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INVASION NOTE

What's coming eventually comes: a follow-up on an invader's spread by the world's largest water diversion in China

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Abstract Zhan et al. (Biological Invasions, 2015, 17:3073–3080) stressed that China's South-to-North Water Transfer Project (SNWTP)—the world's largest constructed water diversion—could create an invasion highway by facilitating spread of non-native species, including invasive golden mussel *Limnoperna fortunei*. However, most available literature indicated that golden mussels could not survive the cold winter in Northern China. We proposed that phenotypic plasticity and rapid environmental adaptation, combined with relatively high water temperature derived from wastewater treatment plant effluents and a large potential inoculum continuously transported from southern source populations, could jointly contribute to golden mussel spread into northern locations. We conducted surveillance for the species both before and after the waterway was opened in late 2014 in the diversion destination—Beijing. While all surveys in the whole area were negative between 2014 and 2018, we detected rapid geographical expansions in 2019–2021 across multiple waterbodies based on traditional field surveys and environmental DNA (eDNA)-based methods. Surprisingly, we subsequently observed populations that had successfully survived a cold winter in Beijing. The SNWTP may facilitate further spread of cold-adapted populations, placing high-latitude areas at risk. This case study highlights the need for robust scientific assessment and management to predict and mitigate non-native species' distributional changes that may accompany large-scale hydraulic projects.

Keywords Invasive species · Water diversion · Hydraulic project · Golden mussel (*Limnoperna fortunei*) · Early detection · Eradication · Environmental DNA

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Water scarcity has become a serious world-wide problem (United Nations water scarcity at http://www.un.org/waterforlifedecade/scarcity.shtml), and it is particularly acute in Northern China (Zhan et al. 2015). In order to alleviate water shortage in megacities in China such as Beijing and Tianjin, the South-to-North Water Transfer Project (SNWTP)—the world's largest water diversion—was launched on December 12th, 2014. This project has improved the availability and distribution of water resources in Northern China, thus providing support for rapid and sustainable social and economic development, particularly for the Beijing-Tianjin-Hebei Metropolitan region. Thus far, SNWTP has diverted more than 53 billion m^3 of water to Northern China, of which 8.5 billion m^3 and 5 billion m^3 were used for ecological water compensation in more than 50 rivers/streams and aquifers, respectively. More importantly, the SNWTP serves as the major drinking water resource for > 140 million people in more than 280 counties/cities (all data above from reports from SNWTP office at http://nsbd.mwr.gov.cn/).

As the SNWTP was nearing completion, we opined that an "invasion highway" could be created by linking different biogeographic regions, inevitably resulting in extremely rapid transportation and subsequent colonization by an array of invaders from Southern to Northern China (Zhan et al. 2015). Specifically, we predicted that the golden mussel *Limnoperna fortunei*, which is a notorious mollusc native to the Pear River basin and middle-low reaches of the Yangtze River, would rapidly colonize and negatively affect human-created water diversion channels and natural habitats in downstream areas, notably in the biggest water recipient area and also diversion destination—Beijing. This mussel species is one of the world's worst biofouling species in aquatic ecosystems, causing significant changes to ecosystem properties and industrial development (see Boltovskoy 2015). We used this mussel species as an example of unintended and unexpected consequences that might accompany large-scale water diversion projects to call on governments to conduct risk assessments prior to initiating such projects (Zhan et al. 2015).

It was believed that the golden mussel cannot survive the cold weather in winter in Northern China, particularly in Beijing, based on reports in available literature—a minimum water temperature of ~ 16–17 °C for reproduction and largely increased mortality rate at < 5 °C, as well as known geographical distributions of tropical and subtropical regions (see references in Boltovskoy 2015 and Xia et al. 2021). However, water supply to a majority of waterbodies in Beijing, Tianjin, and many other cities in Northern China (i.e., arid and semi-arid areas) is unique, as nonconventional water sources predominate, such as effluents from wastewater treatment plants (see data at Beijing Water Authority at http://swj.beijing.gov.cn/). As a result, water temperature is typically > 5 °C higher than that in natural water bodies, particularly during winters (personal observations). In addition, the transport of large numbers of propagules of southern populations in SNWTP flow (average of 4 million m^3 daily) provides invasion opportunities in recipient areas including Beijing. Indeed, soon after the SNWTP started, a large number of propagules, including adults, juveniles, and larvae, have been detected to migrate and settle down along the water diversion channels, and some rapid invasions are not limited in SNWTP but also other water diversion projects in China (e.g., Xu et al. 2015).

In addition, we proposed that interactions between biological characteristics and local environments might contribute to golden mussels' invasiveness and range extensions. While we lacked direct evidence at the time we proposed the possibility of phenotypic plasticity contributing to local environmental adaptation and winter survival, subsequent field studies in Beijing supported this hypothesis. For example, we found that populations could successfully survive in the wild in winter for 6 days at < 1 °C, 41 days at < 2 °C, and 108 days at < 5 °C, with 27% survival overall (Xia et al. 2021). Thus, SNWTP provided an opportunity for selection of populations thermally-adapted to cold. Species distribution modelling has illustrated possible survival and range expansions in mid-latitude regions, including the Laurentian Great Lakes (Xia et al. 2021).

Owing to the strong ecological effects associated with golden mussels elsewhere (e.g., Zhan et al. 2012; Xia et al. 2021 and references therein), in 2014 our research group initialized intensive routine surveillance (three times annually, including winter) in streams, rivers, and reservoirs in Beijing. Briefly, the routine surveillance included the collection and identification of all fauna and flora such as benthos and plankton, as well as 26 water chemistry factors such as temperature and eutrophication/pollution index. We did not identify invaded locations between 2014 and 2018 but detected established populations at four sites in 2019 (Fig. 1). As colonizing species usually have a lag time to reach a detectable population density, it is possible that successful colonization occurred earlier. As traditional methods (benthic sampling, plankton sampling for veligers, questionnaires of workers on vulnerable waterbodies) have low detection probabilities when populations are very small (Harvey et al. 2009; Xiong et al. 2016), we then developed and applied environmental DNA (eDNA)-based surveys (Xia et al. 2018) in 2020 and 2021. As expected, we detected more positive sites—from 4 in 2019 (using non-genetic methods) to 18 in 2020 and 30 in 2021 (Fig. 1). Generally, golden mussels were detected early from water recipient and surrounding areas in Beijing and subsequently spread further along rivers/streams (Fig. 1). All positive sites were confirmed by subsequent surveys, including eDNA-based surveys in winter. Such a finding illustrates that golden mussels have likely formed small but established populations at those new sites and confirm overwintering in the wild in Beijing. Subsequently, we found well-established populations at six sites with a population density of 50–100 individuals/m^2 (Fig. 1). Based on these surveys, the established populations could reach the detectable level using traditional field surveys soon after (usually 1–2 years) these sites were detected positive in eDNA-based detection. The patterns suggest that golden mussels have adapted well to the environments in Beijing, and that local spread may be more rapid than expected and the lag time may become shorter before newly established populations outbreak. So far, golden mussels have spread to all five drainages in Beijing, including Yongding, Chaobai, Beiyun, Daqing, and Jiyun Rivers (Fig. 1). We predict that additional local spread is likely in Beijing and beyond, as natural dispersal in

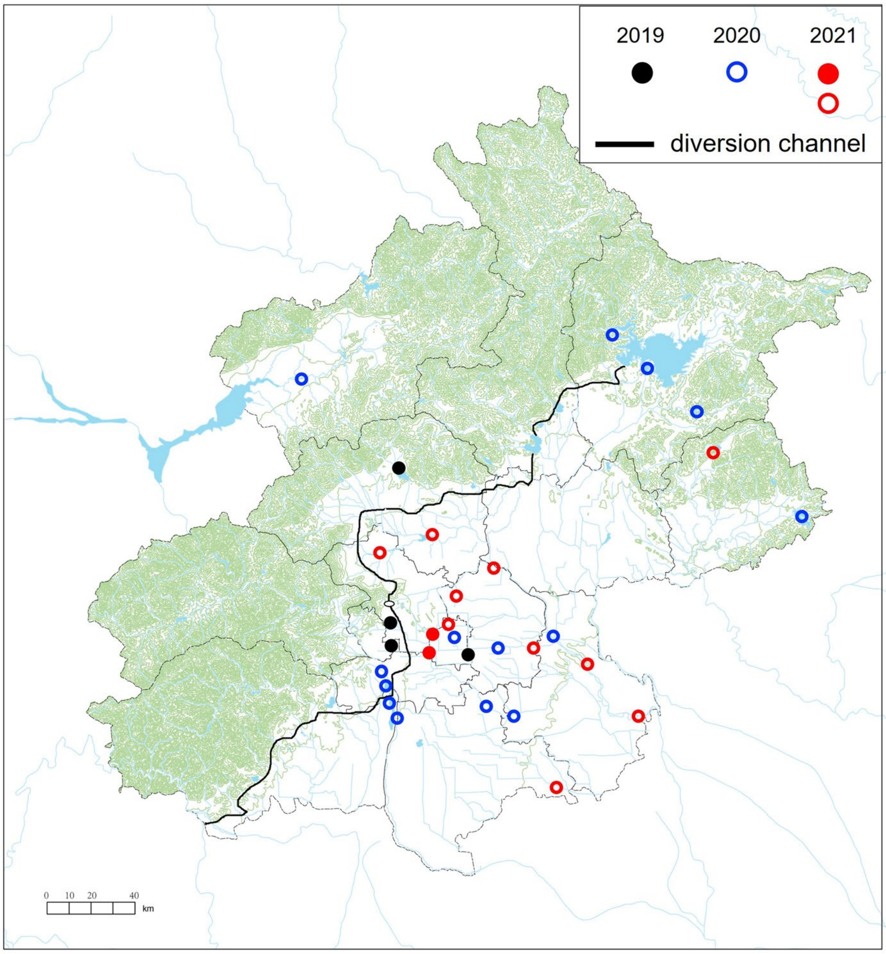

Fig. 1 Locations colonized by the highly invasive golden mussel, *Limnoperna fortunei* in Beijing, China. Solid circles are surveillance sites confirmed by both environmental DNA (eDNA)-based method and traditional field surveys, while open circles denote positive signals by eDNA only

water currents and fellow travelers with animals cannot be easily interrupted and stopped.

It is well-known that the management of invasive species is most effective and economical at early stages of invasions. Unfortunately, precautions were not implemented after we raised concerns prior to opening of the SNWTP invasion highway that began in Danjiankou Reservoir in the south. Still, based on the "better late than never" management philosophy, we propose that preventative measures be taken in vulnerable areas. When compared with traditional field surveys, the use of newly developed eDNA-based methods can successfully detect mussel presence at the earliest stage of invasions (limit of detection: 1×10^{-7} ng/uL, Xia et al. 2018). Our improved Taqman probe-based, real-time, quantitative PCR assay has decreased this detection limit further to 50 copies/uL (Chinese patent: CN202010943818.2). The high sensitivity of eDNA-based methods provides the best estimate of current distribution and allows managers to consider control options (e.g., eradication) when populations in new areas are very low. A variety of eradication strategies have been developed (see references in Boltovskoy 2015), including biological (e.g., predation), physical (e.g., antifouling materials and coatings, ultraviolet light), and chemical (e.g., oxidizing chemicals) methods. Recently, we found that negatively-charged polyethylene glycol-coated Fe_3O_4-nanoparticles could significantly down-regulate the expression of an essential protein in byssus (foot protein 2) and energy-related metabolic pathways, thus inhibiting byssus production, reducing plaque size, and weakening byssus performance (Li et al. 2021). The development of new antifouling strategies based on recoverable magnetic nanoparticles from the environment provides new opportunities to effectively eradicate colonizing golden mussels, particularly in man-made structures such as critical water diversion channels.

In addition to golden mussels, several other species have been observed to quickly spread through the SNWTP and colonize local waterbodies, including fish (e.g., *Taenioides cirratus*, *Tridentiger bifasciatus*) (Guo et al. 2020), molluscs (e.g., *Radix ovate*, *Anodonta globosula*, *Assiminea lutea*) (Yu et al. 2020), and highly invasive aquatic plants (e.g., *Alternanthera philoxeroides*, *Eichhornia crassipes*, *Cabomba caroliniana*) (Liu et al. 2017; personal observations). It should be noted that the number of known dispersing species is limited by the relatively low research effort devoted to this issue. We propose that a systematic and comprehensive survey be conducted to identify the full complement of species currently spreading through the SNWTP.

Lessons from the SNWTP:

1. Inland water diversions open an invasion highway facilitating spread of an array of invaders that strongly parallels major shipping-based canals (e.g., Suez, Panama, Don-Volga). Inland canals may prove particularly troublesome when they span different biogeographic regions, as with SNWTP.
2. Water diversions may open ecological and evolutionary highways by requiring extreme-environment-adapted populations for survival in new regions. Such evolutionary change can in turn push invasion fronts forward very quickly.
3. Management of non-native species is crucial both before and after the opening of water diversion projects. Otherwise, benefits from water diversion will be offset by ecological surprises associated with spreading invaders.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by HW, ZX, SL, and AZ. The first draft of the manuscript was written by HW, HJM, and AZ, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

Conflict of interest The author declare that they have no competing interest.

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