



Comparative growth, feeding and reproduction of hatchery-reared and wild mandarin fish *Siniperca chuatsi* in a shallow Yangtze lake, China

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ABSTRACT: Stocking hatchery-reared fish in natural shallow lakes is a common practice in Chinese fisheries. The success of these fisheries depends on the balance between the commercial value of the stock and the growth performance of stocked fish to rapidly reach commercial size. The mandarin fish *Siniperca chuatsi* has become a commercially important fishery in China. However, the performance of hatchery-reared mandarin fish (HMF) after release into natural environments and their interactions with wild mandarin fish (WMF) have received little attention. In this study, we compared the growth, feeding and reproduction of HMF with WMF in a shallow Yangtze lake. We found that 11 mo after release, the growth of HMF was significantly slower than that of WMF but rapidly caught up after 16–19 mo. This suggests that HMF may experience compensatory growth after 11 mo, which may be a result of a low reproductive investment compared to WMF. In addition, the trophic niche of HMF differed significantly from that of WMF, with a lower diversity of prey and a single dominant prey species. Furthermore, there was no significant diet overlap between HMF and WMF. Our findings demonstrated that the growth performance of HMF can equal or exceed that of wild conspecifics, and that there was limited diet overlap with WMF, suggesting that the current stock enhancement programmes of releasing HMF can result in fish similar to that of WMF, with limited foraging competition.

KEY WORDS: Hatchery-reared and wild fish · Growth · Feeding · Reproduction · Interactions · Fisheries management

1. INTRODUCTION

Stock enhancement is a common fisheries management tool used extensively in both freshwater and marine environments (Huusko & Vehanen 2011). The practice consists of releasing hatchery-reared stocks to increase the abundance and yield of a fishery population (Lorenzen 2005, Li et al. 2014a). Stocking hatchery-reared fish has been used for fisheries practice since the mid-nineteenth century. In 2010, there

was a total of 94 countries practising stock enhancement with 180 fish species (FAO 2010). Successful stock management can not only increase socio-economic benefits and create new work opportunities, it can also provide high-quality food and increase protein availability (Pinkerton 1994, Lorenzen & Garaway 1998). However, stocking hatchery-reared fish may also have negative ecological and genetic impacts on wild fish, e.g. genetic contamination (Jonsson & Jonsson 2006, Kitada 2020), predation (Weber

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& Fausch 2003), competition (Nakajima et al. 2013, Pinter et al. 2018), induction of premature migration (Lorenzen et al. 2012) and introduction of pathogens (Lorenzen et al. 2012). Long-term releases can alter the genetic composition and may cause a decline in fitness of wild populations when the proportion of hatchery fish is very high (Kitada 2020). Therefore, stocking hatchery-reared fish has often been a subject of controversy; its effectiveness and side-effects on wild stocks being questioned (Lorenzen 2005, Jonsson & Jonsson 2006, Araki & Schmid 2010).

Previous studies have shown that hatchery-reared fishes can have competitive advantages over their wild counterparts due to their higher aggressiveness and usually larger size compared to wild conspecifics when released into the wild (Rhodes & Quinn 1998, Johnsson & Bjornsson 2001, Yamamoto et al. 2008, Vehanen et al. 2009, Nakajima et al. 2013, Taylor et al. 2017). However, hatchery-reared fish may take some time to acclimatize to the unfamiliar natural conditions (Shurov et al. 1987, Sundström & Johnsson 2001). A reduction of prey availability in the wild would also lead to slower growth and higher mortality of hatchery-reared fish (Sosiak 1982, Sundström et al. 2004). Despite some studies comparing the survival and growth of hatchery-reared and wild fish, no clear pattern has emerged, which is probably due to behavioural, morphological and physiological differences between wild and hatchery-reared fish (Einum & Fleming 2001, Vehanen et al. 2009, Pinter et al. 2018).

The mandarin fish *Siniperca chuatsi* (Basilewsky) is one of the most important commercial freshwater fish species in Asia, with a wide latitudinal spread from the Zhujiang River basin (south) to the Amur River system (north) (Li et al. 2014b). In China, it is popular because of its extensive distribution and high commercial value. It is a top predator at all stages, feeding on live fish or shrimp only (Liu et al. 1998, Li et al. 2013, 2014a). However, the wild populations of mandarin fish have declined rapidly in the last decades as a consequence of habitat degradation, fewer spawning grounds, overfishing and eutrophication (Yao & Li 2018). This has led to a decrease in piscivorous fishes at the highest trophic level and the dominance of small-sized fishes in the Yangtze lakes (Cao et al. 1991). To maintain or en-

hance the yield of recreational fisheries and utilize the abundant small-sized fish resources, hatchery-reared mandarin fish (HMF) have been stocked in many lakes and reservoirs in China since the 1990s (Cui & Li 2005, Li et al. 2014b). In many cases, stocking natural lakes with HMF contributes to immediate resource enhancement and increased economic benefits (Cui & Li 2005, Li et al. 2014b). However, the performance of HMF that are released into natural environments and their interaction with the wild population have received little attention (Li et al. 2014a).

In this study, we compared the growth, feeding and reproductive characteristics of HMF and wild mandarin fish (WMF) with similar genetic backgrounds in a shallow Yangtze lake. Our aim was to test the performance of HMF under natural settings and their potential impact to WMF populations.

2. MATERIALS AND METHODS

2.1. Study site

Xiaosihai Lake (30° 16' N, 114° 41' E) is located in the middle reach of the Yangtze River, Hubei Province, Central China, with an area of 133.3 ha and a depth ranging from 1.0–1.7 m (Fig. 1). In 2007, the lake was mostly covered by *Trapa bispinosa* (a floating plant), and only a small part of the littoral zone was sparsely vegetated with *Myriophyllum spicatum*

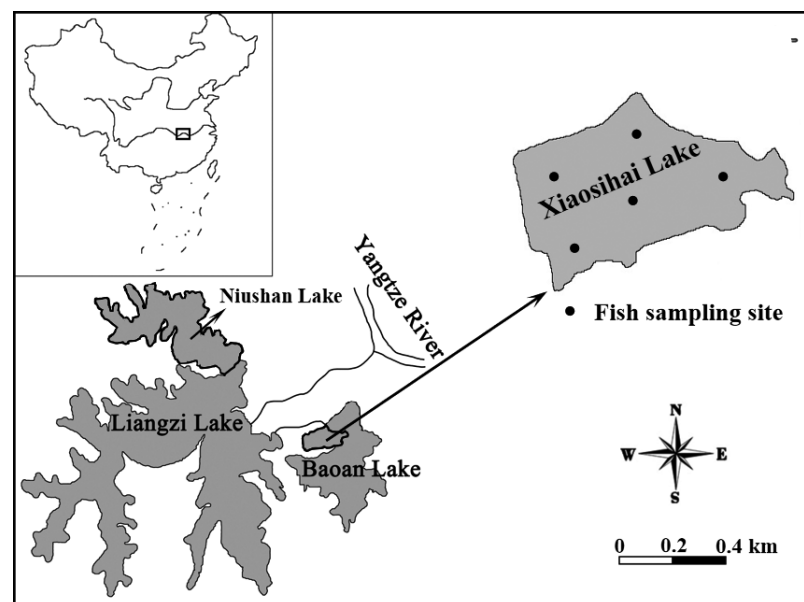


Fig. 1. Location of Xiaosihai Lake, showing the gill-net sampling sites

(a submersed plant). Based on the trophic state index, the lake was slightly eutrophic (Li et al. 2013). The fish community of the lake comprised 42 fish species belonging to 13 families. Common carp *Cyprinus carpio*, bighead carp *Aristichthys nobilis*, silver carp *Hypophthalmichthys molitrix*, mandarin fish and Chinese snakehead *Channa argus* were the most important commercial fishes (Zhang 2005). The total catches of mandarin fish in Xiaosihai Lake in 2005 and 2006 were 1656 and 1859 kg, respectively. Quantitative sampling of the small fish in 2007 showed that the density was 1.93 ind. m⁻², and the topmouth gudgeon *Pseudorasbora parva* was the most abundant species (Li et al. 2010).

2.2. Mandarin fish stocking

On 23 June 2006, a total of 6000 juvenile HMF (mean \pm SD: total length [TL] = 63.1 \pm 4.94 mm, body weight [BW] = 3.17 \pm 0.70 g), originated from 24 spawners from a state-owned hatchery, were stocked in Xiaosihai Lake. The brood stock was captured from Niushan Lake, which belongs to the same water system as Xiaosihai Lake (Fig. 1). HMF juveniles were reared on live silver carp fry in concrete tanks for 40 d. All HMF juveniles were marked using coded wire tags (CWTs; 0.25 mm diameter, 1 mm length; Northwest Marine Technology [NMT]) before release. CWTs were injected between the base of the dorsal fin and the lateral line of each fish. CWT marking has been used successfully and has shown negligible effects on mortality and growth of mandarin fish (Zhang & Li 2007, Li et al. 2014a). Three days after marking, they were transported in oxygen-filled plastic bags (20 l) from the hatchery to Xiaosihai Lake and released across the littoral zone by boat.

2.3. Fish sampling

Mandarin fish were sampled by gill net during (1) April–May 2007 (spring, ca. 11 mo after release), (2) July–August 2007 (summer, ca. 14 mo after release), (3) October–November 2007 (autumn, ca. 16 mo after release) and (4) December–January 2008 (winter, ca. 19 mo after release). During each season, 30 gill nets of 6 different mesh sizes (30, 40, 50, 60, 70 and 80 mm) were used to capture mandarin fish. There were 5 gill nets of each mesh type, and each net was 30 m long and 1.5 m high. Throughout the lake, 5 sampling sites were selected, and 6 nets (6 different

mesh nets connected together) were set in each site. The 30 gill nets were pulled up and examined for fish after 4 h during daytime and 10–12 h during nighttime. Fishing was conducted at least 3 days and nights during each season. Additionally, electrofishing was conducted at night (from 20:00–23:00 h) in the autumn and winter along the littoral zones, with a generator-powered machine (DC, 4 kW, 220–380 V, 50 Hz) (Li et al. 2013a).

Once captured, mandarin fish were immediately anesthetized with MS222, then placed in a box with ice and transported to the laboratory. An NMT handheld detector was used to detect the CWTs to distinguish HMF from the WMF. TL (to the nearest mm) and BW (to the nearest 0.1 g) were also individually measured. The operculum was removed and frozen for later age determination (Chiang 1959). Stomachs were removed and preserved in 10% buffered formalin solution for contents analysis. A total of 118 HMF (spring: 24; summer: 0; autumn: 33; winter: 61; and 51 electrofished) and 424 WMF (spring: 161; summer: 38; autumn: 43; winter: 182; and 69 electrofished) were sampled. All HMF (177–325 mm), and 290 WMF (91–539 mm), were analyzed for stomach contents. All procedures of stocking and capturing fish complied with the animal welfare regulations of the Government of China and the ethical rules of the Institutional Animal Care and Use Committee of the Institute of Hydrobiology (Approval ID: Keshuizhuan 08529).

2.4. Stomach content analysis

The stomach contents of mandarin fish were analyzed by counting and measuring prey organisms under a stereo binocular microscope (Olympus SZ61-ILST-SET). Prey fish in stomach contents were identified to species when possible; otherwise, the identification stopped at the genus or order level (Li et al. 2013a). The lengths of intact prey fish were directly measured. For slightly digested prey fish that could be identified to species by external morphology, their size was back-calculated by means of the linear equations between their standard length and TL. Heavily digested prey fish were identified to species based on the morphology of intact species-specific bones of the prey fish that remained in stomachs, and TL and BW of the digested prey fish were back-calculated theoretically according to the regression equations made by Zhang (2005). The index of relative importance (%IRI) was used to describe the importance of all possible prey taxa (Pinkas et al.

1971, Liao et al. 2001), which provides an optimal balance of frequency of occurrence, numerical abundance and abundance by weight of taxa in fish diets (Liao et al. 2001).

2.5. Reproduction parameters

In Yangtze lakes, the breeding season of mandarin fish occurs from April–July with a water temperature above 20°C. Most WMF reach sexual maturity at age 2 yr; a few individuals may reach maturity at 1 yr (Yao & Li 2018). Gonads were collected in May 2007 and were weighed to the nearest of 10^{-3} g (gonad weight, GW), then preserved in 10% buffered formalin solution for later analysis. Based on macroscopic appearance, female gonads were classified into 6 stages (stage I–VI) following Chiang (1959). The gonado-somatic index (GSI), absolute fecundity (AF), relative fecundity (RF) and egg diameters (ED) were only measured on mature HMF with stage IV and V gonads and WMF of the same age (WMF-SA). In total, 8 HMF and 15 WMF-SA were analyzed.

The GSI was calculated as: $GSI (\%) = 100 GW / BW$. AF was obtained by counting eggs, and RF was calculated as $RF = AF / BW$ (Pompei et al. 2016). We randomly selected 50 oocytes from each female and measured ED (in mm) using the software Image J to calculate the mean value of egg diameter.

2.6. Data analysis

The length–weight relationships of HMF and WMF were described by the equation: $\ln BW = \ln a + b \ln TL$, where $\ln a$ and b are the intercept and coefficient of the regression curve, respectively (Froese 2006). A 1-sample *t*-test was used to verify if there was a significant difference between the *b*-value of each individual and the isometric value 3. An independent-samples *t*-test was used to test for possible significant differences of *b*-values and condition factors (CFs) between HMF and WMF. CF was calculated as: $CF = 10^5 \times BW / TL^3$.

WMF-SA were selected from each survey season based on the results of age determination. Then, growth, feeding and reproduction were compared between HMF and WMF-SA. A 2-way ANOVA was used to test for differences in TL, BW and CF between HMF and WMF-SA at a period of 11, 16 and 19 mo after release. Tukey's HSD post hoc test was used to detect the significance of differences among treatment means after ANOVA. Specific growth rates

(%) of TL (SGR_{TL}) and BW (SGR_{BW}) between HMF and WMF-SA at different growth periods were calculated as: $SGR_{TL} = 100 (\ln TL_f - \ln TL_i) / T$ and $SGR_{BW} = 100 (\ln BW_f - \ln BW_i) / T$, using mean lengths and weights (Siikavuopio et al. 2009), where TL_f and TL_i are the final and initial total length, and BW_f and BW_i are the final and initial body weight, and T is the number of days of fish growth between the 2 survey periods.

To examine size-dependent variation in the diet, HMF and WMF were divided into small (<216 mm TL) and large (≥ 216 mm TL) size groups based on the average TL of age-1 HMF (216 mm). The differences in the diet composition from stomach content analysis with respect to species, seasons and size groups were assessed by a chi-squared test (χ^2) of the frequency of a given prey (Sley et al. 2009, Li et al. 2014a). Schoener's index was used to measure the dietary overlap (Schoener 1970). This index expresses diet similarity between 2 species on a scale from 0, representing no overlap, to 1, representing complete overlap between species. Biologically meaningful diet overlap is indicated by index values exceeding 0.60 (Schoener 1970).

The differences in GSI values between HMF and WMF were assessed using an independent-samples *t*-test following an arcsine transformation of GSI data. AF, RF and ED data were log-transformed, and the independent-samples *t*-test was used to compare HMF and WMF. Statistical analyses were performed using SPSS v.16.0 for Windows (SPSS). Normality and homogeneity of data were assessed using a 1-sample Kolmogorov-Smirnov test and Levene's test. Results of statistical tests were considered significant at $p < 0.05$.

3. RESULTS

3.1. Length–weight relationships

The length–weight relationships were highly significant for both HMF and WMF (HMF: $\ln BW = 3.17 \ln TL - 12.03$, $R^2 = 0.986$, $F = 8026.2$, $p < 0.001$, $n = 118$; WMF: $\ln BW = 3.06 \ln TL - 11.49$, $R^2 = 0.993$, $F = 59575.6$, $p < 0.001$, $n = 424$) (Fig. 2). The *b*-values for both HMF and WMF were significantly larger than 3.0, indicating a tendency towards positive allometric growth (HMF: $t = 107.1$, $df = 117$, $p < 0.05$; WMF: $t = 87.8$, $df = 423$, $p < 0.05$). Significant differences in the slopes (*b*) were observed between HMF and WMF ($t = 61.998$, $df = 540$, $p < 0.05$) despite a lack of significant difference in body condition ($t = 0.232$, $df = 540$, $p = 0.817$).

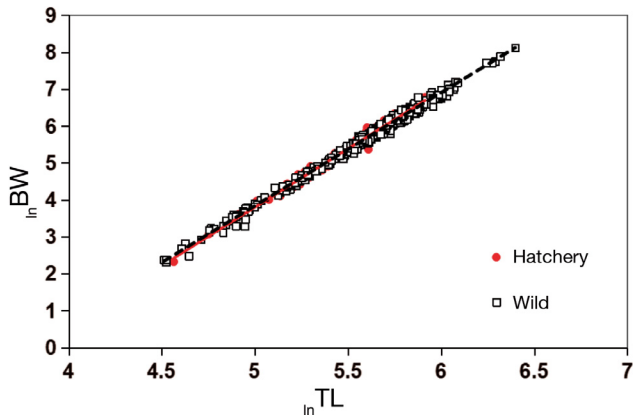


Fig. 2. Linear regression between total length (TL) and body weight (BW) for hatchery (●) and wild (□) mandarin fish *Siniperca chuatsi* in Xiaosihai Lake

3.2. Growth

Growth of HMF and WMF-SA was monitored at 11, 16 and 19 mo following release (Fig. 3). TL and BW differed significantly between groups and among survey times (Table 1). CF varied significantly by survey time, but not by group (Table 1). No significant interaction was found between group and survey time for TL, BW and CF (Table 1). There were significant pairwise differences in TL, BW and CF of HMF and WMF-SA at 3 different survey times after release (Tukey's HSD, HMF and WMF-SA: all $p < 0.05$). TL and BW of HMF were significantly lower than those of WMF-SA 11 mo after release, respectively (Tukey's HSD, TL: $p = 0.031$; BW: $p = 0.041$), but no significant difference was found between these 2 strains after 16 and 19 mo (all $p > 0.05$).

For HMF, SGR_{TL} and SGR_{BW} showed a decreasing trend with increasing age after release. Compared with WMF-SA, SGR_{TL} and SGR_{BW} of HMF from May 2007 to October 2007 and from October 2007 to January 2008 were higher (Table 2).

3.3. Feeding

In total, 25 recognizable prey taxa were confirmed in diet composition, including 20 fish taxa, 4 invertebrate taxa (*Macrobrachium* sp., *Caridina* sp., Odonata, *Bellamyia* sp.) and some plant detritus (Table 3). The dominant prey taxa of HMF were *Pseudorasbora parva* and *Hemiculter leucisculus*, with a mean prevalence of 60.74 and 12.96%, respectively. In contrast, the diets of WMF were dominated by *P. parva*, *Caridina* sp. and *Macrobrachium* sp., with a mean prevalence of 38.68, 18.34 and 8.43%, respectively (Table 3). Chi-squared

test showed that diet composition was significantly different between the 2 groups ($\chi^2 = 113.6$, $p < 0.05$). HMF ate more fish and less shrimp than WMF.

Regardless of whether the fish were HMF or WMF, size-dependent variation in diet composition was significant (Fig. 4). For HMF, the diets of the small-size group were dominated by *Rhodeus* sp., *H. leucisculus*, shrimps and *P. parva*, with average %IRI values of 34.28, 19.96, 14.75 and 14.08%, respectively. In contrast, large-size group diets were dominated by *P.*

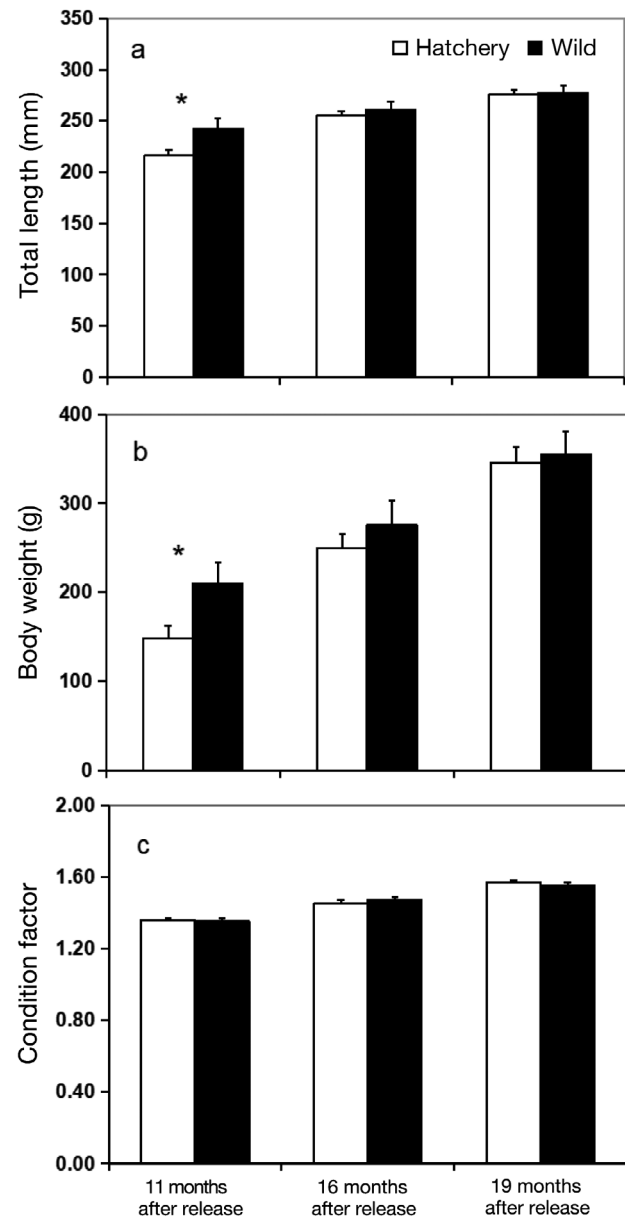


Fig. 3. Comparison of (a) total length, (b) body weight and (c) condition factor between hatchery mandarin fish and wild mandarin fish at the same age in 3 surveys 11, 16 and 19 mo after release. Values are means (\pm SE). *Significant differences between hatchery and wild fish ($p < 0.05$)

Table 1. Two-way ANOVA for comparison of differences in total length, body weight and condition factor between hatchery-reared mandarin fish and wild mandarin fish of the same age in 3 surveys 11, 16 and 19 mo after release.

Bold type indicates significant differences ($p < 0.05$)

Source of variance	F	df	p
Total length			
Group	4.707	1	0.031
Survey time	32.603	2	<0.001
Group × survey time	2.331	2	0.100
Body weight			
Group	4.250	1	0.041
Survey time	39.497	2	<0.001
Group × survey time	0.818	2	0.443
Condition factor			
Group	0.669	1	0.414
Survey time	73.308	2	<0.001
Group × survey time	1.776	2	0.172

parva (67.48%) and *H. leucisculus* (10.25%). There was a significant difference in diet composition between the 2 size groups ($\chi^2 = 86.48$, $p < 0.05$). For WMF, while the most important food items of both the small- and large-size groups were *P. parva* and shrimps, a significant difference in diet composition was also observed ($\chi^2 = 32.24$, $p < 0.05$), with the small-size group having more shrimps in their stomach contents. Comparing the diet composition of the same sized HMF and WMF, the results showed that both small ($\chi^2 = 93.73$, $p < 0.05$) and large ($\chi^2 = 69.27$, $p < 0.05$) fish differed. Small HMF had more *Rhodeus* sp. and *H. leucisculus* and less *P. parva* and shrimps in their stomach contents compared to same-sized WMF, while large HMF displayed more *P. parva* and fewer shrimps.

For both HMF and WMF, there were significant seasonal differences in diet composition (HMF: $\chi^2 = 127.25$, $p < 0.05$; WMF: $\chi^2 = 183.17$, $p < 0.05$) (Fig. 5). For HMF, the diet composition in spring was dominated by *H. leucisculus*, *Rhodeus* sp. and *Caridina* sp., with average %IRI values of 62.94, 15.01 and 11.14%, respectively, while *P. parva* was the most important food source, accounting for 57.55 and 67.20% respectively in autumn and winter (Fig. 5a). For WMF, the diet composition in spring was dominated by *Caridina* sp. (32.62%), followed by *P. parva* (18.76%) and *Rhodeus* sp. (13.87%). In summer, it was dominated by *Caridina* sp. (47.05%) and *Macrobrachium* sp. (20.21%). In autumn, it was dominated by *P. parva* (34.57%), followed

by *Macrobrachium* sp. (22.76%) and *Caridina* sp. (9.30%). In winter, it was dominated by *P. parva* (55.42%), followed by *Macrobrachium* sp. (7.44%) and *C. auratus* (6.89%) (Fig. 5b). Significant differences were also observed in diet composition between HMF and WMF in different seasons (spring: $\chi^2 = 62.65$, $p < 0.05$; autumn: $\chi^2 = 27.50$, $p < 0.05$; winter: $\chi^2 = 18.78$, $p < 0.05$).

The Shannon-Wiener diversity index and Levin's niche breadth index of HMF were smaller than those of WMF (Table 4), suggesting that HMF consumed fewer types of prey items and that single prey items dominated. The diet overlap index between HMF and WMF was 0.571, which was lower than a threshold of 0.6 identified as a biologically meaningful diet overlap level. This result revealed the non-significant diet overlap between these 2 groups.

3.4. Reproduction

The reproductive biological characteristics of age-1+ HMF and WMF were compared (Table 5). The TL and BW of HMF were on average smaller than those of WMF, but no significant difference was found. However, significant differences between HMF and WMF were found in the GSI, AF, RF and ED (Table 5).

4. DISCUSSION

This study, for the first time, compared the growth, feeding and reproductive traits of HMF with WMF in the wild. Our results demonstrated that 11 mo after release, HMF were smaller than WMF. This observation suggests lower growth in hatchery-reared specimens relative to wild ones, which has been widely documented in a range of fish and invertebrate species (Stoner & Davis 1994, Kellison et al. 2000, Malavasi et al. 2004, Smith & Fuiman 2004, Davis et al. 2005, Vehanen et al. 2009). However, some studies

Table 2. Specific growth rate in terms of total length (TL) and body weight (BW) between hatchery-reared mandarin fish (HMF) and wild mandarin fish of the same age (WMF-SA) in 3 stages after release. n/a: no available value

Group	Specific growth rate (% d ⁻¹)					
	June 2006 to May 2007		May 2007 to October 2007		October 2007 to January 2008	
	TL	BW	TL	BW	TL	BW
HMF	0.103	0.320	0.042	0.129	0.026	0.111
WMF-SA	n/a	n/a	0.015	0.068	0.017	0.084

Table 3. Percentage occurrence (%O), number (%N), weight (%W), and index of relative importance (%IRI) of the prey taxa in the stomach contents of hatchery-reared mandarin fish (HMF) and wild mandarin fish (WMF) in Xiaosihai Lake. n:number of individuals

Prey taxa	HMF (n = 118)				WMF (n = 290)			
	%O	%N	%W	%IRI	%O	%N	%W	%IRI
Fish								
<i>Pseudorasbora parva</i>	37.14	35.20	40.05	60.74	29.61	20.04	18.06	38.68
<i>Cultrichthys erythropterus</i>	10.00	4.08	9.83	3.02	6.15	5.49	8.97	3.05
<i>Hemiculter leucisculus</i>	17.14	9.18	25.61	12.96	8.94	4.43	14.19	5.71
<i>Carassius auratus</i>	4.29	2.04	2.33	0.41	6.70	3.80	13.45	3.96
<i>Abbottina rivularis</i>	8.57	4.08	6.57	1.98	3.91	1.48	0.98	0.33
<i>Sarcocheilichthys nigripinnis</i>	1.43	0.51	0.24	0.02	6.15	5.06	5.57	2.24
<i>Rhodeus</i> sp.	11.43	5.10	1.78	1.71	15.08	8.65	2.59	5.81
<i>Acheilognathus chankaensis</i>	2.86	1.02	0.52	0.10	1.12	0.63	0.57	0.05
<i>Acheilognathus macropterus</i>	0.00	0.00	0.00	0.00	2.23	0.84	1.91	0.21
<i>Rhinogobius giurinus</i>	5.71	3.06	0.56	0.45	5.59	2.11	0.47	0.49
<i>Odontobutis obscurus</i>	5.71	2.04	7.52	1.19	5.03	1.90	5.24	1.23
<i>Toxabramis swinhonis</i>	1.43	1.02	0.05	0.03	2.23	0.84	1.13	0.15
<i>Squalidus nitens</i>	0.00	0.00	0.00	0.00	1.68	0.63	0.42	0.06
<i>Mycropercops swinhonis</i>	2.86	1.02	0.14	0.07	1.12	0.63	0.09	0.03
<i>Paracheilognathus imberbis</i>	2.86	1.02	0.11	0.07	5.03	2.32	0.54	0.49
<i>Channa argus</i>	1.43	0.51	0.46	0.03	0.56	0.21	0.21	0.01
<i>Pelteobagrus fulvidraco</i>	1.43	0.51	0.24	0.02	1.12	0.42	0.18	0.02
<i>Siniperca chuatsi</i>	0.00	0.00	0.00	0.00	0.56	1.48	19.37	0.40
<i>Mastacembelus sinensis</i>	1.43	0.51	0.50	0.03	2.23	1.05	1.76	0.22
Unidentified fish	1.43	1.02	0.08	0.03	0.56	0.21	0.01	0.01
Other prey								
<i>Macrobrachium</i> sp.	15.71	6.63	1.24	2.69	19.55	10.34	2.24	8.43
<i>Caridina</i> sp.	24.29	10.20	0.55	5.68	31.28	16.46	0.64	18.34
Odonata	0.00	0.00	0.00	0.00	1.12	0.42	0.04	0.02
<i>Bellamyia</i> sp.	0.00	0.00	0.00	0.00	1.12	0.42	0.02	0.02
Plant detritus	31.43	11.22	1.60	8.76	26.26	10.13	1.32	10.04

also reported that hatchery-reared fish released in the wild displayed faster growth rates than wild fish (Kallio-Nyberg & Koljonen 1997) or at least similar growth and survival in pond culture (Ut et al. 2007). Therefore, to date, no consistent conclusions have been reached regarding growth performance between hatchery-reared and wild fish. This inconsistency probably arises from behavioural, morphological and physiological differences between hatchery-reared and wild fish. Hatchery-reared and wild fishes also differ in learning, phenotypic traits and genotypic selection (Einum & Fleming 2001, Weber & Fausch 2003). Such differences are produced by both genetic and environmental drivers (Weber & Fausch 2003). In our study, the smaller size of HMF in Xiaosihai Lake at 11 mo post-release is likely due to environ-

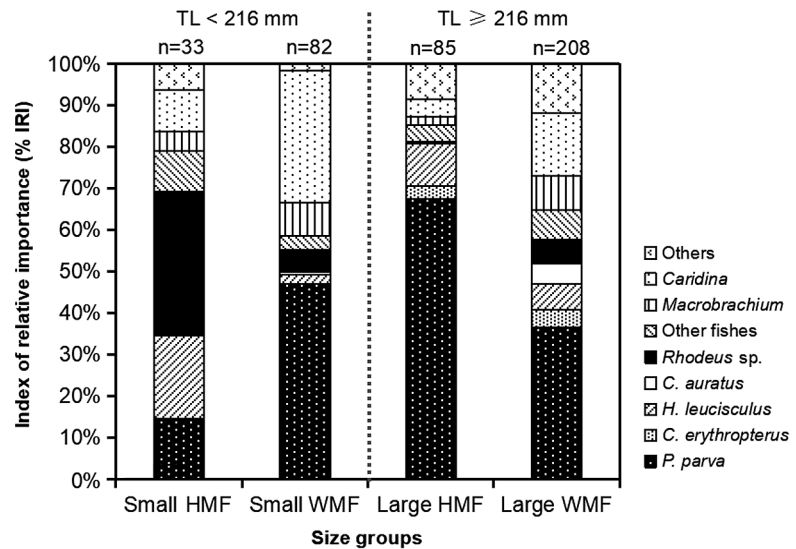


Fig. 4. Comparison of diet composition of hatchery-reared mandarin fish (HMF) and wild mandarin fish (WMF) size groups in Xiaosihai Lake, based on the index of relative importance (%IRI) of major prey groups from stomach content analysis. Sample sizes are above bars. TL: total length

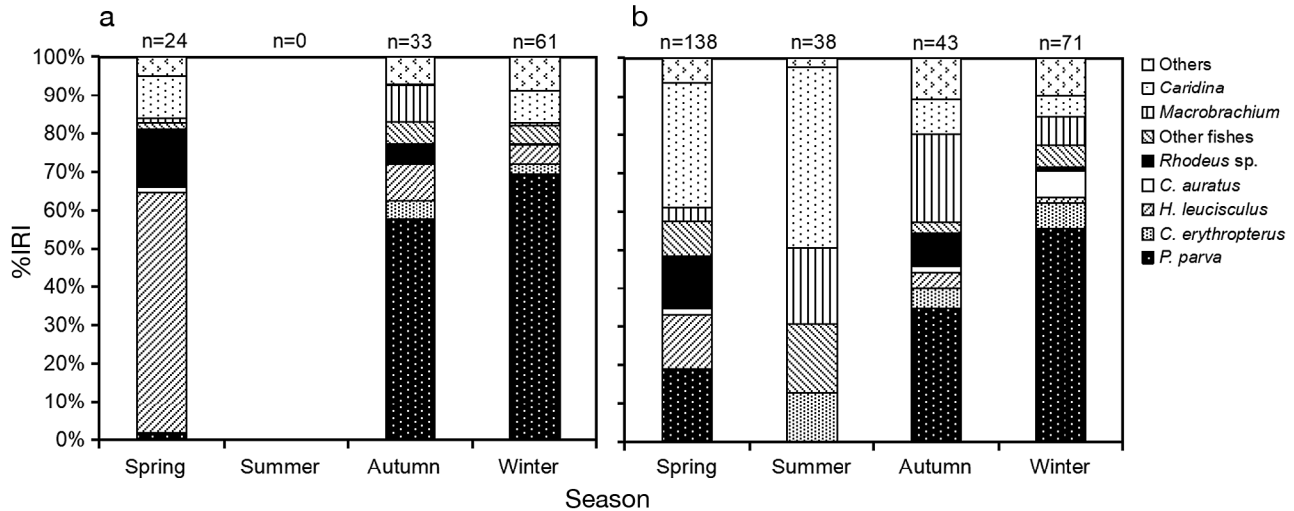


Fig. 5. Diet composition of (a) hatchery-reared mandarin fish and (b) wild mandarin fish in different seasons in Xiaosihai Lake, based on the index of relative importance (%IRI) of major prey groups from stomach content analysis. Sample sizes are above bars

Table 4. Shannon-Wiener diversity index, Levin's niche breadth index and Schoener's overlap index based on prey importance from stomach content analysis comparing hatchery-reared mandarin fish (HMF) and wild mandarin fish (WMF) in Xiaosihai Lake

Index	HMF	WMF
Shannon-Wiener diversity	1.42	1.97
Levin's niche breadth	0.079	0.156
Schoener's overlap	0.571	

mental drivers rather than genetic ones, as the broodstock of hatchery-reared juveniles were captured from the same water system.

Because the mandarin fish is a piscivore that specializes in feeding on live fish or shrimp throughout its life (Liu et al. 1998, Li et al. 2013a, 2014a), the survival and growth of HMF juveniles are directly affected by their ability to catch prey fish after being released into the natural environment (Yao & Li 2018). In hatcheries, juveniles were provided with

adequate and palatable prey fish to maximize their survival and growth. But after being released into the lake, the availability and palatability of prey fish inevitably decreased; thus, the growth of HMF juveniles may be hindered initially due to the difficulty in acquiring food before they can adapt to the new environment. Additionally, previous studies have confirmed the important role of habitat in foraging success and growth performance (Ren et al. 2019, Li et al. 2019). Mandarin fish catch prey with a pursuit strategy at the juvenile stage, and complex habitats inhibit their foraging success (Yao & Li 2018, Li et al. 2019). The roots of *Trapa bispinosa* and leaves of *Myriophyllum spicatum* in Xiaosihai Lake provide a complex habitat which impairs foraging success and may subsequently inhibit the growth of HMF after release from the hatchery into the lake. Moreover, HMF need to balance the trade-off between the energetic gain of foraging and the risk of predation by other natural predators in the lake (Grant 1993, Weber & Fausch 2003).

Table 5. Reproductive characteristics of age 1+ hatchery-reared mandarin fish (HMF) and wild mandarin fish (WMF) in Xiaosihai Lake, and test statistics

Parameter	HMF (n = 8)		WMF (n = 15)		t	df	p
	Mean ± SD	Range	Mean ± SD	Range			
Total length (mm)	219 ± 20	184–247	229 ± 16	194–254	-1.276	21	0.216
Body weight (g)	152.4 ± 46.4	84–230	172.1 ± 34.3	98–221	-1.163	21	0.258
Gonado-somatic index (%)	4.51 ± 1.45	2.86–6.41	7.99 ± 1.61	5.66–10.36	-2.663	21	0.016
Absolute fecundity (no. eggs)	8983 ± 1763	6150–11021	14814 ± 4213	9897–21951	-4.365	18.82	<0.001
Relative fecundity (no. eggs g ⁻¹)	67.8 ± 18.6	41.4–92.9	89.1 ± 17.6	61.6–115.1	2.810	21	0.010
Egg diameter (mm)	0.84 ± 0.06	0.77–0.94	1.09 ± 0.06	1.01–1.18	-10.519	21	<0.001

Previous studies indicate that hatchery-reared fish could exhibit modified behavioural patterns due to a lack of natural selection pressures in the psychosensory-deprived hatchery environment (Berejikian 1995, Olla et al. 1998, Kellison et al. 2000). Compared with WMF, HMF juveniles can suffer higher predation-induced mortality rates post-release and slower growth due to more time spent swimming (Kellison et al. 2000). In hatcheries, HMF juveniles are often fed a single species of prey fish, such as silver carp. However in the wild, HMF prey on a wide variety of fish species that differ from that in hatcheries. HMF juveniles may suffer low foraging success and slow growth due to the monotonous predation ability formed in the hatchery.

There was no significant difference in TL or BW between HMF and WMF-SA in Xiaosihai Lake 16 and 19 mo after release. Previous studies showed that it can take some time for hatchery-reared fish to adapt to the new natural environment and switch prey (Olla et al. 1998, Sundström & Johnsson 2001). The foraging deficits of hatchery-reared juveniles due to lack of natural selective pressures in the hatchery environment may diminish with exposure to natural conditions or wild conspecifics (Kellison et al. 2000). The differences in prey consumption and behaviours between HMF and wild conspecifics are expected to disappear in a few weeks or more (Johnsen & Ugedal 1986, Shurov et al. 1987, Johnsen & Ugedal 1990). Adaptation to the natural environment and an improvement in foraging ability may explain the expansion of food items and compensatory growth of HMF after 11 mo post-release in the lake. In addition, the poorest performing foragers of the HMF die and only those that are effective foragers survive; thus, the extent of increase in body size and growth of HMF may in part simply reflect natural selection operating on the HMF, with the removal of the poorest performers.

Comparing the dietary characteristics between HMF and their WMF counterparts can be an effective way of assessing the successful naturalization of hatchery-reared fish after released into the wild and their ecological effects on wild fish (Ogawa et al. 2008). The significant differences in diet composition between HMF and WHF suggest limited feeding competition during the critical periods of the early stocking stages. This result is consistent with our previous study about the trophic niche of mandarin fish that was conducted in another shallow Yangtze lake (Biantang Lake) on the basis of stomach contents and stable isotope mixing model analysis (Li et al. 2014a). The differentiation in trophic niche between hatchery-reared and wild fish has also been observed in

several other species (Ogawa et al. 2008, Simpson et al. 2009, Larsson et al. 2011). The difference in diet between HMF and WMF was presumably induced by domestication effects and the need for HMF to adapt to the change in quantity and quality of food in the natural environment, as mentioned above. Previous studies have suggested that hatchery fish select small, easy-to-capture prey that are consumed in large quantities or large-sized prey with high energy profit (Mikheev 1984, Li et al. 2014a). Our observations support this conclusion, as *Pseudorasbora parva* and *Hemiculter leucisculus* were small but the most abundant prey fish for HMF in Xiaosihai Lake (Li et al. 2010).

A size-dependent diet shift in HMF and WHF was observed in Xiaosihai Lake. On the basis of the stomach content analyses, both small-size groups clearly displayed more shrimps compared to their corresponding large-size groups. Similar cases were found by Mittelbach & Persson (1998) based on data of 27 piscivorous fish species. Moreover, there were significant differences in diet composition between HMF and WMF in both the small- and large-size groups, suggesting dietary separation persists between HMF and WMF as they grow in Xiaosihai Lake. Also, the breadth of diet for HMF (20 species of fish, invertebrates, plant detritus) was large but not as large as that observed for WHF, which is probably a key reason why HMF can survive and coexist with WMF in Xiaosihai Lake. The dietary overlap based on prey importance from stomach content analysis between HMF and WMF was much less than 0.6, suggesting limited diet overlap exists between them. Therefore, it could be concluded that the current stock enhancement program of releasing HMF in Yangtze lakes results in little, if any, negative food competition on the WMF during the period of study.

Even with a limited sample, this study revealed that HMF had significantly lower GSI, AF, RF and ED than WMF-SA at age-1+. In our study, we infer that the change to less energy-dense natural foods in the wild and acclimatization to an unfamiliar natural environment by HMF after release into the lake may limit its energy gain and growth, thus resulting in smaller size and lower reproductive potential at the initial stage of stocking (11 mo after stocking) compared to WMF.

5. CONCLUSIONS

This study is the first to compare the growth, feeding and reproduction of the HMF with WMF to eval-

uate the performance of HMF after release into the natural environment and their ecological interactions with wild conspecifics in a shallow Yangtze lake. Our results demonstrated that the growth performance of HMF can equal or exceed that of WMF-SA in the lake at 16 and 19 mo after release, suggesting that stocked HMF can acquire a size similar to that of WMF. Moreover, HMF had limited diet overlap with WMF, suggesting that the current stocking program results in little foraging competition.

Acknowledgements. This study was financially supported by the National Key Research and Development Program of China (Grant No. 2019YFD0900601), the Projects of the National Natural Science Foundation of China (Grant No. 31201994 and 31670542), the Youth Innovation Promotion Association CAS (2019331) and China Agriculture Research System (CARS-45-23).

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Editorial responsibility: Ian Fleming,
St. John's, Newfoundland and Labrador, Canada
Reviewed by: 4 anonymous referees

Submitted: October 19, 2020
Accepted: August 6, 2021
Proofs received from author(s): October 18, 2021