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Better Fitness of Sharpbelly, *Hemiculter leucisculus* (Basilewsky, 1855) in Invaded Habitats: Evidence from Body Length-Weight Relationships Across the World

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YZ: Data curation, formal analysis, writing-original draft; TJ and XD: Conceptualization, methodology, writing- review and editing; LG, ZW, CL, WW, TX, LS, HH, SZ, MA, HJ: Data curation and language editing.

Key words
***Hemiculter leucisculus*, Body length-weight relationships, Difference analysis, Fitness, Growth patterns**

ABSTRACT

As one of the main driving factors of biodiversity loss, biological invasion has attracted wide attention. Among the many scientific issues in this field, the most noteworthy one is to figure out the ecological mechanisms behind successful invasions since relevant knowledge is extremely important for conservation and management, but we still know very little about that to some species. In view of this, the notorious sharpbelly *Hemiculter leucisculus* (Basilewsky, 1855) was selected as the research object, by analyzing the difference between its fitness in the native habitats and the invaded habitats at global scale through data integration technology and body length-weight relationships, this study attempted to reveal the ecological mechanisms underlying the global rapid successful invasion of this invasive species. The results showed that the fitness of the invasive populations was higher than the native populations ($t = 3.85$; $P < 0.05$). Based on the above, this study put forward a series of measures and suggestions for prevention and control so as to mitigate the potential harm of its further dispersal in the near future.

INTRODUCTION

With the continuation of global climate change, international trade and transportation industry development, biological invasion has become the second factor leading to global biodiversity loss (Duenas *et al*., 2021; Early *et al*., 2016; Leuven *et al*., 2017). Generally, biological invasion means the process that a species was transferred from its original habitat to a new habitat which is outside the biogeographical barrier by natural or anthropogenic assistances, and formed breeding populations in the new habitat, and afterward caused adverse impacts on the local biodiversity, agricultural, and forestry production as well as human health, or ecological disasters (Richardson *et al*., 2011). Compared with terrestrial ecosystems, aquatic ecosystems are more vulnerable to alien species invasion (Pyšek *et al*., 2020).

The sharpbelly *Hemiculter leucisculus* (Basilewsky, 1855) is a small freshwater fish belonging to Cypriniformes, Cyprinidae, Culterinae (Chen *et al*., 1998; Zhang *et al*., 2016), and usually dwells in the middle and upper layers of lakes, rivers, and reservoirs. It mainly feeds on invertebrates and phytoplankton. It can be sexually mature at the age of 1 year, spawns from April to October, with peak period of May and June, and its body length is usually 10–14 cm (https://fishbase.mnhn.fr/search.php; Huang *et al*., 2022). This cyprinid is native to China, Mongolia, Russia, Vietnam,

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and the Korean Peninsula (Khurshut, 2016). However, due to improper management during introduction, it has spread beyond its native range to many regions including Georgia, Afghanistan, Iran, Iraq, Kazakhstan, Uzbekistan, Turkmenistan, and Azerbaijan (Epitashvili *et al.*, 2023; Khurshut, 2016; Mustafayev *et al.*, 2015). In addition, this fish also possesses typical characteristics of invasive species (Wang *et al.*, 2013, 2016). For example, on the one hand, its life history pattern is r type, i.e. it shows short life span, fast growth rate, early sexual maturity, long breeding period, high fertility, and batch spawning. On the other hand, it also shows a certain degree of plasticity, e.g. with the change of climate or geographical environment, it can not only produce eggs with different ecological types, but also make its own brain grow with different patterns (Huang *et al.*, 2022; Liu *et al.*, 2022; Sun, 1987; Wang *et al.*, 2016; Wu and Yi, 1959). Therefore, some studies even made a bold prediction that, with the continuation of global climate change and increase of human activities, the areas with high invasion risk by this fish will spread all over the world except Antarctica (Dong *et al.*, 2020). In light of this species' strong invasive potential, it is reasonable to speculate that it may have higher fitness in the invaded habitats than the native habitats.

However, after a systematic review and anatomizing of the existing works on this fish all over the world, it is not hard to find that they still just focused on its basic biology (Wang *et al.*, 2016), ecology (Guo *et al.*, 2021; Hung *et al.*, 2015), physiology (Huang and Zeng, 2016), behavior (Lu, 2015), molecular biology (Luo *et al.*, 2022), phylogeny and adaptive evolution (Liu *et al.*, 2022; Vasileva *et al.*, 2022), phylogeography or zoogeography (Sun *et al.*, 2022; Vasileva *et al.*, 2022), environmental toxicology (Hung *et al.*, 2015; Zhang, 2007) as well as morphology and population genetics (Cho *et al.*, 2012; Sun *et al.*, 2022; Wang, 2021). By far, comparative research on the difference between its fitness in the native habitats and the invaded habitats has not been reported.

In view of this, by integrating the body length-weight data of *H. leucisculus* around the world and comparatively analyzing that data in both the native habitats and the invaded habitats, we attempted to uncover the ecological mechanisms behind the global rapid successful invasion of this species, and provide basic data or science and technology support for the scientific management of *H. leucisculus* and other similar invasive species.

MATERIALS AND METHODS

Data collection

The body length-weight relationships data of *H. leucisculus* were collected by retrieving with the key words *Hemiculter leucisculus*, body length-weight relations, total length, and body length, etc. in both English and Chinese databases including the Web of Science (https://www.webofscience.com/wos), Google Scholar (https://scholar.google.com), and China National Knowledge Infrastructure (https://www.cnki.net), and data types include journal articles, dissertations, government reports and materials. By statistics, 71 valid records were initially gleaned, of which 45 and 26 were in the native areas and the invaded areas, respectively (Supplementary materials). The spatial distribution of relevant research sites is shown in Figure 1.

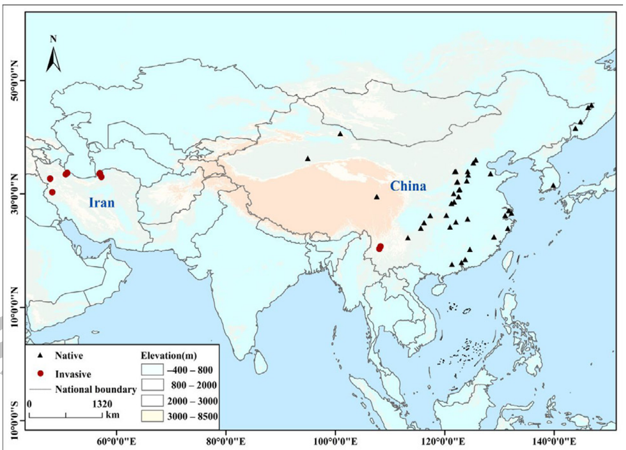

Fig. 1. Map showing spatial distribution locations of *Hemiculter leucisculus* populations in the present study.

Data cleansing

Before taking next steps, this study cleansed the data obtained previously in order to get more reliable information or results. To be specific, firstly, we removed the records that were duplicative, obviously incorrect, and incomplete with key information (e.g. sampling location and time, sample sizes, body length-weight relationship, as well as length types and units); Secondly, using the equations $a`_{cm} = a_{mm}\ 10^{b}$ and $a_{TL} = a_{LS}\ (TL/LS)^{-b}$ (if the relationship between total length and standard length or fork length is a proportional function) or $a_{TL} = a_{LS}(2f/L_{max} + g)^{-b}$ (if that relationship follows the linear function $TL = f + gLS$), we standardized the a in the filtered body length-weight relationship into a', so as to make the results of different studies with different body length types or units comparable to each other (i.e. unifying the body length in the body length-weight relationship into total length, and standardizing the units of body length and body weight into centimeter and gram, respectively). In the above formulas, LS is the standard length (SL) or fork length (FL) in the body length-weight relationship in the original records;

TL is total length; a_{LS} is the parameter corresponding to the length type before conversion; a_{TL} is the parameter corresponding to the total length. L_{max} is the maximum of standard length or fork length in the original studies. f and g are the regression intercept and slope, respectively, of the linear function describing the relationship between the total length and the standard length or the fork length (Froese, 2006). According to FishBase (https://fishbase.mnhn.fr/search.php) and relevant information (Qin *et al.*, 2017), the conversion formulas of TL and FL, and, TL and SL for *H. leucisculus* in this study are TL/FL = 1.15 and TL = 0.02 + 1.19SL, respectively. Thirdly, based on the theoretical relationship between lg(a') and b (Fig. 2), outliers (i.e. points outside the 95% confidence interval of the fitting line) are removed. Finally, a total of 48 data (36 and 12 from the native areas and the invaded areas, respectively) were obtained for following analysis.

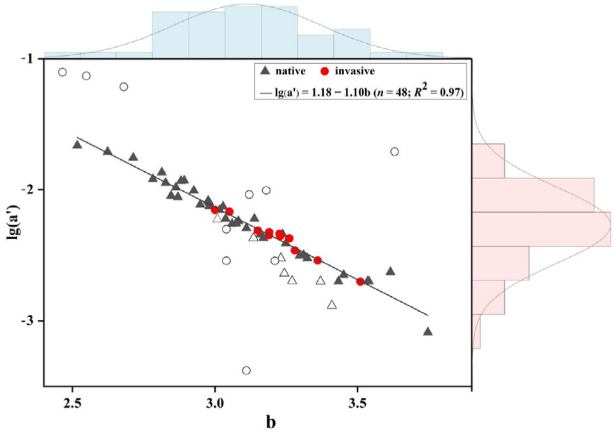

Fig. 2. Regression relationship between lg(a') and b in the body length-weight relationships for *H. leucisculus* (blank triangles represent the outliers in the data from the native areas; the blank circles represent the outlier in the data from the invaded areas; the blue parts represent the b-value frequency distribution histogram and the superimposed normal distribution curve; the pink parts represent the lg(a') frequency distribution histogram and the superimposed normal distribution curve).

Statistical analysis

Shapiro-Wilk and Levene tests were applied to evaluate normality and variance homogeneity of the b values of the body length-weight relationship of *H. leucisculus* populations, respectively. If the normal distribution and the variance homogeneity were both verified, an independent (single) sample *t* test was adopted; otherwise, non-parametric Mann-Whitney (Wilcoxon) tests were used to analyze whether there were significant differences between the b values of the native populations and the invasive populations (that two sets of b values and the theoretical value 3, respectively). All statistical analyses and graphics in this study were performed in ArcGIS 10.2 (Esri Co., USA) and OriginPro 2022 (OriginLab Corporation, USA). Unless otherwise specified, all statistics are expressed as mean ± standard error. The significance level (α) was set to 0.05 according to the past practice.

RESULTS

Value ranges of b

The results showed that b values of *H. leucisculus* populations in the native habitats and the invaded habitats were 2.52–3.75 (3.07±0.05) and 3.00–3.54 (3.25±0.05), respectively (Table I). Both manifest normal distribution ($W = 0.98$; $P > 0.05$) and variance homogeneity ($W = 2.53$; $P > 0.05$).

Table I. b values of both the invasive populations and the native populations of *H. leucisculus* (CI represents confidence interval for the median of b; SE represents standard error).

	n	Min	Max	Mean	Median	SE	95%CI
Native	36	2.52	3.75	3.07	3.03	0.05	2.98–3.16
Invasive	12	3.00	3.54	3.25	3.23	0.05	3.15–3.35

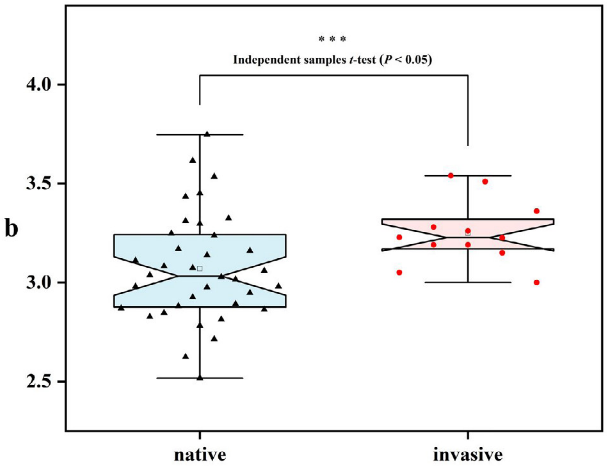

Fig. 3. Difference analysis on the b values of both the invasive populations and the native populations of *H. leucisculus* (the blank boxes refer to the means).

Difference analysis on the invasive populations and the native populations

The results showed that there was significant difference in b values between the invasive populations and the native populations ($t = 3.85$; $P < 0.05$; Fig. 3); the b values of the invasive populations were greater than 3 with significance ($t = 5.35$; $P < 0.05$), while the b values of the native populations were greater than 3 with no significance ($t = 1.53$; $P > 0.05$).

DISCUSSION

Value range of b

The b value of fish's body length-weight relationship should theoretically be within the range from 2.50 to 3.50 (Carlander, 1977), with which our results are roughly consistent. However, we noticed that the b values in the Erlongshan reservoir of Jilin Province (3.62) and the Beijiang river of Guangdong Province (3.75) deviated far from the upper limit of the theoretical range. Looking up the primary data, it is not difficult to find that: due to the lack of food-competing fishes (e.g. silver carp *Hypophthalmichthys molitrix* (Valenciennes, 1844) and bighead carp *Aristichthys nobilis* (Richardson, 1845), *H. leucisculus* population in the Erlongshan reservoir is rich in food resources, which means better growth conditions, i.e. a larger b value. By contrast, because of sampling bias (the samples were all females with gonadal development stages of from IV to V), the b value in the Beijiang river had a large deviation from the theoretical value as well. This demonstrates that it is correct to cleanse the data after data collection or before further analysis, and hence our conclusions are reliable.

Fitness comparison between the native habitats and the invaded habitats

As mentioned above, the invasive populations' b values (3.25 ± 0.05) were significantly greater than 3, and thus manifest positive allometry; the native populations' b values (3.07 ± 0.05) were insignificantly greater than 3, and thus manifest isometry (Fig. 4). For this reason, it can be inferred that our previous conjecture is highly probably correct, i.e. *H. leucisculus* population may have better fitness in the invaded habitats than the native habitats. However, unlike previous studies, Lin *et al.* (2023) found that *Pseudorasbora parva* (Temminck and Schlegel, 1846) showed good fitness at both habitats. In contrast, Sun *et al.* (2023) discovered that *Oreochromis niloticus* (Linnaeus, 1758) owned poor fitness at both the native regions and the invaded regions, although the fitness in the latter is still higher than the former.

Management recommendations

Based on the results of this paper, we find that *H. leucisculus* has a strong invasion potential, which further supports the speculation that this fish may spread to new habitats in the near future. Hence, this study attempts to propose a series of adaptive management recommendations: (1) adopting new technologies (e.g. eDNA and eRNA) to conduct continuous monitoring on its global population dynamics; (2) attempting to analyze the mechanisms behind this fish's rapid successful global invasion from other perspectives, e.g. the molecular level; (3) increasing input in the basic research on this fish so as to comprehensively understand its ecological habits; (4) enhancing transnational cooperation to achieve more coordinated and effective prevention and control.

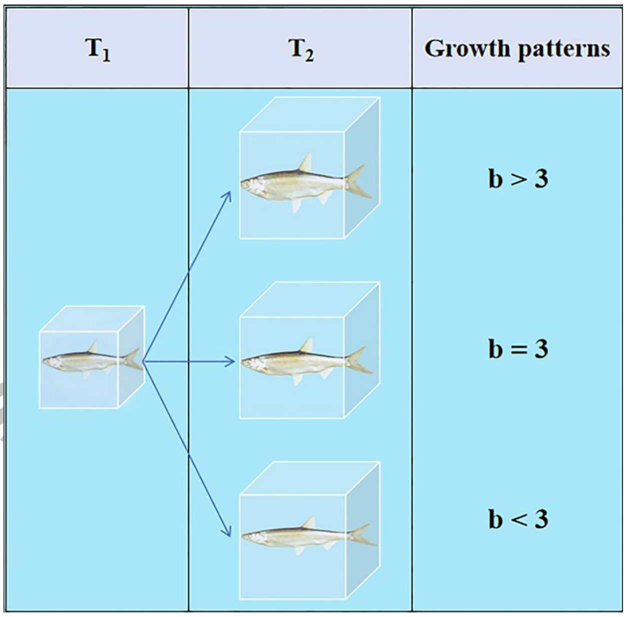

Fig. 4. Growth patterns of *H. leucisculus* (The difference forms between the parameter b and 3 represent different growth patterns of the fish. When the fish grows from T_1 to T_2, that b = 3 means isometry, i.e. the fish is in the same shape and nutrient conditions during T_2 and T_1; b < 3 means negative allometry, i.e. the fish is thinner and in worse nutritional conditions during T_2; b > 3 means positive allometry, i.e. the fish is thicker and in better nutritional conditions during T_2. The differences between b values in different populations reflect the suitability of different habitats to the species).

DECLARATIONS

Acknowledgments

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Supplementary material

There is supplementary material associated with this article. Access the material online at: https://dx.doi.org/10.17582/journal.pjz/20240420084908

Statement of conflict of interest

The authors declare that there is no conflict of interests regarding the publication of this article.

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Supplementary Material

Better Fitness of Sharpbelly *Hemiculter leucisculus* (Basilewsky, 1855) in Invaded Habitats: Evidence from Body Length-Weight Relationships Across the World

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Supplementary Table S1. Body length-weight relationships of *H. leucisculus* at global scale.

No.	Country	Location	Sampled year(s)	Gender	n	L_{min}–L_{max}	a'	b	R^2	References
1	China (N)	Fenhe Reservoir	1984–1985	F	426	5.90–19.00 cm	0.0060	3.14	1.00	Xie et al., 1986
2		Fenhe Reservoir	1984–1985	M	388	6.00–18.80 cm	0.0082	2.98	1.00	Xie et al., 1986
3		Fenhe Reservoir	2019	C	60	5.00–15.82 cm	0.0020	3.27	0.99	Xue, 2020
4		Dongjiangyuan	2010	C	248	7.90–16.30 cm	0.0013	3.41	0.87	Deng, 2013
5		Dong Jiang	NA	C	246	6.20–13.50 cm	0.0022	3.45	0.90	Deng, 2013
6		Gui Lin	NA	C	279	5.00–18.90 cm	0.0031	3.30	0.94	Deng, 2013
7		Hu Bei	NA	C	238	6.00–13.50 cm	0.0032	3.31	0.95	Deng, 2013
8		Bei Bing	NA	C	300	8.60–18.50 cm	0.0121	2.78	0.96	Deng, 2013
9		Hei Long Jiang	NA	C	120	6.00–13.70 cm	0.0023	3.24	0.94	Deng, 2013
10		Lake Jingwei	2018	C	96	NA	0.0195	2.62	1.00	Gong, 2019
11		Bei Jiang	2006–2007	F	63	12.30–21.50 cm	0.0008	3.75	0.90	Li et al., 2008
12		Bei Jiang	2005–2006	C	591	8.80–22.80 cm	0.0055	3.07	0.97	Zhao et al., 2009

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No.	Country	Location	Sampled year(s)	Gender	n	L_{min}–L_{max}	a'	b	R²	References
13		Luhun Reservoir	2010	C	85	9.50–15.50 cm	0.0075	3.03	0.95	Liu et al., 2016
14		Luhun Reservoir	2010	F	21	NA	0.0099	2.93	0.84	Liu et al., 2016
15		Luhun Reservoir	2010	M	19	NA	0.0136	2.81	0.92	Liu et al., 2016
16		Erlongshan Reservoir	NA	C	108	NA	0.0024	3.62	NA	Sun, 1987
17		Luohe River	2008	C	145	9.20–15.30 cm	0.0117	2.88	0.89	Liu and Li, 2015
18		Luohe River	2008	F	44	NA	0.0118	2.89	0.94	Liu and Li, 2015
19		Luohe River	2008	M	101	NA	0.0176	2.71	0.84	Liu and Li, 2015
20		Lake Dalai	1990–1992	C	600	NA	0.0218	2.52	NA	Li and Wang, 1995
21		Lake Xingkai	2007	C	205	8.00–19.00 cm	0.0043	3.14	0.99	Xun, 2009
22		The main stream of the Yangtze River	2007	C	42	8.50–12.50 cm	8.5117	2.82	0.86	Luo and Chen, 2009
23		Amur River	2012	C	30	6.60–16.40 cm	0.0043	3.17	0.99	Huang et al., 2014
24		Liuxihe	2012	C	310	9.80–27.40 cm	0.0020	3.37	0.99	Li et al., 2014
25		Xingkai (Khanka) Lake	2007	C	20	12.80–19.70 cm	0.0020	3.43	0.95	Liu et al., 2012
26		the Mainstream of Yellow River	2018	C	19	5.10–17.80 cm	0.0070	3.02	0.98	Wang et al., 2022
27		Dengzhou section	2015–2020	C	785	6.50–29.00 cm	0.0058	3.08	0.99	Wang et al., 2023
28		Beijing-Hangzhou grand canal	2020–2021	C	274	8.20–22.50 cm	0.0090	2.85	0.95	Zhang et al., 2022b
29		Oujiang River	2019	C	49	10.40–23.00 cm	0.0030	3.23	0.97	Zhang et al., 2022a
30		Dongting Lake	2017–2019	C	709	4.57–20.31 cm	0.0046	3.24	0.93	Huang et al., 2022
31		Lake Niushan,Yangtze River	2002–2004	C	128	8.90–21.40 cm	0.0077	2.95	0.90	Ye et al., 2007
32		Lake Niushan,Yangtze River	2002–2004	M	106	11.70–18.10 cm	0.0113	2.83	0.84	Ye et al., 2007
33		Lake Niushan,Yangtze River	2002–2004	F	152	11.70–18.30 cm	0.0104	2.86	0.86	Ye et al., 2007
34		Tian-e-zhou Oxbow, Yangtze River	2010–2011	C	223	3.20–13.90 cm	0.0046	3.16	0.99	Wang et al., 2012
35		Yiluo River	2016	C	2092	4.20–21.40 cm	0.0039	3.25	0.96	Qin et al., 2017
36		Dianshan Lake	2013	F	217	7.30–72.90 cm	0.1332	1.70	0.66	Kindong et al., 2017
37		Three Gorges Reservoir	2010–2011	C	375	6.50–14.80 cm	0.0060	3.04	0.92	Perera et al., 2022
38		Three Gorges Reservoir	2010–2011	C	326	5.50–14.70 cm	0.0020	3.54	0.95	Perera et al., 2022
39		Three Gorges Reservoir	2010–2011	C	119	6.50–17.10 cm	0.0030	3.32	0.95	Perera et al., 2022
40		Songhua River	2020–2021	C	1258	NA	0.0060	3.01	NA	Lu et al., 2023
41		Wujiang River	2006–2014	C	3205	4.30–19.50 cm	0.0075	2.98	0.98	Yang et al., 2016
42		Tarim River	2009–2010	C	501	4.00–18.80 cm	0.0055	3.06	0.98	Huo et al., 2012
43		Chishui River	2007–2012	C	187	7.80–17.20 cm	0.0080	2.98	0.97	Liu et al., 2014
44		Xiangjiang River	2010	C	33	7.40–17.70 cm	0.0088	2.87	0.97	Lei et al., 2015
45	Korea (N)	Upo Wetland	2007–2014	C	43	12.00–25.30 cm	0.0051	3.11	0.96	Kim et al., 2017
46	China (I)	Lake Erhai	2009–2011	F	2443	4.30–19.10 cm	0.0042	3.26	0.96	Wang, 2012
47		Lake Erhai	2009–2011	M	1290	4.60–12.30 cm	0.0048	3.19	0.97	Wang, 2012

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No.	Country	Location	Sampled year(s)	Gender	n	L_{min}–L_{max}	a'	b	R^2	References
48		Lake Erhai	2009–2012	C	2620	2.40–23.20 cm	0.0034	3.28	0.99	Tang et al., 2013
49		Lake Erhai	2009–2012	F	298	5.80–16.80 cm	0.0045	3.19	0.96	Tang et al., 2013
50		Lake Erhai	2009–2012	M	218	6.70–15.00 cm	0.0049	3.15	0.97	Tang et al., 2013
51	Iran (I)	Kaboudval/Zarrineh	2010–2017	C	14	11.04–14.41 cm	0.0050	3.04	0.95	Mouludi-Saleh and Eagderi, 2019
52		Anzali wetland	2010–2011	C	51	14.80–20.00 cm	0.0068	3.05	0.91	Moradinasab et al., 2012
53		Anzali Lagoon	2000–2001	M	46	5.00–16.40 cm	0.0046	3.23	0.92	Mohammad and Davood, 2002
54		Anzali Lagoon	2000–2001	F	44	NA	0.0044	3.23	0.96	Mohammad and Davood, 2002
55		Zarinehrud River	2013	C	77	6.60–14.20 cm	0.0070	3.00	0.89	Radkhah and Eagderi, 2015
56		Alma-Gol (wetlands of northern Iran)	2000–2002	F	233	NA	0.0004	3.11	0.98	Patimar. et al., 2008
57		Alma-Gol (wetlands of northern Iran)	2000–2002	M	202	NA	0.0029	3.04	0.98	Patimar. et al., 2008
58		Adji-Gol	2000–2002	F	54	NA	0.0195	3.63	0.97	Patimar. et al., 2008
59		Adji-Gol	2000–2002	M	41	NA	0.0099	3.18	0.98	Patimar. et al., 2008
60		Ala-Gol	2000–2002	F	214	NA	0.0020	3.51	0.99	Patimar. et al., 2008
61		Ala-Gol	2000–2002	M	210	NA	0.0029	3.36	0.99	Patimar. et al., 2008
62		Anzali wetland	2015	C	32	10.22–16.23 cm	0.0092	3.12	0.95	Radkhah et al., 2016
63		Shadegan, Dez, and Karkheh	2015	C	6	9.50–14.00 cm	6.7900	3.19	0.94	Valikhani et al., 2020
64		Caspian	NA	C	10	9.50–16.40 cm	0.0020	3.54	0.99	Esmaeili et al., 2014
65		pond Gonbad kavoos	2008	F	36	1.93–2.94 mm	NA	3.19	0.99	Asgardon et al., 2018
66		pond Gonbad kavoos	NA	M	16	NA	NA	3.23	0.99	Asgardon et al., 2018
67		pond Gonbad kavoos	NA	C	52	NA	NA	3.24	0.99	Asgardon et al., 2018
68		Sefidroud River	2012–2013	C	235	9.10–18.10 cm	0.0790	2.47	0.87	Mousavi-Sabet et al., 2013
69		Sefidroud River	2012–2013	M	99	9.30–16.90 cm	0.0740	2.55	0.93	Mousavi-Sabet et al., 2013
70		Sefidroud River	2012–2013	F	136	9.10–18.10 cm	0.0610	2.68	0.87	Mousavi-Sabet et al., 2013
71	Russia (I)	Khanka Lake	1972	C	NA	15.10–21.50 cm	0.0029	3.21	0.70	Gavrenkov and Ivankov, 1976

Note: N refers to the native population; I refers to the invasive population; F means female samples; M means male samples; C means the samples with mixed sexes or indistinguishable sexes.

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