# INCREASING INVASION RISK FROM THE NORTHWARD EXPANSION OF LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*) IN CHINA UNDER MULTIPLE INFLUENCES

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**Abstract.** The introduction of non-native aquatic species to develop aquaculture may inadvertently cause substantial adverse ecological impacts. Largemouth bass (*Micropterus salmoides*) is farmed with high production across a wide range of territory in China, yet is among the "world's worst invaders". Despite its extensive cultivation, the potential spawning area (PSA) of largemouth bass in China's natural waterbodies has hitherto not been systematically assessed. This paper statistically analyzes aquaculture production (1983−2020) and distribution records (literature, media, field) of largemouth bass in China. In addition, water temperature requirements which support vital life-history processes of largemouth bass were investigated and its PSA (1970−2010) in China was simulated based on environmental suitability curves. The results show that 90.3% of the provinces in mainland China farmed largemouth bass, with production increasing from 126,374 t in 2003 to 619,519 t in 2020, an average annual increase in production of 9.8%. From 1970 to 2010, the PSA of largemouth bass expanded by 183.7 km from the Pearl Basin to the high-latitude watersheds in northern China ($P < 0.001$). Largemouth bass can spawn in the Niulan and Gan Rivers in the Yangtze Basin and pose an invasion risk to the entire Basin regardless of habitat fragmentation. Analysis shows that multiple influences including aquaculture escapement, climate change and reduced fishing pressure combine to increase the invasive risk of largemouth bass in the Yangtze Basin. Currently, 17 exotic aquatic species used for aquaculture have become established in the waters of southern China alone, highlighting the necessity to assess PSA and formulate both specific and generalized management countermeasures to mitigate the ecological risks posed by exotic cultured fish.
**Keywords:** *largemouth bass, non-native aquatic species, habitat suitability curve, potential spawning area, multiple influences, biological invasion*


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## Introduction

With increasing economic integration of aquaculture production throughout the world, damage caused to the economy, ecology and society by escapement of exotic species has become ever more serious. Protection of biodiversity and natural resources faces severe challenges as a consequence of these biological invasions (Perrings et al., 2002; Simberloff et al., 2013; Li et al., 2016). Notwithstanding this issue, the introduction and utilization of non-native species has injected vitality into the rapidly developing global aquaculture industry and brought considerable economic benefits (Lin et al., 2015; FAO, 2020). Introduction of non-native fish to increase aquaculture production is the most widespread route for new aquatic invasions (Ellender and Weyl, 2014; Khosa et al., 2019). Climate change may interact with other environmental stressors to affect the distribution and reproduction of non-native species, and promote their establishment as invasive populations (Hellmann et al., 2008; Britton et al., 2010). The world has been pursuing sustainable development of its wild fisheries through limiting harvests, and implementing spatial fishing bans and seasonal moratoria to reduce fishing pressure, especially during the spawning season (Zhang et al., 2020a). Economic value and fishing pressure affect the probability of non-native fish establishing populations in rivers (Gu et al., 2022). The invasive process of non-native fish may benefit from multiple influences which promote their invasion; therefore, it is urgent to assess the invasion risk of non-native fish (Lin et al., 2015; Li et al., 2020).

The largemouth bass (*Micropterus salmoides*) is naturally distributed among freshwater basins from the central and eastern United States to northern Mexico in North America (Near et al., 2003). Largemouth bass are commonly found in pools and backwaters of rivers and streams (Stuber et al., 1982), and are habitat generalists in lotic systems (Wheeler and Allen, 2003). Largemouth bass are eurythermic fish that can tolerate water temperatures of 1−36 °C rendering them capable of surviving in a broad variety of habitats (Wheeler and Allen, 2003; Gui et al., 2018). In addition, largemouth bass are voracious predators, considered one of the "*100 of The World's Worst Invasive Alien Species*" (Lowe et al., 2000), and thereby harmful to native aquatic species (Pereira and Vitule, 2019). Invasion of largemouth bass into ecosystems is latent and long-term, with high and long-lasting ecological impacts on the invaded system (Ellender et al., 2018; Luger et al., 2020).

China's rich climate zones and complex terrain have created diverse habitats, which are conducive to the growth, development and reproduction of a rich array of native species. Non-native species may also find suitable habitats in which they can establish novel populations which flourish, even if the original area of introduction does not provide ideal environmental conditions (Ding et al., 2008; Lin et al., 2015). More than 660 invasive alien species have been found throughout China according to the "2020 China Ecological Environment Bulletin" published by the Ministry of Ecology and Environment of the People's Republic of China (2020). Largemouth bass farming and recreational fishing is widespread in China, and all freshwater waterbodies in China can be potentially invaded by largemouth bass.

Perch cultured in China include largemouth bass, jade perch (*Scortum barcoo*), pike perch (*Sander lucioperca*) and eurasian perch (*Perca fluviatilis*), all from the order Perciformes. Largemouth bass was introduced into the island of Taiwan (China) in the late 1970s, and following successful artificial propagation in 1983 was introduced into Guangdong (China) on the mainland. At present, largemouth bass which is the most extensively farmed in area and scale of operations, is regarded as one of the most


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successful exotic species in Chinese aquaculture (Gui et al., 2018; Hussein et al., 2020). China's largemouth bass aquaculture production reached 619,519 t in 2020. Guangdong has the largest production of largemouth bass in China, with an annual output of more than 360,000 t, accounting for about 58% of the total largemouth bass aquaculture production (China Fisheries Statistical Yearbook, 2021). There are two main modes of largemouth bass culture in China: pond culture and cage culture, and its aquaculture production is enhanced through polyculture, intensive culture, out-of-season spawning and other aquacultural techniques (Gui et al., 2018). Out-of-season spawning induces spawning during the non-reproductive season and compresses the annual spawning cycle into several months (Hussein et al., 2020). Cage culture has been shown to significantly increase the risk probability of non-native fish establishing populations in natural waters via escapement ($P < 0.001$) (Gu et al., 2022). Introduction of non-native species at a certain frequency in a given area will determine the risk probability of establishment and dispersion (Simberloff, 2009; Pereira and Vitule, 2019).

Climate change models generally concur that water temperatures are rising globally, with average water temperatures rising globally by 0.16 °C per decade between 1960 and 2014 as predicted, with the rate of warming accelerating towards 2014 (Wanders et al., 2019). Water temperature is the most important environmental factor affecting the distribution of largemouth bass and their habitat availability (Krause et al., 1998; Caissie, 2006). Ambient temperature controls reproductive behavior, it determines the rate of growth and development, ability to move and feed, and affects spatial distribution among rivers and lakes (Coutant, 1975; Caissie, 2006). Climate change affects fish habitat area, with increased thermally suitable habitat for warm-water fish (Mohseni et al., 2003).

In the past seven decades, most rivers in China have experienced a stage of over-exploitation, with significant changes in their fish community structure and aquatic biodiversity, and an increase in available habitat space due to reduced fish density (Zhang et al., 2020a). Non-native species may pose a greater invasion risk in fragile and disturbed ecosystems (Stachowicz et al., 1999; O'Loughlin and Green, 2017). According to a research study conducted by the Yangtze River Fisheries Research Institute of the Chinese Academy of Fisheries Sciences, about 30 exotic fish species (predominately channel catfish, tilapia, mosquito fish, and largemouth bass) were identified in the Yangtze River Basin from 2017−2020 (Yang et al., 2022). Under new protective management arrangements for the Yangtze River Basin, fishery stressors have been reduced to low levels (Zhang et al., 2020a), which ironically reduces the fishing mortality of exotics as well as native species, thereby increasing the possibility for non-native fish to establish populations and proliferate.

As one of the world's major aquaculture countries, China has introduced a large number of foreign aquatic species for commercial production. Under the multiple influences of continuing expansion of aquaculture, strengthening of the fishing ban policies, and climate change, it is necessary to comprehensively and systematically assess the ecological risks posed by escapement and establishment of exotic cultured species in the wild. In our study of the invasion risk from cultivated largemouth bass in China, aquaculture production during the period from its introduction to the mainland in 1983 until 2020 was statistically analyzed to gain an understanding of the temporal and spatial pattern and scale of largemouth bass farming. Secondly, distribution records of largemouth bass in China were collected based on data from scientific literature searches, media reports, and field surveys, which were subsequently used to test the


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accuracy of predictions. Finally, the water temperature requirements of largemouth bass life-history processes were investigated including simulations of PSA based on suitability curves. The purpose of this study was to predict the PSA of largemouth bass in China and its changing trend under multiple influences, and to provide a useful reference for a comprehensive and systematic assessment of the invasion risk posed by exotic cultured species more generally.

## Methods

### *Study area*

China has diverse climatic zones and complex terrain (*Fig. 1*). All five of the main Koppen-Geiger climate types are present in China (*Fig. 1a*), with the dominant by land area being the arid B (41.38%), followed by cold D (28.44%), temperate C (25.53%), polar E (4.48%) and tropical A (3.8%) (Peel et al., 2007; Wang et al., 2020). The topography of China is complex and diverse (*Fig. 1b*) being high in the west and low in the east, creating a three-stage gradient from west to east (Liu and Diamond, 2005). Chinese water catchments are divided into nine major basins: Songhua-Liaohe Rivers, Haihe River, Huaihe River, Yellow River, Yangtze River, Pearl River, Southeast, Southwest and Continental Basins.

### *Investigation of aquaculture status*

Official source information to enumerate and tabulate aquaculture production of largemouth bass in China were obtained from the Ministry of Agriculture and Rural Affairs of China (China Fishery Statistical Yearbook, 2021), and the China Engineering Science and Technology Knowledge Center (Fishery Expertise Service System Platform, http://fishery.ckcest.cn/index.html). Appendix 1 details the largemouth bass aquaculture production in each province of China from 2003 to 2020.

### *Collection of records in natural waters*

Global and China-only distribution records for largemouth bass were investigated and tabulated (Appendix 2). The global distribution statistics were obtained from the Global Biodiversity Information Facility (GBIF, http://www.data.gbif.org/, last accessed in 08 August 2022). The data available for China's distribution records derive from three sources: literature searches, media coverage, and field observation.

Literature research and media coverage data were obtained from an extensive search for largemouth bass records in a professional knowledge database (e.g. http://www.cnki.net, http://www.webofscience.com), and news media websites (e.g. http://news.qq.com, http://news.sina.cn, http://baijiahao.baidu.com). For each of these distribution records, the longitude and latitude were checked, and if the data source did not include geographic coordinates, then the approximate distribution range was recorded based on descriptive location information.

The field survey data were acquired from the Yangtze River Fisheries Resources and Environment Survey, within the Yangtze River Basin, led by the Chinese Academy of Fishery Sciences. This survey covers about 6,300 km of the main stream of the Yangtze River from its source (Chumal and Tuotuo Rivers) to its mouth at Shanghai. This included the large first-class tributaries Yalong, Min, Dadu, Heng, Chishui, Tuo, Jialing, Wu, and Han Rivers, and the lakes through which the Yangtze River passes,


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including Dongting and Poyang Lakes. A total of 65 Yangtze River resource and environmental survey stations were established with surveys conducted over the 5-year period 2017−2021 (*Fig. A1*).

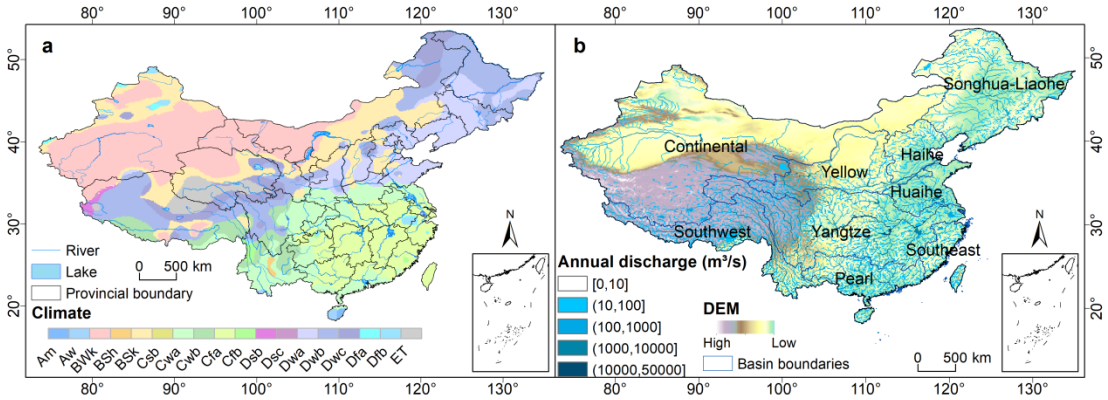


***Figure 1.*** *Study area of China. Koppen-Geiger climate type and provincial boundaries (a): Af (Tropical - Rainforest), Am (Tropical - Monsoon), Aw (Tropical - Savannah), BWh (Arid - Desert - Hot), BWk (Arid - Desert - Cold), BSh (Arid - Steppe - Hot), BSk (Arid - Steppe - Cold), Csa (Temperate - Dry Summer - Hot Summer), Csb (Temperate - Dry Summer - Warm Summer), Csc (Temperate - Dry Summer - Clod Summer), Cwa (Temperate - Dry Winter - Hot Summer), Cwb (Temperate - Dry Winter - Warm Summer), Cwc (Temperate - Dry Winter - Clod Summer), Cfa (Temperate - Without dry season - Hot Summer), Cfb (Temperate - Without dry season - Warm Summer), Cfc (Temperate - Without dry season - Clod Summer), Dsa (Cold - Dry Summer - Hot Summer), Dsb (Cold - Dry Summer - Warm Summer), Dsc (Cold - Dry Summer - Cold Summer), Dsd (Cold - Dry Summer - Very Clod Summer), Dwa (Cold - Dry Winter - Hot Summer), Dwb (Cold - Dry Winter - Warm Summer), Dwc (Cold - Dry Winter - Clod Summer), Dwd (Cold - Dry Winter -Very Clod Summer), Dfa (Cold - Without dry season - Hot Summer), Dfb (Cold - Without dry season - Warm Summer), Dfc (Cold - Without dry season - Clod Summer), Dfd (Cold - Without dry season - Very Clod Summer), ET (Polar - Tundra), EF (Polar - Frost) (Peel et al., 2007). (b) Topographic and nine major watershed areas; the annual average flow data are predicted by the dynamical 1-D water energy routing model (DynWat) (Wanders et al., 2019)*

## *Prediction of potential spawning area*

### *Method selection*

MaxEnt is one of the most popular tools for modeling species distribution and environmental niches during recent years, as it generally outperforms other methods in predictive accuracy (Merow et al., 2013; Bae et al., 2018). MaxEnt has a wide range of applicable scenarios, and has utility for studying the distributions of birds, mammals, plants, and reptiles (Phillips and Dudík, 2008). Species distribution models make predictions based on distribution records, and sample selection bias can impact model accuracy (Elith et al., 2011; Yackulic et al., 2013). Therefore, the species distribution model may have certain limitations for fish due to difficulty in sample collection and high selection bias, especially for non-native fish when there is uncertainty about whether their populations have become established in the wild following introduction or escapement.

Habitat suitability curves quantitatively describe the habitat preference and tolerance range of organisms, and have been widely used in fish habitat simulations (Lamouroux et al., 1999; Lauria et al., 2015). We logically combined habitat suitability curves with data


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maps to intuitively identify PSA. The analytical process comprised the following three steps: (1) identifying abiotic factors influencing the life-history of the largemouth bass, and its tolerance range; (2) acquisition of raster data for abiotic factors within the study area; and (3) coupling suitability curves with abiotic factor raster data to predict the PSA.

*Suitability on water temperature*

Many factors have an impact on the ability of non-native species to become established in the wild following their introduction, mediated by latency in rates of spread throughout natural landscapes (Theoharides and Dukes, 2007). Water temperature is considered the most important environmental factor affecting the invasive pattern and eventual distribution of largemouth bass outside their native habitat (Krause et al., 1998; Caissie, 2006). It controls reproductive behavior, determines their rate of growth and development, determines their ability to move and feed, and affects their distribution in rivers and lakes (Coutant, 1975; Caissie, 2006).

The water temperature requirement during the spawning period is the basis for predicting the PSA, and will also be the most important inhibiting factor affecting the distribution of species. It is worth noting that invasive fish can have migratory characteristics during life history phases and activities such as spawning, feeding, and overwintering, that expand the area where they pose ecological risks beyond the primary area suitable for their spawning. Evidence from various studies (*Table 1*) shows that largemouth bass can spawn in areas with water temperatures of 15−25 °C from March to June (PSA), and can survive in areas with water temperatures within the range of 1−36.8 °C (potential survival area).

***Table 1.*** *Water temperature tolerance ranges or thresholds of largemouth bass*

| Life-history process | Describe | Water temperature | Data sources |
|---|---|---|---|
| Survival lower limit | Lethal temperature | 1 °C | Carmichael et al., 2013; Gui et al., 2018 |
| Digestion rates is zero | / | 5 °C | Coutant, 1975 |
| Feeding | Natural foraging activities | 10 °C | Coutant, 1975 |
| | | 6−12 °C | Carmichael et al., 2013 |
| | | 10−16 °C | Markus, 1932 |
| Spawning | Nesting and spawning begin in late March | 15−25 °C | Coutant, 1975 |
| | | 14−16 °C | Miranda and Muncy, 1987 |
| | | 15 °C | Landsman et al., 2011 |
| Incubation | Eggs hatch into juveniles | 18.9−20 °C | Coutant, 1975 |
| Maximum digestion rates | The temperature suitable for the growth of adult fish | 20−27 °C | Coutant, 1975 |
| Digestion rates is zero | / | 35.5 °C | Coutant, 1975 |
| Survival limit | Lethal temperature | 36 °C | Gui et al., 2018 |
| | | 36.8 °C | Coutant, 1975 |
| | | 36.4 °C | Eaton et al., 1995 |


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*Temperature in natural waters*

The water temperature raster data for this study were obtained from DynWat (dynamical 1-D water energy routing model). The DynWat model (Wanders et al., 2019) predicts water temperature. Its resolves both the energy and water balances, to simulate river temperatures for the period 1960−2014 at a nominal 10-km and 50-km resolution. The DynWat model accounts for surface water abstraction, reservoirs, riverine flooding, and formation of ice, enabling a realistic representation of the water temperature. Validated results against 358 stations worldwide show that it has an accuracy with a root-mean-square error of 0.2 °C and bias of 0.7 °C in its simulations.

*Potential spawning area calculation*

The calculation process of the PSA of largemouth bass was completed using ArcGIS (SERI Inc. version 10.8). Specifically, the Spatial Analyst Tools, Multidimension Tools, Analysis Tools and allied functions were used in the analysis. The years 1970, 1980, 1990, 2000 and 2010 were selected as the key years to calculate the PSA with a resolution of a 10-km. Box-plots of latitudinal trends in PSA of largemouth bass were created using GraphPad prism (GraphPad Software Inc. version 8.0.2).

## Results

### *Aquaculture development*

Largemouth bass were farmed extensively in 90.3% of the provinces in mainland China (*Fig. 2a*), especially those regions characterized by warm temperature and high rainfall, Cfa and Cwa, climate types. Most largemouth bass production in 2020 (619,519 t) occurred in Guangdong (361,220 t, 58.3%), Zhejiang (85,574 t, 13.8%), Jiangsu (40,074 t, 6.4%), Sichuan (22,053 t, 3.5%), Hunan (21,410 t, 3.5%), Hubei (21,317 t, 3.4%), Jiangxi (18,749 t, 3.0%) and Fujian (11,623 t, 1.9%) Provinces. The heat map of this distribution (*Fig. 2a*) clearly shows that many provinces in the Yangtze River Basin are farming largemouth bass on a large scale.

The production of largemouth bass in China is increasing year by year (*Fig. 2b*). Largemouth bass production in mainland China increased from 126,374 t in 2003 to 619,519 t in 2020 with an average annual growth rate in production of 9.8%. Largemouth bass production in Guangdong province increased from 89,218 t in 2003 to 361,220 t in 2020 at an average annual rate of 8.6%.

### *Potential spawning area*

The predicted results show that the PSA of largemouth bass in China is concentrated in the southern watershed (*Fig. 3*). The Pearl River Basin is the main PSA and is gradually expanding towards the north. The climate of the PSA is dominated by Cwa and Cfa.

In extracting the latitudes of each raster of the predictive results to construct a box and whisker plot (*Fig. 3f*) the whiskers included 1−99% of the original latitude data to avoid the extreme values. From 1970 to 2010, the PSA of largemouth bass continued to expand from the Pearl Basin to the high-latitude watersheds ($P < 0.001$). The average, 75$^{th}$ percentile and 99$^{th}$ percentile latitude values for key years were calculated, indicating that the PSA of largemouth bass expanded to high latitude waters by 89.1 km, 137.5 km and 183.7 km, respectively (1970−2010).


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### *Distribution records*

Taking the 2010 PSA as a base for comparison, the regional correspondence between the distribution records and the forecast results showed that the origin climates of largemouth bass were mainly Cfa, Dfa, Dfb, Cwa and Cwb (*Fig. 4a*) and the climates of PSA in China were predominantly Cfa, Cwa and Cwb (*Fig. 4b*). The distribution records and PSA of largemouth bass are concentrated in the southern watershed of China, mainly in the Pearl River Basin and the Yangtze River Basin, with good correlation.

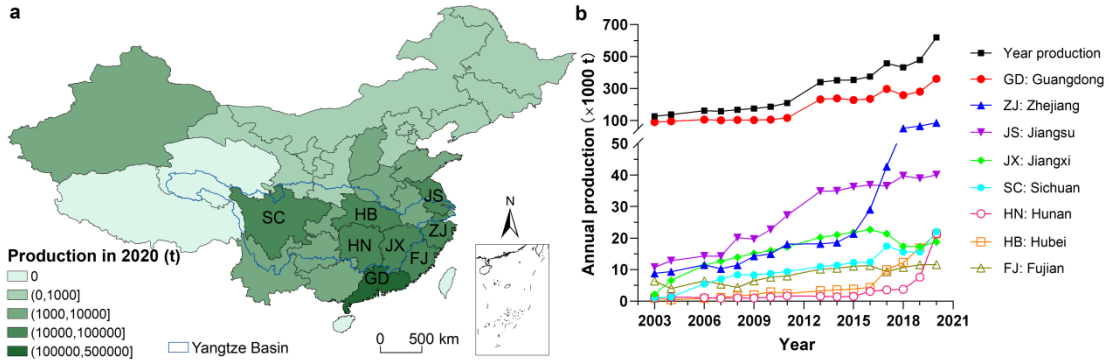


***Figure 2.*** *Spatial and temporal distribution of largemouth bass aquaculture production. Heat map of largemouth bass aquaculture production in mainland China in 2020 (a). This heat map is province-based. It illustrates the distribution of largemouth bass farming spatially. The trend of change in the scale of largemouth bass farming in mainland China is depicted in (b). It lists the provinces which produced more than 10,000 t of largemouth bass in 2020, comprising the provinces of Guangdong, Zhejiang, Jiangsu, Jiangxi, Sichuan, Hunan, Hubei and Fujian. Data for 2005 and 2012 are missing*

### *Invasion risk in the Yangtze*

In the Yangtze River Basin, the high-risk regions for largemouth bass invasion are mainly distributed in Jinsha (tributaries Niulan, Pudu and Longchuan Rivers) and Gan Rivers (*Fig. 5*). The Medium-risk regions are mainly distributed in Tuo and Xiang Rivers. The Low-risk regions are mainly distributed in Jialing, Han and Wu Rivers. The Yangtze River Basin provides almost the entire water temperature range for survival of largemouth bass, implying that in the absence of habitat fragmentation, largemouth bass may cause ecological impacts throughout the whole Yangtze River Basin (*Fig. 5*).

## Discussion

### *Potential spawning area prediction*

Criteria for habitat suitability were determined based on water temperature. Nevertheless, other abiotic factors such as depth, flow velocity, slope and substrate type may also play an important role in determining the habitat suitability for fish (Lamouroux et al., 1999; Lauria et al., 2015). Notwithstanding the role of these other factors, water temperature is considered the most important influence on life history processes and the distribution of largemouth bass (Coutant, 1975). Many studies on water temperature thresholds for spawning and survival of largemouth bass are highly consistent, effectively reducing possible biases in habitat suitability curves constructed using expert judgement


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(Coutant, 1975; Miranda and Muncy, 1987; Gui et al., 2018). Division of water temperature requirements for the life-history process of largemouth bass into spawning and survival requirements is an important step to predicting PSA, and corresponds well with the habitat preferences of non-native species invading recipient environments. Colonization of largemouth bass may occur in waters with a water temperature of 15−25 °C from March to June, and population dispersal may occur in waters with a water temperature of 1−36.8 °C (Coutant, 1975). However, we ignored possible changes in species environmental tolerance (Sheth and Angert, 2014), and biases in water temperature datasets (Wanders et al., 2019), which may reduce the accuracy of PSA.

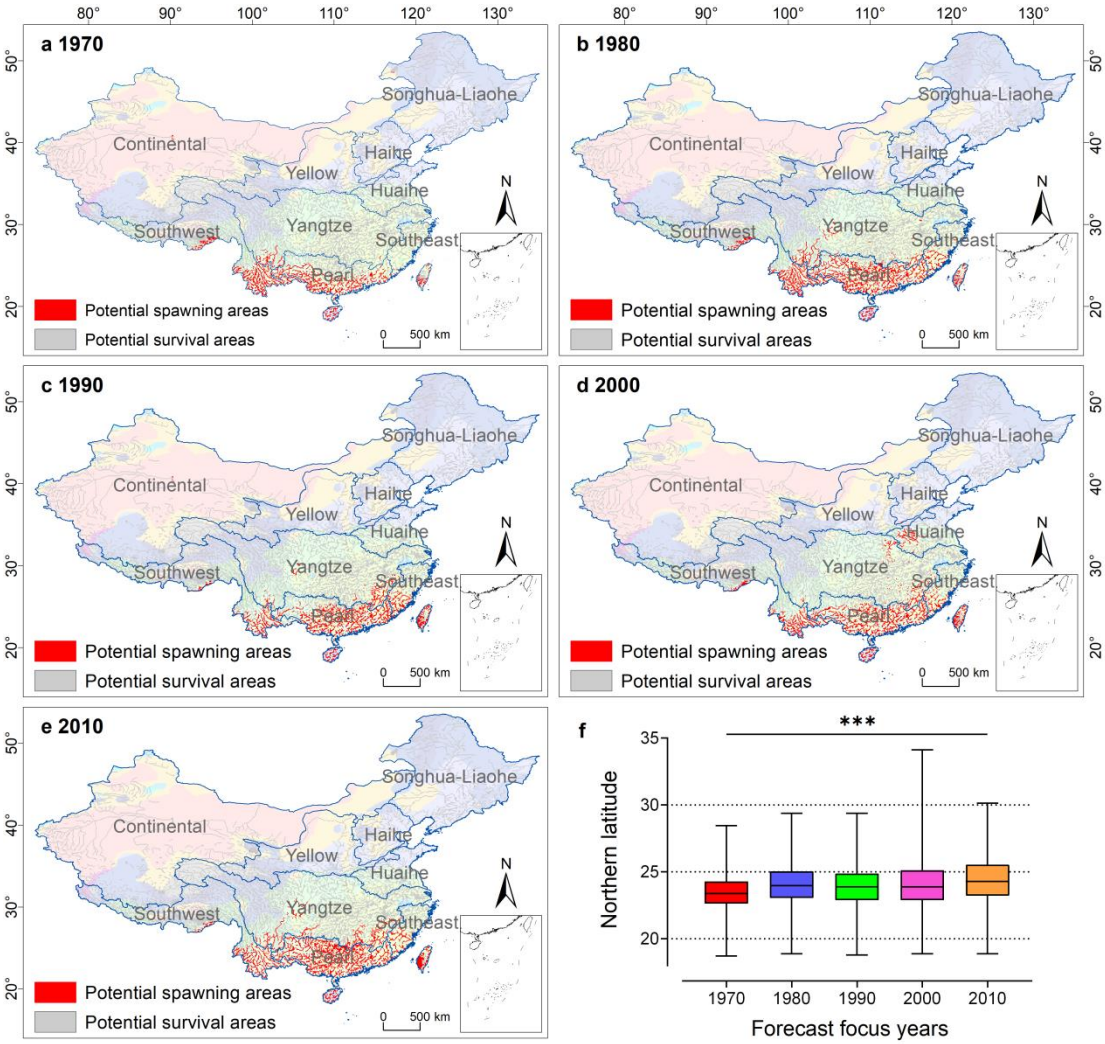


***Figure 3.*** *PSA of the largemouth bass in China based on water temperature tolerance. (a−e) Different forecast results in 1970, 1980, 1990, 2000, and 2010; the background colors indicate climate zones which is similar as in Figure 1a. (f) Latitudinal box plot of PSA of largemouth bass is shown for each forecast focus year*

For assessing the PSA of invasive fish, habitat suitability curves are more suitable than species distribution models. Species distribution models require unbiased distribution records to predict potential geographic distributions, but sometimes this important consideration (dealing with deviations and removing duplication) has not be


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addressed in other studies (Newbold, 2010; Elith et al., 2011; Kramer-Schadt et al., 2013). Predicting the potential geographic distributions of Malay civet (*Viverra tangalunga*) in Borneo (Kramer-Schadt et al., 2013) showed that dealing with uneven sampling effort can significantly improve model prediction. However, with field studies of fish, it is difficult to collect unbiased distribution records due to factors such as heterogeneity in fishing effort, net gear specifications, and weather. In contrast, the method used in this study does not require species distribution records at the prediction stage, which is consistent with assessing non-native species prior to their introduction.

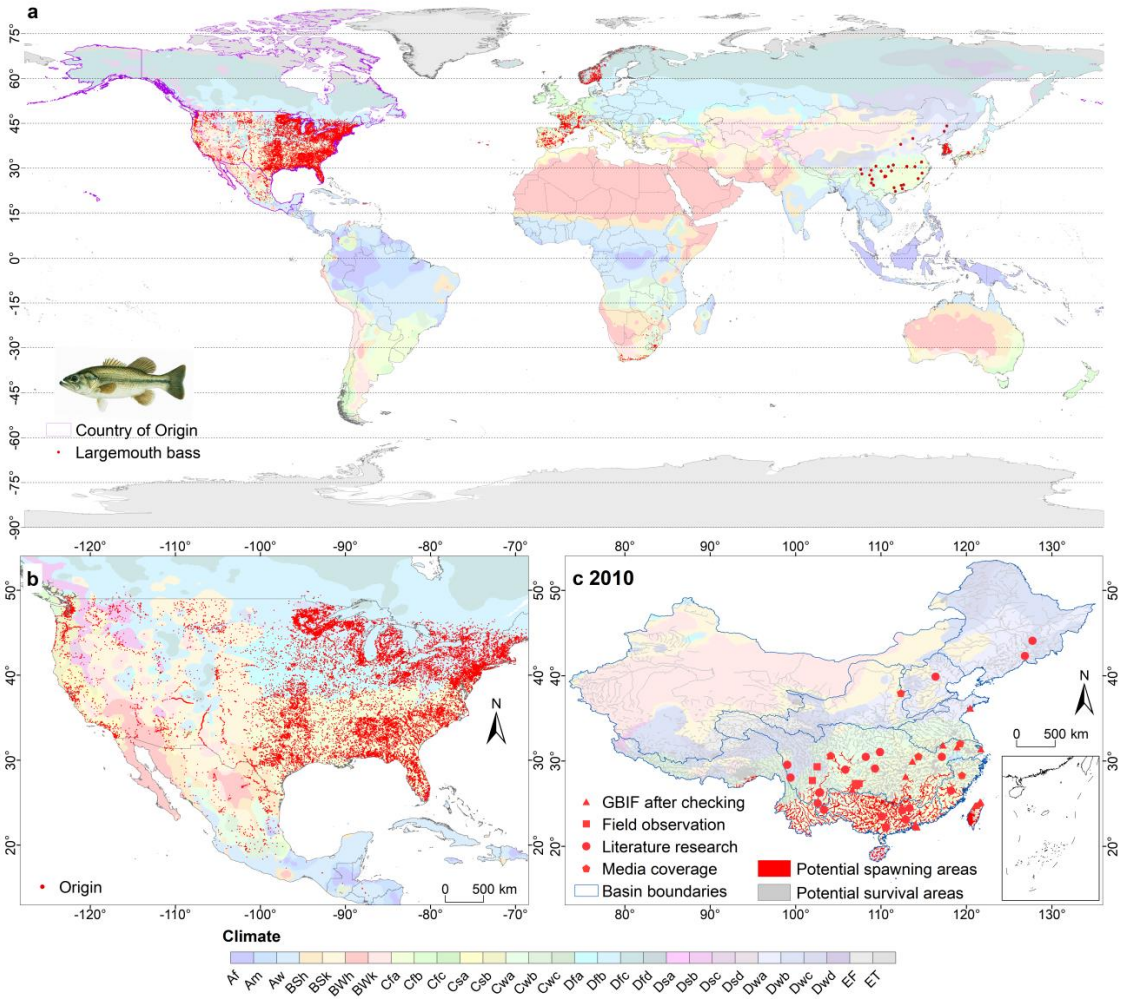


***Figure 4.*** *PSA checkout map (Data source: Appendix 2; GBIF, http://www.data.gbif.org/, last accessed on 08 August 2022). Largemouth bass world distribution map (a). Largemouth bass origin (parts of the United States, Canada and Mexico) distribution map (b). PSA (China) for largemouth bass in 2010 (c)*

### *Increasing risk with aquaculture development*

Aquaculture is the main contemporary means through which non-native fish are introduced into natural ecosystems (Grosholz et al., 2015; Khosa et al., 2019). To date, the Food and Agriculture Organization of the United Nations (FAO) has collected 5,623 species introduction records (Introduced Species Fact Sheets,


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https://www.fao.org/fishery/en/introsp). Eight species of fish are included in the "*100 of The World's Worst Invasive Alien Species*", six of these (including Mozambique tilapia, Brown trout, Common carp, Largemouth bass, Rainbow trout, Walking catfish and Nile perch) were introduced through aquaculture (Lowe et al., 2000; Ottinger et al., 2016; Gu et al., 2018). These non-native fish have caused severe negative impacts on their recipient environments, including adverse habitat changes for native species and environmental quality e.g. common carp consume vast quantities of native plants and increase turbidity through sediment resuspension (Miller and Crowl, 2006), and reduced biodiversity (e.g. tilapia prey on native biota depleting their abundance, Russell, 2012; Gu et al., 2019).

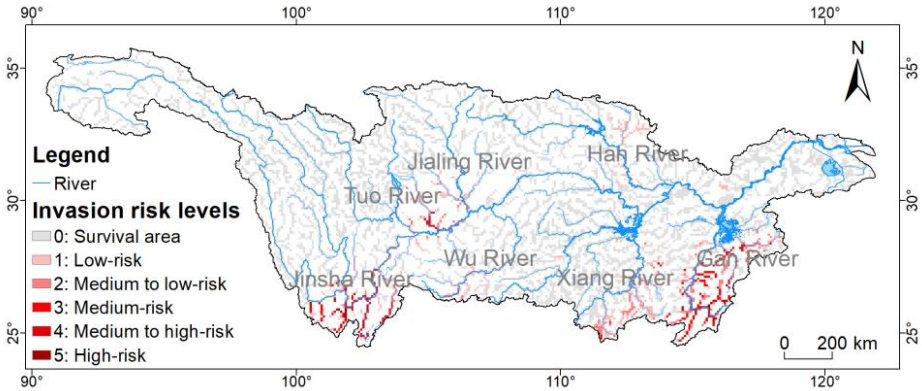


***Figure 5.*** *Invasion risk levels of largemouth bass in different parts of the Yangtze River Basin. The number of occurrences of the PSA (0–5), was the criterion for assigning the level of invasion risk from low to high respectively*

Farming of non-native fish is likely to increase their chances of colonization of natural habitats. The escape of non-native fish from farms is unavoidable, resulting in the continued transport of propagules into natural waters (Lima et al., 2018). The propagule pressure hypothesis states that the reproductive stress of alien species, a product of the number of individuals released or escaping per instance by the frequency of instances of release or escapement (Jeschke and Starzer, 2018), determines the degree of invasion (Simberloff, 2009). When the propagule pressure is high, it is beneficial to the invader to reduce the adverse effects of constraints such as bottlenecks and Allee's effect on the alien species, so that more individuals can overcome environmental resistance and survive to lay a genetic foundation for subsequent population expansion (Simberloff, 2009; Pereira and Vitule, 2019).

### *Climate change and expansion of potential spawning area*

Air and water temperature trends are broadly consistent across the globe, and the differences between their overall trends are not statistically significant (O'Reilly et al., 2015). Under the current emissions scenario, continued greenhouse gas emissions would make a median global temperature rise of 3.2 °C (2.2−3.5 °C) by 2100 very likely under the Intended Nationally Determined Contributions target of the 26th UN Climate Change Conference of the Parties aka COP26 (Wang et al., 2022). The comprehensive observations of the climate system and several key indicators show that the global warming trend is continuing, and extreme weather such as high temperatures and heavy rainfall in China is becoming more frequent and more intense (China


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Meteorological Administration Climate Change Centre, 2022). Water temperature is mainly affected by ambient air temperature, the amount of water flow and the proportion of base flow or surface flow (Liu et al., 2018). Compared with 1971−2000, global mean and high (95$^{th}$ percentile) water temperature is projected in one scenario to increase by 0.8−1.6 (1.0−2.2) °C during 2071−2100 (van Vliet et al., 2013).

With future climate change, habitat extent and function will continue to be affected. Global warming has caused the thermally suitable spawning habitat of Atlantic cod (*Gadus morhua*) and polar cod (*Boreogadus saida*) to shift to higher latitudes, and the original spawning habitat in such instances may shrink or even disappear (Dahlke et al., 2018). Invasive species tend to have a broad adaptive capacity to changing water temperature, and climate change-induced increases in water temperatures in turn increase the availability of thermal habitats suitable for warm-water fish (Mohseni et al., 2003; Johnson et al., 2009). Water temperature is the most important factor affecting the distribution of largemouth bass (Coutant, 1975), and the water temperature during the spawning period is the most important limiting factor for largemouth bass distribution. Driven by rising water temperature in China, the PSA of largemouth bass continued to expand by 183.7 km to the high-latitude watershed from 1970 to 2010 ($P < 0.001$), and this expansion will continue in the future with climate change. Furthermore, the ecological impacts of the expansion of non-native fish habitats to higher latitudes may be more severe than at lower latitudes. Without considering the role of habitat fragmentation, enough river sections are suitable for largemouth bass to spawn, so that largemouth bass will cause invasion risks in the entire Yangtze River Basin (*Figs. 3* and *5*).

### *Fishing and colonization of non-native species*

Economic value and associated fishing pressure on non-native fish influences their colonization. High-value fish are subject to greater fishing pressure, and the probability of successful colonization of exotic species can be significantly negatively correlated with the price ($P < 0.001$) (Gu et al., 2022). Moreover, waters in which fishing is banned, either temporarily or permanently, are increasing, and in 2019 seven large watersheds accounting for 68.1% of China's natural water area have implemented a seasonal fishing moratorium system (Zhang et al., 2020b). This fishing ban has greatly promoted conservation of fish diversity and recovery from depleted fish biomass for many watersheds in China (Yangtze River, Yellow River, Pearl River, etc.) due to reduced fishing mortality (Zhang et al., 2020a). However, the flourishing tilapia populations in the Pearl River Basin have demonstrated how a reduction in fishing can inadvertently promote an invasion of non-native fish (Gu et al., 2018). Therefore, it is particularly important to pay attention to the species composition and abundance of fish populations in rivers where fishing is not permitted.

### *Increasing risk in multiple influences*

Multiple factors contribute to increased risk of invasion from non-native fish species. Propagule introduction, abiotic environment and biotic interactions are major components that influence successful establishment and dispersal of non-native species (Wallingford et al., 2020). In addition to aquaculture being an important way to introduce non-native fish, recreational fisheries (Largemouth bass are delicious and easy to catch, popular with anglers and even released without permission), and biological control (Grass carp was introduced to the United States for the control of aquatic weeds)


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may also introduce non-native fish thereby posing an invasion risk (Clavero and García-Berthou, 2006; Ellender and Weyl, 2014). Global change has directly or indirectly altered the drivers of species' distribution, such as increased estuarine species richness due to reduced salinity, increased invasion of warm-water species due to global warming, and non-native species able to achieve maximum biomass under low dissolved oxygen conditions (Lauchlan and Nagelkerken, 2020). As previously mentioned, high-value exotic fish tend to face higher fishing pressures, which may prevent them from maturing or spawning, whereas fishing bans in natural waters may cause this constraint to disappear (Gu et al., 2018). Our understanding about how multiple factors may influence trends in PSA is still in its infancy, but the ecological risks posed by biological invasions are worrisome.

## Conclusions

Invasion risks and associated management challenges posed by non-native fish continue to increase (Li, 2020). Globally, 63 countries or regions have introduced largemouth bass (*Fig. 4a*), and the PSA of this species worldwide may be more extensive than is currently perceived. Moreover, the impact of multiple factors on the invasion of non-native fish is ubiquitous and may also promote the invasion of additional non-native fish species such as tilapia and common carp. Therefore, it is necessary to assess the ecological risks of non-native fish comprehensively and systematically, and the assessment of largemouth bass in this study can provide a reference for related work on other potentially invasive species.

There are more than 50 international agreements and guidelines related to biological invasion, of which the "Convention on Biological Diversity" is the most important internationally for managing invasive species. The guiding principles of biological invasion management include precepts and precautionary principles from the Conference of the Parties of the "Convention on Biological Diversity". Our study suggests that under existing management principles, there should be focus on the following aspects: (i) first, risk assessments need to be conducted prior to the introduction of exotic fish for farming, which can effectively avoid introducing them into high-risk natural waters; (ii) second, the impacts of climate change on fish life histories and habitats should be systematically analyzed in the area where farming exotics is planned; and (iii) finally, there is an urgent need to establish exotic fish monitoring stations strategically in no-fishing waterways adjacent to fish farming areas to closely monitor their fish species composition.

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## APPENDIX

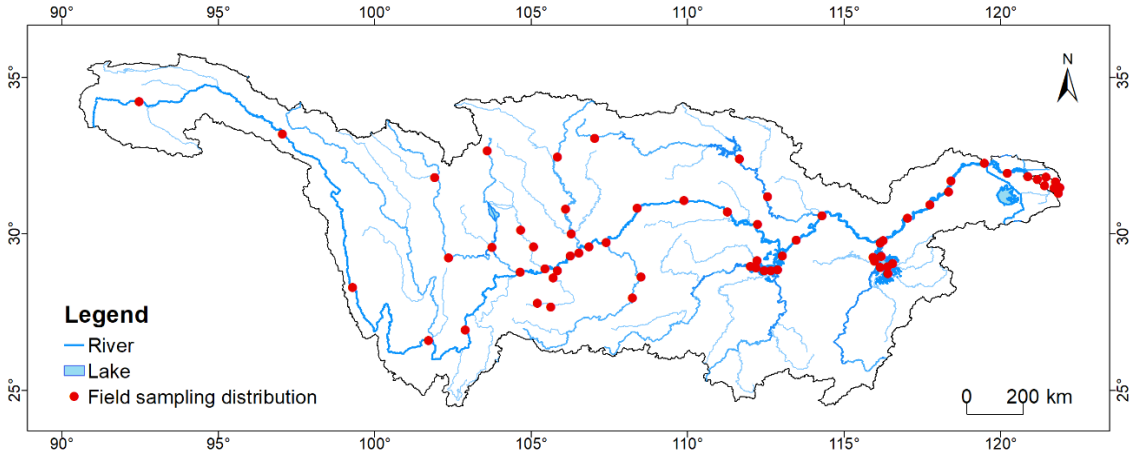


***Figure A1.*** *Distribution map of Yangtze River resource and environmental survey stations*

## ELECTRONIC APPENDIX

This manuscript has two electronic appendices with basic data:

***Appendix 1.*** *Largemouth bass aquaculture production in each province of mainland China from 2003 to 2020*

***Appendix 2.*** *Distribution records of largemouth bass*


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