Research Article

Climate, habitat and human disturbance driving the variation of life-history traits of the invasive goldfish *Carassius auratus* (Linnaeus, 1758) in a Tibetan Plateau river

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Abstract

Explaining variation in life-history traits of invasive species is a key goal in invasion ecology. The goldfish, *Carassius auratus,* is one of the most successful invaders in freshwater systems and has successfully invaded the Yarlung Zangbo River located in the Qinghai-Tibetan Plateau, China. Although many studies on life-history trait variations in goldfish have been carried out worldwide, few have focused on plateau areas, and factors driving this variation have received little attention. In this study, six life-history traits of goldfish and twenty-five environmental variables, including climate, habitat and human disturbance, were selected to examine their impacts on life-history traits. Multiple regression and hierarchical partitioning analyses were performed to determine the relationships between life-history traits and environmental variables. Maximal body length (MaxL), corrected total fecundity (TFecC) and egg diameter (EggD) were significantly explained by environmental variables. MaxL was positively related to elevation (ELE), population density (POP) and precipitation of the wettest month (BIO13) but negatively related to isothermality (BIO3). TFecC was positively related to ELE, POP and BIO13 but negatively related to BIO3, whereas EggD was negatively related to ELE and BIO13. Body size, fecundity and egg size were significantly affected by the environment, which suggested that a trade-off between growth and reproduction was the key to goldfish adaptation to plateau environments. Climate, habitat and human disturbance are closely related to the life history, suggesting that goldfish will expand their distribution in response to future global environmental changes. Therefore, we advocate that current efforts should focus on taking targeted action and preventing future introductions of goldfish to other areas. Education to promote public awareness of the threats caused by goldfish and other non-native species should be the first priority.

Key words: alpine freshwater ecosystems, invasive fish, life history plasticity, environment

Introduction

Invasive fish cause significant environmental damage to freshwater ecosystems and lead to changes in the community structure and alterations in ecosystem function and services (Vitule et al. 2009; Cucherousset and

Olden 2011; Piria et al. 2018). Considering the adverse impact of invasive fish, there is a particularly urgent need to understand the factors that facilitate the invasion process in order to implement measures for successful prevention and management of invasive species (Kolar and Lodge 2002). Among the possible factors, life-history traits have been widely recognized as important contributing factors that have determined the current distributions and potential spread of invasive species (Grabowska and Przybylski 2015). Life-history traits are a reflection of organisms adapting to their natural environments (Stearns 1976), and their plasticity will increase the fitness of introduced fish with regard to colonization and dispersal in new habitats (Sol et al. 2012; Grabowska and Przybylski 2015; Colangelo et al. 2017). Simultaneously, habitat can function as a template ("habitat templet" theory, Southwood 1977) that can influence the life histories of species and result in intraspecific variation (Jonsson and Jonsson 2011). Therefore, understanding the adaptive significance of life-history traits of invasive species relative to their introduced environments has become a central issue in exploring the invasion mechanism (Partridge and Harvey 1988). Numerous studies have explored the relationships between life-history traits and environmental factors to explain invasion patterns and processes (e.g., Alcaraz and García-Berthou 2007; Carmona-Catot et al. 2011; Masson et al. 2015; Wei et al. 2018). For example, Alcaraz and García-Berthou (2007) found that salinity mainly affected invasive mosquitofish (*Gambusia holbrooki*) females, which led to earlier maturation, higher reproductive investment and a reduced condition and density. Carmona-Catot et al. (2011) studied invasive mosquitofish along latitudinal and upstream-downstream gradients and found that lower reaches and lower latitudes led to higher reproductive efforts and lower body conditions. Masson et al. (2015) showed that thermal regimes significantly affected some life-history traits of invasive pumpkinseed sunfish (*Lepomis gibbosus*) and resulted in faster juvenile growth and greater reproductive investment. Wei et al. (2018) tested the impact of nutrient enrichment on the life history of *Pterygoplichthys* spp. and found that female *Pterygoplichthys* spp. matured to a larger size with increasing total phosphorus, whereas the mean size and age at maturity of males increased due to increasing total nitrogen concentrations. Although these works have improved our understanding of life histories and the environment, changes in the life-history traits of invasive species under extreme environmental conditions, especially on plateaus, remain poorly understood.

The Yarlung Zangbo River, which is located on the Qinghai-Tibetan Plateau, is the longest plateau river in China and one of the highest rivers in the world. The Yarlung Zangbo River is very sensitive and vulnerable to fish invasion due to its fragile ecosystem and unique fish fauna (Favre et al. 2015). To date, 13 non-native fish species have been found in the region, and eight of them have been established, which has resulted in a reduction in native fish resources (Zhang 2013). The goldfish *Carassius auratus* (Linnaeus, 1758) is one of the most widely distributed non-native species in the Yarlung Zangbo River (Chen and Chen 2010).

A common cyprinid fish, the goldfish has been introduced into numerous countries worldwide (Marr et al. 2013). Their invasive potential arises from their life-history traits that facilitate colonization of new habitats. Tarkan et al. (2010) summarized some growth and reproduction life-history traits and found that invasive European goldfish populations displayed relatively early maturity and variable growth compared with a non-native Australian population. Liu et al. (2015) revealed that spawning times and growth rates in the early life history of invasive goldfish varied between the Chabalang and Chongdui populations in the Yarlung Zangbo River basin. In addition, higher investment in reproduction (earlier maturation and higher relative fecundity and gonadosomatic index) was considered the key factor for establishment success of the gibel carp (*Carassius gibelio*), which belongs to the same genus as goldfish (Emiroğlu et al. 2012). These studies have suggested that non-native goldfish can regulate their growth and reproductive activities to adapt to new environments, which in turn increases the rate of successful colonization. However, our present knowledge of the mechanisms involved in the life-history plasticity of goldfish and the environmental drivers across the Yarlung Zangbo River basin is still limited. In this study, six life-history traits of goldfish representing growth, development and reproduction were measured, and 25 environmental variables, including climate, habitat and human disturbance, were selected to examine their impacts on life-history traits. According to the "habitat templet" theory (Southwood 1977), first we hypothesized that the life-history traits of goldfish would be significantly affected by the environment of the Yarlung Zangbo River basin. Second, based on previous studies on the life-history traits of invasive goldfish, we hypothesized that growth and reproduction performance were crucial for dispersal of the goldfish in the plateau and would respond to environmental gradients in the Yarlung Zangbo River Basin.

Materials and methods

Study area

The Yarlung Zangbo River, which is located in the Tibet Autonomous Region in China, is the highest river in the world. According to data from 1956–2010, the annual average temperature of the Yarlung Zangbo River is approximately 5.2 °C and decreases with increasing elevation (Wang et al. 2015). The annual average precipitation is approximately 412.7 mm and decreases gradually from east to west; the uneven distribution of precipitation in the basin is mainly concentrated over 6–9 months, which

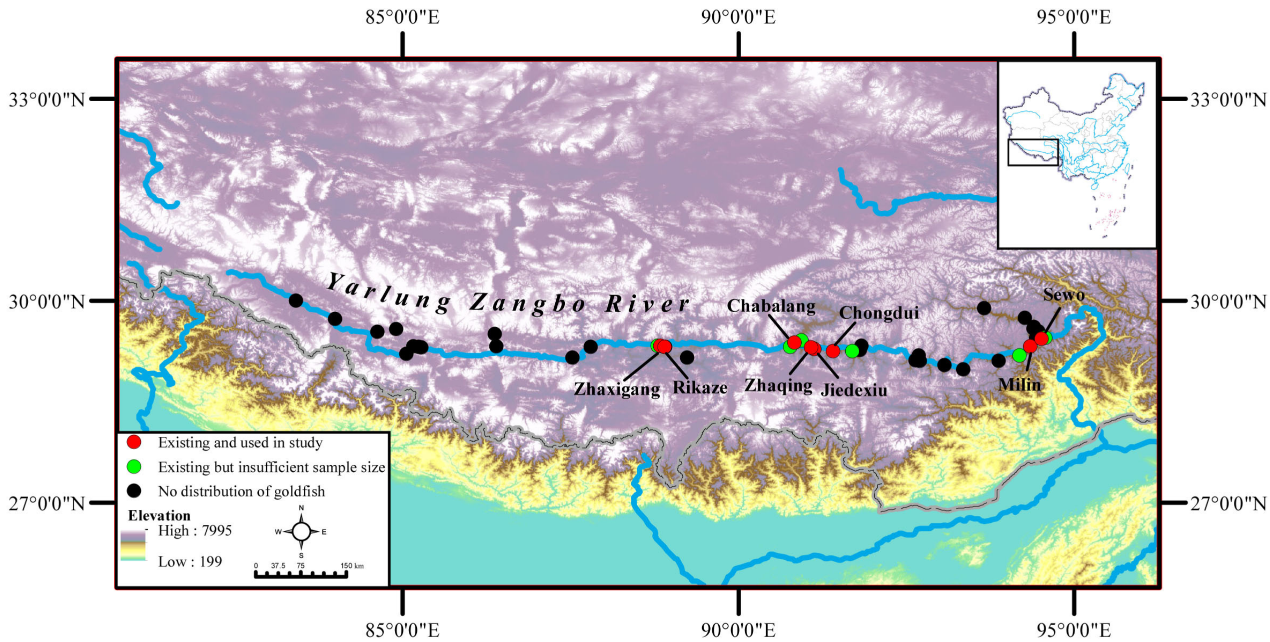

Figure 1. Map of sampling sites in the Yarlung Zangbo River.

Table 1. Habitat description for the eight sampling sites. Geographic coordinates system: GCS_WGS_1984 (unit: degree); Elevation (m): altitude above sea level; Water body: water body type; Macrophytes: Yes = presence, No = absence.

Sampling site	Longitude	Latitude	Elevation (m)	Water body	Macrophytes
Zhaxigang	88.836	29.331	3840	Wetland	Yes
Rikaze	88.901	29.315	3830	Pond	No
Chabalang	90.832	29.380	3605	Wetland	Yes
Zhaqing	91.078	29.307	3593	Pond	Yes
Jiedexiu	91.129	29.281	3605	Pond	Yes
Chongdui	91.410	29.252	3562	Wetland	Yes
Milin	94.348	29.323	2930	Pond	Yes
Sewo	94.517	29.435	2915	Pond	Yes

accounts for 86.6% of the annual precipitation (Wang et al. 2015). To collect life-history data for goldfish at a broad spatial scale, a total of 45 randomly selected sites were sampled along elevational gradients in the Yarlung Zangbo River Basin (83°24′–94°34′E; 29°27′–30°0′N) (Figure 1). The elevation of the sampling sites ranged from 2915 to 4580 m (Figure 1).

Fish sampling

Sampling was conducted from April to June 2015. For wadeable sites (water depth less than 1 m), electrofishing (12 V, 2000–3500 W) was used to collect samples due to its low selectivity (CEN 2003; Beier et al. 2007). For non-wadeable sites with a water depth greater than 1 m, multiple types of sampling gear were used, including floating gillnets (mesh size from 1 to 7.5 cm), set gillnets (mesh size from 1 to 7.5 cm) and trap nets (mesh size 1.5 mm). Goldfish were observed at 14 of 45 surveyed sites (elevation ranged from 2915 m to 3840 m). Among them, six sites were excluded from our study due to an insufficient sample size. A total of 372 specimens from the remaining eight sampling sites (five ponds and three wetlands (Table 1);

electrofishing sampling) were used to determine the life-history traits of the goldfish. More than 30 specimens were examined at each site.

During the sampling process, relevant biological data were collected, including the body standard length, eviscerated weight, total weight and gender. The body length was measured to the nearest 0.01 mm with an electronic calliper. The body weight and gonad weight were taken using an electronic balance to the nearest 0.01 g and 0.001 g, respectively. Age was determined from their scales following the method described by Chen (2009). The fish scales were taken from above the lateral line of each individual; then, three to five complete scales from each specimen were cleaned and sealed, and their rings were counted under an optical microscope (BH2: Olympus Optical, Tokyo, Japan).

Life-history traits

Six life-history traits were selected to reflect the growth, development and reproduction of the goldfish. The following traits were measured: (1) Maximal body length (MaxL): maximum standard length measured for the species at eight sampling sites (mm); (2) Longevity (Long): maximum age observed for the species at eight sampling sites (years); (3) Length at first maturation (LenFMat): the minimum length of an individual with a mature gonad (mm) (Stage IV). The gonadal development stages were determined visually following Yin (1995); (4) Total fecundity (TFec): the number of eggs in the ovaries (Stage IV) of mature females. A subsample of ovary weighing 1–2 g was taken from the anterior, middle and posterior portions of each ovary for egg counts and egg diameters measurement (Yin 1995). Calculation of total fecundity: number of oocytes per gram of subsamples × weight of the entire ovary; (5) Relative fecundity (RFec): the number of eggs per gram of fish calculated using the formula: Relative fecundity = Total fecundity/ Eviscerated weight; (6) Egg diameter (EggD): mean diameter of mature fully yolked oocytes (mm) (Stage IV). The egg diameter was measured with software (tpsDig2) after image acquisition.

Environmental variables

Twenty-five environmental variables in the following three categories were considered: climate (BIO1-19, water vapour pressure (kPa), solar radiation (kJ m^{-2} day^{-1}) and wind speed (m s^{-1})), habitat (elevation (m) and watershed area (m^2)) and human disturbance (population density (ind/km^2)) (Table 2). The climatic data used in this study were obtained from the WorldClim database (http://www.worldclim.org) (resolution: 1 km^2). For the habitat variables, elevation was measured with a GPS device (Garmin Montana 650). The polygon tool of Google Earth was used to estimate the area of the watershed by hand-drawing perimeters and calculating the area. The population density was estimated as that of the township to the sampling site.

Table 2. Description of the environmental variables.

Variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temperature - min temperature))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter
Vapr	Water Vapor Pressure
Srad	Solar Radiation
Wind	Wind Speed
ELE	The Altitude above Sea Level at the Sampling Site
WAT	Watershed Area at the Sampling Site
POP	Township Population Density at the Sampling Site

Table 3. Correlation between body size and other life-history traits. b: slope of the linear regression for the given trait; Long: longevity; TFec: total fecundity; RFec: relative fecundity; EggD: egg diameter; LenFMat: length at first maturation.

	Long	TFec	RFec	EggD	LenFMat
R^2	0.608	0.626	0.019	0.203	0.222
P	0.023	0.019	0.742	0.262	0.238
b	0.690	1.978	0.231	−0.067	0.216

The data were obtained from the Fifth National Census reported by the National Bureau of Statistics of the People's Republic of China (http://www.stats.gov.cn/).

Data analysis

To normalize the data, all life-history traits and environmental variables were $\log_{10}$ transformed.

Correction for body size effects

Due to the high correlation between body size and other life-history traits (Table 3), traits significantly related to body size should be corrected as follows: The correction formula is trait (corrected for body size) = trait/$(\text{MaxL})^b$, where b is the slope of the linear regression for the given trait (Blanck et al. 2007).

Multicollinearity analysis of environmental variables

Collinearity refers to the non-independence of predictor variables in statistical models, which may lead to misidentification of relevant predictors (Dormann et al. 2013). To detect collinearity between explanatory variables, Pearson's correlation analysis was performed. When a pair of environmental variables had a correlation coefficient greater than 0.70, which indicated a high degree of collinearity among the variables (Dormann et al. 2013), the more ecologically significant variable was included.

Multiple regression and hierarchical partitioning

We performed multiple regression (MR) and hierarchical partitioning (HP) analyses to evaluate the relationships between life-history traits and environmental variables. The MR analysis was used to develop models that described the effects of the explanatory variables on the response variables (James and McCulloch 1990; Graham 2003). For the MR analysis, a backwards stepwise procedure was used to remove statistically non-significant variables and identify variables that explained variation in life-history traits. After the models were obtained, a second-order Akaike's information criterion (AICc), which corrected for the small sample size, was used to evaluate the candidate model (Burnham and Anderson 2004). The model with the lowest AICc was regarded as the most suitable model. HP analysis was used to evaluate the independent influence of environmental variables on each life-history trait (Mac Nally 1996). The SPSS 18 and R version 3.4.4 (R Development Core Team 2018) statistical software were used for the MR and HP analyses, respectively.

Results

Correction for body size effects

Both Long ($r^2 = 0.608$, $P = 0.023$) and TFec ($r^2 = 0.626$, $P = 0.019$) were significantly correlated with MaxL (Table 3). Therefore, Long and TFec were corrected for body size, and the corrected traits (hereafter referred to as LongC and TFecC, respectively) were used in the analysis.

Multicollinearity analysis of environmental variables

The correlation analysis demonstrated that some pairs of environmental variables had higher coefficients, which revealed some potential collinearity (correlation coefficient > 0.7) (Figure 2). Twenty environmental variables were excluded due to high collinearity. Therefore, only five variables were considered: BIO3 (isothermality), BIO13 (precipitation of the wettest month), ELE (elevation), WAT (watershed area) and POP (population density).

Environmental effects on variations in life-history traits

Generally, the MR and HP analysis results were consistent, but the significance and relative importance of the variables obtained using these methods were slightly different. When evaluated by both methods, MaxL, TFecC and EggD were significantly explained by environmental variables.

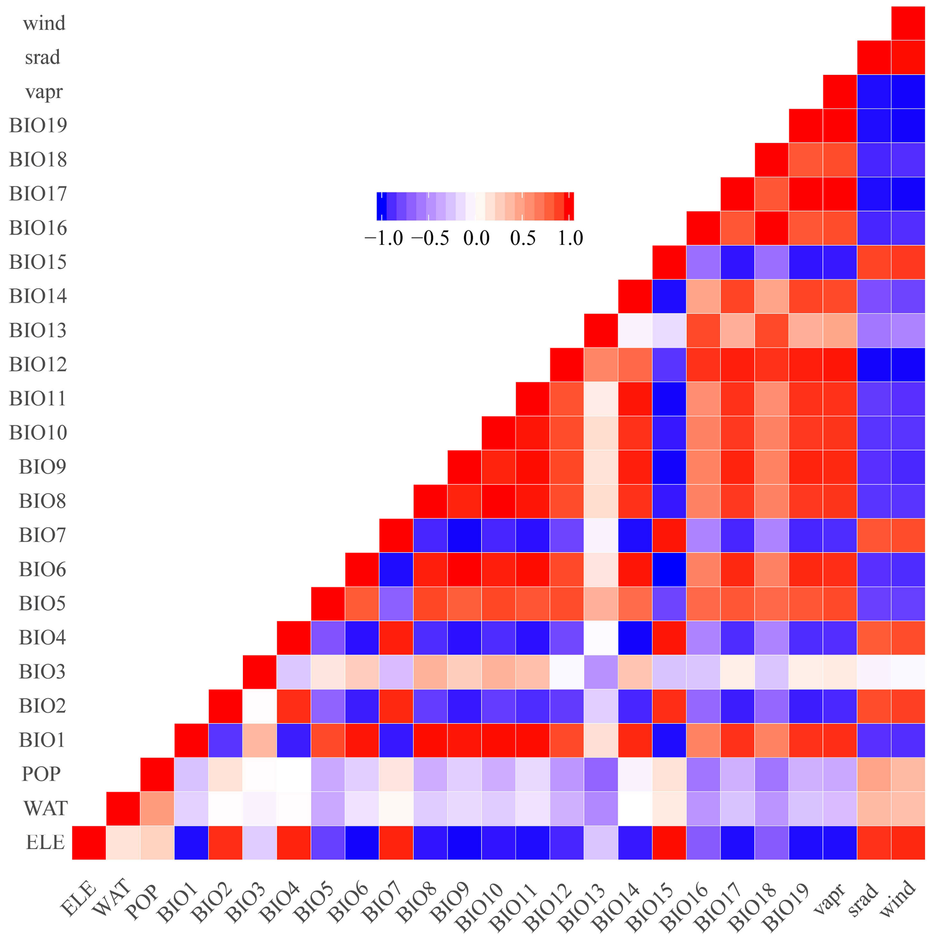

Figure 2. Pearson's correlation coefficients between environmental variables. Abbreviations are defined in Table 1.

Table 4. Multiple regression models for the correlation between life-history traits and environmental variables. AICc: second-order Akaike's information criterion corrected for the small sample size; MaxL: maximum body length; LongC: longevity after controlling for body size; TFecC: total fecundity after controlling for body size; ELE: elevation; POP: population density; BIO3: isothermality; and BIO13: precipitation of wettest month. RFec, EggD and LenFMat see Table 3 for codes.

Variables	Model	AICc	R^2	R^2_{adj}	*p*
MaxL	ELE, POP, BIO3, BIO13	53.079	0.961	0.908	0.019
LongC	Nonsignificant				
TFecC	ELE, POP, BIO3, BIO13	54.279	0.956	0.898	0.022
RFec	Nonsignificant				
EggD	ELE, BIO13	−37.504	0.759	0.663	0.028
LenFMat	Nonsignificant				

For MaxL, the best model in the MR analysis included ELE, POP, BIO3 and BIO13, which explained 90.8% (P = 0.019) of the total variation (Table 4). MaxL was positively related to ELE, POP and BIO13 but negatively related to BIO3. In the HP analysis, BIO3 showed the largest independent effect (42.09%), followed by BIO13 (30.42%), ELE (11.17%) and POP (8.45%) (Figure 3).

For TFecC, the best model in the MR analysis included ELE, POP, BIO3 and BIO13, which explained 89.8% (P = 0.022) of the total variation (Table 4). TFecC was positively related to ELE, POP and BIO13 but negatively related to BIO3. The relative importance of the variables in the HP analysis was 40.63% for BIO3, 30.80% for BIO13, 12.10% for ELE and 8.38% for POP (Figure 3).

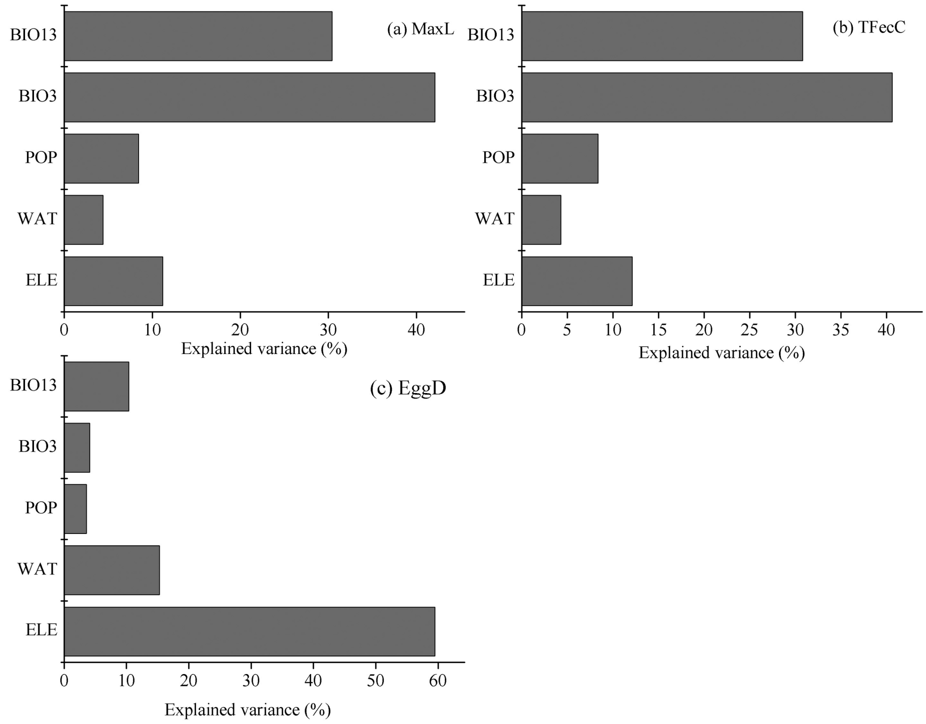

Figure 3. Variance in life-history traits explained by different environmental variables (data from the HP analysis).

For EggD, the best model in the MR analysis included ELE and BIO13, which explained 66.3% (P = 0.028) of the total variation (Table 4). EggD was negatively related to ELE and BIO13. The HP analysis showed that ELE (59.49%), WAT (15.28%) and BIO13 (10.36%) had relative higher independent effects (Figure 3).

Discussion

Responses of life-history traits to environmental variables

The results of the present study supported our first hypothesis and suggested that some life-history traits of goldfish were significantly affected by elevation, population density, isothermality and precipitation of the wettest month. The response of life history to environmental conditions often reflects the highest fitness in a given environment (Endler 1995). Populations in high-elevation areas demonstrate a typical Bergmann's rule response to temperature (Millien et al. 2006). In this case, the variation in body size in goldfish from the plateau is consistent with Bergmann's rule. The maximal length and total fecundity of the goldfish increased and the egg diameter decreased with increasing elevation. The difference in altitude in river systems is related to the unparalleled gradient of glacier effects, substrate, water temperature and oxygen saturation (Hamerlik and Jacobsen 2012; Favre et al. 2015), and these effects are even more extreme in the plateau. A larger body size may confer survival benefits to the goldfish by increasing their reproductive success and competitive ability and reducing their predation risk (Kingsolver and Huey 2008). Populations at higher altitudes that experience lower temperatures and shorter breeding periods tend to produce as many offspring as possible to fully utilize the short-term resources and appropriate environmental conditions (Iverson et al. 1993). The effect of elevation on EggD may be related to temperature, since natural selection favours individuals with smaller egg diameters at low temperatures; individuals with smaller egg diameters have shorter incubation times and greater hatchability, which can facilitate establishment of goldfish in the plateau (Einum and Fleming 2000a).

Human activities always significantly influence water chemistry (Morrice et al. 2007). Population density is the best predictor of the total phosphorus concentration (Osborne and Wiley 1988; Paul and Meyer 2001). In our study, population density was positively related to MaxL and TFecC, probably due to increases in the total phosphorus and total nitrogen concentrations resulting from pollution caused by human activities (Morrice et al. 2007). As a result, the goldfish body size and fecundity increased, possibly due to the abundant resource supply.

Isothermality, which reflects the seasonal change in temperature and is related to species distributions, was negatively related to MaxL and TFecC. The seasonal temperature change in the Qinghai-Tibetan Plateau is greater than that in other regions (Bai et al. 2018). Frequent or extreme changes in seasonal temperature have negative effects on aquatic environments and increase the possibility of droughts or floods (Tytar and Makarova 2015). An increase in seasonal temperature changes could affect the concentrations and distributions of dissolved oxygen and nutrients in the water and in turn affect the life processes of aquatic organisms, resulting in a smaller body size and lower fecundity of these organisms (Carpenter et al. 1992; Cordellier and Pfenninger 2009).

Precipitation of the wettest month, which reflects the greatest water availability in a year, was positively related to MaxL and TFecC but negatively related to EggD. In aquatic systems, lower water availability may lead to low respiration and primary productivity and smaller sizes of top predators, such as fish (Sheridan and Bickford 2011). Additionally, the increase in precipitation enriches nutrients in the aquatic environment and thus increases the reproductive investment (Andrade and Braga 2005; Souza et al. 2015). Therefore, precipitation can determine the body size of goldfish by affecting the availability of food.

Life-history trade-offs of goldfish in the plateau

Our results reveal dramatic changes in the goldfish body size, fecundity and egg diameter in response to environmental changes that are consistent with our second hypothesis, indicating that trade-off between growth and reproduction is the key to the ability of goldfish to adapt to plateau environments. However, the present study further illustrated that the body size and fecundity of goldfish increased with elevation while the egg diameter decreased, suggesting that goldfish exhibited a periodic strategy along altitudinal gradients. Variation in body size is regarded as a trade-off between energy intake, metabolic costs and net energy allocation to different structures and activities (Garvey and Marschall 2003; Millien et al. 2006). Individuals in high-elevation and cold environments can reach a relatively large size by prolonging growth and delaying reproduction (Atkinson 1994; Belk and Houston 2002; Angilletta et al. 2004). For goldfish in the plateau, a larger body size at higher elevations may enhance performance and fitness (Kingsolver and Huey 2008), which improve survival and fecundity (Kingsolver and Pfennig 2004). However, the total reproductive energy in the plateau is limited due to the shortage of resources and cold temperatures. The trade-off between egg diameter and fecundity is closely related to maternal fitness and larval survival (Quinn et al. 1995; Closs et al. 2013; Smalås et al. 2017). The variation in egg diameter appeared to be governed by adaptation to environmental variability and plastic responses to maternal effects among individuals (Feiner et al. 2016). The parents produce smaller eggs and more offspring when total reproductive energy is limited, which can increase survival in plateau environments (Crump 1984; Einum and Fleming 2000b). Smaller eggs require less time to complete development, which can reduce the cumulative risk of offspring being preyed upon (Caldwell et al. 1980).

Management of invasive goldfish in the plateau

The present study reveals that goldfish have a considerable ability to adapt to the plateau environment. Climate, habitat and human disturbance were closely related to the life history, suggesting that goldfish will expand their distribution in response to future global environmental changes. In this respect, Tibetan management needs to take action to prevent their dispersal. Numerous actions have been proposed to eradicate and control non-native fish, such as eradication and removal programmes (Britton et al. 2011). Unfortunately, fish sacrifice-based methods may not be ideal for management of non-native fish in Tibet, where fish are considered sacred. Also, fishing is prohibited, and many religious people act spontaneously to safeguard fish populations in Tibet (Gupta et al. 2016). In addition, the public in Tibet buy small fish (e.g., goldfish and *Pseudorasbora parva*) from local markets and release them into the wild for religious reasons, which is considered a secondary pathway for goldfish dispersal in Tibet (Chen and Chen 2010). Therefore, we advocate that current efforts should focus on taking targeted action to prevent future introductions of goldfish to other areas rather than their eradication and control. Education to promote public awareness of the threats caused by goldfish and other non-native species should be the first priority (Britton et al. 2011), including knowledge dissemination on goldfish identification and their ecological impacts on ecosystems through national media avenues (e.g., newspaper and TV). Further investigations of the habitat preferences of goldfish are also required to predict the potential invasive risk of goldfish in the future.

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