

Golden mussel (*Limnoperna fortunei*) survival during winter at the northern invasion front implies a potential high-latitude distribution

Zhiqiang Xia^{1,2}  | Justin R. Barker¹  | Aibin Zhan^{2,3}  | Gordon Douglas Haffner¹ | Hugh J. MacIsaac^{1,4}

¹Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada

²Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

³University of Chinese Academy of Sciences, Beijing, China

⁴School of Ecology and Environmental Science, Yunnan University, Kunming, China

Correspondence

Zhiqiang Xia, Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON N9B 3P4, Canada.
Email: xiab@uwindsor.ca

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Abstract

Aim: Golden mussel *Limnoperna fortunei* is an invasive bivalve in many freshwater ecosystems in Asia and South America. Cold winter temperatures are expected to restrict its spread to high-latitude areas. Cold tolerance and potential distribution of this species remain largely unstudied because the most extensively studied populations occur in tropical and sub-tropical areas. We sought to investigate cold tolerance of golden mussels and to model their potential distribution at higher latitudes.

Location: China, Global.

Methods: We investigated overwintering survival of caged golden mussels in a reservoir located at the northern invasion front in north China. We then determined the lowest water temperature at which mussel filtering occurred in laboratory. Finally, we modelled relative environmental suitability globally based on Maximum Entropy using the species' most updated occurrence records.

Results: Golden mussels in a northern invasion front reservoir could survive over a course of 6 days at <1°C, or 41 days at <2°C, or 108 days at <5°C, with 27% survival overall. Caged mussels were inaccessible to local predators and reproduced, with the subsequent population size increasing in early summer by ~280%, representing a potential source population. Laboratory tests demonstrated that the lowest water temperature at which mussels could filter water was 5.5°C, and 50% of individuals became active when temperature rose to 7.5–8.0°C. Species distribution modelling illustrated a potential distribution of golden mussels at higher latitude than presently found. Models that considered updated high-latitude occurrence records predicted a significantly larger suitable area than currently exists, including near the lower Laurentian Great Lakes.

Main conclusions: Our findings suggest enhanced cold tolerance of golden mussels and wider potential distribution than currently exists. We emphasize the importance of examining samples from invasion fronts when developing distribution predictions for spreading invasive species.

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KEY WORDS

cold tolerance, invasion front, *Limnoperna fortunei*, low water temperature, overwintering survival, species distribution modelling, thermal heterogeneity

1 | INTRODUCTION

Species invasions represent a critical driver of ecological change around the globe (Liu et al., 2017; Melotto et al., 2020) and often cause tremendous economic losses (Wan & Yang, 2016). Preventing invasions is more cost-effective than post-invasion management, but this requires detailed knowledge of introduction pathways and environmental tolerance (Kramer et al., 2017; Reaser et al., 2020; Xia, Johansson, et al., 2018). Aside from dispersal constraints, local environmental conditions often serve as key barriers to establishment of newly introduced non-indigenous species (NIS), with highest success occurring in areas that exhibit environmental similarity with native habitats (Kramer et al., 2017; Petsch et al., 2020). For example, temperature is directly linked to species survival and physiological performance (Karanova & Gakhova, 2007), and represents a critical factor constraining potential distribution for a wide variety of invasive species including fish (Van Zuiden et al., 2016), aquatic invertebrates (Churchill et al., 2017; Zhao et al., 2019) and terrestrial insects (Formby et al., 2018).

The potential distribution of a NIS can be estimated through knowledge of its dispersal vectors and environmental tolerance (Kramer et al., 2017; McGarvey et al., 2018; Petsch et al., 2020). Species distribution modelling, which combines occurrence records and associated environmental variables, represents a valuable method by which to identify ranges with suitable environmental conditions (e.g. Hattab et al., 2017; Pearson et al., 2007). Despite being routinely used, species distribution models (SDM) have some critical caveats in predicting possible range of an invading species. For example, predicting suitable habitats for a rapidly spreading NIS is often challenging as a result of temporary dispersal constraints (i.e. not all suitable environments are colonized yet) (Kramer et al., 2017) or merely owing to sample bias (i.e. species are not recorded in all environments in which they occur; Stolar & Nielson, 2015). Hence, newly identified occurrence records, especially those from distinct habitats, may greatly influence the performance of SDM in predicting the potential distribution of NIS by increasing the sample size and expanding the range of environmental tolerance.

The freshwater bivalve golden mussel *Limnoperna fortunei* is considered to be native to South and Southeast Asia. It has widely expanded its distribution to include neighbouring regions in Asia (since the 1960s) and South America (beginning in the early 1990s), predominantly through inland water diversions and discharge of ships' ballast water (Boltovskoy, 2015; Ricciardi, 1998; Zhao et al., 2019). Golden mussels cause severe fouling problems in municipal water supply systems (Ricciardi, 1998; Xu et al., 2013; Zhao et al., 2019) and serve as "ecosystem engineers" that profoundly impact invaded ecosystems (Boltovskoy, 2015; Ricciardi, 1998). Recently, poleward expansion of this species—from either native or invasive ranges—has

raised increasing concerns, especially under a scenario of global warming combined with the emergence of new introduction pathways (e.g. new international shipping routes and inland water diversion projects) (Kramer et al., 2017; Mackie & Brinsmead, 2017; Petsch et al., 2020; Xia et al., 2020; Zhan et al., 2015). As an example, the recently opened South to North Water Diversion Project will likely facilitate the dispersal of the species to northern from southern China because the source reservoir is inhabited by the species (Xia, Zhan, et al., 2018; Zhan et al., 2015; Zhao et al., 2019).

Golden mussels exhibit wide tolerance to many environmental factors such as pH, dissolved oxygen, calcium concentration, conductivity and ammonia concentration (Boltovskoy, 2015; Liu et al., 2020; Ricciardi, 1998). However, low water temperature is expected to restrict distribution of golden mussels in high-latitude areas by affecting reproduction, filtering rates, growth rates and overwintering survival (Boltovskoy, 2015; Oliveira et al., 2010; Ricciardi, 1998; Tagliarolo et al., 2016; Zhao et al., 2019). Field surveys indicate that golden mussels require a minimum water temperature of ~16–17°C to reproduce (e.g. Choi & Shin, 1985; Xu et al., 2013), which is commonly observed during warm months in many vulnerable but not yet invaded water bodies in northern China and elsewhere (e.g. Zhao et al., 2019). A laboratory-based study revealed that filtering activities and survival rate of golden mussels declined dramatically when water temperature was <10 and <5°C, respectively (Oliveira et al., 2010), suggesting that cold winter conditions could potentially regulate the spatial distribution of the species. However, the most intensively studied populations occur in waters that seldom reach the species' cold limit, thereby increasing the possibility of underestimating potential range of the species. In Asia, the golden mussel has been found in Lake Paldang, South Korea, where minimum surface water temperature is ~0°C; however, detailed information such as the duration of exposure to very low temperature remains unknown (Choi & Shin, 1985). In addition, Lake Paldang is part of a complex water system, and understanding the cold tolerance of golden mussels in such a system is challenged by considering only the presence of larvae in warm months as evidence of overwintering survival because free-swimming larvae may have originated from advective transport from contiguous locations. Therefore, investigation of cold tolerance of golden mussels using cold-adapted (i.e. northern) populations is needed to estimate the potential distribution and to inform management of this nuisance species.

Several recent studies have attempted to predict environmentally suitable range for the golden mussel, particularly in mid-latitude areas like the North American Mississippi River systems and Laurentian Great Lakes region, by directly comparing agreement of thermal conditions between present and possible target areas (Mackie & Brinsmead, 2017; Oliveira et al., 2010) or by conducting species distribution modelling (Campos et al., 2014; Kramer

et al., 2017; Petsch et al., 2020). These efforts contribute to our understanding of the potential distribution of the species; however, occurrence records considered in these studies were highly concentrated in South America and Southern China, where low water temperature was highly unlikely to serve as a limiting factor for the species. Such bias in occurrence records can compromise the efficacy of these efforts to predict potential distribution of this NIS (Kramer et al., 2017).

In this study, we conducted field and laboratory experiments to test overwintering survival and to determine the effect of water temperature on filtering activity of golden mussels collected from the Shisanling Reservoir, Northern China, respectively. The reservoir is the highest latitude water body known to support established populations of the species (Xia, Zhan, et al., 2018; Xu et al., 2013). We then modelled the potential range with suitable environmental conditions for the species on global and regional scales—with an emphasis on cold tolerance—by incorporating recent, higher latitude occurrence records in addition to older ones from mainly more tropical and temperate locations. In addition, we investigated the effects of including high-latitude occurrence records on predictions and model performance.

2 | METHODS

2.1 | Study area

Shisanling Reservoir (40°15'11"N, 116°15'53"E) is a small-to-medium size reservoir (~220 km² catchment area) located in the north suburb of Beijing, China. It was built in 1958, mainly for flood control and irrigation. The reservoir is located at upstream of Wenyu River (a tributary of Hai River) with intermittent inflow and flood discharge in the rainy season. There is no shipping traffic between the reservoir and other water bodies though it was once used for recreational swimming and fishing. The maximum depth exceeds 10 m, while the water level fluctuates by <1 m daily because this reservoir serves as the lower reservoir of a pumped-storage power plant (i.e. a type of hydro power plant; capacity: 800 MW) that can regulate water level. This hydro power plant may recirculate very limited amount of heated water from its cooling system back to the reservoir. The reservoir was invaded accidentally by golden mussels sometime after 1980, while the exact date and pathway are unknown (Xu et al., 2013). It is believed that their introduction was likely due to recreational activities or fisheries stock enhancement. We observed golden mussels in areas with hard substrates in the reservoir, while a large part of the reservoir's benthic environment was identified as unsuitable for colonization because of soft-bottom conditions (Figure 1; Xia et al., 2020; Xia, Johansson, et al., 2018; Zhan et al., 2015). The highest mussel density was ~20,000 individuals m⁻², which was observed on a submerged metal structure during a 2016 survey (Z. Xia, unpublished data). However, animals were much more sparsely distributed in natural habitats (e.g. rocks), and mussel clumps (i.e. druses) were rarely found.

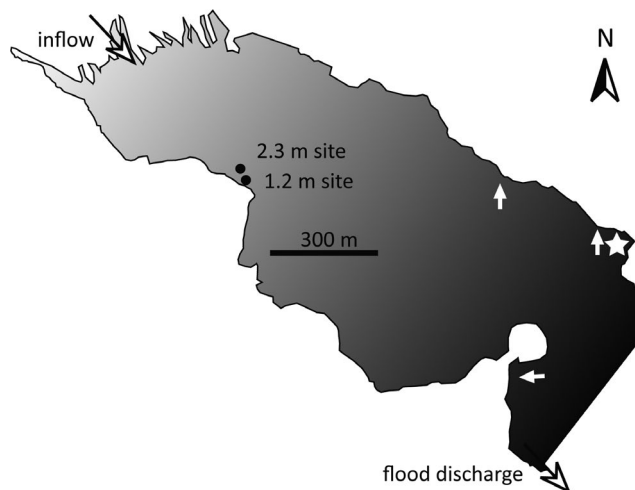


FIGURE 1 Map of experimental deployment sites (showing water depth) in Shisanling Reservoir, China. Water depth increases with shading, with the deepest locations >10 m. White arrows indicate areas where golden mussels have also been observed, and the white star indicates a pumped-storage power plant. Intermittent inflow and flood discharge are located at the northwest and southeast of the reservoir, respectively (open arrows)

2.2 | Experimental design

To test the overwintering survival of living golden mussels, we caged and deployed animals at varying depths; cages also served to eliminate potential predation. Specifically, rocks with attached golden mussels were collected and placed into six cages before being deployed back to the original area with different depths. Colonized rocks with suitable size (1–3 rocks per cage depending on rock size and mussel density) for caging were collected from ~1 m depth (Figure 1). This area was selected because its rocky bottom allowed us to deploy the experimental cages on the bottom without considerable accumulation of soft sediment which may impact mussel survival. Each steel cage was 40 × 25 × 20 cm (length × width × height) in dimension, with 5 mm mesh on the walls to prevent entry of potential predators (e.g. fish and crayfish) (Nakano et al., 2010), while allowing water to flow through and to retain golden mussels or their shells.

The number of animals on each rock was counted without separating them from the rock to keep animals intact and to minimize disturbance, and each rock was photographed before deployment. Exposure time of the animals in the air (i.e. animal counting and photographing) was <5 min. The bottom surface of rocks had more mussels than the upper side, consistent with observations by Nakano et al. (2010) and Xu et al. (2013, 2015), which remained unchanged when placed in the cage. A data logger (HOBO Water Temp Pro v2) was secured on the top (~10 cm vertically to animals) of each cage to record water temperature with a one-hour measurement interval. We deployed a total of six cages at sites at depths between ~1 and ~6 m; however, only two cages were successfully retrieved at the end of experiment.

Cage deployment was carried out on 14 July 2017 and retrieved on 26 June 2018. Daily minimum and maximum air temperature of the local area (Changping District, Beijing) was compiled from weather records (<http://www.tianqihoubao.com>) for the same period.

2.3 | Survivor identification and mussel size measurement

Following retrieval, cages were transported back to the laboratory in pre-chilled lake water, and the same side of the rock at deployment was photographed. Image pairs—before and after deployment—were carefully examined by eyes to identify surviving animals. Here, survivors were conservatively defined as those animals that retained their establishment spot and orientation on the rock. In addition, a presumed survivor was further confirmed if no old byssal threads existed underneath the mussel after we carefully detached it by cutting byssal threads. This method was used since we observed appreciable old byssal thread accumulation on the rock after mussel detached (i.e. died or moved, see examples in Figure S2). Following image comparison, all living mussels were carefully separated from the rock before they were counted and size (shell length: SL) measured to the nearest 0.01 mm using a digital caliper. We also counted all dead animals (i.e. empty shells) retained in the cage and sized each by measuring the right valve. Based on the size distribution of living animals, we were able to estimate their overwintering survival rate. Specifically, overwintering survivors were expected to reach a larger

SL than that of animals that died during winter or recruited following the winter because the former had a longer growth period than the latter (i.e. ~ one versus half year). Growth rates of golden mussel are positively related to water temperature (Nakano et al., 2010; Spaccesi, 2013; Xu et al., 2015). Previous studies have demonstrated that SL of newly recruited golden mussel could increase as much as 16 to >20 mm throughout a year, depending on water temperature (Table 1). In particular, the maximum SL of golden mussels in Lake Ohshio, Japan (~36.2°N), never exceeded 18 mm during a growth period slightly over 1 year (Nakano et al., 2011). From August to December, Shisanling Reservoir had a similar maximum but lower minimum water temperature than Lake Ohshio (Nakano et al., 2010; Table 1, Figure 2). The former also has a much higher latitude (i.e. with presumably lower water temperature) than the latter (40.3° vs. 36.2°N, Table 1); thus, we expected that mussels in the Shisanling Reservoir would have a slower growth rate than lower-latitude populations (Table 1). Therefore, we used a threshold of >18 mm SL to distinguish overwintering survivors from post-deployment recruitment in this study. This represented a conservative estimation of survival rate because we expected that it was unlikely that post-deployment recruitments, even for those established shortly following deployment, could exceed 18 mm during the presumed growth period (July 14–June 26) (Table 1). Similarly, according to the growth rate estimated for post-winter recruitment (see Results), we expected that mussels that died in winter should reach a minimum SL of 14 mm, representing the youngest individuals at deployment. Thus, we consider dead mussels with SL >14 mm to estimate the overwintering mortality rate.

TABLE 1 Summary of growth rates reported for golden mussels in literature. Records are ordered by latitude of locations

Habitat	Growth rate (SL)	Water temperature (°C)	Latitude	Reference
Xizhijiang River, China	Mean: 0.4–3.5 mm/month	16–30 (monthly average)	~23°N	Xu et al. (2015)
Bela Vista Reservoir, Brazil	Mean: 36 mm in 1.3 years	min. air temperature >16	~25.4°S	Belz et al. (2010)
Parana River, Argentina	20 mm in 1 year	12.9–26.5	~33.9°S	Boltovskoy and Cataldo (1999)
Río Santiago Reservoir, Argentina	<21 mm in 6.2 months (Jun–Dec)	13–26	~34.8°S	Darrigran et al. (2011)
Bagliardi Beach at Río de la Plata, Argentina	The first cohort: 8.1 mm in 0.74 year; or 10.4 mm in 0.9 year; or 11.8 mm in 1.12 years; or 15.8 mm in 1.5 years	14–24 (monthly average)	~34.9°S	Maroñas et al. (2003)
Bagliardi Beach and Punta Indio at Río de la Plata, Argentina	Mean: <20 mm in 1 year; Even for the earliest cohort, it is hard to reach 16 mm during the first half year	8.5–28.6	~34.9°S	Spaccesi (2013)
Lake Ohshio, Japan	<6 mm in 105 days	25–9 (Aug 30–Dec 12)	~36.2°N	Nakano et al. (2010)
Lake Ohshio, Japan	Max. <18 mm (very rare in 16–18 mm) and most are <16 mm in 12 months (Sep–Sep)	4.2–23.6 (8 m depth)	~36.2°N	Nakano et al. (2011)
Shisanling Reservoir, China	Min. 18 mm was adopted as the threshold for ~11.4 months growth period	0.1–31.0 (1.1–2.3 m depth): similar warmest but lower coldest than Lake Ohshio during the same period	~40.3°N	Present study

2.4 | Activities in cold water

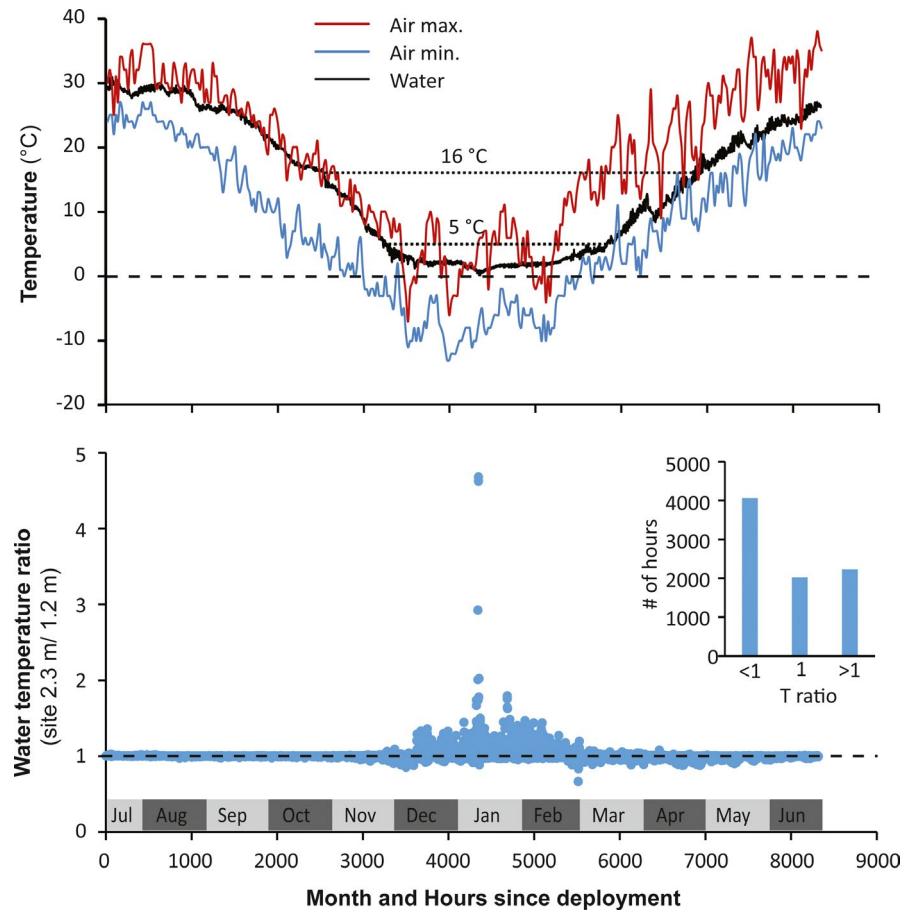
To determine the effect of temperature on golden mussel filtering, we examined the lowest water temperature at which mussels were active (i.e. filtering) by mimicking a natural water temperature increase from a point below which all mussels were inactive (i.e. non-filtering). Specifically, mussels were collected from the same area of the cage experiment and were raised under 24°C using well-aerated dechlorinated tap water for at least 1 week before the experiment. Mussels were fed with commercial fish food (i.e. concentrated culture of *Chlorella vulgaris*) during the experiment. Three mussel clumps consisting of 25, 25 and 27 individuals (mixed size), respectively, were then acclimated at 2°C (the lowest temperature our incubator can reliably achieve) to allow all mussels to become inactive before water temperature was gradually increased. Specifically, we placed each mussel clump in a 2-L beaker filled with original water and a thermometer to monitor exact water temperature, which was then manipulated to drop by 1°C per day from 16 to 10°C and 1°C per 2 days from 10 to 2°C. Each beaker was aerated by an air stone, and mussels were not fed throughout this process. We checked beakers daily to ensure that any dead mussels were removed. A beaker containing 30 mussels was set as a control, which was raised under the same settings but at room temperature (~25°C). After standing at 2°C for 2 days, each experimental beaker was moved out of the incubator to room temperature, allowing water temperature to increase

gradually, during which the number of active animals was identified by eyes with a 0.5°C interval. An active mussel was identified as one with valves gaped and siphon extended, which indicates water filtering (Xia et al., 2020). Mortality rate of each mussel clump during acclimation was compared with that in the control beaker by using a one-sample *t* test. Here we examined mussel activities in a warming (i.e. water temperature increasing) rather than a cooling (i.e. water temperature declining) process because a) our cooling system did not allow for observing mussels at fine temperature intervals (0.5°C) without interrupting the cooling process, and b) it was easier to observe a mussel became active from inactive (i.e. siphon extending) than vice versa.

2.5 | Species distribution modelling

We collated a total of 113 golden mussel occurrence records representing 1969 to 2020 from open databases after removal of duplicates and spatial thinning by 2.5 km (Global Biodiversity Information Facility, USGS Biodiversity Information Serving Our Nation, Fish Base, Berkeley Ecoinformatics Engine, iNaturalist, and Integrated Digitalized Biocollections). An additional 11 samples from either open database or literature, and all records were found in East Asia and South America. We assigned the former dataset as southern (113 records) and the latter as northern (11 records) records according to

FIGURE 2 Maximum and minimum air temperature (daily) of the study area and average water temperature (hourly) of the two sites where experimental cages deployed (Upper), and the water temperature ratio of 2.3 m site: 1.2 m site (Lower) during the cage experiment (July 14, 2017–Jun 26, 2018). The inset (lower panel) indicates the total number of hours during which the 2.3 m site had higher (>1), same (1) or lower (<1) water temperature relative to the 1.2 m site over an annual cycle (T Ratio). Dotted lines in upper panel indicate reproductive threshold (16°C) and cold limit (5°C), respectively (Oliveira et al., 2010). Inset: T ratio = temperature ratio of 2.3 to 1.2 m site. Broad horizontal dashed line indicates temperature of 0°C (Upper) or a T Ratio of 1 (Lower)



their geographical locations (Figure 5), and to our knowledge, the northern records have not been considered in any previous modelling. Specifically, northern records consist of seven localities in China, Japan and South Korea that were available in literature (Choi & Shin, 1985; Nakano et al., 2011; Xia, Johansson, et al., 2018; Xia, Zhan, et al., 2018) and four recorded in Global Biodiversity Information Facility.

For environmental predictors, we calculated all 19 bioclimatic variables in the “DISMO” R package (Hijmans et al., 2017) from 1969–2019 monthly WorldClim historical monthly temperature and precipitation values at a 2.5 km² resolution (Fick & Hijmans, 2017). Multicollinearity among predictors was assessed by a Spearman's correlation matrix. We transformed bioclimatic variables following Kramer et al. (2017) to reduce collinearity and improve model stability. The minimal temperature of the coldest month (BIO6) was selected to determine potential distribution relative to overwintering survival. Additional environmental variables were selected through an iterative removal of the lowest contributing variable of remaining non-correlated ($r < .7$) bioclimatic variables (Zeng et al., 2016), which resulted in the selection of annual precipitation (BIO12).

We implemented Maximum Entropy (MaxEnt) species distribution modelling v3.4.1 (Phillips et al., 2006). We considered model training with either the southern (S) or the southern and northern (SN) occurrence records, respectively, to explore whether inclusion of samples from high latitude affected model projection. Models were trained with a fivefold cross-validation of 113 occurrences from either S (S model) or SN (SN model) with 40 repetitions and 1,500 iterations. Specifically, SN training sets consisted of 102 randomly selected southern and all 11 northern occurrences to rule out potential impacts of sample size on model performance. Background points were restricted to areas accessible by golden mussels and were generated within a radius of 200 km from occurrences based on known dispersal range of golden mussels (Darrigran & Ezcurra de Drago, 2000; Darrigran & Pastorino, 1995) and similar species (Stoeckel et al., 1997) with respect to sampling bias. The sampling bias was determined through a target group sampling layer for all unique mollusc species records within a 200 km radius of included occurrences (Phillips et al., 2009). It was approximated by kernel density of records at a 2.5 km² resolution and restricted to water features as defined by the world water bodies and world linear water (Esri, 2011a, 2011b) for complete hydrographic coverage.

To improve predictions and limit overfitting or underfitting, we further tuned models regarding the regularization multiplier (0.5 to 5), the number of background points (100, 500, 1,000, 2,500, 5,000, 7,500, 10,000) and MaxEnt features classes (Merow et al., 2013) following Radosavljevic and Anderson (2014). We implemented all possible combinations of the three settings above. Models with the lowest average difference of area under the receiver operating curve (AUC) between training and testing (AUC_{Diff}) (Radosavljevic & Anderson, 2014), and the highest average AUC_{Test} of 40 repetitions for both training sets were selected. AUC is a threshold-independent measure of model performance based on true- and false-positive rates (i.e. sensitivity and 1-specificity), which measures

the probability that the model scores a random presence site a higher occurrence probability than a random site (Hanley & McNeil, 1982; Phillips et al., 2009). AUC_{Diff} minimizes the risk that a model is over-parameterized (i.e. overfitting) to the training data, such that a properly fit model will have equal training and testing AUC (i.e. $AUC_{Diff} = 0$; Warren & Seifert, 2011). Final models included a regularization multiplier of four, 1,000 background points, only quadratic and hinge feature classes, and all remaining default setting.

The effect of MaxEnt training with S or SN occurrences was determined by its ability to classify a testing occurrence set, which consisted of the excluded 11 SN occurrences per replicate to represent the entire known distribution. Model performance was assessed by AUC_{Test} , Boyce index and threshold-dependent minimal training omission rate (OR_{min}). The Boyce index details the average agreement between the predicted suitability and observed values, which ranges from -1 (no agreement) to 1 (perfect agreement), with values close to zero indicating that the prediction is no better than random as determined by the corresponding function in “ECOSPAT” R package (Boyce et al., 2002; Broennimann et al., 2018). A lowest presence threshold (i.e. no omission) of withheld training occurrences was applied to determine the presence/absence binary map following pilot comparisons with 10% omission (Pearson et al., 2007). OR_{min} is the percentage of testing points with relative suitability scores lower than the training point with the lowest predicted suitability score (Radosavljevic & Anderson, 2014). Higher values of OR_{min} indicate reduced predictive ability. Additionally, niche similarity between S and SN training projections were determined by Schoener's D (Schoener, 1968) and minimal predicted area (MPA) through the “ECOSPAT” R package (Broennimann et al., 2018). Schoener's D ranges from 0 to 1 with 0 indicating no similarity (i.e. no overlap) and 1 identical prediction (i.e. complete overlap) between the S and SN projections, respectively (Warren et al., 2010). MPA is the minimal surface obtained by considering all predicted cells with a relative suitability >0.7 which encompass 90% of known occurrences (Engler et al., 2004). Further, a Multivariate Environmental Similarity Surfaces (MESS) analysis was conducted to determine novel areas at risk for each training set (Elith et al., 2010). MaxEnt response curves were extracted and back-transformed to raw values for interpretation. Tests of model performance metrics and MPA values between training sets were conducted Mann-Whitney U test in R v4.0.2. We applied the selected model at both global and smaller regional scales. Specifically, we focused on East Asia and the North American Great Lakes region where the species has raised severe concerns.

3 | RESULTS

3.1 | Water temperature during cage experiment

Only two cages were successfully retrieved at the end of the experiment (Figure 1). A total of 8,321 hr were recorded with water temperature for each site. Water temperature ranged from 0.1 to 31.1°C and

from 0.1 to 30.9°C for 1.2 and 2.3 m deep sites, respectively, with an average of 0.1–31.0°C (Figure 2, Upper). In most instances, water temperature at the 2.3 m site was lower than (48.9%, 4,071 of 8,321 hr) or equal to (24.3%, 2,019 of 8,321 hr) that at 1.2 m site, except that in the coldest season when relatively higher water temperature was observed at the 2.3 m site (Figure 2, Lower & Inset). The two locations experienced a similar duration of water temperature <5°C (Figure S1), lasting 2,581 and 2,585 hr (i.e. ~108 days), respectively. However, the 1.2 m site experienced slightly more hours of extreme cold than that the 2.3 m site (e.g. 0–1°C: 149 vs. 129 hr; 1–2°C: 1,063 vs. 923 hr; Figure S1). As expected, water temperature fluctuated much less than air temperature during the experiment (Figure 2, Upper).

3.2 | Mussel survival and recruitment

Fifty-nine and 55 mussels were caged and deployed at the 1.2 and 2.3 m site, respectively, of which at least 1 and 11 were identified as overwintering survivors according to the before-after comparison (Figure S2), indicating that 10.5% (12 of 114) initial mussels survived the winter without displacement. SL of these 12 survived mussels ranged 16.8–31.2 mm and averaged 21.2 ± 0.4 mm (\pm SD). The abundance of living mussels in the two cages increased sharply (i.e. by 280%), and dead mussels were found at the end of experiment. Specifically, a total of 264 and 167 living mussels, and 47 and 23 dead animals were found within the experimental cages from the 1.2 and 2.3 m site, respectively (Figure 3a). The SL of living mussels ranged from <6 to 31 mm, which were dominated by young-of-year individuals (i.e. SL <12–14 mm) (Figure 3b,c). These mussels might be a combination of the earliest cohorts following winter and late cohorts after deployment (see Discussion). A total of 31 living (SL >18 mm) (Figure 3b,c) and 48 dead mussels (SL >14 mm) (Figure 3d,e) produced an overwintering survival rate of 27% (31 of 114 initial mussels) and a mortality rate of 42% (48 of 114), respectively.

3.3 | Mussel activities in cold water

$28.5 \pm 4.7\%$ (Mean \pm SD) of mussels died during the acclimation at 2°C, which was not significantly different from the control (30%, 9 of 30 mussels) ($t_2 = -0.58$, $p = .62$). The lowest water temperature at which mussels began to filter water was 5.5°C, and the percentage of active individuals increased rapidly with water temperature (Figure 4). 50% of mussels filtered water when temperature ranged between 7.5°C ($38.2 \pm 5.7\%$) and 8°C ($63.7 \pm 7.5\%$) before levelling off at 9°C and above (Figure 4).

3.4 | Species distribution modelling

Models exhibited excellent training performance with the AUC 0.89 and 0.88, and Boyce Index 0.81 and 0.96 for S and SN trained

models, respectively (Table 2). SN model performed significantly better than the S model for classification of testing locations ($W = 1,600$ – $5,200$, p -values <.01; Table 2; Figure S3). Predicted niches were highly overlapped between S and SN models with Schoener's D values of 0.94 ± 0.00 for global, North America and Asia extents. The projected range with suitable environmental conditions suggested a potential global distribution of the golden mussel, of which the south and southeast of North America, north and east of Australia, New Zealand, most central Africa and West Europe have no occurrences reported though they have medium to high suitability (Figure 5). The SN occurrence-calibrated model predicted more suitable areas than the S-calibrated model, with the MPA significantly larger for the former than latter model ($W = 1,600$, $p <.01$; Figure S4). Each calibration further demonstrated similar response curves (Figure S5). Peak relative suitability for minimum temperature of the coldest month was 4.6 and 4.8°C, while the minimal coldest temperature of no omission was -6.8 and -4.1 °C for SN and S occurrences, respectively (Figure S5a). At smaller scales, SN models projected slightly higher relative suitability at higher latitudes (Figure 6), particularly within the Laurentian Great Lakes (Figure 6c,d). Further, the MESS analysis illustrated increased global areas (Figure S6a) of environmental similarity at higher latitudes including the Laurentian Great Lakes (Figure S6b) and east Asia (Figure S6c) when the northern occurrences were considered.

4 | DISCUSSION

Low water temperature has been suggested as a critical environmental factor that might restrict the expansion of golden mussels to higher latitudes (Kramer et al., 2017; Oliveira et al., 2010; Ricciardi, 1998). Shisanling Reservoir (40°15'11"N, 116°15'53"E) represents the first location beyond the 40th parallel N that supports introduced golden mussel populations (Xu et al., 2013). This population occurs much farther north than previously reported (e.g. Lake Paldang, South Korea: 37.5°N; Lake Ohshio, Japan: 36.2°N). The water temperature recorded in this reservoir was lower than that in other relatively high-latitude systems inhabited by the species as well (e.g. Choi & Shin, 1985; Nakano et al., 2011; Table 1). These findings provide direct evidence that golden mussels can tolerate chronic exposure to low water temperature in situ. Using a population from the Paraguay River (Brazil), Oliveira et al. (2010) found that golden mussels reached 100% mortality after 38 days at 5–7°C and suggested that 5°C was a critical lower threshold for extended (i.e. weeks to months) survival in winter. This threshold (5°C) was subsequently used to estimate their distribution (Mackie & Brinsmead, 2017; Oliveira et al., 2010). In our study, however, golden mussels from both sites lived for more than 2,580 hr (~108 days) in water <5°C, and some individuals survived near-freezing conditions in situ, indicating greater cold tolerance. Though the underlying mechanisms (e.g. genetic or physiological plasticity) for such enhanced cold tolerance remains unstudied,

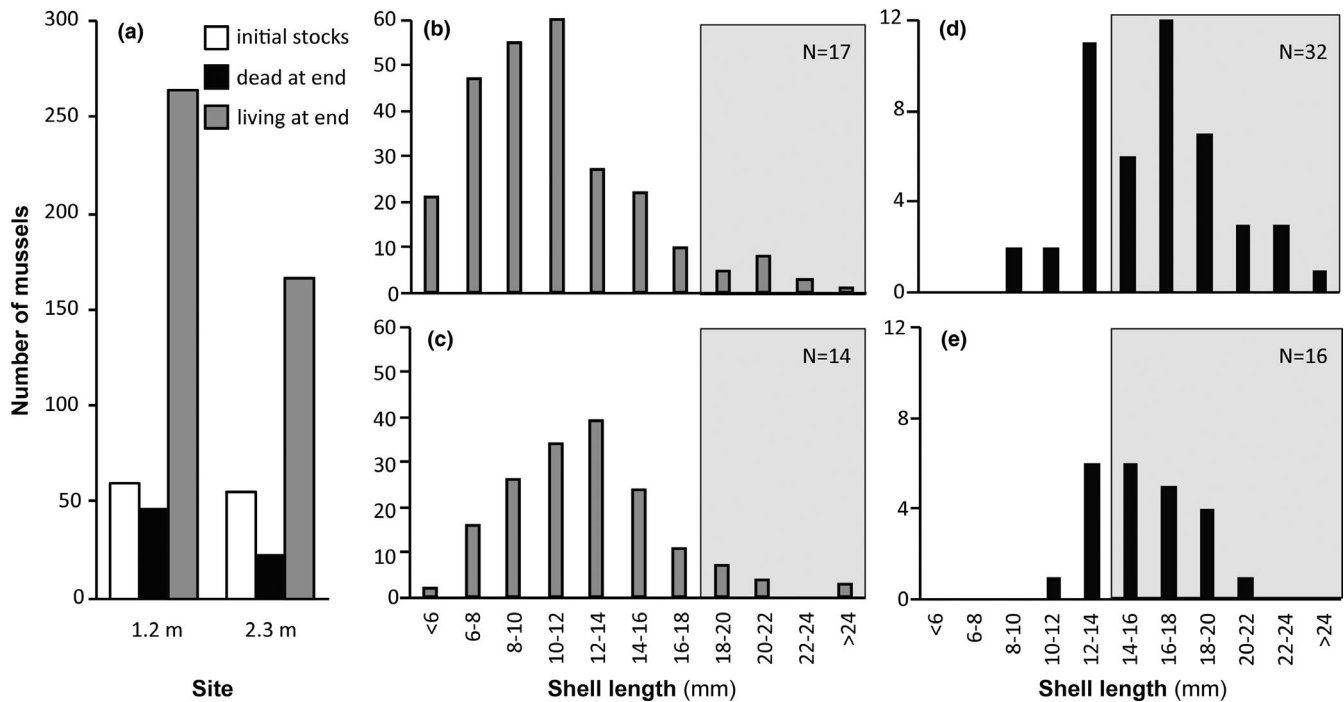


FIGURE 3 Mussel abundance and size distribution, showing (a) the number of living mussels on encrusted rocks at the beginning and end of the cage experiment as well as the dead mussels retained in cages at the end; (b, c) size distribution of living; and (d, e) dead mussels at each site. b and d: 1.2 m site; c and e: 2.3 m site. The presumed overwintering survivors and dead mussels were identified in grey boxes

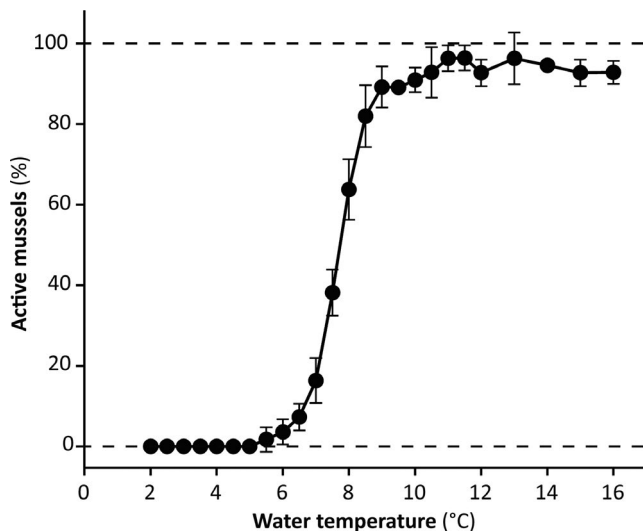


FIGURE 4 Mean (\pm SD) mussel activity as a function of water temperature from 2°C to 16°C. Mussels were deemed active and filtering water when they had their siphon extended. Dashed lines indicate 0% and 100%, respectively

our study suggests a higher latitude distributional range than previous predictions based on the proposed cold limit (Mackie & Brinsmead, 2017; Oliveira et al., 2010). For example, the upper Mississippi River was suggested as unsuitable for golden mussels because of extended low water temperature (i.e. <5°C for ~3–4 months) (Oliveira et al., 2010), while our findings provide direct evidence that they can survive such chronic exposure to low

water temperatures (i.e. 108 days in Shisanling Reservoir versus ~3–4 months in the upper Mississippi River). If our assessments are broadly applicable, they indicate that many other water bodies are potentially vulnerable to the establishment of golden mussels associated with inland water diversion projects (e.g. South to North Water Diversion Project in China) or other invasion routes that enhance the transfer propagules (Zhan et al., 2015). Our SDMs suggest that the southern margin of the Laurentian Great Lakes is susceptible to invasion by the golden mussel (see later Discussion), while previous studies provided contrasting predictions. For example, Mackie and Brinsmead (2017) predicted that the probability of survival and establishment of golden mussels in Ontario, Canada, was low because of intolerance to cold winter. However, Kramer et al. (2017) reported possible support for reproduction of the species in Lake Erie and southern Lake Michigan by considering habitat-specific water temperatures. According to our in situ results, the former study might underestimate the cold tolerance of the species by taking the 5°C as a cold limit.

Power plants on lakes and rivers may provide thermal refugia to warm-water species in temperate regions during winter (Raptis et al., 2017), thereby artificially enhancing survival and distribution of aquatic species. For example, the Asian clam *Corbicula fluminea* has been reported in Lakes Erie and St. Clair adjacent to power plants and their warm-water effluent (French & Schloesser, 1991; Scott-Waslik et al., 1988). While the Shisanling Reservoir also has a power plant, it is unlikely to affect the thermal condition of our deployment location since a hydro power plant does not produce large amount of warm water as nuclear or coal-fuelled power plants

TABLE 2 Summary of model performance in model training and testing validation sets, showing means and SDs (in brackets). Model training and testing validation were against the fivefold cross-validation and all excluded occurrences (11 occurrences), respectively, for southern records (S) or southern and northern records (SN) training sets. Testing performance between S and SN model was compared by using Mann–Whitney *U* test

Performance measure	S training	SN training	S testing	SN testing	Testing performance comparison: SN vs. S
AUC	0.89 (0)	0.88 (0)	0.72 (0)	0.9 (0.03)	$W = 1,600, p < .01$
AUC _{Diff}	–	–	–0.02 (0.03)	0.17 (0)	$W = 1,600, p < .01$
OR _{min}	0 (0)	0 (0)	0.27 (0)	0 (0)	$W = 1,600, p < .01$
Boyce Index	0.81 (0)	0.96 (0)	0.31 (0)	0.65 (0)	$W = 5,200, p < .01$

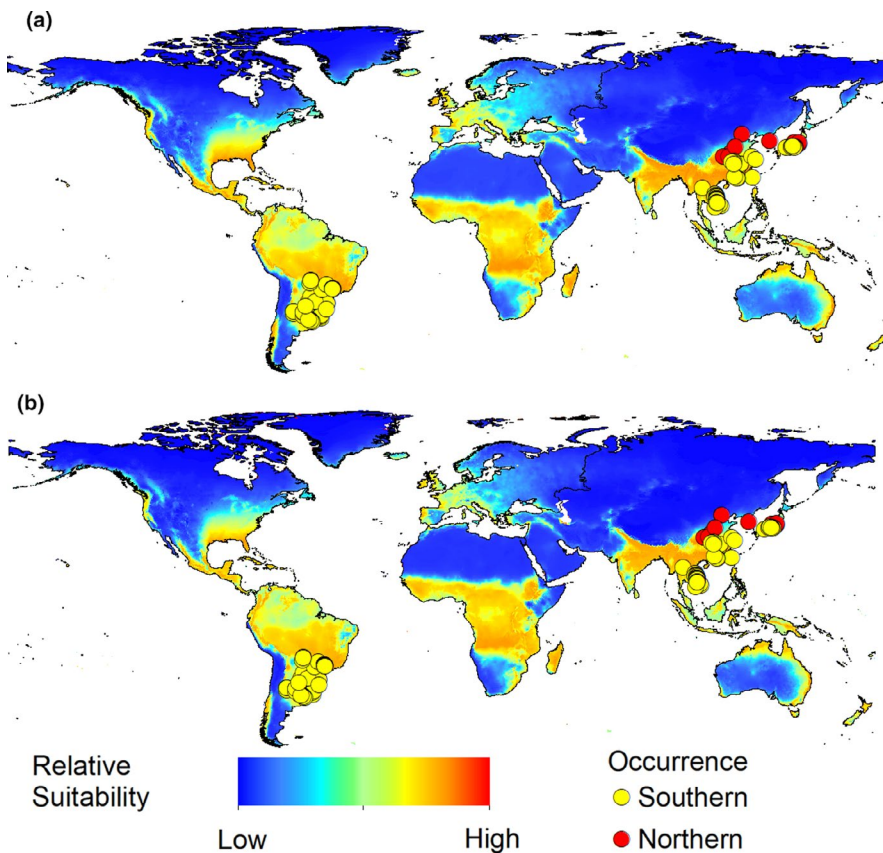


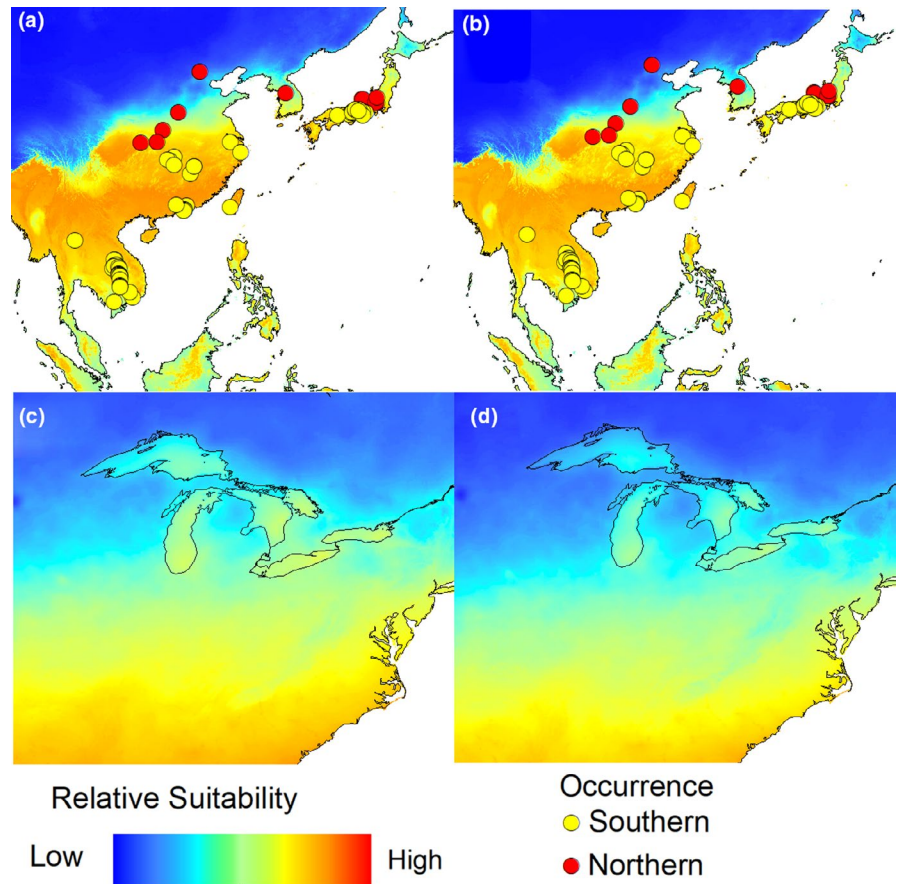
FIGURE 5 Modelled relative suitability for golden mussels on global scale. Models were trained with (a) southern and northern occurrences or with (b) southern-only occurrence records

(Raptis et al., 2017). In addition, cage deployment was distant from the power plant, located at almost opposite ends of the reservoir (Figure 1). Furthermore, our hourly temperature reading never detected a thermal signal consistent with a warm-water plume. Thus, winter survival of golden mussels that we observed appears to be biologically based rather than an artefact stemming from protection of human activities. We expected that mortality of golden mussel would be mainly associated with low water temperature because they have very wide tolerance to other environmental factors (Boltovskoy, 2015; Liu et al., 2020). Even if we could not fully rule out contributions of other factors to mortality, it suggests even stronger cold tolerance of the species (i.e. stronger cold tolerance if other factors did cause mortality).

Despite the limited difference in trap deployment depth (~1.1 m) and the fact that the two sites had almost identical water

temperatures, the sites exhibited divergent thermal conditions during the coldest—and perhaps most critical—period (Figure 2, Lower). Mussels at the 1.2 m site experienced a more protracted period of extremely low water temperature (i.e. $<2^{\circ}\text{C}$) relative to those at the 2.3 m site (Figure S1). The coldest period corresponded to surface ice formation on the surface of the reservoir (December through February), though we did not quantify freezing days. In general, organisms at a shallower site may experience increased mortality due to either longer exposure time or lower water temperature or both (Karanova & Gakhova, 2007; Murphy, 1983). In contrast, mussels inhabiting deeper sites may be provided with a thermal refuge during extremely cold periods, permitting higher overwintering survival. Such differences among microhabitats have been previously suggested as having significant ecological consequences with other species. For example, microsite-based thermal stress variation led to

FIGURE 6 Modelled relative suitability for golden mussels in East Asia (a, b) and Eastern North America (c, d), showing difference between training with southern and northern occurrence records (a, c) and those with southern-only occurrence records (b, d), respectively



varying physiological performance in mussels *Mytilus californianus* living in the intertidal zone (Helmuth & Hofmann, 2002). Such thermal heterogeneity can lead to a situation in which temporally unsuitable habitats—such as shallow waters exposed to freezing temperature—are repeatedly recolonized by propagules from suitable source microhabitats (Pulliam, 2000). Lack of replicated cages at different depths prevented us from making inferential comparisons of survival rates between depths; however, we believe that golden mussels in the study site would follow a similar mechanism. In our system, golden mussels could repopulate shallow sites *via* propagules produced at deeper locations or by individuals in shallow water that survived winter. Given that golden mussels seemingly prefer relatively deep water, likely due to their negative phototaxis (e.g. 4–10 m, Nakano et al., 2011; Liu et al., 2020; Xu et al., 2013), it is reasonable to expect that the species can inhabit more northern water bodies that are connected to the Shisanling Reservoir. Relative to the Shisanling Reservoir, large water bodies such as the Laurentian Great Lakes represent more complicated systems due to greater depths. In addition, the Great Lakes region and some Mississippi basins are extensively affected by thermal pollution from thermal effluent discharges of coal-fuelled and nuclear power plants (Raptis et al., 2017), which may result in some “hot spots” in cold winter and provide thermal refugia. Therefore, knowledge of water temperature at local habitats, and especially in any potential thermal refugia (e.g. Kramer et al., 2017), would be highly valuable to forecasting habitats where successful overwintering of golden mussels might occur.

In this study, we adopted two methods to identify mussels that survived cold water exposures at the end of experiment, and both suffer from some uncertainties. First, counting only non-displaced individuals (10.5%) as survivors can underestimate the survival rate because some mussels might have survived but moved to other locations (within the cage) *via* release of byssal threads and use of their foot (Duchini et al., 2015). This point is supported by the fact that more large animals were identified at the end of the field exposure (e.g. 31 mussels >18 mm). Second, while the true growth rate of mussels in the studied reservoir is unknown, we believe that our selection of size threshold was reasonable but conservative. The total number of living and dead mussels accounted for 69% of mussels at deployment (79 of 114), indicating that some initial mussels were not considered either survivors or mortalities. These mussels might have survived but not reached 18 mm or have died before reaching 14 mm. Following winter, water temperature increased to >16°C in late April, allowing spawning (Xu et al., 2013) and about 2 months growth for early cohorts until the end of the experiment (Figure 2). The dominant size of living mussels at 1.2 and 2.3 m sites was 10–12 and 12–14 mm, respectively (Figure 3b,c). They are highly likely post-deployment recruitments before the winter because a 2-month growth period could unlikely support the post-winter recruitments to reach such large sizes. Similar uncertainties might apply to the mortality rate as well, and such errors might be inevitable without marking every single mussel. As a result, survival and mortality rates in this study should be considered tentative.

We found that all golden mussels were inactive when the water temperature was very low (e.g. $<5^{\circ}\text{C}$), consistent with findings that bivalves reduce metabolic rate or enter dormancy when exposed to low water temperature (Ansart & Vernon, 2003; Peck & Conway, 2000). Golden mussels began to filter water once water temperature increased to 5.5°C , while 50% of individuals were active at $7.5\text{--}8^{\circ}\text{C}$ (Figure 4). These values are lower than previous suggestions for water filtering by golden mussels (e.g. $\sim 10^{\circ}\text{C}$ by Oliveira et al., 2010). Such a difference is potentially very important since a lower activation temperature results in a shorter period of dormancy and greater acquisition of food, both of which could facilitate overwintering survival (Karanova & Gakhova, 2007). There might be a time-lag between water temperature increased to the lowest point allowing for an active mussel and an extended siphon. This indicates that mussels in our study would have become active at an even lower water temperature (e.g. 5°C for the lowest temperature or $7\text{--}7.5^{\circ}\text{C}$ for 50% to begin to filter).

Our SDMs suggest a broader potential distribution of the golden mussel, consistent with some other studies made at the global scale (Campos et al., 2014; Kramer et al., 2017). The inclusion of several high-latitude occurrence records enhanced the performance and prediction of SDMs, emphasizing the importance of including comprehensive distribution data to reduce underprediction of range by SDMs (e.g. Campos et al., 2014). Using a range-bagging model, Kramer et al. (2017) found distinct climates between current invasive and native populations of golden mussels, which was likely due to its spreading stage or inadequate inclusion of occurrence records in their work such as failure to consider the northern invasive records in the present study. Our SDMs with updated distribution data support the contention that golden mussels can survive at a higher latitude and experience an expanded range, consistent with our admittedly tentative in situ survival results. Based on benthic water temperature, Kramer et al. (2017) predicted that the reproduction of golden mussels be restricted to only Lake Erie, southern Lake Michigan and some shallow bays of other lakes. These findings together suggest some risk to the aforementioned areas of invasion by the golden mussel because of their reproduction potential and overwintering survival (i.e. the present study). Furthermore, they highlight the importance of vector control to ensure that the species is never introduced (likely via ballast water discharge or vessel fouling) to potentially vulnerable systems. In 2017, the United Nations ratified new global ballast water discharge regulations limiting permissible abundance of viable organisms in treated ballast water (i.e. IMO D-2 performance standard). It is critical that these regulations be applied to the affected global shipping fleet as quickly as possible and that the selected limit for discharge of viable zooplankton-sized organisms (<10 individuals m^{-3} of discharge) be effective in preventing successful introduction of this species via its larval (veliger) stage.

To conclude, the golden mussel *L. fortunei* has a greater ability to survive at low water temperatures than previously reported. Thermal habitat heterogeneity associated with water depth and potential thermal pollution may allow overwintering survival of the species even in systems with winter surface ice formation. For

spreading invasive species like the golden mussel, inclusion of new occurrence records from the invasion front can improve SDM-based predictions of their distribution.

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DATA AVAILABILITY STATEMENT

All supplementary information can be found online for this article.

ORCID

Zhiqiang Xia  <https://orcid.org/0000-0002-9201-1043>

Justin R. Barker  <https://orcid.org/0000-0001-6363-1959>

Aibin Zhan  <https://orcid.org/0000-0003-1416-1238>

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BIOSKETCH

Our research focuses on a wide variety of questions in invasion ecology, with special emphasis on aquatic ecosystems. Major research interests of the research team include but are not limited to early detection, risk assessment, local adaptation and species distribution modelling of invasive species.

Author contributions: Z.X. conceived the study, collected and analysed the data; J.B. performed the species distribution modelling; Z.X. drafted the manuscript; J.R.B., A.Z., G.D.H. and H.J.M. revised the manuscript. All authors reviewed and approved the final manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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