Understanding invasion success of *Pseudorasbora parva* in the Qinghai-Tibetan Plateau: Insights from life-history and environmental filters

Yintao Jia [a], Mark J. Kennard [b], Yuhan Liu [a,c], Xiaoyun Sui [a], Yiyu Chen [a], Kemao Li [d], Guojie Wang [d], Yifeng Chen [a,*]

[a] Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China
[b] Australian Rivers Institute, Griffith University, Brisbane, Queensland, Australia
[c] University of Chinese Academy of Sciences, Beijing 100049, China
[d] Qinghai Provincial Fishery Environmental Monitoring Center, Xining, China

HIGHLIGHTS

- Mechanisms of invasion success of topmouth gudgeon were explored in the Tibetan Plateau.
- Invasive and native populations had distinct life history strategies.
- Sex-specific life history plasticity along an elevational gradient was observed.
- Important environmental correlates of occurrence patterns were identified.

GRAPHICAL ABSTRACT
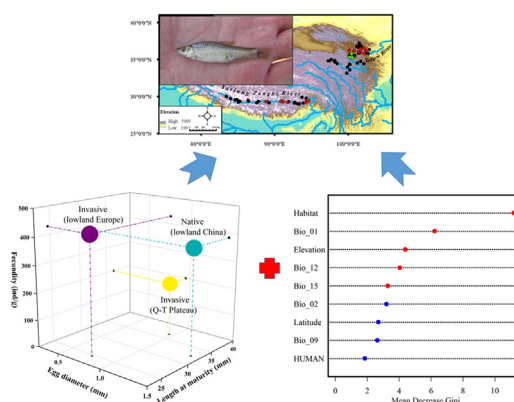
ARTICLE INFO

ABSTRACT

Understanding mechanisms of fish invasion success is crucial to controlling existing invasions and preventing potential future spread. Despite considerable advances in explaining successful fish invasions, little is known about how non-native fish successfully invade alpine freshwater ecosystems. Here, we explore the role of fish life history and environmental factors in contributing to invasion success of *Pseudorasbora parva* on the Qinghai-Tibet Plateau. We compared life history trait differences between native populations in lowland China with introduced populations in lowland Europe and the high elevation Qinghai-Tibet Plateau. Linear mixed-effects models were used to analyse life-history trait variation across elevation gradients. A random forest model was developed to identify the key environmental filters influencing *P. parva* invasion success. Life history characteristics differed substantially between native and introduced populations. Compared with native Chinese populations, introduced populations in lowland Europe had smaller body size, higher fecundity, smaller oocytes and earlier maturation. Introduced populations in the Qinghai-Tibet Plateau had smaller body size, lower fecundity, smaller oocytes and later maturation compared with native populations. 1-Year-Length and fecundity in all age classes

* Corresponding author at: Laboratory of Biological Invasion and Adaptive Evolution, Institute of Hydrobiology, Chinese Academy of Sciences, 7 Donghu South Road, Wuhan, Hubei 430072, China.
E-mail address: chenyf@ihb.ac.cn (Y. Chen).

of females significantly increased with increasing elevation. 2-Year-Length and 3-Year-Length of male signifi-
cantly increased while maximal longevity and length at first maturity were significantly decreased with the ele-
vation gradient. Habitat type, annual mean temperature, elevation, annual precipitation and precipitation
seasonality, were the 5 most important predictors for the occurrence of the *P. parva*. Our study indicates that in-
vasive *P. parva* adopt different life history strategies on the plateau compared with invasive populations at low
elevations, highlighting that more studies are required for a better understanding of biological invasion under ex-
treme conditions. Considering the ongoing hydrologic alteration and climate change, our study also highlighted
that *P. parva* may expand their distribution range in the future on the Qinghai-Tibet Plateau.

1. Introduction

Non-native fishes pose a considerable threat to freshwater ecosys-
tems around the world and can have catastrophic ecological and eco-
nomic consequences (Vitule et al., 2009; Cucherousset and Olden,
2011; Piria et al., 2018). Non-native fish disrupt native fish communities
through several potential mechanisms (Cucherousset and Olden, 2011),
including hybridization and introgression (Muhlfeld et al., 2017), her-
bivory (Miller and Provenza, 2007), competition (Marras et al., 2015),
predation (Correa et al., 2012), disease transmission and parasitism
(Poulin et al., 2011), changes in food webs (Britton et al., 2010), and
habitat alteration (Koehn, 2004). These processes may alter community
structure, ecosystem functioning and provision of ecosystem services
for people (Vilà et al., 2010; Cucherousset and Olden, 2011). Consider-
ing the pervasive ecological and economic impacts of non-native fishes
on freshwater ecosystems, an understanding of the mechanisms of fish
invasion success are needed to inform management of existing inva-
sions and prevent future invasions (García-Berthou, 2007; Aschonitis
et al., 2018).

Many biotic and abiotic factors have been proposed as potential de-
terminants of invasion success of fish (Kennard et al., 2005; Moyle and
Marchetti, 2006; Fitzgerald et al., 2016; Gavioli et al., 2018; Wellband
et al., 2018). Although these factors may be species- and/or region-
specific, life history traits of the invasive species and environmental
characteristics of the invaded system are recognized as important filters
for the outcome of the invasion (Grabowska and Przybylski, 2015;
Howeth et al., 2016). Several theories about life history have been
used to explain the successful invasion of fishes, such as r-and K-
selection (Pianka, 1970), life history theory (Stearns, 1992) and alterna-
tive ontogenies and developmental plasticity (Vilizzi and Kováč, 2014).
For example, life-history theory predicts that invasive populations will
display fast (opportunistic) strategies with early maturity, high repro-
ductive investment, and a short lifespan (Stearns, 1992; Winemiller
and Rose, 1992). Life-history traits have also been widely used as pre-
dictors of fish invasion success and species invasiveness (Olden et al.,
2006). In addition, examination of intra-specific variation in life-
history traits of invasive species at large spatial scales (e.g. along latitu-
dinal or salinity gradients) can provide insight into mechanisms
influencing potential invasiveness of species and environmental factors
limiting their spread (e.g. Alcaraz and Garcia-Berthou, 2007; Benejam
et al., 2009; Carmona-Catot et al., 2011). For instance, invasive
mosquitofish (*Gambusia holbrooki*) populations in lower latitudes allo-
cated more energy to reproduction and had a lower condition
(Carmona-Catot et al., 2011). In addition, mosquitofish females exhib-
ited earlier maturation, higher reproductive investment and a reduced
condition and density along a gradient of increasing salinity (Alcaraz
and Garcia-Berthou, 2007). Understanding how life history trait charac-
teristics vary along environmental gradients can also be used to predict
shifts in distributions in response to global environment changes
(Benejam et al., 2009). In terms of environment, Moyle and Light
(1996) highlight the important role of abiotic factors in determining
fish invasion success and suggest in some systems that, if abiotic factors
are suitable for an introduced species, it will invade successfully regard-
less of biotic factors.

Despite these advances in general understanding of mechanisms of
invasion success, evidence from ecosystems exposed to extreme envi-
ronmental conditions, especially plateau or mountain freshwater eco-
systems, remains limited. Alpine ecosystems, which can be considered
as bioclimatic and biogeographic islands (Burke, 2003), are regarded
as inherently more susceptible than other ecosystems to fish invasion
(Grêt-Regamey et al., 2012). This environment typically supports a
high concentration of endemic aquatic species within a small geograph-
ical range and which are particularly vulnerable to the adverse effects of
invasion (McNeely et al., 2009). However, the rate of fish invasion in
these ecosystems is rising because of the increasing incidence of inten-
tional and accidental introductions of non-native species, and because
anthropogenic disturbance and climate change is likely to increase the
inherent invasibility of these regions (Adams et al., 2001; Ilhéu et al.,
2014).

The Qinghai-Tibetan Plateau (Q-T Plateau) in China provides an ex-
cellent model system to improve our ecological understanding of fish
invasion success in alpine freshwater ecosystems. At least 15 non-
native fish species have successfully established on the Q-T Plateau,
the most wide-spread and abundant of which is the topmouth gudgeon,
Pseudorasbora parva. This small freshwater cyprinid species is native to
eastern Asia, including lowland China, but has spread widely through-
out central Asia, Europe and north Africa. The invasion success of this
species has been attributed to its high plasticity of life history traits
and broad environmental tolerances (Gozlan et al., 2010; Záhorská
et al., 2014).

The aim of our study was to explore the role of life history and envi-
ronmental filters in influencing invasion success of *P. parva* in the Q-T
Plateau. Our specific objectives were to: (1) Compare trait characteris-
tics of *P. parva* from native and introduced populations in China and
Europe to clarify how life history plasticity may contribute to invasion
success of this species in the Qinghai-Tibet Plateau; (2) quantify trait
variation of *P. parva* along an altitudinal gradient in Tibetan rivers to elu-
cidate how trait plasticity in *P. parva* facilitates invasion and spread in
the plateau; (3) quantify potential environmental determinants of inva-
sion success in Tibetan rivers to identify which environmental filters are
important for determining the *P. parva* occurrence in the Qinghai-Tibet
Plateau. We expect that our study will contribute to a broader under-
standing of the mechanism for fish invasion success in alpine freshwater
ecosystems.

2. Material and methods

2.1. Study area and focal species

The Q-T Plateau, often referred to as the 'Third Pole', is the highest
and largest plateau on Earth, covering about 2.5 million km² with an av-
erage elevation of 4000 m above sea level (Wu, 2001; Qiu, 2008). The Q-
T Plateau is the source of some major rivers, such as the Yangtze, Yellow
River and Yarlung Zangbo River, and is known as the "water tower of
Asia" (J. Xu et al., 2009). Aquatic biota in the Q-T Plateau are character-
ized as highly specialised and of low diversity (Hamerlik and Jacobsen,
2012; Favre et al., 2014). There are estimated to be at least 152 fish spe-
cies in Q-T Plateau, 74 of which are endemic species (Wu and Wu,

1991). However, freshwater ecosystems of the Q-T Plateau have experienced multiple fish invasions. Past surveys have documented 13 non-native species in Yarlung Zangbo River and 15 non-native species in the Yellow River (unpublished data). The biomass of non-native fishes accounted for 42.5% of the total biomass in some reaches of the Yarlung Zangbo River (Chen and Chen, 2010). Among the non-native species, topmouth gudgeon *Pseudorasbora parva* is one of the most abundant and widely distributed species (unpublished data).

Topmouth gudgeon is a small freshwater cyprinid species native to East Asia (e.g. Japan, China and Korea) that has successfully established in 32 countries from Central Asia to North Africa and its spread is associated with the introduction of Chinese carps for aquaculture (Gozlan et al., 2010). The native range of *P. parva* in China occurs across a broad geographical extent, including the middle and lower reaches of the Yangtze River. Human translocations have led to the invasion of the *P. parva* in western China, such as Qinghai and Tibet where they were recorded in the 1980s (Wu and Wu, 1990, 1991). The invasive success of this species has been attributed to their high plasticity of life history traits and broad environmental tolerance limits (Gozlan et al., 2010; Záhorská et al., 2014). Following introduction, their opportunistic life-history strategy with a short generation time, protracted spawning, parental care and overall high reproductive effort will enhance their ability to colonize new environments. Moreover, *P. parva* exhibited a great plasticity in habitat utilization in their introduced range, and they can survive in diverse habitat types of lentic and lotic waters (Gozlan et al., 2010).

2.2. Sample collection

To quantify present-day distributions of *P. parva* in relation to environmental gradients and to collect life history trait data for this species, a total of 100 randomly selected sites were sampled along altitudinal gradients in the Yellow River and the Yarlung Zangbo River (Fig. 1). Although the *P. parva* is also found in other rivers on the Q-T Plateau (e.g. Salween River; W.Y. Xu et al., 2009), this species is most widely distributed and abundant in the Yellow River and Yarlung Zangbo River (Chen and Chen, 2010; Tang and He, 2015). Sampling sites covered a large geographical extent for each river, with elevation ranging from 1736 m to 4735 m, and most sites were sampled twice over a four-year period from April to June in 2013 to 2016. Sampling occurred over a broad range of habitats, including rivers, lakes, reservoirs and ponds. An intensive fish sampling strategy was employed to reliably estimate the presence or absence of *P. parva* at each site. For wadeable sites (water depth < 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 (water depth > 1 m), multiple sampling gear types were used, including backpack electrofishing (12 V, 2000–3500 W), 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). A combination of multiple gear types is the most widely recommended way to minimize the gear-specific sampling inefficiency and personality-related sampling bias (Jackson and Harvey, 1997; Biro and Dingemanse, 2009). Electric fishing was conducted according to the CEN (2003) with length equal to 20 times the channel width (rivers) or at least 200m² of fished area (ponds). Gillnets and trap nets were deployed overnight for 12-hour duration (1800 to 0600 h).

All captured *P. parva* were frozen for subsequent laboratory analyses. The standard length was measured to the nearest 0.01 mm using dial callipers. The body weight and gonad weight were measured to the nearest 0.01 g and 0.001 g, respectively. Scales were collected to determine the age of each fish using the methods described by Yan (2005).

2.3. Life-history traits

Eight life-history traits were selected to reflect growth, survival and reproductive performance. The following traits were used: (1) maximum and mean body length (MaxBodyS; MeanBodyS) - maximum and mean standard length present in the samples (mm); (2) length at age (N-Year-Length) - mean standard length for each age-class (from 1 to 3) present in the sample; (3) longevity (Long; MeanLong) - maximum and mean age identified in the samples (years); (4) length at first maturation (LenFMat) - the minimum standard length at which individuals of the species have the ability to reproduce (mm); (5) age at first maturation (AgeFMat) - the minimum age at which individuals of the species have the ability to reproduce (years); (6) fecundity for age (N-Year-RFec) - the mean number of eggs per gram of fish for each age-class (from 1 to 3) present in the sample and calculated using the formula: Relative fecundity = Total fecundity / Eviscerated weight; (7) egg diameter for age (N-Year-ED) - the mean diameter of mature oocytes (mm) for each age-class (from 1 to 3) present in the sample; (8) sex ratio (SexR) - the ratio of females to males in the species.
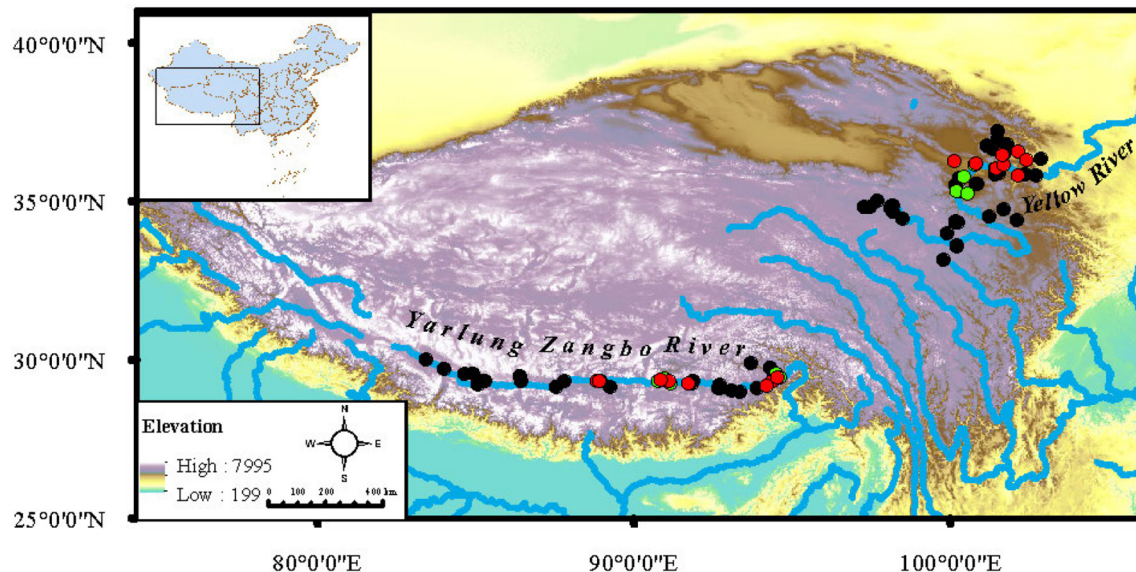

Fig. 1. Sampling sites on the Q-T Plateau. Black dots indicated no distribution of *P. parva*. Green dots indicated the presence of *P. parva* but with insufficient sample sizes. Red dots indicated the presence of *P. parva* and life history traits were used in study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.4. Environmental descriptors

For each sampling location, we obtained data for 23 environmental variables to determine the possible environmental filter(s) influencing invasion success of *P. parva* in terms of climate, habitat and anthropogenic disturbance which have well-documented effects on fish invasion success (Table 1). For the climatic variables, climate data were sourced from the WorldClim database (records from 1950 to 2000; Hijmans et al., 2005; http://www.worldclim.org/). For habitat variables, elevation (m) and latitude were measured in the field with a handheld GPS device. Two habitat types were recorded at field sampling: lotic and lentic. When fish were sampled in flowing rivers, with relatively high velocities, the habitat was defined as lotic. Whereas sampled in lakes, ponds and reservoirs, with low mean column velocities, the habitat was defined as lentic (Blanck and Lamouroux, 2007). Human disturbance intensity at each sampling site was characterized using the Global human footprint (HUMAN) index (Sanderson et al., 2002; http://sedac.ciesin.columbia.edu/). The HUMAN is an integrated measure including nine datasets that represent four data types as proxies for human influence, including: human population density, land transformation (built-up areas, nighttime lights, land use/land cover), and accessibility (coastlines, roads, railroads, navigable rivers).

Prior to analysis, one of each pair of highly correlated variables ($|r| > 0.7$, Spearman's correlation coefficients) was removed to reduce collinearity among predictors (Dormann et al., 2013). All removals were based on a selection criterion of ecological relevance to fish invasion. The final set of environmental predictors included: elevation, latitude, habitat, human, annual mean temperature, mean diurnal range of temperature, mean temperature of driest quarter, annual precipitation, and precipitation seasonality.

2.5. Statistical analyses

2.5.1. Correction for body size effects

A linear regression was performed to explore the possible effects of body size on some life-history traits (Blanck et al., 2007). If the traits were significantly related to body size, then the following equation was fit to eliminate the body size effect (performed separately for each population): trait (corrected for body size) = trait / (MaxL)$^\beta$, where β is the slope of the linear regression for the given trait (Blanck et al., 2007). The corrected trait was then used in the subsequent analyses. In our study, only longevity required correction as it exhibited a significant linear correlation with body size. Egg size was unexpectedly independent of body size, which was possibly due to male parental care of *P. parva*, because parental care plays an essential role in regulating the egg size of fishes (Sargent et al., 1987).

2.5.2. Comparing life history traits variation between native and invasive populations

We compared the life-history traits of native and invasive populations of *P. parva* to evaluate the extent of intraspecific life history trait plasticity and how this may contribute to invasion success of this species. Trait data were assembled for invasive populations from the Qinghai-Tibet Plateau (with mean temperature 5.81 ± 2.81 °C), and invasive populations from low elevations (<300 m) of Europe (with mean temperature 10.55 ± 0.67 °C) and native populations from low elevations (<300 m) in China (with mean temperature 15.46 ± 2.20 °C) were selected. Life history traits of native (Meng, 1982; Han and Li, 1995 (n = 51); Zhang, 1997 (n = 1121); Jin et al., 1996; Wang and Hu, 2015 (n = 31); Yan, 2005 (n = 348 for Chao Lake and 373 for Dongting Lake); Hu, 2017 (n = 59); Li et al., 2017 (n = 167)) and European populations (Adamek and Siddiqui, 1997 (n = 52); Britton et al., 2008 (n = 62 for top and 57 for bottom pond); Záhorská and Kováč, 2009 (n = 226), 2013 (n = 448); Záhorská et al., 2013 (n = 384); Švolíková et al., 2016 (n = 183)) were assembled from the literature. Data for populations from the Q-T Plateau (n = 494, see Appendix S1 for detailed information) were collected as part of this study. Similar to our study, most of the lowland China and European populations were sampled by electrofishing or multiple gear types (e.g. electric fishing and a micro-mesh seine net in Britton et al., 2008; electrofishing and/or by nets in Záhorská and Kováč, 2009, 2013; casting net and gillnet in Wang and Hu, 2015). Unfortunately, most published studies of *P. parva* life history from low elevation regions of Europe and China focused on one or two life history traits and generally do not distinguish gender, which resulted in poor data availability. Only four life history traits of females were finally included in our comparative study:

Table 1
Summary of the environmental parameters in our study.

Abbr.	Environmental parameters	Unit	Minimum	Maximum	Average	S.D.	Data source
Bio_1	Annual mean temperature	°C	−8.67	10.17	3.84	4.22	WorldClim database http://www.worldclim.org/
Bio_2	Mean diurnal range	°C	10.74	15.95	13.48	1.09	
Bio_3	Isothermality		30.68	45.95	39.08	3.84	
Bio_4	Temperature seasonality	°C	5.55	10.25	7.66	1.34	
Bio_5	Max temperature of warmest month	°C	8.30	27.80	20.88	3.64	
Bio_6	Min temperature of coldest month	°C	−23.90	−4.40	−13.95	5.35	
Bio_7	Temperature annual range	°C	26.80	42.80	34.83	4.39	
Bio_8	Mean temperature of wettest quarter	°C	−16.98	19.28	11.20	6.93	
Bio_9	Mean temperature of driest quarter	°C	−14.72	7.22	−4.17	5.71	
Bio_10	Mean temperature of warmest quarter	°C	0.08	20.67	12.73	3.83	
Bio_11	Mean temperature of coldest quarter	°C	−16.98	2.53	−6.04	4.98	
Bio_12	Annual precipitation	mm	186.00	724.00	433.52	119.67	
Bio_13	Precipitation of wettest month	mm	26.00	147.00	97.83	28.11	
Bio_14	Precipitation of driest month	mm	0.00	6.00	1.58	1.38	
Bio_15	Precipitation seasonality	mm	44.70	142.49	96.37	20.39	
Bio_16	Precipitation of wettest quarter	mm	68.00	395.00	255.68	74.18	
Bio_17	Precipitation of driest quarter	mm	2.00	34.00	8.89	7.72	
Bio_18	Precipitation of warmest quarter	mm	34.00	395.00	248.57	87.75	
Bio_19	Precipitation of coldest quarter	mm	2.00	109.00	16.61	27.77	
Elevation	Elevation	m a.s.l.	1736.00	4735.00	3271.72	788.89	Handheld GPS device
Latitude	Latitude	Dec. degrees	28.98	37.25	32.81	3.15	
Habitat	Habitat types (lotic/lentic)						Wild survey
HUMAN	Global human footprint	%	4.00	76.00	25.41	12.75	Global Human Footprint database http://sedac.ciesin.columbia.edu/

maximum body length, length at first maturation, fecundity and egg size. Nonparametric Kruskal-Wallis one-way analysis of variance was used to test for regional differences in life history traits. Prior to the analysis, the Kruskal-Wallis test assumption of equal within-group variance was verified.

2.5.3. Quantifying trait variation of P. parva along an elevational gradient in rivers of the Q-T Plateau

P. parva were observed at 28 of 100 surveyed sites and they always co-occurred with at least one other native species (e.g. *Gymnocypris eckloni* and *Schizopygopsis younghusbandi younghusbandi, Triplophysa pseudoscleroptera*) and non-native species (e.g. *Carassius auratus, Misgurnus anguillicaudatus, Abbottina rivularis*) (Appendix S2). Life history traits of populations from 16 sites (eight from Qinghai Province and eight from Tibet) were used to examine how the life history characteristics of *P. parva* varied along elevational gradients in each river. The remaining 12 sites were excluded from our study due to insufficient sample sizes of *P. parva*. A total of 1168 specimens were examined to determine the life-history traits of *P. parva* at each site (see Appendix S1 for detailed information).

Linear mixed-effects models (R packages lme4 (Bates et al., 2018)) were used to analyse life-history trait variation for each sex separately across elevation gradients (used here as a proxy for variation in climate and habitat (Körner, 2007)). In the analyses, elevation was included as a fixed factor and river was considered as a random effect. To satisfy normality assumptions (Zuur et al., 2009), elevation and all life-history traits except for SexR were log-transformed priori to analyses. SexR was transformed using arcsine square-root transformation (Blanck et al., 2007).

2.5.4. Quantify potential environmental determinants of invasion success in rivers of the Q-T Plateau

A random forest model relating environmental characteristics to *P. parva* occurrence was developed to predict the presence or absence of *P. parva* and quantify the relative importance of environmental factors in influencing fish invasion success (R packages "randomForest" package by Liaw and Wiener (2002)). The random forest model is a non-parametric method which constructs a large number of classification or regression trees (500 trees in our case) to produce accurate predictions (Breiman, 2001). The algorithm begins with the random selection of approximately 2/3 of the whole data as training dataset ('in-bag' data) and the remaining 1/3 data are used for model validation ('out-of-bag' data) (Cutler et al., 2007). Each decision node is then split using the best among a randomized subset of the predictors at each node (Liaw and Wiener, 2002). The 'out-of-bag' data are used to estimate the prediction accuracies and error rates for each tree (Cutler et al., 2007). The final outcome is the average of the predictions from all the trees (Breiman, 2001; Cutler et al., 2007). In addition, Cohen's Kappa was also calculated from the out-of-bag data to measure model fit. Those with a value > 0.81 are considered almost perfect agreement, values of 0.61–0.80 substantial agreement, and values of 0.41 to 0.60 moderate agreement (Landis and Koch, 1977). The importance of each predictor was measured using the Gini index (Strobl et al., 2007). Larger Gini index for a feature is an indication of higher importance. Partial dependence plots were created to visualize the marginal effect of each variable on the occurrence of *P. parva* (Cutler et al., 2007).

3. Results

3.1. Comparison of traits from native and introduced populations in China and Europe

Spatial differences in the four morphology and life history traits were observed between invasive populations of *P. parva* from the Q-T plateau, lowland Europe, and native populations in lowland China. Native Chinese (p = 0.059, marginally significant) and invasive

European populations (p = 0.082, marginally significant) from low elevations had larger maximal length than high elevation populations from the Q-T plateau (Fig. 2a). In contrast, fish from the Q-T plateau were larger at first maturity (Fig. 2b) compared with European native populations (p < 0.001), while native populations were of intermediate size. Invasive populations from lowland Europe had higher fecundity (Fig. 2c) and smaller egg sizes (Fig. 2d) than populations from both other regions. Invasive populations from the Q-T plateau had the lowest fecundity and intermediate egg sizes compared with the other two regions. In addition, the native and invasive populations occupied different locations of a trivariate life history space defined by fecundity, length at first maturity and egg diameter (Fig. 3).

3.2. Quantifying trait variation of P. parva along an elevational gradient in rivers of the Q-T Plateau

The linear mixed models revealed that differences in effect of elevation on the various life-history traits of the *P. parva*, and there were also differences between females and males (Table 2) along the altitudinal gradients. When considering females, length of 1-year fish increased significantly with increasing elevation. Higher elevation populations also showed higher fecundity for all age classes. Variation in all other female life history traits was not significantly related to elevation. In the case of males, 2-Year-Length and 3-Year-Length significantly increased with the elevation gradient, while longevity and length at first maturity were significantly negatively associated with elevation.

3.3. Potential environmental determinants of invasion success in rivers of the Q-T Plateau

The *P. parva* were observed at 28 of 100 surveyed sites. In the RF model, the estimate of classification error rate (the out-of-bag or OOB estimate) was low at 10.0%, and the Cohen's Kappa coefficient was 0.752, which indicated that the model performed well in predicting the occurrence of the *P. parva*. The variable importance results indicated that habitat type (lentic vs lotic) had the highest relative importance value, and followed by annual mean temperature, elevation, annual precipitation and precipitation seasonality, whose were the five most important predictors among the nine environmental predictors (Fig. 4). Other environmental variables showed low levels of importance, with the HUMAN was the least important one (Fig. 4). Results from partial dependence plots indicate that environmental predictors related to *P. parva* occurrence generally non-linearly, including polynomial forms and sudden change after thresholds (Fig. 5). Habitat showed a strong threshold effect, with a low probability of *P. parva* occurrence at lotic habitat type. Annual mean temperature had a positive relationship *P. parva* occurrence, with a sharp increase when annual average temperature more than about 0 °C. Elevation has a negative relationship while annual precipitation has a humped relationship with *P. parva* occurrence (Fig. 5). With the increased elevation, when elevation near 4000 m, the *P. parva* occurrence sharply declined, whereas *P. parva* occurrence showed a slight upward trend when the annual average rainfall is greater than about 300 mm. The partial dependence plots also show that the *P. parva* occurrence increases with precipitation seasonality up to about 100, and then remains relative stable at the higher values (Fig. 5).

4. Discussion

4.1. Variation in traits from native and introduced populations in China and Europe

Plasticity in life-history traits has been recognized as an important advantage of invasive species, which allow them to optimize life history traits in response to environmental conditions of colonized habitats and play an essential role in invasion success (Chun et al., 2007; Valiente
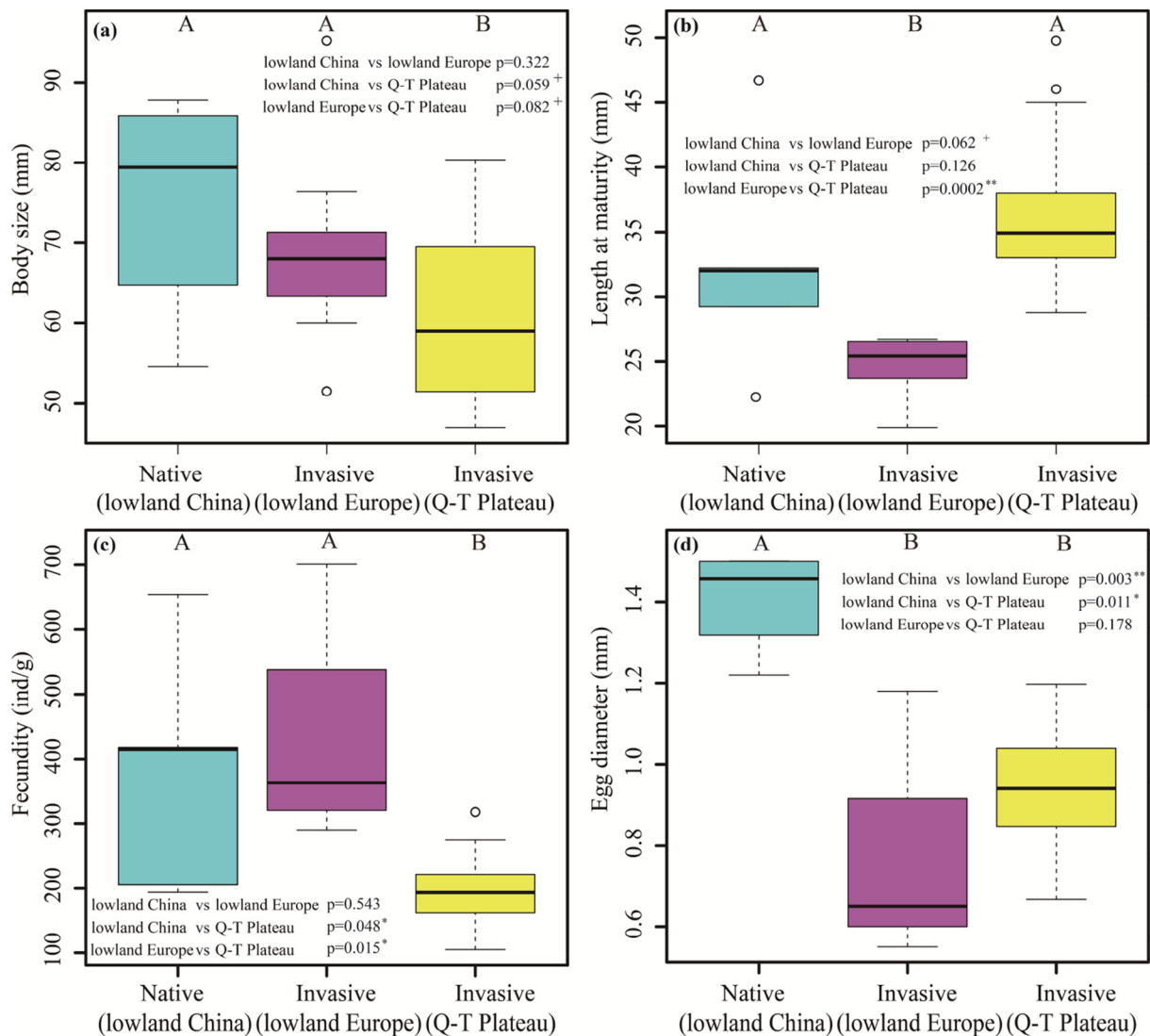
Fig. 2. Differences in morphological and life history traits between invasive and native populations. Different capital letter indicates a significant difference between regions. *p < 0.05; **p < 0.01; [+]p < 0.1 (marginally significant).

et al., 2010). Consistent with this assertion, invasive populations of *P. parva* at low elevations in Europe and extremely high elevations on the Q-T Plateau exhibit different biological trait characteristics from populations in the native range in lowland China. Considering these differences in terms of the tri-variate life-history strategy model (similar to Winemiller and Rose, 1992), the invasive lowland European populations followed a more opportunistic life history strategy characterized by smaller body size, higher fecundity, smaller oocytes and earlier maturation than native populations. This strategy may maximize colonizing capacity for an invasive species in a new environment (Fox et al., 2007). However, the invasive population at the Q-T Plateau adopted a very different life history strategy with small body size, lower fecundity, smaller oocytes, and later maturation compared with the species' native populations. This strategy may be more advantageous in environments with limited resources and/or intense density dependence (Winemiller and Rose, 1992). It is well recognized that the ability to switch to a more opportunistic life-history strategy may facilitate the expansion of an invading species (Vila-Gispert et al., 2005; Fox et al., 2007). Invasive populations at low elevation support this theory, while populations at high elevation exhibit almost the opposite strategy. This difference may be explained by life history trade-offs among traits that can contribute to an organism's fitness and which are a pivotal element of life history theory (Stearns, 1989). No species can

simultaneously maximize all their life history functions within a given environment (Olden et al., 2006), i.e. increasing fitness in one life history trait is generally countered by reducing fitness in other traits (Stearns, 1977). Our findings provide evidence that *P. parva* optimizes the trade-off between investment in reproduction and growth to facilitate the successful invasion and spread.
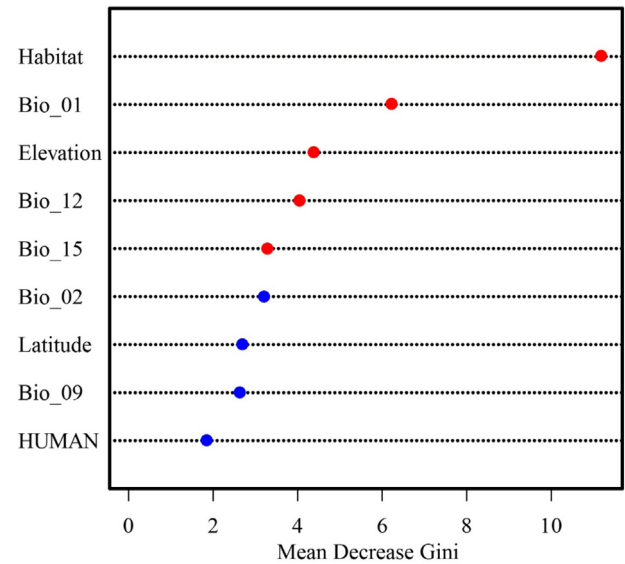
Life-history traits of fishes are expected to change in populations in response to abiotic factors such as thermal and hydrologic regimes (Jonsson et al., 2013; Bennett et al., 2016), biotic factors including resource availability, competition or predation (Reznick et al., 2001; Gozlan et al., 2010; Jonsson et al., 2013), as well as environmental changes caused by human activities (Hendry et al., 2008; Milardi et al., 2018a). However, lack of quantitative data to characterize these potential abiotic and biotic mechanisms for our study regions in the Q-T Plateau, lowland China and Europe, limits our understanding of the factors influencing life-history plasticity of *P. parva*. Another source of uncertainty is the potential for differences in sampling methods used in studies from the three regions to introduce biases in characterization of population-level life history traits of *P. parva*. This is because different sampling methods and fish behavioral traits can affect capture probability of individuals, and these traits may be correlated with other physiological and life history traits (Redpath et al., 2009; Biro, 2013). We minimized this potential source of bias by consistently using multiple
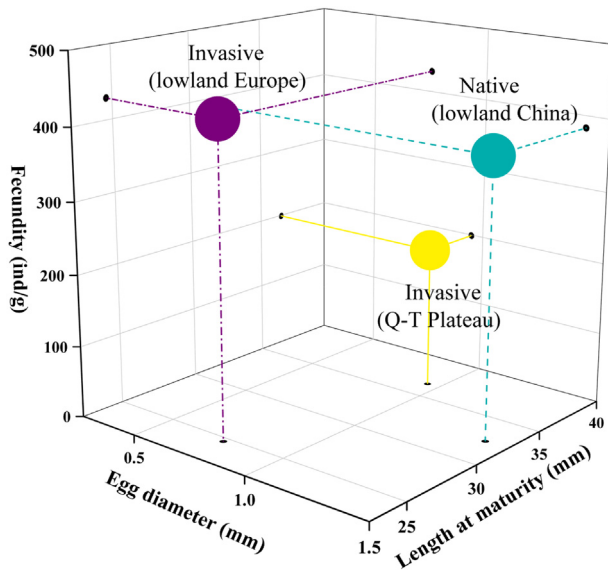
Fig. 3. The location of native and invasive populations in the three-dimensional space established by fecundity, length at maturity and egg diameter (data is the average for each region).

Fig. 4. Variable importance for the 9 predictors from random forest models for the presence of the *P. parva* (Habitat: habitat types; Bio_1: annual mean temperature; Bio_12: annual precipitation; Bio_15: precipitation seasonality; Bio_02: mean diurnal range; Bio_09: mean temperature of driest quarter; HUMAN: global human footprint).

gear types for our sampling in the Q-T plateau but lack of information meant we were unable to control for this for other studies from lowland China and Europe. Nevertheless, we do not expect that sampling-induced biases explain the observed differences in life history traits between the three study regions. According to current empirical and theoretical knowledge and our available data, we speculate that cold temperatures, poor resource availability, lower predation risk and lower human disturbance intensity in the Q-T Plateau compared with lowland China and lowland Europe are potential contributing factors in shaping the observed trade-off patterns of *P. parva*.

Temperature is a critical abiotic factor regulating growth, development and reproduction performance of fishes (Angilletta et al., 2004; Samsing et al., 2016). It is widely reported that temperature strongly influences the entire life cycle of fishes from embryo development (Hanel et al., 1996), larval and juvenile development and survival (Pankhurst and Munday, 2011), to sexual maturation and reproductive output in adults (Miller et al., 2015). In addition, temperature can also affect rates of primary productivity (O'Beirne et al., 2017) and energy transfer between trophic levels (Barneche and Allen, 2018). Water temperature was considered as the major determinant of the expression of life history traits of *P. parva* (Gozlan et al., 2010). Comparing the average annual temperature in various regions, as a surrogate for water temperature, it can be seen that native populations inhabit the highest temperature, followed by invasive populations at Europe and invasive populations at plateau regions. Selective pressures of different thermal environments may cause tradeoffs between growth and reproduction for invasive populations, which then lead to apparent divergent regional life history strategies (Blanck and Lamouroux, 2007).

Resource availability has also been recognized to influence life history expression (McBride et al., 2015). The food composition of *P. parva* is diverse and includes microcrustaceans, molluscs, chironomid

Table 2
Linear mix model results of relationships between elevation and variation in each life history traits. MaxBodyS: maximum body length; MeanBodyS: mean body length; Long: maximum age; MeanLong: mean age; LenFMat: length at first maturation; AgeFMat: age at first maturation; RFec: relative fecundity; ED: egg diameter; SexR: sex ratio.

Traits	Female				Male			
	Estimate	SE	t	p	Estimate	SE	t	p
MaxBodyS	−0.074	0.197	−0.376	0.712	−0.015	0.097	−0.159	0.875
MeanBodyS	0.074	0.126	0.589	0.564	0.040	0.127	0.317	0.756
1-Year-Length	0.137	0.067	2.045	0.059[+]	0.192	0.110	1.751	0.100
2-Year-Length	0.002	0.064	0.034	0.973	0.213	0.080	2.651	0.017[*]
3-Year-Length	0.039	0.121	0.318	0.758	0.102	0.043	2.372	0.031[*]
Long	−0.013	0.095	−0.134	0.895	−0.179	0.053	−3.362	0.004[**]
MeanLong	−0.132	0.110	−1.199	0.248	−0.104	0.093	−1.114	0.282
LenFMat	0.055	0.176	0.312	0.759	−0.358	0.199	−1.799	0.091[+]
AgeFMat	0.238	0.239	0.999	0.333	−0.346	0.352	−0.985	0.339
RFec	0.849	0.223	3.802	0.002[**]				
1-Year-RFec	1.035	0.394	2.629	0.019[*]				
2-Year-RFec	0.863	0.364	2.372	0.032[*]				
3-Year-RFec	1.096	0.207	5.287	0.001[**]				
ED	0.226	0.154	1.466	0.162				
1-Year-ED	0.248	0.197	1.263	0.226				
2-Year-ED	0.415	0.261	1.587	0.133				
3-Year-ED	−0.237	0.278	−0.853	0.419				
SexR (F:M)	−4.881	18.264	−0.267	0.793				

[*] p < 0.05.
[**] p < 0.01.
[+] p < 0.1 (marginally significant).
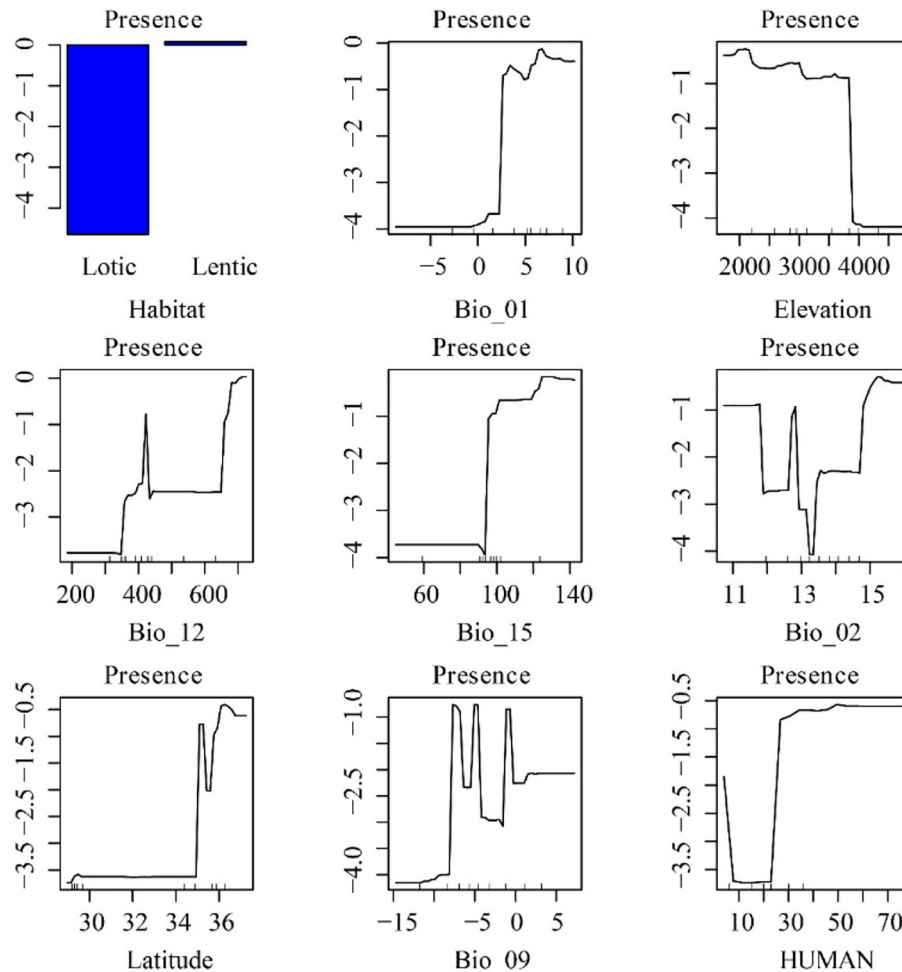
Fig. 5. Partial dependency plots for the 9 predictors from random forest models for the presence of the *P. parva* (Habitat: habitat types; Bio_1: annual mean temperature; Bio_12: annual precipitation; Bio_15: precipitation seasonality; Bio_02: mean diurnal range; Bio_09: mean temperature of driest quarter; HUMAN: global human footprint).

larvae, rotifers, detritus and algae (Gozlan et al., 2010). However, food resource availability is much lower in the Q-T Plateau compared with low elevation regions. For example, the biomass of macroinvertebrates in the high elevation Yarlung Zangbo Rivers is 0.01 g/m² for main stream and 0.06 g/m² for tributaries while the biomass for the low elevation rivers in the Yangtze River range from 0.21 g/m² to 0.42 g/m² (Zhao and Liu, 2010). Food quality might be another factor to take into account (Jonsson et al., 2013). *P. parva* has very diverse food preferences and exhibits enormous flexibility in attaining it. *P. parva* have a broad diet breadth and the feeding types change with native and introduced range. For native populations, the diet of *P. parva* was dominated by cladocerans (52.43%), aquatic insect larvae (27.71%) and non-animal food (10.28%) (Xie et al., 2001). In contrast, the items most frequently ingested by invasive *P. parva* in the lowlands of Europe were benthic crustaceans, insect larvae and zooplankton, with 2% non-animal food in Hungary (Hliwa et al., 2002), and *P. parva* fed almost exclusively on chironomids in Austria (Wolfram-Wais et al., 1999). Algae were the dominant species in terms of abundance in prey item of the Q-T plateau populations, accounting for 54.19% in terms of weight (Ding et al., 2018). Abundance and quality of the food determined an organism's intake of resources, and allocation of resources to fitness-related activities may change the growth and maturation schedules of the invader, resulting a shift in life history strategies (Boggs, 1992; Winemiller and Rose, 1992).

Variations in the local species pool and hence the potential for biotic interactions (i.e. competition and predation) may also have led to differential plasticity in life-history for populations in Q-T Plateau, lowland China and Europe (Reznick et al., 2001). Populations of *P. parva* in the Q-T Plateau coexisted with relatively few fish species (ranging from 1 to 9 species), compared with populations in lowland Europe (5 to 13 species) and lowland China (26 species in Niushan Lake and 27 species in Biandantang Lake) (Appendix S2). Lack of information on species relative abundances, resource use and availability means it is not possible to infer competition among coexisting species as a mechanism explaining observed differences in life history characteristics of *P. parva*. However, no piscivorous fishes were found co-occurring with *P. parva* in the Q-T plateau. In contrast, *P. parva* populations in lowland China and Europe are likely exposed to intense predation pressure by coexisting with piscivores such as *Cultrichthys erythropterus* in lowland China and *Sander lucioperca* in lowland Europe (Appendix S2).

Finally, populations may also exhibit differential phenotypic responses when exposed to different levels and sources of environmental perturbation (Hendry et al., 2008). Among our study areas, the Q-T Plateau had the lowest human footprint (mean 25.41 ± 12.75 SD), followed by lowland China (33.20 ± 21.08) and Europe (52.43 ± 18.32). These spatial differences in human disturbance intensity may also have contributed to observed differences in life history strategies of *P. parva* between the three regions.

4.2. Influence of elevation gradients on trait variation of P. parva in rivers of the Q-T Plateau

Life-history plasticity is often crucial for invasion success in high elevation environments (Morrison and Hero, 2003). Some key life-history

traits of *P. parva* varied substantially across the elevational gradient, with a significant increase in 1-Year-Length and fecundity-at-age at higher elevation for female and increase in 2-Year-Length and 3-Year-Length but a decrease in longevity and length at first maturity for males. For females, the increasing 1-Year-Length highlights the importance of investing resources in female growth during the first years to obtain larger body size to enhance the probability of surviving to first reproduction (Blanckenhorn, 2000). According to the "bigger is better" hypothesis (Miller et al., 1988; Sogard, 1997), larger larvae or juveniles are expected to be more resistant to starvation, less vulnerable to predators and better able to tolerate environmental extremes, which will help them gain a survival advantage over smaller conspecifics. Our study found that fecundity of *P. parva* at all age classes was increased along the altitudinal gradient, which suggests that this may produce more oocytes to adapt to the more unfavorable alpine habitats. Two theories have been proposed to explain this variation: (1) Life history theory predicted that individuals from a fluctuating environments usually have larger reproductive effort, such as higher fecundity than individuals from a stable habitat (Stearns, 1992); (2) the 'Moreau-Lack's rule' (proposed by Moreau (1944) and Lack (1954)) suggested that fecundity increases predictably with increasing latitude (or elevation) to adapt environmental differences along geographic gradients (e.g. seasonality, length of breeding season, food availability, temperature) (Pincheira-Donoso and Hunt, 2017). In contrast to females, larger adult body size in males will be favored by predation, feeding, competition, mating success and survival (Gross and Sargent, 1985; Parker, 1992; Konishi and Takata, 2004), which will improve the fitness for males adapting to the higher altitudes. Decrease in the maximal age along elevational gradient might be caused by possible increased energetic cost of male parental care (Forsgren et al., 2004), or (and) male-male competition (Maekawa et al., 1996). The fitness benefits of early maturation in male are short generation times and higher survival rate to maturity (Vrtílek et al., 2018).

4.3. Quantifying potential environmental determinants of invasion success in rivers of the Q-T Plateau

According to the community assembly theory, the environment functions like the most critical filter in determining the outcome of invasions (Moyle and Light, 1996; Bae et al., 2018; Radinger et al., 2019). The environmental filter is thus defined as "abiotic factors that prevent the establishment or persistence of species in a particular location" (Kraft et al., 2015). Habitat, annual mean temperature, elevation, annual precipitation and precipitation seasonality were ranked as the five most important features for predicting the distribution of *P. parva* in the Q-T Plateau, which also suggested that these factors could be environmental filters determining the future susceptibility of recipient regions to *P. parva* invasion. *P. parva* can inhabit both lentic and lotic waters in their native range. However, their highest abundances commonly occur in relatively small lentic systems in their invasive range in Europe (Jackson et al., 2015), which are consistent with our observation in the Q-T Plateau. Although the *P. parva* also occurred at lotic habitats in the Q-T Plateau, it could be explained as the function of the both habitats. Lentic waters function as spawning, nursery and adult habitats, while the lotic water merely serves as a dispersal corridor for the *P. parva* (Pollux and Korosi, 2006). Following habitat, the annual mean temperature was among the most influential variables predicting the *P. parva* occurrence. All freshwater fish species are poikilotherms, thermal regime will strongly affect their physiology, bioenergetics, and behavior (Rahel and Olden, 2008). The ability to tolerate wide ranges of temperature was therefore determined the outcome of invasive species. Our study showed that the occurrence of the *P. parva* increased when annual mean temperature was higher than 0 °C, which suggested that 0 °C may be near their lower temperature threshold. This thermal constraint will likely limit the presence of *P. parva* at temperatures lower than 0 °C. High-elevation is always considered as natural barriers to

prevent biological invasion (Lapointe and Light, 2012). Many studies have illustrated the importance of elevation in controlling the *P. parva* distribution in Japan (Fukuda et al., 2013) and Slovakia (Jakubčinová et al., 2018). Our study confirmed this result, and suggested the possible high altitudinal threshold for *P. parva* was slightly below 4000 m. Annual precipitation and precipitation seasonality were strongly positively associated with the presence of the *P. parva*, and these may be caused by the habitat use of the fish. *P. parva* tended to use lentic waters including wetlands and ponds in the Q-T Plateau, and changes in precipitation modified the amount and quality of habitat for the *P. parva*, which directly influence their distribution (Poff et al., 2002; Liu et al., 2017). Interestingly, spatial variation in human disturbance intensity was not an important predictor of the occurrence of *P. parva*, despite being generally considered to be a major driver of non-native species distributions and ecosystem invasibility (Vitousek et al., 1997; Ellis, 2015). This finding probably relates to generally low human population densities (e.g. <3 people per square kilometer in Tibet; National Bureau of Statistics of the People's Republic of China 2017, http://www.stats.gov.cn/) and hence generally low human footprint index values across our study sites (mean 25.41 ± 12.75 SD) in the Q-T Plateau (Table 1). Notwithstanding our findings, we caution the reader of an important limitation of our study. Data limitations meant that we could not include other potentially important abiotic and biotic determinants of invasion success by *P. parva* in our analyses (e.g. spatial data describing relative invasibility or propagule pressure; Guo et al., 2015; Milardi et al., 2018b).

4.4. Potential for future spread of P. parva in the Q-T plateau

Our study confirmed that high plasticity in life history is an important attribute that may have helped *P. parva* to become established and spread in the Q-T plateau. In addition, our findings also highlight that environmental characteristics (including lentic habitat type, climate factors and elevation) were important correlates of the current distribution of the *P. parva* in the Q-T plateau. In addition, the prospect of future environmental changes in conjunction with life history advantages may promote the spread of the *P. parva* in the Q-T plateau. For example, several large dams have already been built on the Q-T Plateau three dams are currently under-construction, and nine dams will be built in the future at source of the Yellow River (Xie et al., 2018). The conversion of lotic to lentic habitat caused by these dams is likely to create new niche opportunities for *P. parva* and promote their spread in the Q-T Plateau (Liew et al., 2016). Climate change may affect aquatic invasive species through altering thermal and hydrologic regimes (Rahel and Olden, 2008). The Q-T Plateau has experienced significant warming during the last half century (Liu and Chen, 2000) and temperatures are projected to continue increasing at a faster rate than the global average (Zhang et al., 2015). These thermal changes, combined with likely changes to runoff associated with changes in precipitation and snowmelt, mean a further range expansion of *P. parva* in the Q-T Plateau may be expected.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.133739.

Acknowledgements

References

Adamek, Z., Siddiqui, M.A., 1997. Reproduction parameters in a natural population of topmouth gudgeon, *Pseudorasbora parva*, and its condition and food characteristics with respect to sex dissimilarities. Pol. Arch. Hydrobiol. 1, 1–2.

Adams, S.B., Frissell, C.A., Rieman, B.E., 2001. Geography of invasion in mountain streams: consequences of headwater lake fish introductions. Ecosystems 4, 296–307. https://doi.org/10.1007/s10021-001-0012-5.

Alcaraz, C., Garcia-Berthou, E., 2007. Life history variation of invasive mosquitofish (*Gambusia holbrooki*) along a salinity gradient. Biol. Conserv. 139, 83–92. https://doi.org/10.1016/j.biocon.2007.06.006.

Angilletta, M.J., Steury, T.D., Sears, M.W., 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integr. Comp. Biol. 44, 498–509. https://doi.org/10.1093/icb/44.6.498.

Aschonitis, V.G., Gavioli, A., Lanzoni, M., Fano, E.A., Feld, C., Castaldelli, G., 2018. Proposing priorities of intervention for the recovery of native fish populations using hierarchical ranking of environmental and exotic species impact. J. Environ. Manag. 210, 36–50. https://doi.org/10.1016/j.jenvman.2018.01.006.

Bae, M.J., Murphy, C.A., García-Berthou, E., 2018. Temperature and hydrologic alteration predict the spread of invasive Largemouth Bass (*Micropterus salmoides*). Sci. Total Environ. 639, 58–66. https://doi.org/10.1016/j.scitotenv.2018.05.001.

Barneche, D.R., Allen, A.P., 2018. The energetics of fish growth and how it constrains food-web trophic structure. Ecol. Lett. 21, 36–844. https://doi.org/10.1111/ele.12947.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., 2018. Package 'lme4'. https://cran.r-project.org/web/packages/lme4/index.html, Accessed date: 22 December 2018.

Beier, U., Degerman, E., Melcher, A., Rogers, C., Wirlöf, H., 2007. Processes of collating a European fisheries database to meet the objectives of the European Union Water Framework Directive. Fish. Manag. Ecol. 14, 407–416. https://doi.org/10.1111/j.1365-2400.2007.00579.x.

Benejam, L., Alcaraz, C., Sasal, P., Simon-Levert, G., Garcia-Bethou, E., 2009. Life history and parasites of the invasive mosquitofish (*Gambusia holbrooki*) along a latitudinal gradient. Biol. Invasions 11, 2265–2277. https://doi.org/10.1007/s10530-008-9413-0.

Bennett, M.G., Whiles, M.R., Whitledge, G.W., 2016. Population-level responses of life history traits to flow regime in three common stream fish species. Ecohydrol 9, 1388–1399. https://doi.org/10.1002/eco.1734.

Biro, P.A., 2013. Are most samples of animals systematically biased? Consistent individual trait differences bias samples despite random sampling. Oecologia 171, 339–345. https://doi.org/10.1007/s00442-012-2426-5.

Biro, P.A., Dingemanse, N.J., 2009. Sampling bias resulting from animal personality. Trends Ecol. Evol. 24, 66–67. https://doi.org/10.1016/j.tree.2008.11.001.

Blanck, A., Lamouroux, N., 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. J. Biogeogr. 34, 862–875. https://doi.org/10.1111/j.1365-2699.2006.01654.x.

Blanck, A., Tedesco, P.A., Lamouroux, N., 2007. Relationships between life-history strategies of European freshwater fish species and their habitat preferences. Freshw. Biol. 52, 843–859. https://doi.org/10.1111/j.1365-2427.2007.01736.x.

Blanckenhorn, W.U., 2000. The evolution of body size: what keeps organisms small? Q. Rev. Biol. 75, 385–407. https://doi.org/10.1086/393620.

Boggs, C.L., 1992. Resource allocation: exploring connections between foraging and life-history. Funct. Ecol. 6, 508–518. https://www.jstor.org/stable/2390047.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Britton, J.R., Davies, G.D., Brazier, M., 2008. Contrasting life history traits of invasive topmouth gudgeon (*Pseudorasbora parva*) in adjacent ponds in England. J. Appl. Ichthyol. 24, 694–698. https://doi.org/10.1111/j.1439-0426.2008.01163.x.

Britton, J.R., Davies, G.D., Harrod, C., 2010. Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: a field investigation in the UK. Biol. Invasions 12, 1533–1542. https://doi.org/10.1007/s10530-009-9566-5.

Burke, A., 2003. Inselbergs in a changing world-global trends. Divers. Distrib. 9, 375–383. https://doi.org/10.1046/j.1472-4642.2003.00035.x.

Carmona-Catot, G., Benito, J., García-Berthou, E., 2011. Comparing latitudinal and upstream-downstream gradients: life history traits of invasive mosquitofish. Divers. Distrib. 17, 214–224. https://doi.org/10.1111/j.1472-4642.2011.00743.x.

CEN (European Committee for Standardization), 2003. Water quality: sampling of fish with electricity. European Standard EN 14011. E. CEN, Brussels, p. 2003.

Chen, F., Chen, Y.F., 2010. Investigation and protection strategies of fishes of Lhasa River. Acta Hydrobiol Sin 34, 278–285 (in Chinese).

Chun, Y.J., Collyer, M.L., Moloney, K.A., Nason, J.D., 2007. Phenotypic plasticity of native vs. invasive purple loosestrife: a two-state multivariate approach. Ecology 88, 1499–1512. https://doi.org/10.1890/06-0856.

Correa, C., Bravo, A.P., Hendry, A.P., 2012. Reciprocal trophic niche shifts in native and invasive fish: salmonids and galaxiids in Patagonian lakes. Freshw. Biol. 57, 1769–1781. https://doi.org/10.1111/j.1365-2427.2012.02837.x.

Cucherousset, J., Olden, J.D., 2011. Ecological impacts of nonnative freshwater fishes. Fisheries 36, 215–230. https://doi.org/10.1080/03632415.2011.574578.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 88, 2783–2792. https://doi.org/10.1890/07-0539.1.

Ding, H., Gu, X., Zhang, Z., Huo, B., Li, D., Xie, C., 2018. Growth and feeding habits of invasive *Pseudorasbora parva* in the Chabalang Wetland (Lhasa, China) and its trophic impacts on native fish. J. Oceanol. Limnol. 1–12. https://doi.org/10.1007/s00343-019-8004-5.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking,

B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Ellis, E.C., 2015. Ecology in an anthropogenic biosphere. Ecol. Monogr. 85, 287–331. https://doi.org/10.1890/14-2274.1.

Favre, A., Päckert, M., Pauls, S.U., Jähnig, S.C., Uhl, D., Michalak, I., Muellner-Riehl, A.N., 2014. The role of the uplift of the Qinghai–Tibetan Plateau for the evolution of Tibetan biotas. Biol. Rev. 90, 236–253. https://doi.org/10.1111/brv.12107.

Fitzgerald, D.B., Tobler, M., Winemiller, K.O., 2016. From richer to poorer: successful invasion by freshwater fishes depends on species richness of donor and recipient basins. Glob. Chang. Biol. 22, 2440–2450. https://doi.org/10.1111/gcb.13165.

Forsgren, E., Amundsen, T., Borg, A.A., Bjelvenmark, J., 2004. Unusually dynamic sex roles in a fish. Nature 429, 551–554. https://doi.org/10.1038/nature02562.

Fox, M.G., Vila-Gispert, A., Copp, G.H., 2007. Life-history traits of the introduced Iberian pumpkinseeds *Lepomis gibbosus* relative to native populations. Can differences explain colonization success? J. Fish Biol. 71, 56–69. https://doi.org/10.1111/j.1095-8649.2007.01683.x.

Fukuda, S., De Baets, B., Onikura, N., Nakajima, J., Mukai, T., Mouton, A.M., 2013. Modelling the distribution of the pan-continental invasive *Pseudorasbora parva* based on landscape features in the northern Kyushu Island, Japan. Aquat. Conserv. 23, 901–910. https://doi.org/10.1002/aqc.2336.

García-Berthou, E., 2007. The characteristics of invasive fishes: what has been learned so far. J. Fish Biol. 71, 33–55. https://doi.org/10.1111/j.1095-8649.2007.01668.x.

Gavioli, A., Mancini, M., Milardi, M., Aschonitis, V., Racchetti, E., Viaroli, P., Castaldelli, G., 2018. Exotic species, rather than low flow, negatively affect native fish in the Oglio River, Northern Italy. River Res. Appl. 34 (8), 887–897. https://doi.org/10.1002/rra.3324.

Gozlan, R.E., Andreou, D., Asaeda, T., Beyer, K., Bouhadad, R., Burnard, D., Caiola, N., Cakic, P., Djikanovic, V., Esmaeili, R., Falka, I., Golicher, D., Harka, A., Jeney, G., Kováč, V., Musil, J., Povz, M., Nocita, A., Poulet, N., Virbickas, T., Wolter, C., ̌ Tarkan, A., Tricarico, E., Trichkova, T., Verreycken, H., Witkowski, A., Zhang, C., Zweimueller, I., Britton, J.R., 2010. Pan-continental invasion of Pseudorasbora parva, towards a better understanding of freshwater fish invasions. Fish Fish. 11, 315–340. https://doi.org/10.1111/j.1467-2979.2010.00361.x.

Grabowska, J., Przybylski, M., 2015. Life-history traits of non-native freshwater fish invaders differentiate them from natives in the Central European bioregion. Rev Fish Biol Fisher 25 (1), 165–178. https://doi.org/10.1007/s11160-014-9375-5.

Grêt-Regamey, A., Brunner, S.H., Kienast, F., 2012. Mountain ecosystem services-who cares? Mt. Res. Dev. 32, 3–34. https://doi.org/10.1659/MRD-JOURNAL-D-10-00115.S1.

Gross, M.R., Sargent, R.C., 1985. The evolution of male and female parental care in fishes. Am. Zool. 25, 807–822. https://doi.org/10.1093/icb/25.3.807.

Guo, Q., Fei, S., Dukes, J.S., Oswalt, C.M., Iannone III, B.V., Potter, K.M., 2015. A unified approach for quantifying invasibility and degree of invasion. Ecology 96, 2613–2621. https://doi.org/10.1890/14-2172.1.

Hamerlik, L., Jacobsen, D., 2012. Chironomid (Diptera) distribution and diversity in Tibetan streams with different glacial influence. Insect Conserv. Divers. 5, 319–326. https://doi.org/10.1111/j.1752-4598.2011.00161.x.

Han, X.F., Li, S.H., 1995. The biology of *Pseudorasbora parva* in Baiyangdian Lake. Hebei Fish 2, 3–6 (In Chinese).

Hanel, R., Karjalainen, J., Wieser, W., 1996. Growth of swimming muscles and its metabolic cost in larvae of whitefish at different temperatures. J. Fish Biol. 48, 937–951. https://doi.org/10.1111/j.1095-8649.1996.tb01488.x.

Hendry, A.P., Farrugia, T.J., Kinnison, M.T., 2008. Human influences on rates of phenotypic change in wild animal populations. Mol. Ecol. 17, 20–29. https://doi.org/10.1111/j.1365-294X.2007.03428.x.

Hijmans, R., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276.

Hliwa, P., Martyniak, A., Kucharczyk, D., Sebestyn, A., 2002. Food preferences of juvenile stages of *Pseudorasbora parva* (Schlesinger, 1842) in the Kis-Balaton Reservoir. Arch. Pol. Fish. 10, 121–127.

Howeth, J.G., Gantz, C.A., Angermeier, P.L., Frimpong, E.A., Hoff, M.H., Keller, R.P., Mandrak, N.E., Marchetti, M.P., Olden, J.D., Romagosa, C.M., Lodge, D.M., 2016. Predicting invasiveness of species in trade: climate match, trophic guild and fecundity influence establishment and impact of non-native freshwater fishes. Divers. Distrib. 22, 148–160. https://doi.org/10.1111/ddi.12391.

Hu, Y., 2017. Sexual Dimorphism and Female Individual Fecundity of Six Species of Gobioninae in the Jialing River, Southwest China. MSc thesis. China West Normal University (In Chinese).

Ilhéu, M., Matono, P., Bernardo, J.M., 2014. Invasibility of Mediterranean-climate rivers by non-native fish: the importance of environmental drivers and human pressures. PLoS One 9, e109694. https://doi.org/10.1371/journal.pone.0109694.

Jackson, D.A., Harvey, H.H., 1997. Qualitative and quantitative sampling of lake fish communities. Can. J. Fish. Aquat. Sci. 54, 2807–2813. https://doi.org/10.1139/f97-182.

Jackson, M.C., Ruiz-Navarro, A., Britton, J.R., 2015. Population density modifies the ecological impacts of invasive species. Oikos 124, 880–887. https://doi.org/10.1111/oik.01661.

Jakubčinová, K., Haruštiaková, D., Ševcove, B., Švolíková, K., Makovinská, J., Kováč, V., 2018. Distribution patterns and potential for further spread of three invasive fish species (*Neogobius melanostomus*, *Lepomis gibbosus* and *Pseudorasbora parva*) in Slovakia. Aquat. Invasions 13 (4), 513–524. https://doi.org/10.3391/ai.2018.13.4.09.

Jin, K., Shi, W., Yu, X., Hu, H., Li, W., 1996. The preliminary observation on eight small freshwater fishes eating adhesive fish eggs. J. dalian Fish. Coll 11, 24–30 (In Chinese).

Jonsson, B., Jonsson, N., Finstad, A.G., 2013. Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. J. Anim. Ecol. 82, 201–210. https://doi.org/10.1111/j.1365-2656.2012.02022.x.

Kennard, M.J., Arthington, A.H., Pusey, B.J., Harch, B.D., 2005. Are alien fish a reliable indicator of river health? Freshw. Biol. 50, 174–193. https://doi.org/10.1111/j.1365-2427.2004.01293.x.

Koehn, J.D., 2004. Carp (Cyprinus carpio) as a powerful invader in Australian waterways. Freshw. Biol. 49, 882–894. https://doi.org/10.1111/j.1365-2427.2004.01232.x.

Konishi, M., Takata, K., 2004. Size-dependent male–male competition for a spawning substrate between Pseudorasbora parva and Pseudorasbora pumila. Ichthyol. Res. 51, 184–187. https://doi.org/10.1007/s10228-003-0203-5.

Körner, C., 2007. The use of 'altitude' in ecological research. Trends Ecol. Evol. 22, 569–574. https://doi.org/10.1016/J.TREE.2007.09.006.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Funct. Ecol. 29, 592–599. https://doi.org/10.1111/1365-2435.12345.

Lack, D., 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. Biometrics, 159–174. https://www.jstor.org/stable/2529310.

Lapointe, N.W., Light, T., 2012. Landscape-scale determinants of non-native fish communities. Divers. Distrib. 18, 282–293. https://doi.org/10.1111/j.1472-4642.2011.00858.x.

Li, H.J., Wang, Y.P., Leng, Q.L., Li, X.J., Li, X.F., Yu, T.L., Huang, B., 2017. Study on the age and growth of Pseudorasbora parva from Nanwan Lake upstream the Huaihe River. Acta Hydrobiol. Sin. 41, 835–842 (In Chinese).

Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. R News. vol. 2 pp. 18–22.

Liew, J.H., Tan, H.H., Yeo, D.C., 2016. Dammed rivers: impoundments facilitate fish invasions. Freshw. Biol. 61, 1421–1429. https://doi.org/10.1111/fwb.12781.

Liu, X., Chen, B., 2000. Climatic warming in the Tibetan Plateau during recent decades. Int. J. Climatol. 20, 1729–1742. https://doi.org/10.1002/1097-0088(20001130)20:14<1729::AID-JOC556>3.0.CO;2-Y.

Liu, Q., Yu, H., Liang, L., Ping, F., Xia, X., Mou, X., Liang, J., 2017. Assessment of ecological instream flow requirements under climate change Pseudorasbora parva. Int. J. Environ. Sci. Technol. 14, 1–12. https://doi.org/10.1007/s13762-016-1166-1.

Maekawa, K., Iguchi, K., Katano, O., 1996. Reproductive success in male Japanese minnows, Pseudorasbora parva: observations under experimental conditions. Ichthyol. Res. 43, 257–266. https://doi.org/10.1007/BF02347598.

Marras, S., Cucco, A., Antognarelli, F., Azzurro, E., Milazzo, M., Bariche, M., Butenschön, M., Kay, S., Di Bitetto, M., Quattrocchi, G., Sinerchia, M., Domenici, P., 2015. Predicting future thermal habitat suitability of competing native and invasive fish species: from metabolic scope to oceanographic modelling. Conserv. Physiol. 3, 1–14. https://doi.org/10.1093/conphys/cou059.

McBride, R.S., Somarakis, S., Fitshugh, G.R., Albert, A., Yaragina, N.A., Wuenschel, M.J., Alonso-Fernández, A., Basilone, G., 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish Fish. 16, 23–57. https://doi.org/10.1111/faf.12043.

McNeely, J.A., Kapoor-Vijay, P., Lu, Z., Olsvig-Whittaker, L., Sheikh, K.M., Smith, A.T., 2009. Conservation biology in Asia: the major policy challenges. Conserv. Biol. 23, 805–810. https://doi.org/10.1111/j.1523-1739.2009.01284.x.

Meng, Q.W., 1982. On the morphological characteristics of the larvae of seven species of freshwater fishes. J. Fish. China 6, 65–76.

Milardi, M., Lanzoni, M., Gavioli, A., Fano, E.A., Castaldelli, G., 2018a. Long-term fish monitoring underlines a rising tide of temperature tolerant, rheophilic, benthivore and generalist exotics, irrespective of hydrological conditions. J. Limnol. 77, 266–275. https://doi.org/10.4081/jlimnol.2018.1745.

Milardi, M., Aschonitis, V., Gavioli, A., Lanzoni, M., Fano, E.A., Castaldelli, G., 2018b. Run to the hills: exotic fish invasions and water quality degradation drive native fish to higher altitudes. Sci. Total Environ. 624, 1325–1335. https://doi.org/10.1016/j.scitotenv.2017.12.237.

Miller, S.A., Provenza, F.D., 2007. Mechanisms of resistance of freshwater macrophytes to herbivory by invasive juvenile common carp. Freshw. Biol. 52, 39–49. https://doi.org/10.1111/j.1365-2427.2006.01669.x.

Miller, T.J., Crower, L.B., Rice, J.A., Marshall, E.A., 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45, 1657–1670. https://doi.org/10.1139/f88-197.

Miller, G.M., Kroon, F.J., Metcalfe, S., Munday, P.L., 2015. Temperature is the evil twin: effects of increased temperature and ocean acidification on reproduction in a reef fish. Ecol. Appl. 25, 603–620. https://doi.org/10.1890/14-0559.1.

Moreau, R.E., 1944. Clutch-size: a comparative study, with special reference to African birds. Ibis 86, 286–347. https://doi.org/10.1111/j.1474-919X.1944.tb04093.x.

Morrison, C., Hero, J., 2003. Geographic variation in life history characteristics of amphibians: a review. J. Anim. Ecol. 72, 270–279. https://doi.org/10.1046/j.1365-2656.2003.00696.x.

Moyle, P.B., Light, T., 1996. Fish invasions in California: do abiotic factors determine success? Ecology 77, 1666–1670. https://doi.org/10.2307/2265770.

Moyle, P.B., Marchetti, M.P., 2006. Predicting invasion success: freshwater fishes in California as a model. Bioscience 56, 515–524. https://doi.org/10.1641/0006-3568(2006)56[515:PISFFI]2.0.CO;2.

Muhlfeld, C.C., Kovach, R.P., Al-Chokhachy, R., Amish, S.J., Kershner, J.L., Leary, R.F., Lowe, W.H., Luikart, G., Matson, P., Schmetterling, D.A., Shepard, B.B., Westley, P.A.H., Whited, D., Whiteley, A., Allendorf, F.W., 2017. Legacy introductions and climatic variation explain spatiotemporal patterns of invasive hybridization in a native trout. Glob. Chang. Biol. 23, 4663–4674. https://doi.org/10.1111/gcb.13681.

O'Beirne, M.D., Werne, J.P., Hecky, R.E., Johnson, T.C., Katsev, S., Reavie, E.D., 2017. Anthropogenic climate change has altered primary productivity in Lake Superior. Nat. Commun. 8, 15713. https://doi.org/10.1038/ncomms15713.

Olden, J.D., Poff, N.L., Bestgen, K.R., 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. Ecol. Monogr. 76, 25–40. https://doi.org/10.1890/05-0330.

Pankhurst, N.W., Munday, P.L., 2011. Effects of climate change on fish reproduction and early life history stages. Mar. Freshw. Res. 62, 1015–1026. https://doi.org/10.1071/MF10269.

Parker, G.A., 1992. The evolution of sexual size dimorphism in fish. J. Fish Biol. 41, 1–20. https://doi.org/10.1111/j.1095-8649.1992.tb03864.x.

Pianka, E.R., 1970. On r-and K-selection. Am. Nat. 104, 592–597. https://doi.org/10.1086/282697.

Pincheira-Donoso, D., Hunt, J., 2017. Fecundity selection theory: concepts and evidence. Biol. Rev. 92, 341–356. https://doi.org/10.1111/brv.12232.

Piria, M., Simonović, P., Nikolić, V., Ristovska, M., Apostolou, A., Adrović, A., Povž, M., Zanella, D., Mrdak, D., Milošević, D., Vardakas, L., Koutsikos, N., Kalogianni, E., Gregori, A., Kostov, V., Škrijelj, R., Korro, K., Bakiu, R., Tarkan, A.S., Joy, M.K., 2018. Alien freshwater fish species in the Balkans - vectors and pathways of introduction. Fish Fish. 19, 138–169. https://doi.org/10.1111/faf.12242.

Poff, N., Brinson, M., Day, J., 2002. Aquatic Ecosystems and Global Climate Change. Pew Center on Global Climate Change, Arlington.

Pollux, B.J.A., Korosi, A., 2006. On the occurrence of the Asiatic cyprinid Pseudorasbora parva in the Netherlands. J. Fish Biol. 69, 1575–1580. https://doi.org/10.1111/j.1095-8649.2006.01218.x.

Poulin, R., Paterson, R.A., Townsend, C.R., Tompkins, D.M., Kelly, D.W., 2011. Biological invasions and the dynamics of endemic diseases in freshwater ecosystems. Freshw. Biol. 56, 676–688. https://doi.org/10.1111/j.1365-2427.2010.02425.x.

Qiu, J., 2008. The third pole. Nature 454, 393–396.

Radinger, J., Alcaraz-Hernández, J.D., García-Berthou, E., 2019. Environmental filtering governs the spatial distribution of alien fishes in a large, human-impacted Mediterranean river. Divers. Distrib. https://doi.org/10.1111/ddi.12895.

Rahel, F.J., Olden, J.D., 2008. Assessing the effects of climate change on aquatic invasive species. Conserv. Biol. 22, 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x.

Redpath, T.D., Cooke, S.J., Arlinghaus, R., Wahl, D.H., Philipp, D.P., 2009. Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish. Evol. Appl. 2, 312–323. https://doi.org/10.1111/j.1752-4571.2009.00078.x.

Reznick, D., Butler IV, M.J., Rodd, H., 2001. Life-history evolution in guppies. VII. The comparative ecology of high-and low-predation environments. Am. Nat. 157, 126–140. https://doi.org/10.1086/318627.

Samsing, F., Oppedal, F., Dalvin, S., Johnsen, I., Vågseth, T., Dempster, T., 2016. Salmon lice (Lepeophtheirus salmonis) development times, body size, and reproductive outputs follow universal models of temperature dependence. Can. J. Fish. Aquat. Sci. 73, 1–11. https://doi.org/10.1139/cjfas-2016-0050.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. BioScience 52, 891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2.

Sargent, R.C., Taylor, P.D., Gross, M.R., 1987. Parental care and the evolution of egg size in fishes. Am. Nat. 129 (1), 32–46. https://doi.org/10.1086/284621.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60, 1129–1157.

Stearns, S.C., 1977. The evolution of life history traits: a critique of the theory and a review of the data. Annu. Rev. Ecol. Syst. 8, 145–171. https://doi.org/10.1146/annurev.es.08.110177.001045.

Stearns, S.C., 1989. Trade-offs in life-history evolution. Funct. Ecol. 3, 259–268. https://www.jstor.org/stable/2389364.

Stearns, S.C., 1992. The Evolution of Life Histories. Oxford University Press, Oxford, UK.

Strobl, C., Boulesteix, A.-L., Zeileis, A., Hothorn, T., 2007. Bias in random forest variable importance measures. BMC Bioinf 8, 25. https://doi.org/10.1186/1471-2105-8-25.

Švolíková, K., Záhorská, E., Kováč, V., 2016. Unusually high production of oocytes in two invasive populations of topmouth gudgeon Pseudorasbora parva (Temminck and Schlegel, 1846). J. Appl. Ichthyol. 32, 978–981. https://doi.org/10.1111/jai.13107.

Tang, W.J., He, D.K., 2015. Investigation on alien fishes in Qinghai Province, China (2001–2014). J. Lake Sci. 27, 502–510 (In Chinese).

Valiente, A.G., Juanes, F., Nuñez, P., Garcia-Vazquez, E., 2010. Brown trout (Salmo trutta) invasiveness: plasticity in life-history is more important than genetic variability. Biol. Invasions 12, 451–462. https://doi.org/10.1007/s10530-009-9450-3.

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., DAISIE partners, 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Front. Ecol. Environ. 8 (3), 135–144. https://doi.org/10.1890/080083.

Vila-Gispert, A., Alcaraz, C., García-Berthou, E., 2005. Life-history traits of invasive fish in small Mediterranean streams. Biol. Invasions 7, 107–116. https://doi.org/10.1007/s10530-004-9640-y.

Vilizzi, L., Kováč, V., 2014. Alternative ontogenies and developmental plasticity: implications for ecological and evolutionary studies on species complexes. Fish Fish. 15, 523–531. https://doi.org/10.1111/faf.12048.

Vitousek, P.M., D'antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. N. Z. J. Ecol. 21, 1–16.

Vitule, J.R.S., Freire, C.A., Simberloff, D., 2009. Introduction of non-native freshwater fish can certainly be bad. Fish Fish. 10, 98–108. https://doi.org/10.1111/j.1467-2979.2008.00312.x.

Vrtílek, M., Žák, J., Pšenička, M., Reichard, M., 2018. Extremely rapid maturation of a wild African annual fish. Curr. Biol. 28, R822–R824. https://doi.org/10.1016/j.cub.2018.06.031.

Wang, M.J., Hu, J., 2015. Study on the individual fecundity of the Pseudorasbora parva in Nanyi Lake. Jiangxi Fish. Sci. Technol. 2, 8–10 (In Chinese).

Wellband, K.W., Pettitt-Wade, H., Fisk, A.T., Heath, D.D., 2018. Standing genetic diversity and selection at functional gene loci are associated with differential invasion success in two non-native fish species. Mol. Ecol. 27, 1572–1585. https://doi.org/10.1111/mec.14557.

Winemiller, K.O., Rose, K.A., 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49, 2196–2218. https://doi.org/10.1139/f92-242.

Wolfram-Wais, A., Wolfram, G., Auer, B., Mikschi, E., Hain, A., 1999. Feeding habits of two introduced fish species (Lepomis gibbosus, Pseudorasbora parva) in Neusiedler See (Austria), with special reference to chironomid larvae (Diptera: Chironomidae). Hydrobiologia 408/409, 123–129. https://doi.org/10.1007/978-94-017-2986-4_12.

Wu, T., 2001. The Qinghai-Tibetan plateau: how high do Tibetans live? High Alt. Med. Biol. 2, 489–499. https://doi.org/10.1089/152702901753397054.

Wu, Y.F., Wu, C.Z., 1990. A preliminary study of the fishery resources and the countermeasures of fishery development in the region of the Karakorum-Kunlun Mountains. China. J Nat Resour. 5, 354–364 (In Chinese).

Wu, Y.F., Wu, C.Z., 1991. The Qinghai-Tibetan Plateau Fish. Sichuan Science and Technology Press, Chengdu, China (In Chinese).

Xie, S.Q., Cui, Y.B., Li, Z.J., 2001. Dietary-morphological relationships of fishes in Liangzi Lake, China. J. Fish Biol. 58, 1714–1729. https://doi.org/10.1111/j.1095-8649.2001.tb02325.x.

Xie, J.Y., Tang, W.J., Yang, Y.H., 2018. Fish assemblage changes over half a century in the Yellow River, China. Ecol. Evol. 8, 4173–4182. https://doi.org/10.1002/ece3.3890.

Xu, J., Grumbine, R.E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., Wilkes, A., 2009a. The melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods. Conserv. Biol. 23, 520–530. https://doi.org/10.1111/j.1523-1739.2009.01237.x.

Xu, W.Y., Miao, X.J., Qiu, J.R., He, W.P., He, R.L., Guo, Z.Y., 2009b. Investigation report of fish in Nujiang Prefecture. J Hydroecology 2, 37–41 (In Chinese).

Yan, Y.Z., 2005. Adaptive Evolution in Life-history Strategies of Invasive Fishes in Lake Fuxian. PhD thesis. Inst. of Hydrobiology, Chinese Academy of Science (In Chinese).

Záhorská, E., Kováč, V., 2009. Reproductive parameters of invasive topmouth gudgeon Pseudorasbora parva (Temminck and Schlegel, 1846) from Slovakia. J. Appl. Ichthyol. 25, 466–469. https://doi.org/10.1111/j.1439-0426.2009.01190.x.

Záhorská, E., Kováč, V., 2013. Environmentally induced shift in reproductive traits of a long-term established population of topmouth gudgeon (Pseudorasbora parva). J. Appl. Ichthyol. 29, 218–220. https://doi.org/10.1111/jai.12039.

Záhorská, E., Švolíková, K., Kovác, V., 2013. Do invasive populations of topmouth gudgeon (Pseudorasbora parva, Temminck and Schlegel) from disturbed and undisturbed habitats follow different life-histories? Int. Rev. Hydrobiol. 98, 61–70. https://doi.org/10.1002/iroh.201201446.

Záhorská, E., Kováè, V., Švolíková, K., Kapusta, A., 2014. Reproductive parameters of topmouth gudgeon (Pseudorasbora parva) from a heated Lake Licheñskie (Poland). Cent. Eur. J. Biol. 9, 212–219. https://doi.org/10.2478/s11535-013-0252-3.

Zhang, T.L., 1997. The Biology, Standing Crop and Production of Topmouth Gudgeon Pseudorasbora parva in the Baoan Lake, Hubei. MSc thesis. Inst. of Hydrobiology, Chinese Academy of Science (In Chinese).

Zhang, R.H., Su, F.G., Jiang, Z.H., Gao, X.J., Guo, D.L., Ni, J., You, Q.L., Lan, C., Zhou, B.T., 2015. An overview of projected climate and environmental changes across the Tibetan Plateau in the 21st century. Chin. Sci. Bull. 60, 3036–3047 (In Chinese).

Zhao, W.H., Liu, X.Q., 2010. Preliminary study on macrozoobenthos in Yarlung Zangbo River and its branches around Xiongcun, Tibet, China. Resour. Environ. Yangtze Basin 19, 281–286 (In Chinese).

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer, New York.