to allow for scoring of each of the nine criteria (C1-9) in the following: CPI = A1 + A2 + A3, where A1 is the Distribution and Population Status index and calculated as $A1 = \sum_{i=1}^{3} 0.555\ \mathrm{X}_i$, A2 is the Life History Limitations index and calculated as $A2 = \sum_{i=4}^{7} 0.417\ \mathrm{X}_i$, and A3 is the Recovery Importance and Potential index and calculated as $A3 = \sum_{i=8}^{9} 0.833\ \mathrm{X}_i$, where i is the number of the criterion, and χ_i is the score given for the respective criterion. The CPI ranges from 0 to 10, and each of the three sub-indices (A1-3) are weighted equally with a theoretical maximum value of 3.33.

CPIs were subsequently used to assign a conservation priority class to each species following partitioning criteria given in Table 2. The conservation priority criteria were divided into following four ranking levels to facilitate direct translation to protection categories under Article 9 of the "Law of the People's Republic of China on the Protection of Wildlife" (Xie & Wang, 1995; Wang & Xie, 2004; Fan & Bau, 2008): "First Priority" (protection category "First State Protection"), "Second Priority" (protection category "Second State Protection"), "Third Priority" (protection category "Third State Protection"), and "Least Priority" (protection category "Least State Protection").

RESULTS

Two families, three subfamilies, 18 genera and 69 species of freshwater mussels have been documented from the middle and lower reaches of the Yangtze River in various earlier studies (Appendices 1 and 2). *Lamprotula* was the most speciose genus (11 species), followed by *Lanceolaria* (7 species). A complete checklist of species included in the database from the middle and lower reaches of the Yangtze drainage can be found in Appendix 1.

The regional conservation status of these 69 species in the study region was evaluated based on IUCN criteria (Table 3, Appendix 13). The results showed that 35 (50.7%) of the species are threatened or NT, with 11 EN (15.9%), 20 VU (29.0%), and four NT (5.8%); 18 LC (26.1%) and 16 DD (23.2%). The genera *Aculamprotula*, *Gibbosula*, *Lamprotula*, *Pseudodon*, *Ptychorhynchus* and *Solenaia* were identified as particularly threatened with extinction (Appendix 13).

We evaluated 44 species for which we were able to compile a complete data matrix for C1 to C9 using the newly developed QASCP system (Table 3). Only one species (*Solenaia carinata*) ranked as Frist Priority and was also determined as regionally EN under IUCN guidelines. Of the five Second Priority species, one was assessed as regionally EN (*Lamprotula triclava*), three as VU (*Aculamprotula fibrosa*, *A. scripta*, *Gibbosula polysticta*) and one as DD (*Cuneopsis kiangsiensis*). All of these six First and Second priority species are endemic to China, exhibit decreasing population sizes, medium fecundity rates, are restricted to mud substrates, and are of considerable economic value whilst research into artificial reproduction is lacking (Appendices 2-12). The 23 Third Priority species included species with a more variable regional IUCN status, i.e. EN (2), VU (15), NT (2) and LC (3).

DISCUSSION

Chinese freshwater mussels have suffered serious declines in recent decades, especially in the middle and lower reaches of the Yangtze River (Wu et al., 2000; Shu et al., 2009; Xiong et al., 2012; Zieritz et al., 2018a). In this study, 15.9% of species were assessed as EN in the study area using IUCN criteria. Since 2009, when 41% of freshwater mussels in the middle and lower reaches of Yangtze River basin were considered threatened or NT, the proportion of NT and threatened species has increased to 51% (Shu et al., 2009). For some species, the conservation status appears to have remained stable over the last decade. For example, *Sinohyriopsis cumingii* and *Lamprotula caveata* are listed as LC in both our regional IUCN assessment as well as Shu et al's (2009) assessment (Table 4). However, overall, results of the present study indicate that over the past decade, the conservation status of many species has declined and the number of threatened species has increased. For instance, *Lamprotula microsticta,* evaluated as NT by Shu et al. (2009), is now considered EN in the study region. In addition, many species of the study area were not evaluated by Shu et al. (2009) for various reasons, but were assessed as EN in this study (e.g., *Solenaia carinata*, *S. rivularis*, and *S. triangularis*; Table 4). The observed trend indicates that freshwater mussel diversity in the Yangtze drainage is under serious threat, and that conditions necessary for sustaining the current level of freshwater mussels diversity in the region are deteriorating and may rapidly lead to extinctions.

The application of a newly developed method to prioritize freshwater mussels for conservation (QASCP) revealed one First Priority species, five Second Priority species, 23 Third Priority species, and 15 Least Priority species. This suggests that many species in the region are in immediate need of protection to avoid continued or future population declines.

There is considerable distributional data available for freshwater mussels, but historical data on freshwater mussels are scarce and strongly focused on a limited number of genera. Data on fecundity and reproductive periods were particularly scarce and prevented precise determination of conservation priorities. For example, data on host fish identities are available for only five Chinese freshwater mussels (*Aculamprotula scripta*, *A. fibrosa*, *Sinohyriopsis cumingii*, *Sinanodonta woodiana*, *Lamprotula leaii*) and were exclusively obtained in laboratory experiments, which may not reflect hosts under natural field conditions (Wang, Wei, & Peng, 2001; Hu, 2003; Hua, Xu, Wen, & Wang, 2005; Bai, Li, & Pan, 2008; Levine, Lang, & Berg, 2012).

A further limitation to conservation and in-depth research on Chinese freshwater mussel biology and ecology conservation is the unresolved taxonomy of the fauna. Accurate knowledge on species boundaries and their taxonomy is crucial as a basis for protecting species diversity and managing resources (Costello, May, & Stork, 2013). However, the taxonomic validity of many Chinese taxa is still unclear and under intense scientific discussion (e.g. Jiang et al., 2015). That said, advances in the use of molecular approaches to the systematics and taxonomy of the freshwater mussels has resulted in a vastly improved understanding of the evolutionary relationships between freshwater mussel lineages (Graf &

Cummings, 2007; Pfeiffer & Graf, 2015; Lopes-Lima et al., 2018a). In addition, the recent focus on Asian freshwater mussels using molecular systematic approaches has improved our understanding of the species-level diversity and distribution, including the recognition of several new, sometimes morphologically cryptic species (Kongim, Sutcharit, & Panha, 2015; Thach, 2016; Zieritz et al., 2016). More phylogenetic studies using the latest molecular technologies and data are needed to properly and fully assess the taxonomy and conservation status of Chinese freshwater mussels (e.g., Bolotov et al., 2017; Lopes-Lima et al., 2018a).

Major threats to freshwater mussels in China

Major threats to global freshwater biodiversity include loss, fragmentation and degradation of habitat, dam construction, overexploitation, pollution, sand mining, introduction of non-native invasive species, and climate change (Dudgeon et al., 2006; Geist, 2011; Burlakova et al., 2011; Lopes-Lima et al., 2017). In the Yangtze River Basin, freshwater mussels are vulnerable to a combination and accumulation of all these threats. The parasitic larval and juvenile stages of freshwater mussels are thereby particularly sensitive to environmental changes (Bringolf et al., 2007; Taskinen et al., 2011).

Pollution and water quality

Urban, agricultural, and industrial water pollution are all potentially affecting the density and diversity of mussels (Geist, 2011; Haag, 2012). In the Yangtze River basin, the rapid growth of urban areas and industries beginning in the 1970s has resulted in large volumes of untreated domestic and industrial sewage. This has led to major water quality problems throughout the region and a sharp decline in aquatic biodiversity (Fu et al., 2003; Mueller et al., 2008; Zeng, Mcgowan, Cao, & Chen, 2018). In addition, most tailings from mines in the region are discharged directly into the basin without treatment, which leads to serious heavy metal pollution of river water that is likely to have negative effects on the survival of freshwater mussels (Fu et al., 2003; Wu et al., 2004; Mueller et al., 2008). Eutrophication is also an important factor affecting species composition, density and biomass of freshwater mussels. For example, Taihu Lake (Figure 1) with 24 species of freshwater mussels reported (Shu et al., 2009) is in a serious state of eutrophication. Conversely, the less eutrophic Poyang Lake and Dongting Lake (Figure 1) exhibit higher densities and biomass of freshwater mussels (Shu et al., 2009; Xiong et al., 2012).

Habitat loss and fragmentation

Large-scale sand mining operations also destroy the habitat environment of freshwater mussels. With the rapid economic development, demand for building resources in China is increasing (Wu, de Leeuw, Skidmore, Prins, & Liu, 2007). Unrestricted sand mining in many river drainages in China may is likely to heavily impact benthic diversity. Sand mining from rivers results in the removal and mortality of adult mussels, destruction of the benthos, degradation of water quality and clarity, and may be one of the main driving forces causing the decline of freshwater mussel resources in the lakes of the middle and lower reaches of the Yangtze River (Fu et al., 2003; Xie, 2017). However, our understanding of the impact of sand dredging on these animals is currently inadequate and requires further study.

The hydrologic and habitat characteristics of rivers, streams, and lakes in China have been heavily altered, and may have resulted in the rapid destruction of many mussel beds (Haila, 2002; Wu & Hobbs, 2002). Historically, the Yangtze River formed a highly interconnected river–lake system with many lakes and tributary rivers connected to the

Yangtze River mainstem (Fu et al., 2003; Jin, Nie, Li, Chen, Zhou, 2012; Zhang et al., 2013). Since the 1950s, dam construction has had a far-reaching impact on the aquatic ecosystem. Currently, only Poyang Lake and Dongting Lake remain directly connected to the Yangtze River mainstem. The freshwater mussel diversity in these mainstem-connected lake habitats is higher than hydrologically disconnected and impounded lakes (Wu et al., 2000; Shu et al., 2009).

The damming of rivers not only affects the function of aquatic ecosystem, but also affects biodiversity at all scales by changing community composition at the species and possibly even genetic level (Hoffman, Willoughby, Swanson, Pangle, Zanatta, 2017). Dam-induced changes in water depth, water flow, sediment composition and temperature have been shown to cause decline in benthic density, block migration routes of some fishes, which can in-turn affect mussel dispersal, as well as alter mussel habitat directly (Geist & Auerswald, 2007; Mueller, Pander, & Geist, 2011). In general, dams typically promote lentic or generalist taxa and reduce or eliminate lotic species (Burlakova et al., 2011; Mueller et al., 2011). Increased sedimentation and decreased sediment porosity upstream of dams is particularly harmful to rheophilic mussel species - directly by increasing juvenile mortality (Geist & Auerswald, 2007; Osterling, Arvidsson, & Greenberg, 2010) and indirectly by reducing hatching rates of hosts (Sternecker & Geist, 2010; Sternecker, Cowley, & Geist, 2013). Changes to thermal regimes as a result of dams can have strong effects on fish communities, on the reproductive success of freshwater mussels (Heinricher & Layzer, 1999), as well as the timing and successful development of mussel larvae on their hosts (Taeubert, El-Nobi, & Geist, 2014).

Loss of access to hosts

The diversity of freshwater fish species plays an important role in determining the diversity of freshwater mussels resulting from the mussels' parasitic life cycle (Cao et al., 2018; Lopes-Lima et al., 2017). Driven by commercial interests, overfishing has resulted in a sharp decline in fin fish resources in the region (Xie, 2017). The harvesting of host fish laden with encysted glochidia likely has detrimental effects on the reproduction, distribution of freshwater mussels across the region and dispersal among tributaries and the Yangtze River mainstem.

Overharvest of mussels

Freshwater mussels from the middle and lower Yangtze are used for human and livestock food, and shells are used for making buttons, shell inlay, beads, and pearls and thus have high economic value (Xiong et al., 2012; Zhang et al., 2013). Since the middle of the 19th century, a large-scale harvest for button manufacturing and pearl farming in the region has persisted. For example, in 1960, the annual harvest of mussels from Poyang Lake and Dongting Lake exceeded 4000 t and 2000 t, respectively (Wu et al., 2000; Xiong et al., 2012). This excessive exploitation and utilization leads to a serious decline in mussel populations. Many species of freshwater mussels are slow to reach sexual maturity and are long-lived, making it difficult for them to recover from exploitation.

Recommendations for conservation and management

(1) Habitat protection

Habitat degradation and destruction has been identified as one of the primary reasons for the decline of freshwater mussels (Wu et al., 2000; Bogan, 2008; Haag, 2012; Zieritz et al., 2018b). Thus, in order to reduce the impact of human activity imposed on mussel habitats, conservation refuges should be delineated in areas with dense and diverse mussel assemblages and/or high priority species. Also, the construction of dams and related structures that alter water flow and sediment mining should be limited or prohibited and dam removals encouraged where possible to restore natural flow-regimes. In addition, remediation procedures and prevention of continued and future industrial waste, agricultural runoff, and sanitary sewage are needed.

(2) Increased emphasis on life-history and reproductive biology research

Lack of information on host fish identities and reproductive timing is currently restricting conservation assessments and conservation actions for freshwater mussels in China. In addition, development of meaningful conservation actions of threatened species will require collection of data on their population dynamics, population structure, and geographical distribution.

(3) Restrictions on mussel and host fish harvesting during key reproductive periods

Commercial harvest has the potential to cause rapid decline of both freshwater mussels and their host fish. The following actions should be taken: strengthen the management and impose restrictions on commercial fishing operators and vessels, standardize the use of fishing gear, and limit fin fish and mussel harvest to time periods outside of spawning and parasitic stages for the highest priority species.

(4) Establish propagation programs

Since natural populations of many of the threatened and high priority species of freshwater mussels in the middle and lower Yangtze River drainage are rapidly declining, it may become necessary to establish populations in laboratories and hatcheries. The establishment of facilities and protocols for the artificial propagation raising of mussels has been successful in many parts of Europe, North America and Southeast Asia (Geist, 2011; Haag, 2012; Lima et al., 2012). Hatchery-maintained or propagated populations can be used to avoid extirpations and or extinctions until natural habitat conditions are remediated and threats are mitigated.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article: Appendix 1 to Appendix 13.

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Table 1. Evaluation criteria for scoring the nine conservation indices developed in the current study for each of 69 freshwater mussel species recorded from the middle and lower reaches of the Yangtze River. Raw data and data sources for each index can be found in Appendices 2 to 12.

Index	0 point	1 points	2 points
Distribution frequency (C1)	Present at ＞45% of the 28 river/lake basins (Appendix 1 and 2)	Present at ＞15% and <45% of the 28 river/lake basins (Appendix 1 and 2)	Present at <15% of the 28 river/lake basins (Appendix 1 and 2)
Population status and trends (C2)	Increasing population size and large number of juveniles entering cohort	Stable populations with evidence of recruitment and normal distribution of ages	Decreasing population size with no evidence of recent recruitment and age structure skewed toward old adults
Endemism (C3)	Species widely distributed globally	Species endemic to China	Species endemic to Yangtze basin
Fecundity (C4)	High fecundity	Medium fecundity	Low fecundity
Reproductive period (C5)	At least 3 months of the parasitic larval period occur within the closed fishing season	1-2 months of the parasitic larval period occur within the closed fishing season	Parasitic larval period occurs fully outside the closed fishing season
Habitat/substrate preference (C6)	Can live in a wide range of substrates and habitats (including mud, silt and sand)	Can live in a moderate range of substrates and habitats (e.g. mud and silt)	Can live only in restricted habitat and substrate types (e.g. restricted to hard mud or coarse gravel substrate)

Drought resistance (C7)	Strong drought resistance due to thick shell and/or large maximum size	Medium drought resistance due to medium shell thickness and size	Weak drought resistance due to thin shell and/or small maximum size
Economic value (C8)	Low economic value, low value as food source	High economic value, low value as food source	High economic value, high value as food source
Propagation (C9)	Successful artificial reproduction ongoing	Research on artificial reproduction ongoing	No artificial reproduction or research on this ongoing

Table 2. Partition criteria of Conservation priority coefficients to Conservation priority ranks of freshwater mussels in the middle and lower reaches of the Yangtze River.

Conservation priority coefficient interval	Conservation priority rank
≥9.00	First Priority
7.00-8.99	Second Priority
5.00-6.99	Third Priority
＜5.00	Least Priority

Table 3. Conservation status and conservation priority coefficients/ranks for the 69 freshwater mussels recorded from the middle and lower reaches of the Yangtze River as determined by different methods. Abbreviations: CR: Critically Endangered; DD, Data Deficient; EN: Endangered; LC, Least Concern; NA, not assessed; NT, Near Threatened; t: threatened (= CR, EN and VU); VU, Vulnerable

Species	IUCN Global conservation status	Regional conservation status based on Shu et al. (2009)	Regional conservation status based on IUCN criteria 2019 (this study)	Conservation priority coefficient	Conservation priority rank
Unionidae					
Unioninae					
Aculamprotula fibrosa	LC	NT	VU	7.64	Second Priority
Aculamprotula nodulosa	NA	NA	EN	NA	NA
Aculamprotula scripta	NA	NA	VU	7.22	Second Priority
Aculamprotula tientsinensis	DD	t	VU	6.81	Third Priority
Aculamprotula tortuosa	VU	t	VU	6.81	Third Priority
Aculamprotula zonata	DD	t	VU	6.81	Third Priority
Acuticosta chinensis	LC	NT	LC	4.03	Least Priority
Acuticosta jianghanensis	NA	NA	DD	NA	NA
Acuticosta ovata	LC	NT	LC	5.00	Third Priority

Acuticosta retiaria	NA	NA	VU	5.69	Third Priority
Acuticosta sichuanica	NA	NA	DD	NA	NA
Acuticosta trisulcata	NA	NA	VU	5.69	Third Priority
Cuneopsis captiata	LC	t	LC	5.42	Third Priority
Cuneopsis celtiformis	LC	NA	VU	5.42	Third Priority
Cuneopsis heudei	LC	t	LC	4.86	Least Priority
Cuneopsis kiangsiensis	NA	NA	DD	7.08	Second Priority
Cuneopsis pisciculus	LC	t	LC	5.42	Third Priority
Cuneopsis rufescens	VU	t	VU	6.53	Third Priority
Diaurora aurorea	NA	t	VU	NA	NA
Lepidodesma aligera	NA	NA	VU	NA	NA
Lepidodesma languilati	DD	t	NT	5.00	Third Priority
Nodularia douglasiae	LC	LC	LC	2.08	Least Priority
Nodularia persculpta	NA	NA	DD	NA	NA
Ptychorhynchus murinum	NA	NA	DD	NA	NA
Ptychorhynchus pfisteri	NT	t	VU	5.42	Third Priority

Ptychorhynchus schomburgianum	NA	NA	DD	NA	NA
Schistodesmus lampreyanus	LC	t	LC	3.61	Least Priority
Schistodesmus spinosus	LC	t	NT	4.58	Least Priority
Parreysiinae					
Lamellidens liuovatus	NA	NA	DD	NA	NA
Anodontinae					
Anemina arcaeformis	LC	LC	LC	4.17	Least Priority
Anemina euscaphys	DD	t	VU	5.42	Third Priority
Anemina fluminea	LC	NA	LC	5.00	Third Priority
Anemina globosula	NA	NA	VU	5.42	Third Priority
Cristaria plicata	DD	LC	LC	3.89	Least Priority
Cristaria radiata	NA	NA	DD	NA	NA
Lanceolaria eucylindrica	DD	t	VU	5.42	Third Priority
Lanceolaria gladiola	LC	t	LC	4.72	Least Priority
Lancelaria grayii	NA	NT	LC	4.31	Least Priority
Lanceolaria lanceolata	LC	NT	NT	4.44	Least Priority

Lanceolaria oxyrhyncha	NA	NA	DD	NA	NA
Lanceolaria triformis	DD	NA	VU	5.42	Third Priority
Lanceolaria yueyingae	NA	NA	DD	NA	NA
Pletholophus tenuis	NA	NA	LC	NA	NA
Sinanodonta angula	NA	NT	NT	5.42	Third Priority
Sinanodonta lucida	NA	NT	LC	4.86	Least Priority
Sinanodonta qingyuani	NA	NA	DD	NA	NA
Sinanodonta woodiana	LC	LC	LC	2.50	Least Priority
Gonideinae					
Lamprotula bazini	DD	NA	EN	6.25	Third Priority
Lamprotula caveata	LC	LC	LC	3.06	Least Priority
Lamprotula chiai	NA	NA	DD	NA	NA
Lamprotula cornuumlunae	NA	t	VU	5.42	Third Priority
Lamprotula elongata	NA	NA	EN	NA	NA
Lamprotula gottschei	NA	NA	EN	NA	NA
Lamprotula kouangensis	NA	NA	DD	NA	NA
Lamprotula leaii	LC	t	LC	3.75	Least Priority

Lamprotula microsticta	VU	t	EN	6.81	Third Priority
Lamprotula paschalis	NA	NA	EN	NA	NA
Lamprotula triclava	CE	NA	EN	7.36	Second Priority
Pseudodon aureus	NA	NA	DD	NA	NA
Pseudodon nankingensis	NA	NA	DD	NA	NA
Pseudodon pinchoniana	NA	NA	DD	NA	NA
Pseudodon secundus	NA	NA	EN	NA	NA
Sinohyriopsis cumingii	LC	LC	LC	3.47	Least Priority
Solenaia carinata	NA	NA	EN	9.58	First Priority
Solenaia oleivora	NA	t	VU	6.11	Third Priority
Solenaia rivularis	NA	NA	EN	NA	NA
Solenaia triangularis	NA	NA	EN	NA	NA
Margaritiferidae					
Gibbosula polysticta	NA	t	VU	7.64	Second Priority
Gibbosula rochechouartii	VU	t	VU	6.81	Third Priority

Figure Captions:

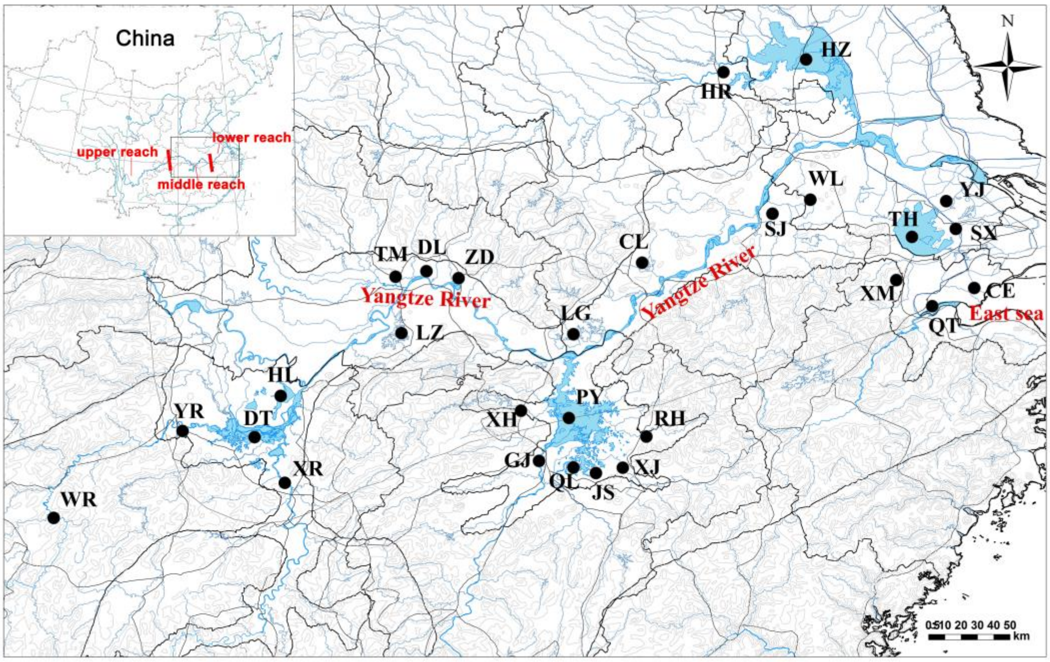

Figure 1. The study area comprising the middle and lower reaches of the Yangtze River, China. Abbreviations: CE, Caoe River; CH, Chaohu Lake; DL, Dong Lake; DT, Dongting Lake; GJ, Ganjiang River; HL, Hong Lake; HR, Huai River; HZ, Hongze Lake; JS, Junshan Lake; LG, Longgan Lake; LZ, Liangzi Lake; PY, Poyang Lake; QL, Qinglan Lake; QT, Qiantang River; RH, Raohe River; SJ, Shijiu Lake; SX, Shaoxi River; TH, Taihu Lake; TM, Tianmen River; WL, Wu Lake; WR, Wujiang River; XH, Xiuhe River; XJ, Xingjiang River; XM, Xiaomei River; XR, Xiang River; YJ, Yongjiang River; YR, Yuan River; ZD, Zhangdu Lake.