

# Growth and feeding habits of invasive *Pseudorasbora parva* in the Chabalang Wetland (Lhasa, China) and its trophic impacts on native fish\*

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Received Jan. 8, 2018; accepted in principle Feb. 22, 2018; accepted for publication May 18, 2018

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**Abstract** In recent years, fish invasion has become one of the main reasons for the decline of native fish stocks. *Pseudorasbora parva* is considered one of the major invasive species worldwide. The present study investigated the fish resources of the Chabalang Wetland (Lhasa, Tibet) during different seasons in 2009 and 2013. Four hundred and twelve individuals were subsampled to estimate age, growth, and feeding habit of *P. parva*. Furthermore, food relationships between *P. parva* and the native Schizothoracinae fish were also examined. The results revealed a significant shift in species composition and community structure characterized by the disappearance of native fish and outbreak of non-native fish. The percentage of non-native *P. parva* in the fish collections significantly increased from 33.64% in 2009 to 64.08% in 2013. The standard length (SL) ranged from 22.00 to 78.71 mm, and their age was 1–5 a. The von Bertalanffy function was used to model the observed length-at-age data as  $L_t = 112.19(1 - e^{-0.1495(t+0.8012)})$  for females and as  $L_t = 123.12(1 - e^{-0.1500(t+0.7132)})$  for males. The results indicated that *P. parva* in Tibet has lower growth and mortality rates compared with that from the native ranges. Ninety-seven prey taxa belonging to 9 prey categories were identified in the gut of 38 *P. parva*. *P. parva* can be considered a generalized and opportunistic predator, competing with the native fish, especially *Schizothorax o'connori*, *Schizopygopsis younghusbandi younghusbandi*, and *Ptychobarbus dipogon*, for Bacillariophyta and Chironomid larvae. This is an important reason for the decline in native fish population.

**Keyword:** *Pseudorasbora parva*; growth; feeding habits; Schizothoracinae fish; biological invasion

## 1 INTRODUCTION

The Qinghai-Tibet Plateau is the highest and youngest plateau in the world with special geographical and ecosystem conditions. Indigenous fishes mainly belonging to the family Schizothoracinae and Sisoridae and *Triplophysa* species are endemic to Tibet, which are also very important fish germplasm resources (Wu and Wu, 1992). In recent years, along with overfishing and water conservancy projects, fish invasion has become another main reason for the

decline of native fish stocks (Chen and Chen, 2010; Yang and Huang, 2011; Huo et al., 2014; Zhu et al., 2017).

*Pseudorasbora parva*, a small cyprinid species native to Eastern China, Japan, Korea, and the

\* Supported by the National Key Technology R&D Program (No. 2015BAD13B06) and the Finance Special Fund of Chinese Ministry of Agriculture (Fisheries Resources and Environment Survey in the Key Water Areas of Tibet)

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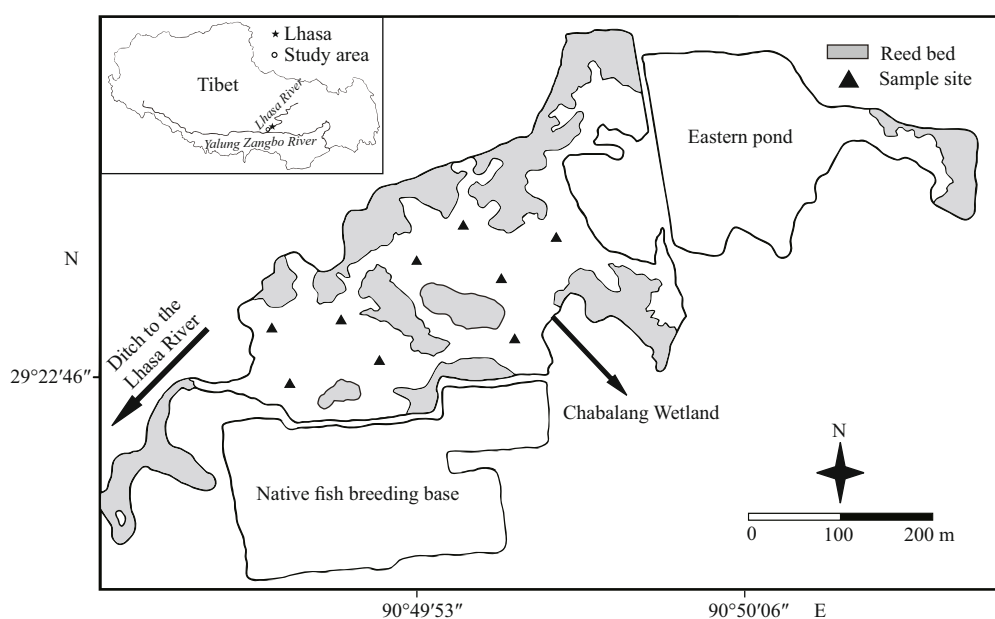


Fig.1 Map of Chabalong Wetland and fish sampling sites

Heilong River Basin, is considered to be the most invasive and threatening species worldwide. It has invaded 32 countries from Central Asia to North Africa in less than 50 years (Gozlan et al., 2010). In Europe, it has been proven to be a highly invasive species, since its initial accidental introduction in 1960s, and has spread throughout Europe (Bianco, 1988; Wildekamp et al., 1997; Pollux and Korosi, 2006). *Pseudorasbora parva* was first introduced in China in the 1950s, as a result of translocation from its native range. Currently, it has invaded almost all the natural waters in China, including the upper reach of the Yellow River, inland waters of Yunnan, Inner Mongolia, Xinjiang, and the Qinghai-Tibet Plateau (Li, 1982; Chu and Chen, 1989; Fan et al., 2011).

However, reports of invasive *P. parva* are sporadic, and description of the population ecology, feeding habits, and relationship with native fishes is scarce, which may cause inadequate understanding of the invasion consequences. In this milieu, the present study intended to document the age, growth, and feeding habits of *P. parva* in the Chabalong Wetland (Lhasa, Tibet), which is one of the most important wetlands along the Lhasa River. Furthermore, the study aimed to clarify its food relationships with native fish in order to provide fundamental information for a better understanding of its effects on native species and to establish the corresponding risk assessment and management policies.

## 2 MATERIAL AND METHOD

### 2.1 Study site and sample collection

The Chabalong Wetland is a shallow marsh (<2.5 m) of 20 hm<sup>2</sup> in Chabalong village (Qushui County, Lhasa), which belongs to the main agricultural area of Tibet, about 1.0 km north of the Lhasa River and 8.5 km from the confluence of the Yarlung Zangbo and Lhasa Rivers (29°22'30"–29°22'59"N, 90°49'20"–90°50'30"E; Fig.1). There are ditches connecting the wetland to the Lhasa River. The average altitude is 3 600 m, annual precipitation is about 441.9 mm, and annual temperature is 7.18°C. *Phragmites australis*, *Typha orientalis* Presl, and *Scirpus tabernaemontani* are the main vegetation. The vulnerability of the wetland is moderate (Bai et al., 2012). Artificially transformed, the wetland is divided into three-interconnected parts: the east is an early-dug fishpond, north is primeval reed marsh, and south is now a native fish breeding research base.

The fish samples were collected by backpack electrofishing at 9 different sampling sites once in January, April, July, and October 2009 and 2013. The fishing equipment set to a frequency of 60 Hz with 6 ms pulse duration and an output of 100 voltages. The voltage, pulse, and frequency were adjusted to maximize the capture probability without injuring the fishes. A micro-mesh gill net investigation was supplemented. After collection, the fishes were sorted according to Zhu (1989), Fishery Bureau in Tibet Municipality (1995), and Xie (2010), and were then

preserved in 10% formaldehyde for laboratory analyses.

## 2.2 Laboratory analyses

In the laboratory, the body weight (BW) and standard length (SL) of each individual were measured to the nearest 0.01 g and 0.01 mm, respectively. Eight to ten well-developed scales were removed from above the lateral line on the left side of the fish, just behind the dorsal-fin origin for age determination. After dissection, the gut contents were removed, weighed (0.1 mg), and preserved in 10% formaldehyde. Sex was determined by visual examination of gonads morphology. The scales were immersed in 4%–5% sodium hydroxide solution for about 5 h, and the extraneous matters were brushed off using a soft brush. Age were estimated by counting the number of annual rings on scales. All scales were analyzed thrice by the same reader after a considerable time interval ( $\geq 3$  weeks).

The relationship between BW and SL was estimated by the power regression analysis described by  $BW = aSL^b$  (a and b are constants) (Le Cren, 1951). The observed length-at-age data was fitted to the von Bertalanffy growth function (VBGF):  $L_t = L_\infty(1 - e^{-k(t-t_0)})$ , where  $L_t$  is the length at age  $t$ ,  $L_\infty$  is the asymptotic length,  $k$  is the growth coefficient, and  $t_0$  is the theoretical age at length 0.

## 2.3 Feeding habits

For dietary analysis, the gut contents were diluted with distilled water and carefully transferred to a counting chamber for microscopic determination. The macro-organisms were identified and counted using a dissecting microscope (Leica EZ4D) and weighed after absorbing excess water with blotting paper. Small organisms were identified and counted under  $10\times$  and  $40\times$  microscopes (Olympus, CX21) using counting chambers (0.1 and 1 mL). The weight was calculated according to mass and volume conversion (Liu et al., 2006).

The contribution of each prey type to the diet was evaluated using the percent of occurrence ( $O\%$ ), number ( $N\%$ ), and weight ( $W\%$ ), and the index of relative importance  $IRI_i = O_i\% (N_i\% + W_i\%)$  (Pinkas et al., 1971). To compare with that of other studies, the values of IRI were expressed in percent (IRI%) (Cortés, 1997). Dominance index was  $IP_i\% = 100 \times O_i\%W_i\% / \sum_1^n (O_i\%W_i\%)$  also calculated (Mohan and Sankaran, 1988).

The Amundsen graphical method (Amundsen et al., 1996), which is applied to the data set of prey taxa identified at genus level, was used to describe the feeding strategy of *P. parva*. In mathematical terms, the prey-specific abundance was summarized as  $P_i\% = 100 \times (\sum S_i / \sum S_{ii})$ , where,  $P_i$  is the prey-specific abundance of prey  $i$ ,  $S_i$  is the gut content ( $W\%$ ) comprised of prey  $i$ , and  $S_{ii}$  is the total gut content of only those fish with prey  $i$  in their guts. Through the position of prey types in the two-dimensional plot ( $P_i$  against  $O\%$ , Fig.3b), information regarding prey importance, feeding strategy, and niche width contribution can be inferred.

## 2.4 Food relationship with the native fishes

Food relationships between *P. parva* and native *Schizothorax o'connori*, *Schizopygopsis younghusbandi younghusbandi*, *Oxygymnocypris stewartii*, *Schizothorax waltoni*, *Ptychobarbus dipogon*, and *Schizothorax macropogon* (Yang et al., 2011; Huo et al., 2014; Ma et al., 2014; Zhou, 2014; Yang, 2015; Liu, 2016) were determined by the diet items in terms of weight percent ( $W\%$ ). Diet items of all the fishes were classified as 21 dietary taxa (Table 3). Trophic level of these dietary taxa was assigned according to Liu (1999), while that of forage fishes was calculated based on their diet items.

Hill's diversity number (Hill, 1973), which is expressed as  $N_0$  (the number of prey taxa),  $N_1 = e^{H'}$  (the number of abundant prey taxa), and  $N_2 = 1 / \sum_1^n P_i^2$  (the number of very abundant prey taxa), was used to discuss diet spectrum. Where,  $H' = -\sum_1^n (P_i \ln P_i)$  is the Shannon-Wiener Index (Shannon, 1948),  $P_i$  is the proportion of prey  $i$ , and  $n$  is the number of dietary taxa. Levin's standardized niche breadth index  $Ba = 1 / (n-1) (1/P_i^2 - 1)$  (Krebs, 1989) was applied to calculate the niche breadth. Diet overlaps of *P. parva* and native fishes were discussed using simplified Morisita's index  $C = 2 \times \sum_1^n P_{xi} P_{yi} / (\sum_1^n P_{xi}^2 + \sum_1^n P_{yi}^2)$  (Hall et al., 1990), where,  $P_{xi}$  and  $P_{yi}$  are the proportions of the common prey  $i$  of fish  $x$  and  $y$ , respectively, and  $C > 0.6$  indicates significance. Trophic levels  $T = 1 + \sum_1^n (t_i P_i)$  (Odum and Heald, 1975) were used to analyze their position in the food chain, where,  $t_i$  is the trophic level of prey  $i$ . Data and images were analyzed using Microsoft Excel 2007 and Origin 8.5.1. Statistical analysis was carried out using the SPSS version 18.0 software at a significance level of 0.05.

**Table 1 Fish species and compositions of Chabalang Wetland in 2009 and 2013**

Family	Genus	Species	2009		2013	
			Number	Percent (%)	Number	Percent (%)
Cyprinidae	<i>Oxygymnocypris</i>	<i>O. stewartii</i>	35	1.19		
	<i>Schizopygopsis</i>	<i>S. younghusbandi younghusbandi</i>	21	0.72		
	<i>Carassius</i>	<i>C. auratus</i> *	875	29.82	51	2.41
		<i>C. (Cyp.) caupio</i> *	1	0.03		
	<i>Ctenopharyngodon</i>	<i>C. idellus</i> *	1	0.03		
	<i>Pseudorasbora</i>	<i>P. parva</i> *	987	33.64	1 356	64.08
	<i>Abbottina</i>	<i>A. rivularis</i> *	29	0.99	292	13.8
Cobitidae	<i>Triplophysa</i>	<i>T. stenura</i>	2	0.07		
		<i>T. orientalis</i>	4	0.14		
		<i>T. tibetana</i>	1	0.03		
	<i>Misgurnus</i>	<i>M. anguillicaudatus</i> *	272	9.27	45	2.13
	<i>Paramisgurnus</i>	<i>P. dabryanus</i> *				
Siluridae	<i>Silurus</i>	<i>S. asotus</i> *	1	0.03		
Eleotridae	<i>Micropercops</i>	<i>M. swinhonis</i> *	705	24.03	372	17.58
Total			2 934	100	2 116	100

Note: \* indicates exotic species.

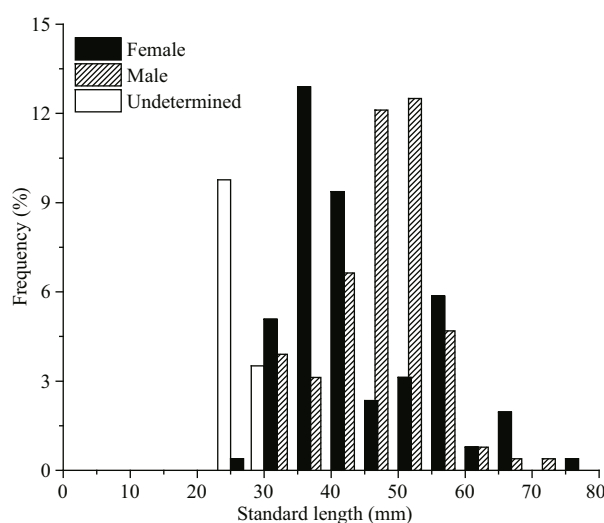
### 3 RESULT

#### 3.1 Fish composition

In total, 2 934 fish were sampled in 2009, with 8 exotic fish species ( $n=2\ 871$ ) accounting for 97.85%. The remaining were native species, including *S. y. younghusbandi* ( $n=21$ ), *O. stewartii* ( $n=35$ ), *Triplophysa stenura* ( $n=2$ ), *Triplophysa orientalis* ( $n=4$ ), and *Triplophysa tibetana* ( $n=1$ ); together they accounted for only 2.15% of the sampled fishes, which is significantly below the estimates recorded for exotic fish. In 2013, 2116 fish belonging to 5 species were captured, and there was no native fish (Table 1). The results showed that the percentage of *P. parva* in the fish community had significantly increased from 33.64% in 2009 to 64.08% in 2013. Furthermore, the occurrence of both juveniles and adults of *P. parva* indicated the establishment of breeding population.

#### 3.2 Age and growth

In total, 256 *P. parva* were subsampled randomly for age determination; 108 were females (SL 32.81–78.71 mm), 114 were males (SL 31.44–71.59 mm), and 34 were unsexed (SL 22.00–29.92 mm). The length-frequency distributions differed significantly between sexes (Kolmogorov-Smirnov;  $Z=2.804$ ,  $P<0.001$ ) (Fig.2). The sexual ratio (F:M) was 1:1.08, which was not significantly different from 1:1



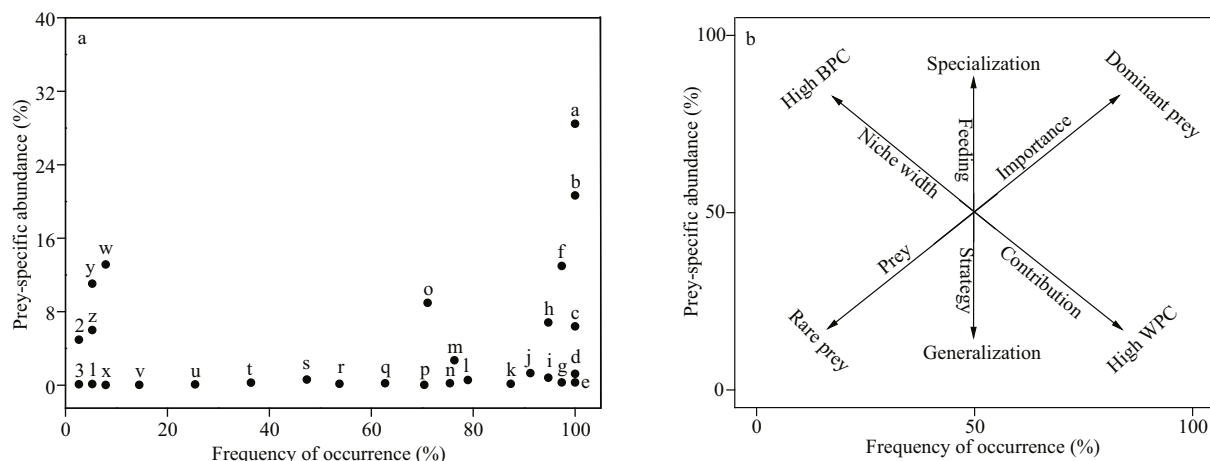
**Fig.2 Frequency distributions of standard length of *P. parva***

( $\chi^2=0.082$ ,  $P=0.775$ ).

Of the 256 *P. parva*, only 2 (approximately 0.78%) were discarded due to regeneration or unidentifiable annulus, the estimated max age was 5 years for both females and males. Age structure differed significantly between sexes (Kolmogorov-Smirnov;  $Z=1.715$ ,  $P=0.006$ ). Most females were 3 a (60.53%), while most males were 2 a (46.23%) (Table 2). The SL-BW relationship was  $BW=2.069 \times 10^{-5} SL^{3.006}$  ( $R^2=0.978$ ,  $n=108$ ),  $BW=8.731 \times 10^{-6} SL^{3.208}$  ( $R^2=0.969$ ,  $n=114$ ), and  $BW=1.516 \times 10^{-5} SL^{3.061}$  ( $R^2=0.868$ ,  $n=34$ ) for females, males, and unsexed, respectively. Significant

**Table 2** Number of specimens and Mean  $\pm$  S.D. and range of standard length at age of *P. parva*

Age (a)	Female			Male			Undetermined		
	<i>n</i>	Range (mm)	Mean $\pm$ S.D. (mm)	<i>n</i>	Range (mm)	Mean $\pm$ S.D. (mm)	<i>n</i>	Range (mm)	Mean $\pm$ S.D. (mm)
1	9	32.81–42.57	38.34 $\pm$ 2.84	8	31.44–39.62	34.74 $\pm$ 2.50	31	22.00–29.33	24.06 $\pm$ 1.66
2	49	31.50–49.01	38.54 $\pm$ 4.10	28	31.44–58.94	43.14 $\pm$ 6.45	3	28.14–29.92	29.07 $\pm$ 0.89
3	35	38.05–67.61	49.74 $\pm$ 9.30	69	35.15–63.62	50.33 $\pm$ 4.63			
4	11	52.44–67.57	58.83 $\pm$ 5.32	7	49.84–60.61	57.84 $\pm$ 3.74			
5	2	52.21–78.71	65.46 $\pm$ 18.74	2	69.00–71.59	70.30 $\pm$ 1.83			

**Fig.3** Graphic representation of diet composition in *P. parva*

a. diagram representing the prey taxa. a: Chironomidae larvae; b: *Nitzschia*; c: *Synedra*; d: *Navicula*; *Scenedesmus*; e: *Fragilaria*; Nauplius; rotifer eggs; f: *Cyclotella*; g: *Ankistrodesmus*; *Diatoma*; h: Cyclopoida; i: *Cymbella*; *Diploneis*; j: unidentified arthropod; *Alona*; *Mougeotia*; k: Nematode; *Chyolorus*; *Brachionus*; *Tetradon*; *Epithemia*; l: *Rhopalodia*; *Monostyla*; m: *Oscillatoria*; n: *Dictyosphaerium*; *Lepadella*; *Cosmarium*; o: Chironomidae pupae; p: *Pinnularia*; *Chodatella*; *Achnanthes*; *Rotaria*; q: *Oedogonium*; *Colurella*; *Chlorella*; *Caloneis*; *Gomphonema*; *Tintinnopsis*; r: plant debris; *Pediastrum*; *Tetrastrum*; *Neidium*; *Dinobryon*; *Merismopedia*; *Keratella*; s: *Ulothrix*; *Araneae*; *Amphora*; t: *Trachelomonas*; Water Bear; *Notholca*; *Cymatopleura*; *Chlorococcum*; *Lyngbya*; u: *Peridinium*; *Treubaria*; *Graptoleberis*; *Golenkinia*; *Arcella*; *Euglena*; *Philodina*; *Diffugia*; *Actinastrum*; v: *Coelastrum*; unidentified Bdelloidea; *Chroococcus*; *Glenodinium*; *Phacus*; *Staurastrum*; *Cyclopyxis*; *Lecane*; w: *Microspora*; x: *Ceriodaphnia*; *Kirchneriella*; *Stauroneis*; *Trichocerca*; y: *Spirogyra*; z: *Zygnema*; l. fish scales, *Cladophora*, *Surirella*, *Ascomorpha*; 2. *Closterium*; 3. other preys; b. explanatory diagram for interpretation of feeding strategy, prey importance and niche width contribution (adapted from Amundsen et al., 1996). BPC and WPC represent between-phenotype component and within-phenotype component, respectively.

differences were found in the SL-BW relationship between sexes (ANCOVA,  $F=44.046$ ,  $P<0.01$ ). The allometric index  $b$  differed significantly from 3 for males ( $t$ -test,  $t=3.836$ ,  $P<0.01$ ), whereas there was no statistical difference from 3 for females ( $t$ -test,  $t=0.137$ ,  $P>0.05$ ). This suggests that the females were isokinetic, while the males were allometric. The von Bertalanffy functions fitted to the observed body length-at-age were given as  $L_t=112.19(1-e^{-0.1495(t+0.8012)})$  and  $L_t=123.12(1-e^{-0.1500(t+0.7132)})$  for females and males, respectively.

### 3.3 Feeding habits

Of the 156 intestines collected randomly for diet analysis, 84 were empty (53.8%), and the remaining 72 contained at least one prey item (46.2%). Thirty-eight specimens with good fullness (SL 36–76 mm) were chosen for food items identification. The diets consisted of a wide variety of algae (57 genera,

belonging to 7 phyla) and animal organisms (23 genera and 5 other taxa, belonging to 5 phyla). A small amount of sand, rotted plant debris, and fish scales were also observed among the intestinal contents (Appendix 1).

According to the frequency of occurrence (O%) data, the prey items most frequently ingested by *P. parva* were algae, Rotifera, Cladocera, Copepod, and aquatic insects, each accounting for 100%. Algae were the most abundant prey item (99.99%) in terms of the index of abundance (N%), which primarily included Chlorophyta (40.60%), Bacillariophyta (30.17%), and Cyanophyta (28.61%). Bacillariophyta were the most important food in terms of weight (45.53%), IRI (41.18%), and IP (47.88%). Chironomidae larvae followed this group in terms of weight (35.01%) and IP (35.63%).

The dietary pattern of *P. parva* based on the Amundsen method is graphically represented in Fig.3a.



**Table 3 Diet composition of *P. parva* and native Schizothoracinae fishes in the middle reaches of Yarlung Zangbo River (in weight percentage, *W*%)**

Dietary item	Fish species						
	1	2	3	4	5	6	7
Algae	54.19	81.26	66.53	-	0.31	0.36	1.59
Protozoa	+	0.02	0.71	-	0.04	+	-
Rotifera	0.11	0.03	+	-	+	+	-
Cladocera	1.68	+	+	-	+	+	-
Copepod	8.44	0.04	+	-	+	+	0.25
Aquatic insect larvae	35.42	18.60	20.70	14.82	99.12	93.59	45.95
Chironomidae larvae	35.01	16.76	9.69	13.19	32.20	79.50	25.54
Hydropsychidae larvae	-	0.30	9.97	1.23	41.25	11.68	12.62
Other aquatic insects	0.41	1.54	1.03	0.39	25.67	2.41	7.79
Fish	0.01	-	-	84.95	0.10	-	5.57
Cobitidae	-	-	-	18.74	-	-	-
Cyprinidae	-	-	-	61.54	0.06	-	-
Sisoridea	-	-	-	0.06	-	-	-
Eleotridae	-	-	-	0.52	0.03	-	-
Other fish	-	-	-	4.09	0.01	-	5.56
Scales and eggs	0.01	-	+	-	-	-	0.01
Amphipoda	-	-	0.01	0.09	-	-	-
Gammaridae	-	-	0.01	0.09	-	-	-
Oligochaeta	-	-	-	-	0.02	-	-
Mollusca	-	+	-	-	0.13	-	-
Umbo-veliger	-	+	-	-	-	-	-
Gastropoda	-	-	-	-	0.13	-	-
Others	0.05	-	-	-	0.00	-	-
Nematode	0.03	-	-	-	0.00	-	-
Water bear	0.03	-	-	-	0.00	-	-
Organic detritus	0.09	0.05	12.06	0.14	0.28	6.05	46.64

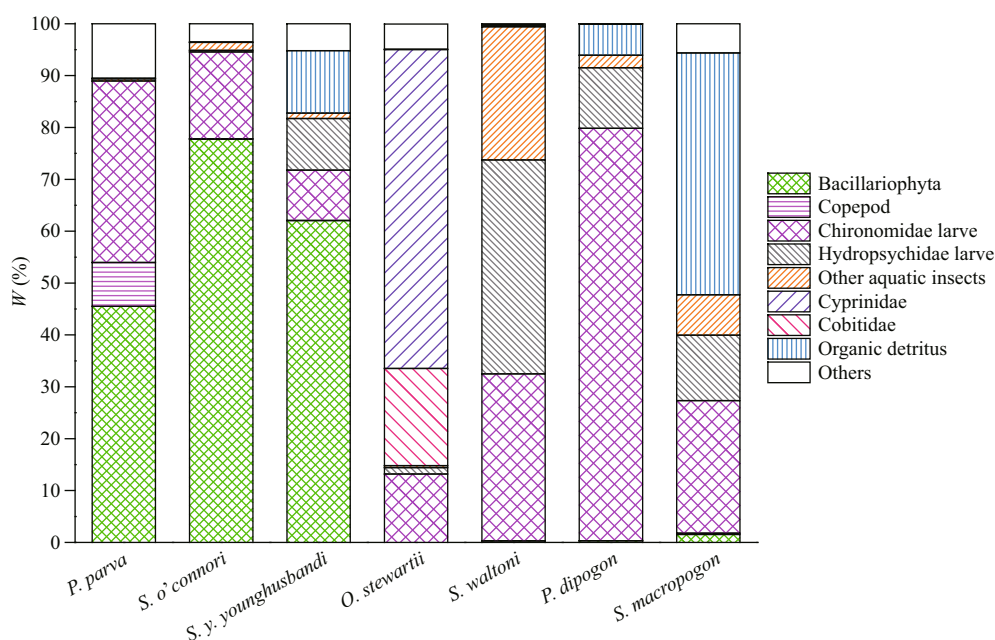
1: *P. parva*; 2: *S. o'connori*; 3: *S. younghusbandi younghusbandi*; 4: *O. stewartii*; 5: *S. waltoni*; 6: *P. dipogon*; 7: *S. macropogon*. “+” indicates percentage <0.01%; “-” indicates none.

Most prey points located toward the lower part indicate a generalized feeding strategy, in which a large number of prey items were usually consumed at a low percent. A preference for the Chironomidae larvae was observed. The Chironomidae larvae were the most important prey item of *P. parva*, with the highest frequency of occurrence ( $O\%=100\%$ ) and prey-specific abundance ( $P_i\%=28.45\%$ ), followed by Nitzschia ( $O\%=100\%$ ,  $P_i\%=20.66\%$ ), and Cyclotella ( $O\%=97.34\%$ ,  $P_i\%=12.98\%$ ). To the niche width, the points toward the lower right part of the graph indicate a relatively high within-phenotype component (WPC), i.e., high diet overlap within individuals. Therefore, *P. parva* is a generalized predator, which relied on a

wide trophic spectrum, and Bacillariophyta and the Chironomidae larvae were the major prey items.

### 3.4 Dietary overlaps between *P. parva* and native fishes

The food compositions (in weight percent, *W*%) of *P. parva* and 6 native Schizothoracinae fishes are listed in Table 3. The Schizothoracinae fishes can be divided into four feeding types. *S. o'connori* and *S. y. younghusbandi* are phytophagous feeding mainly on Bacillariophyta, that accounted for 77.77% and 66.16% of their diet, respectively. *S. waltoni* and *P. dipogon* are zoobenthivores. Hydropsychidae larvae (41.25%) and Chironomidae larvae (32.20%) were the main prey items of *S. waltoni*, while the



**Fig.4** Diet compositions of both *P. parva* and native Schizothoracinae fishes in the middle reaches of Yarlung Zangbo River (in weight percentage, *W*%)

Chironomidae larvae (79.50%) were the main prey item of *P. dipogon*. *O. stewartii* was the only piscivore among the 6 native fishes. Fish accounted for 84.95% in the food composition, followed by the Chironomidae larvae (13.19%). Further, *S. macropogon* was omnivores, which mainly ingested detritus (46.64%) and aquatic insects (45.95%). The Chironomidae larvae accounted for 25.54% of their diet.

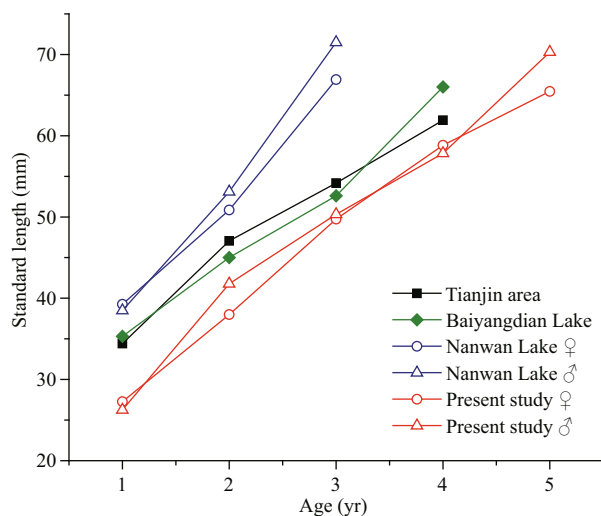
These results revealed that native fishes exhibit some feeding differentiation, which was probably an adaptive strategy of these fishes to deal with food shortage of the Qinghai-Tibetan Plateau. However, the freeloader *P. parva* might disturb this balance, leading to competition for food between the non-native and native fishes (Tables 3 and 4, Fig.4). According to the Morisita index (*C* value), food composition of *P. parva* was the most similar to that of *S. o'connori* and *S. y. youngusbandi*. Furthermore, significant diet overlaps were observed between *P. parva* and *S. o'connori* ( $C=0.90$ ), and between *P. parva* and *S. y. youngusbandi* ( $C=0.88$ ). This will lead to competition for food between *P. parva* and these two fishes for Bacillariophyta and Chironomidae larvae. However, considering the fewer number of abundant prey taxa and narrow dietary niche breadth, the diet spectrum of these two-native fish was actually narrow, placing them in a competitive disadvantage position. Similarly, *P. parva* might also have feeding stress on native *P. dipogon* ( $C=0.52$ ) on the utilization of the Chironomidae larvae. To some extent,

**Table 4** Biodiversity indexes of diet items of both *P. parva* and native Schizothoracinae fishes in the middle reaches of Yarlung Zangbo River

Fishes species	$N_0$	$N_1$	$N_2$	Ba	<i>T</i>
<i>P. parva</i>	11	2.77	2.36	0.12	2.5
<i>S. o'connori</i>	11	1.75	1.45	0.04	2.2
<i>S. youngusbandi youngusbandi</i>	11	2.90	2.10	0.10	2.2
<i>O. stewartii</i>	10	3.11	2.31	0.13	3.5
<i>S. waltoni</i>	16	3.11	2.94	0.12	3.0
<i>P. dipogon</i>	9	2.04	1.54	0.06	2.9
<i>S. macropogon</i>	8	4.08	3.25	0.28	2.6

$N_0$ : number of food items;  $N_1$ : number of important food items;  $N_2$ : number of very important food items; Ba: standardized dietary niche breadths; *T*: trophic level.

*P. dipogon* nearly fed only on the Chironomidae larvae ( $W\%=79.50\%$ ), its food composition was unitary, and the feeding scope was narrow. The overlap index between *P. parva* and other native fish was 0.11–0.30; the Chironomidae larvae were also the common prey item of these fishes. Furthermore, the trophic level of the non-native and native fishes varied by 2.2–3.5. *S. o'connori* and *S. y. youngusbandi* were at the lowest trophic level ( $T=2.2$ ), while *O. stewartii* was at the highest level ( $T=3.5$ ). Although it is piscivorous and the top consumer of the food web, *O. stewartii* hardly ingested *P. parva* ( $W\%=0.09\%$ ) (Huo et al., 2014). Therefore, *P. parva* can be regarded as an exotic competitor.



**Fig.5 Comparison of observed SL of *P. parva* from different regions**

#### 4 DISCUSSION

During the last 50 years, *P. parva* has successfully invaded many countries and regions worldwide and is considered the most invasive fish species (Gozlan et al., 2010). The present study showed that *P. parva* has become established in the Chabalong Wetland and that its population size is constantly increasing. It has invaded many waters of the Yarlung Zangbo River and its tributaries (Shen and Guo, 2008; Chen and Chen, 2010; Fan et al., 2011; Yang et al., 2011). The water temperature and primary productivity of the Yarlung Zangbo River is relatively lower than that of other aquatic environments due to the unique and complex plateau climate, and the special hydrogeomorphology (Wei et al., 2015). The invasive success of *P. parva* partially relates to its strong invasiveness, with a wide ecological amplitude (Sunardi et al., 2005, 2007), high plastic life history traits (Rosecchi et al., 2001; Pinder et al., 2005; Britton et al., 2007; Onikura and Nakajima, 2013), and generalized feeding habits (Rosecchi et al., 1993; Zhang et al., 1998; Xie et al., 2000). On the other hand, based on the food web and co-evolution theories (Elton, 1958), the relatively isolated aquatic ecosystem of the Qinghai-Tibet Plateau is fragile and vulnerable to outer disturbance due to simple fish fauna, low species diversity, and simple interspecific interaction patterns; it is too weak to resist alien fish invasion (Schoenherr, 1981; Minckley and Douglas, 1991; Wu and Tan, 1991; Chen and Chen, 2010). In addition, the adult native Schizothoracinae and Sisoridae species mainly inhabit the main stream of the Yarlung Zangbo River and its tributaries, leaving plenty of favorable

habitats for *P. parva*, such as river branches and wetlands, where the food resources are relatively abundant (Wu and Wu, 1992; Fan et al., 2011). Furthermore, anthropogenic activities, including repeated fish introduction, overexploitation of native fish, hydraulic engineering construction, and religious release (Gozlan et al., 2010; Huo et al., 2014; Zhu et al., 2017), facilitate the invasion success of *P. parva* in Tibet.

Plasticity in life-history strategies is considered as one of the most important reasons for *P. parva* to easily adapt to different habitats, including fast growth, early maturity, short life span, and special reproductive strategy (Rosecchi et al., 2001; Britton et al., 2007). The present study indicated that the growth rate of *P. parva* in the Chabalong Wetland is lower than that in the other regions (Table 5, Fig.5). This might be attributed to the high altitude and microthermal climate of the Qinghai-Tibet Plateau resulting in low mean water temperatures and short growth seasons, which are important determinants of the life history of fish (Cowx, 2001). According to Gaspar et al. (1999), with decrease in water temperature, the lifespan and body size of fish increases, while the growth rate of fish decreases. Studies have shown that the growth rate of *P. parva* varies widely in different places, which is attributed to population density, niche overlap, and food abundance (Yan, 2005; Britton et al., 2007, 2008). These intraspecific differences in the life-history traits between populations inhabiting different habitats indicate that this species can modify its life-history strategy according to environment conditions. This can be regarded as an adaptive evolutionary response of *P. parva* to environmental change.

The results of the present study indicated that *P. parva* in the Chabalong Wetland relies on a wide trophic spectrum and ingested mainly Bacillariophyta and the Chironomid larvae. This is consistent with the findings of previous studies, which described *P. parva* as an omnivore or planktivorous with a broad diet breadth (Rosecchi et al., 1993; Zhang et al., 1998; Wolfram-Wais et al., 1999; Xie et al., 2000). A preference of *P. parva* for the Chironomidae larvae has also been reported by other studies (Wolfram-Wais et al., 1999; Declerck et al., 2002). Therefore, as a generalized and opportunistic predator, *P. parva* can readjust its diet composition based on the abundance and availability of food. The broad diet spectrum enhances their adaptability to different environmental conditions. The results of the present study indicated



**Table 5 Comparison of growth characters of *P. parva* in different areas**

Region	<i>n</i>	Sex	Max age (a)	Sex ratio (F:M)	Growth parameters			References
					$L_{\infty}$	$k$	$t_0$	
※ Tianjin	480	♀+♂	3 <sup>+</sup>	1:0.61	-	-	-	Yang and Li (1989)
※ Baiyangdian Lake	51	♀+♂	3 <sup>+</sup>	1:0.91	64.82	1.142	0.250 7	Han and Li (1995)
※ Niushan Lake	162	♀+♂	1	-	-	-	-	Feng (2003)
※ Chao Lake	90	♀	2 <sup>+</sup>	1:1.31	-	-	-	Yan (2005)
		♂	3 <sup>+</sup>					
※ Dongting Lake	90	♀	2 <sup>+</sup>	1:1.5	-	-	-	
		♂	2 <sup>+</sup>					
※ Nanwan Lake	532	♀	3	1:1.56	107.01	0.246	-0.76	Li et al. (2017)
		♂	3		145.25	0.181	-0.66	
*Fuxian Lake	240	♀	2 <sup>+</sup>	1:1.14	-	-	-	Yan (2005)
		♂	3 <sup>+</sup>					
*Mikri Prespa Lake	296	♀+♂	3 <sup>+</sup>	1:2	-	-	-	Rosecchi et al. (1993)
*Top pond, England	163	♀	4	1:1.63	70.5	0.51	-	Britton et al. (2007)
		♂	4		72.7	0.77	-	
*Bottom pond, England	149	♀	2	1:1.61	79.6	0.81	-	
		♂	2		80.9	0.77	-	
*Šúr pond	143	♀	4 <sup>+</sup>	1:0.34	59.35	0.210	-1.071	Záhorská et al. (2010)
		♂	4 <sup>+</sup>		49.82	0.212	-1.646	
*Present study	256	♀	5	1:1.08	112.19	0.149 5	-0.801 2	
		♂	5		123.12	0.150 0	-0.713 2	

※ indicates native regions for *P. parva*; \* indicates areas *P. parva* invade.

certain overlaps between *P. parva* and six endemic Schizothoracinae species in the trophic niche. Bacillariophyta and Chironomid larvae were their common main prey items. The native fishes are probably well adapted to resist harsh environmental conditions by feeding differentiation; however, they are unable to contend with intruders, such as *P. parva*—a more effective hunter (Schoenherr, 1981; Minckley and Douglas, 1991; Rosecchi et al., 1993). As an exotic intruder, high grazing pressure exerted by dense *P. parva* population can change the prevalent environmental conditions through top-down effects characterized by increased development of phytoplankton and accelerated eutrophication (Adámek and Sukop, 2000; Gozlan et al., 2010). The decline of primary and/or second producers will have bottom-up effects on the upper trophic levels through the aquatic food webs (Power, 1990).

The adult Schizothoracinae fishes mainly inhabit swift current, while *P. parva* inhabit slow-flow waters. Therefore, the direct competition with adult Schizothoracinae for food might not occur very frequently. The competition for food will mainly occur

between *P. parva* and the Schizothoracinae fish larvae and/or fry. However, because of the slow early development and relatively hysteretic first-feeding on live bait (Shao et al., 2012), the Schizothoracinae fish larvae and/or fry were at a competitive disadvantage than *P. parva*. The mortality of these small-sized native fish might increase, which will lead to further decline of recruitment of these native fishes (Huo et al., 2014). Although the trophic competition might not occur frequently between *P. parva* and adult Schizothoracinae, the studies on feeding habits of native Schizothoracinae did not include individuals with SL <100 mm (Yang et al., 2011; Huo et al., 2014; Ma et al., 2014; Zhou, 2014; Yang, 2015; Liu, 2016). Therefore, further studies are necessary to demonstrate food relationships between *P. parva* and these small-sized native fishes.

Although the biological information collected in Chabalang Wetland is incomplete, some more ecological effects of *P. parva* can be speculated. Firstly, *P. parva* has been reported to feed on the eggs and larvae of native fish species (Jin et al., 1996; Xie et al., 2000). In the present study, some fish eggs and scales were found in the intestine of *P. parva*. Further

studies are necessary to elucidate if these belonged to native fish. Secondly, the high abundance of *P. parva* will result in intense competition with native fish for habitat, leading to habitat loss and niche displacement among native fish. This is because the waters that the invader inhabits are exactly the favorable feeding and fattening grounds of native *Triplophysa* and Schizothoracinae fish larvae and/or fry (Wu and Wu, 1992; Fan et al., 2011). Furthermore, *P. parva* has been found to be a vector of many parasites and pathogens, some of which have been documented to cause emergent infectious disease and high rates of mortalities of fish (Urabe et al., 2007; You et al., 2008; Gozlan et al., 2010). Therefore, their invasion might pose new potential threats to native fish and aquatic ecosystem. Further, *P. parva* is a non-target species that was unknowingly released along with intentionally-introduced species (Gozlan et al., 2010). Regarding their increasing distribution and their presence in waters that connect to major river catchments, fluvial dispersal is going on (Pinder et al., 2005). There might be few waters in Tibet immune from their invasion, numerical dominance, and subsequent impacts. To protect the endemic fish and the aquatic ecosystem in Tibet from the invasion, thorough investigation of *P. parva* in Tibet is needed. Further studies on the reproductive strategy, population dynamics, spreading tendency of *P. parva*, and the position it occupies in the plateau aquatic food web are also needed to establish effective risk assessment and management policies.

## 5 CONCLUSION

The invasive *P. parva* in Chabalong Wetland shows plasticity of some life history traits with slow growth and high growth potential. This appeared to be related to the low water temperature and short growth season in the plateau. It can be considered a generalized and opportunistic predator, competing with native fish, especially *S. o'connori*, *S. younghusbandi younghusbandi*, and *P. dipogon*, for Bacillariophyta and Chironomid larvae. However, because the habitats are different, direct competition with adult Schizothoracinae for food might not occur very frequently, the trophic effects of *P. parva* on native adult Schizothoracinae are limited; however, for small-sized native fish living in the same environment, such as Schizothoracinae fish larvae and/or fry, the effects may be significant. Further studies are needed to clarify the food relationships between *P. parva* and small-sized native fish.

## 6 ACKNOWLEDGMENT

The authors would like to thank DUAN Youjian, YANG Xin, and ZHOU Xianjun for help in sample collection.

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## Electronic supplementary material

Supplementary material (Appendix 1) is available in the online version of this article at <https://doi.org/10.1007/s00343-019-8004-5>.