Journal of FISH BIOLOGY
Published for the Fisheries Society of the British Isles

Journal of Fish Biology (2009) **75**, 1158–1172
doi:10.1111/j.1095-8649.2009.02328.x, available online at www.interscience.wiley.com

Effects of the timing of initial feeding on growth and survival of spotted mandarin fish *Siniperca scherzeri* larvae

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(Received 20 September 2008, Accepted 23 April 2009)

The effects of delayed first feeding on growth and survival of spotted mandarin fish *Siniperca scherzeri* larvae were examined under controlled conditions. Morphometric characters [yolk-sac volume, oil globule volume, head depth (H_D), body depth (B_D), eye diameter (E_D), musculature height (M_H), mouth diameter (M_D) and total length (L_T)], body mass (M), specific growth rate (S_{GR}) and survival were evaluated under different first-feeding time (2, 3, 4 and 5 days after hatching). Larvae began to feed exogenously at 2 days after hatching (DAH) and the point of no return (P_{NR}) occurred between 5 and 6 DAH at 23° C, range ±1·0° C. The yolk volume of larvae first-fed at 2 days had a significant difference compared with that of larvae first-fed at 3, 4 and 5 days on 3 and 4 DAH. The larvae first-fed at 2 days achieved comparatively better growth performance than that of 3, 4 and 5 days. On 5 DAH, all morphometric characters had significant differences between 2 and 5 days and 2 and 4 days initial feeding, respectively. Total mortality was recorded on 9 DAH for the larvae first-fed at 5 days. On 12 DAH, significant differences were observed between 2 and 4 days and 3 and 4 days initial feeding for all morphometric characters. From 16 DAH to the end of experiment, all growth variables of the larvae first-fed at 2 days were significantly higher than those in other treatments. The S_{GR} (2–9 DAH) first-fed at 2 and 3 days were significantly higher than 4 and 5 day treatments, and the S_{GR} (9–16 DAH) first-fed at 2 days was significantly higher than 3 and 4 day treatments. There was no significant difference, however, of S_{GR} (16–28 DAH) among treatments. Survival rate was significantly higher at 2 days initial feeding (27·42%) when compared with 3 (15·96%) and 4 days (7·92%) initial feeding at the end of experiment. The present study suggests that the first feeding of *S. scherzeri* larvae should be initiated at 2 days after hatching for achieving good growth and survival.

Key words: fish; growth; point of no return.

INTRODUCTION

Spotted mandarin fish *Siniperca scherzeri* Steindachner is a Sinipercinae native to East Asia, mainly distributed in China, Korea and Vietnam (Zhou *et al*., 1988;

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Li, 1991). If is a valuable commercial fish consumed all year round in Korea and China and there is an increasing demand due to its good taste and high medical value (Zheng, 1993; Su *et al*., 2005; http://www.tigerfish.cn/Article_show.asp?Article1D=16). Due to overexploitation and environmental pressures, *S. scherzeri* stocks have experienced a drastic decline (Liang, 1996; Wu *et al*., 1997). Expanded trade of *S. scherzeri* production has accelerated an extensive culture, and this species has become one of the most promising freshwater fishes in China (Zheng, 1993; Su *et al*., 2005).

In China, some studies on the reproductive biology and artificial reproduction of *S. scherzeri* have been reported (Xu, 1965; Xie, 1983; Wu *et al*., 1996; Zeng *et al*., 2005; Chen, 2006; Jiang *et al*., 2007; Liu, 2007). Only a few reports, however, are available on the larval rearing of this fish (Wang *et al*., 2005; Xia *et al*., 2006, 2007). They are visual feeders, which take feed throughout the day; peak feeding at dusk and dawn with reduced feeding in total darkness indicates the importance of early feeding in the hatchery (Zeng *et al*., 2005). It is necessary to improve growth performance and survival of *S. scherzeri* larvae during initial feeding stages, since the first feeding is critical (Zhang & Ling, 2006).

At the onset of exogenous feeding, fish larvae face death from starvation if the first feeding is delayed past the point of no return (P_{NR}) (Blaxter & Hempel, 1963). First feeding of fish larvae is crucial for their subsequent growth and survival. Most fish larvae develop with an inability to swim and feed adequately resulting in inferior growth if they fail to successfully initiate first feeding (Houde, 1974; Dou *et al*., 2002). Many researchers have reported poor larval survival during the initial feeding period (Paperna, 1978; Houde, 1987; Gisbert & Williot, 1997; Kohno *et al*., 1997; Kohno, 1998; Mookerji & Rao, 1999; Gisbert *et al*., 2004; Dou *et al*., 2005; Pena & Dumas, 2005; Kailasam *et al*., 2007) and this is attributed to factors including temperature, light intensity, food supply, egg size, yolk quantity, feeding behaviour and time of first feeding (May, 1971; Blaxter, 1974; Dou *et al*., 2000).

Morphometric characters of fish larvae are widely used to evaluate the effects of delayed first feeding in many fish species (Ehrlich *et al*., 1976; Yufera *et al*., 1993; Mookerji & Rao, 1999; Pena & Dumas, 2005; Kailasam *et al*., 2007; Shan *et al*., 2008). Previous studies show that larvae are most vulnerable to starvation at the time of first feeding (McGurk, 1984; Yin & Blaxter, 1987; Richard *et al*., 1991; Yufera *et al*., 1993). Since the starvation derived from non-availability of feed or delayed initial feeding can have adverse effect on the growth of fish larvae, it is very important to determine the appropriate time to introduce the first feed. In a previous study, the endogenous feeding period of the *S. scherzeri* larvae was found to be relatively short, lasting 2 days at 23·0° C, range ± 1° C (Wang *et al*., 2005). During this period, the eyes become pigmented and the mouth and anus open for food ingestion and egestion. High mortality often occurs during the first-feeding phase in *S. scherzeri* seed production (Wang *et al*., 2005). The time of initial exogenous feeding, the duration of endogenous energy supply and effects of different time of first feeding on growth performance and survival, however, are not well known. Hence, the present study was conducted to examine the effect of different initial feeding time on yolk depletion, growth performance and survival, and to find out the most appropriate time to initiate first feeding of *S. scherzeri* larvae in the hatchery.

MATERIALS AND METHODS

SPAWNING AND INCUBATION

Fertilized eggs were obtained from hormonally induced ovulation of captive broodstock at the *S. scherzeri* hatchery, Qichun City, Hubei Province, China. After 1 week of rearing, ovarian biopsies of broodstock were taken with a polyethylene cannula and examined as described by Levavi-Zermonsky & Yaron (1986). The stage of oocyte maturation was determined as follows: stage I, central germinal vesicle (GV); stage II, migrating GV; stage III, peripheral GV; stage IV, GV breakdown; stage V, ovulated eggs in ovarian lumen. Only fish having >60% of the oocytes at stage II were selected for the ovulation experiment. Ten females (400–500 g) were selected for induction of ovulation and administered luteinizing hormone-releasing hormone analogue (LHRHa) plus domperidone hormone (DOM) (Ningbo Renjian Pharmaceutical Co., Ltd; www.rjpharm.com) (60 μg kg^{-1} + 4 mg kg^{-1} body mass). Twenty male fish (300–400 g) were administered with half dose of LHRHa and DOM (30 μg kg^{-1} + 2 mg kg^{-1} body mass). After injection, fish were placed in an indoor concrete fish pond with flowing water and a temperature of 23° C, range ±1·0° C. Ovulation was examined by pressing the broodstock abdomen softly manually every hour during the latency period between 7 and 11 h after 38–42 h of hormone administration. When the ovulation occurred, the eggs were stripped manually, and then fertilized with milt from at least two males using a dry fertilization method mixing for 1 min. The average size of fertilized eggs was 1·8–2·0 mm. Fertilized eggs were incubated in jar incubators and provided with a slow flow-through (1·75 l min^{-1}) of fresh water (temperature, 23·0° C, range ± 1° C; dissolved oxygen, 8·0–10·0 mg l^{-1}) with continuous aeration for hatching. Hatching took place 5 days after fertilization.

EFFECT OF DELAYED FIRST FEEDING ON MORPHOMETRIC CHARACTERS OF LARVAE

Newly hatched, healthy larvae were collected and transferred to 12 500 l flow-through white fibreglass-reinforced plastic (FRP) tanks, and continuous water flow was maintained at a daily exchange rate of 20%. Considering the cannibalistic behaviour of this species under a high density, the larvae were stocked at a density of five larvae l^{-1} in the experimental tanks. Light (16 L:8 D) was supplied by two overhead fluorescent tubes set to produce a light intensity between 800 and 1000 lx at the water surface. The timing of initial feeding was set at 2, 3, 4 and 5 days after hatching (DAH). Live feed was supplied to fish larvae at 0800 hours during the experiment according to Xia *et al*. (2006) (Table I). All the treatments were conducted in triplicate under uniform conditions. Mean water temperature recorded in the experimental tanks was 23·0° C, range ± 1° C. A total of 20 larvae from each replicate of all the treatments were sampled from hatching to 28 DAH for measurement of head depth (H_D), body depth (B_D), eye diameter (E_D), musculature height (M_H), mouth diameter (M_D), total length (L_T) (Fig. 1) and body mass (M). Sampling was performed at midday every day. Sampled larvae were anaesthetized in 100 ppm 2-phenoxyethanol solution (Shanghai Experimental Reagent Co., Ltd; www.china.reagent.com) and morphometric characters were measured with an ocular micrometer under a calibrated microscope (MOTIC SMZ-168; www.motic.com). Body mass was recorded using an electronic digital balance (BT25S Sartorius, 0·01 mg; www.sartorius.com) after blotting the larvae with water absorbent paper. Morphometric measurements of the larvae first-fed at 5 days could be done only up to 9 DAH since total mortality was noticed on that day.

The growth rate of larvae was determined using the specific growth rate S_{GR} from: $S_{GR} = 100(\ln L_{Tt} - \ln L_{T0})t^{-1}$, where L_{Tt} is the final L_T of larvae, L_{T0} is the initial L_T and t is the period of time between L_{Tt} and L_{T0} in days.

Yolk volume and oil globule diameter were measured on a daily basis until they were completely depleted. Yolk volume (V_{og}) was measured using the formula $V_Y = \pi(6\ lh^2)^{-1}$, where l is yolk-sac length and h is yolk-sac height. The change in the oil globule (V_Y) was estimated from the formula $V_{og} = \pi(6d^3)^{-1}$, where d is the oil globule diameter. The

TABLE I. The type, size and amount of prey of *Siniperca scherzeri* larvae

Age (DAH)	Type of prey	L_T of prey (mm)	Prey density (number of individuals per fish per day)
2–4	*Megalobrama amblycephala*	5·5–6·5	6
5–6	*Megalobrama amblycephala*	6·0–7·0	3
	Ctenopharyngodon idellus	6·5–7·0	3
	Hypophthalmichthys molitrix	6·5–7·0	3
7–8	*Ctenopharyngodon idellus*	7·0–7·5	5
	Hypophthalmichthys molitrix	7·0–7·5	5
9–10	*Hypophthalmichthys molitrix*	7·5–8·0	6
	Aristichys nobilis	7·5–8·0	6
11–15	*Aristichys nobilis*	8·0–9·0	12
16–21	*Cyprinus carpio*	10–14	5
	Cirrhinus molitorella	10–14	5
	Hypophthalmichthys molitrix	10–14	5
22–28	*Cirrhinus molitorella*	15–18	5
	Ctenopharyngodon idellus	15–18	5

DAH, days after hatching; L_T, total length.

differences on the morphometric characters, yolk and oil globule absorption due to delayed first feeding of fish larvae were assessed.

DETERMINATION OF THE POINT OF NO RETURN

Two thousand five hundred larvae were stocked in a 500 l holding tank and were deprived of food from hatching until all fish died. Other rearing conditions were the same as in the fish experiment. From 2 DAH, 30 starved larvae were taken from each unfed holding tank at 24 h intervals and transferred to a 6 l beaker. Larvae were provided with bluntsnout bream *Megalobrama amblycephala* (Yih) larvae as food at a density of 40 individuals l^{-1} for 4 h, and then sampled and examined with a binocular microscope to identify the presence of prey in their guts. Feeding rate was the percentage of larvae fed food to the total number of larvae stocked (30). The P_{NR} was defined as the time after hatching when the feeding rate of the starved larvae reached approximately half of the initial highest feeding rate under the presence of food (Dou *et al*., 2005). The experiment terminated when no starved larvae could initiate feeding.

EFFECT OF DELAYED FIRST FEEDING ON SURVIVAL RATE

A single experiment was conducted to estimate the survival rate of *S. scherzeri* larvae in different initial feeding treatments. Fish larvae were reared in a 500 l white FRP tank at a density of five larvae l^{-1} and initial feeding was started at 2, 3, 4 and 5 DAH. A starved control treatment without feeding was conducted until all fish larvae died. Dead fish were removed daily and counted. The feeding protocol followed was the same as described above. The experiment was continued up to 28 days and all the treatments were conducted in triplicate. Survival rate was estimated daily for 28 days of rearing.

STATISTICAL ANALYSIS

Data on growth variables were statistically analysed using one-way ANOVA. Prior to the analysis, the data were evaluated for normality using the Kolmogorov–Smirnov non-parametric test and plots of residuals analysed to ensure that assumptions of ANOVA were

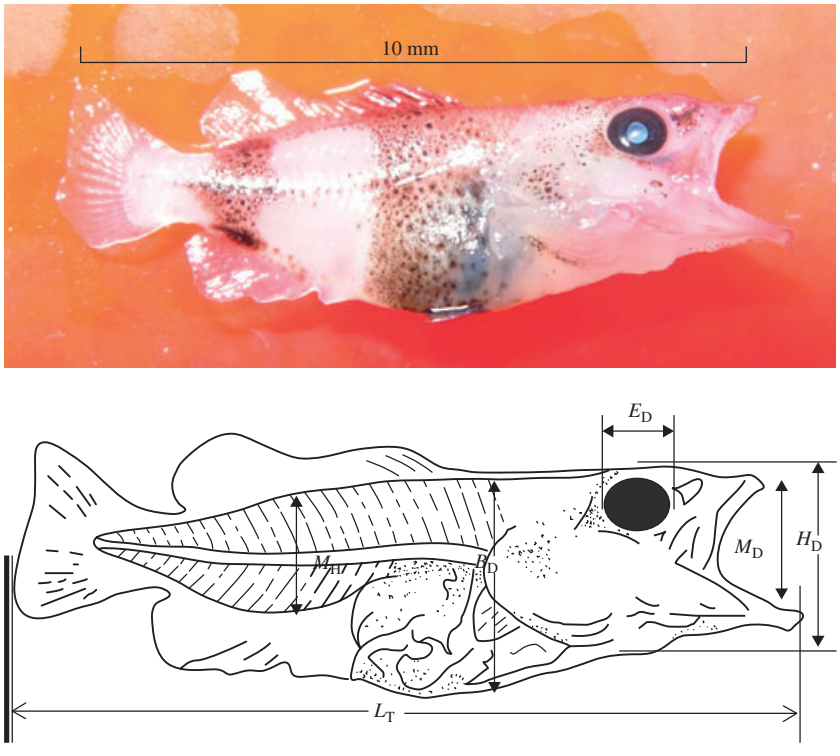

FIG. 1. Morphological characters measured in *Siniperca scherzeri* larvae: L_T, total length; H_D, head depth; B_D, body depth; E_D, eye diameter; M_D, mouth diameter; M_H, musculature height. The line drawing was made from the photograph of a 12 days after hatch larva.

satisfied. Differences among treatments were considered significant at $P < 0{\cdot}05$, and Tukey's HSD *post hoc* multiple range tests were performed to determine which treatments were different. The results are expressed as mean ± S.D. of the data.

RESULTS

CHANGE OF THE YOLK SAC

The newly hatched *S. scherzeri* larvae (4·87 ± 0·10 mm L_T) had a large yolk sac ($V_Y = 1{\cdot}461 \pm 0{\cdot}172 mm^3$). The yolk sac was found to be oval in shape with the presence of a spherical-shaped oil globule. On 1 and 2 DAH, there was no significant difference ($P > 0{\cdot}05$) in the yolk volume change among different treatments (Table II). On 3 DAH, V_Y of larvae first-fed at 2 and 3 days were significantly higher than those of larvae first-fed at 4 and 5 DAH ($P < 0{\cdot}05$) (Table II), and there was a significant difference in V_{og} between treatments first-fed at 2 and 3 days ($P < 0{\cdot}05$) (Table II). Similarly, significant differences were noticed for 4 DAH among treatments ($P < 0{\cdot}05$) (Table II). Complete depletion of yolk was noticed at 5 DAH irrespective of delay in the initial feeding.

The oil globule in *S. scherzeri* larvae was noticed up to 4 DAH and it was completely depleted by 5 DAH. The newly hatched larvae had an V_{og} of 0·0543

TABLE II. Yolk-sac depletion in *Siniperca scherzeri* larvae (ages 1–4 days after hatching, DAH) under different initial feeding times (2, 3, 4 and 5 days after hatching). Values are means ± S.D.

	Volume of yolk (mm^3)			
DAH	2 days	3 days	4 days	5 days
1	0·198 ± 0·011[a]	0·198 ± 0·011[a]	0·196 ± 0·012[a]	0·199 ± 0·011[a]
2	0·092 ± 0·007[a]	0·090 ± 0·007[a]	0·088 ± 0·006[a]	0·088 ± 0·007[a]
3	0·038 ± 0·003[a]	0·025 ± 0·002[b]	0·018 ± 0·002[c]	0·016 ± 0·002[c]
4	0·018 ± 0·001[a]	0·012 ± 0·001[b]	0·007 ± 0·001[c]	0·006 ± 0·001[c]

Different superscript lower case letters in the same row denote significant differences ($P < 0·05$).

TABLE III. Oil globule depletion in *Siniperca scherzeri* larvae (ages 1–4 days after hatching, DAH) under different initial feeding times (2, 3, 4 and 5 days after hatching). Values are means ± S.D.

	Volume of oil globule (mm^3)			
DAH	2 days	3 days	4 days	5 days
1	0·0361 ± 0·0012[a]	0·0361 ± 0·0012[a]	0·0357 ± 0·0013[a]	0·0353 ± 0·0013[a]
2	0·0048 ± 0·0007[a]	0·0048 ± 0·0006[a]	0·0048 ± 0·0007[a]	0·0048 ± 0·0007[a]
3	0·0022 ± 0·0003[a]	0·0022 ± 0·0003[a]	0·0021 ± 0·0003[a]	0·0021 ± 0·0003[a]
4	0·0012 ± 0·0001[a]	0·0012 ± 0·0001[a]	0·0011 ± 0·0001[a]	0·0011 ± 0·0001[a]

The same superscript lower case letters in the same row mean there were no significant differences ($P > 0·05$).

± 0·0018 mm^3 (Table III). No significant differences were found in the oil globule change from 1 to 4 DAH among treatments ($P > 0·05$).

FIRST FEEDING AND P_{NR}

The larvae were hatched 5 days after fertilization and the earliest feeding time was detected at 2 DAH. At first feeding, the larvae had functional mouths and active swimming behaviour. More than 80% of larvae could initiate feeding at 3 DAH (Fig. 2), indicating that most larvae lived through a short period before yolk exhaustion during which they established active feeding. The highest feeding rate (85·46%) of the starved larvae was observed at 3 DAH. There was a significant difference of the daily feeding rate of fish larvae during the P_{NR} experiment ($P < 0·05$; Fig. 2). The time when the feeding rate of the starved larvae dropped to approximately half of the highest feeding rate occurred at 5 DAH (43·33%) (Fig. 2), and then entered irreversible starvation, namely the point of no return (P_{NR}). Unfed larvae never survived beyond 9 days after hatching, and dead larvae usually had morphological deformities, such as undeveloped gut, deformed vertebrae and jaw apparatus.

EFFECT OF DELAYED FIRST FEEDING ON GROWTH

By 5 DAH, the M and L_T of larvae first-fed at 2 and 3 days were significantly higher than those of 4 and 5 days first-fed ($P < 0·05$) and no significant difference

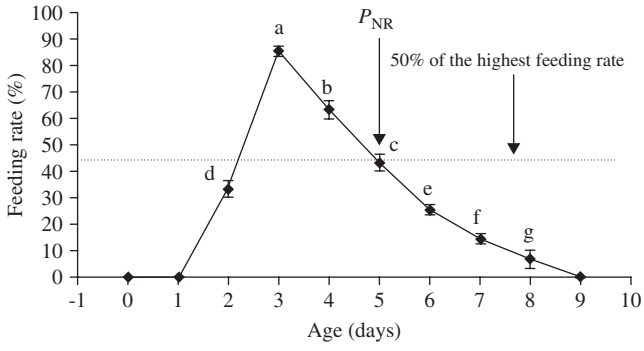

FIG. 2. Changes in the feeding rate of starved *Siniperca scherzeri* larvae when first presented with food (P_{NR}, point of no return). Values are mean ± S.D. Points with different lower case letters are significantly different ($P < 0{\cdot}05$).

could be observed between 2 and 3 days first-fed treatments ($P > 0{\cdot}05$) (Table IV). The H_D and B_D of fish larvae first-fed at 2 and 3 days were significantly higher than those of 4 and 5 days ($P < 0{\cdot}05$) (Table IV). No significant differences of H_D and B_D were observed between 2 and 3 days first-fed treatments ($P > 0{\cdot}05$) (Table IV). There were significant differences of E_D and M_H among the four treatments ($P < 0{\cdot}05$) (Table IV). The M_D recorded at 2 and 3 days first feeding was significantly higher compared with that of 4 and 5 days ($P < 0{\cdot}05$) (Table IV). There were, however, no significant differences of M_D between 2 and 3 days first-fed and between 4 and 5 days first-fed ($P > 0{\cdot}05$) (Table IV).

Total mortality was recorded on 9 DAH in the 5 day first-fed treatment. In this treatment, body shrinkage was observed on 7 DAH (5·60 ± 0·11 cm L_T) and 8 DAH (5·59 ± 0·12 mm L_T) as evidenced by the decrease in L_T from 6 DAH (L_T 5·64 ± 0·13 mm).

On 12 DAH, the M, L_T, H_D, B_D, E_D, M_D and M_H of larvae first-fed at 2 and 3 days were significantly higher than those first-fed at 4 days (Table IV). There were no significant differences of M, L_T, E_D, M_D and M_H between 2 and 3 days first-fed ($P > 0{\cdot}05$). After 16 days rearing, however, significant differences in all growth variables were observed among treatments ($P < 0{\cdot}05$), and such differences were observed up to the end of the experiment (Table IV).

From 2 to 9 DAH, the S_{GR} in 2 and 3 day treatments were significantly higher than the other two treatments ($P < 0{\cdot}05$). The S_{GR} from 9 to 16 DAH in 2 day first-fed was significantly higher than 3 and 4 day treatments ($P < 0{\cdot}05$). From 16 to 28 DAH, however, no significant difference was found among treatments ($P > 0{\cdot}05$) (Fig. 3).

EFFECT OF DELAYED FIRST FEEDING ON SURVIVAL RATE

At 28 DAH, the survival rate recorded in first-fed at the 2 day treatment (27·42 ± 4·50%) was significantly higher ($P < 0{\cdot}05$) than that of the 3 (15·96 ± 2·09%) and 4 day (7·92 ± 0·85%) treatments. On the same day, there was a significant difference ($P < 0{\cdot}05$) in the survival rate of the 3 and 4 day treatments (Fig. 4). Total mortality was recorded on 9 DAH in the 5 day treatment. In all the treatments, the highest mortality rate was recorded between hatching and 9 DAH.

TABLE IV. Development of *Siniperca scherzeri* larvae under different initial feeding times (2, 3, 4 and 5 days after hatching). Values are mean ± S.D. Different superscript lower case letters denote significant differences ($P < 0{\cdot}05$) at a given age

		Age (days after hatching)					
		5	9	12	16	20	28
M (mg)	2 days	$2{\cdot}44 \pm 0{\cdot}26^{a}$	$9{\cdot}86 \pm 0{\cdot}56^{a}$	$16{\cdot}25 \pm 0{\cdot}66^{a}$	$76{\cdot}80 \pm 7{\cdot}79^{a}$	$249{\cdot}38 \pm 23{\cdot}07^{a}$	$670{\cdot}55 \pm 70{\cdot}66^{a}$
	3 days	$2{\cdot}27 \pm 0{\cdot}18^{a}$	$8{\cdot}49 \pm 0{\cdot}49^{a}$	$15{\cdot}30 \pm 0{\cdot}75^{a}$	$58{\cdot}96 \pm 6{\cdot}40^{b}$	$213{\cdot}74 \pm 22{\cdot}84^{b}$	$611{\cdot}24 \pm 67{\cdot}23^{b}$
	4 days	$1{\cdot}36 \pm 0{\cdot}09^{b}$	$4{\cdot}35 \pm 0{\cdot}29^{b}$	$10{\cdot}05 \pm 0{\cdot}54^{b}$	$28{\cdot}59 \pm 4{\cdot}64^{c}$	$115{\cdot}27 \pm 10{\cdot}93^{c}$	$450{\cdot}48 \pm 54{\cdot}85^{c}$
	5 days	$0{\cdot}73 \pm 0{\cdot}19^{c}$	$0{\cdot}62 \pm 0{\cdot}24^{c}$				
L_T (mm)	2 days	$6{\cdot}46 \pm 0{\cdot}28^{a}$	$9{\cdot}50 \pm 0{\cdot}43^{a}$	$10{\cdot}58 \pm 0{\cdot}49^{a}$	$16{\cdot}03 \pm 0{\cdot}82^{a}$	$20{\cdot}70 \pm 0{\cdot}93^{a}$	$32{\cdot}95 \pm 1{\cdot}10^{a}$
	3 days	$6{\cdot}35 \pm 0{\cdot}26^{a}$	$9{\cdot}42 \pm 0{\cdot}35^{a}$	$10{\cdot}45 \pm 0{\cdot}42^{a}$	$13{\cdot}80 \pm 0{\cdot}76^{b}$	$18{\cdot}58 \pm 0{\cdot}99^{b}$	$28{\cdot}66 \pm 1{\cdot}05^{b}$
	4 days	$5{\cdot}87 \pm 0{\cdot}32^{b}$	$8{\cdot}04 \pm 0{\cdot}47^{b}$	$9{\cdot}13 \pm 0{\cdot}52^{b}$	$12{\cdot}05 \pm 0{\cdot}79^{c}$	$14{\cdot}75 \pm 1{\cdot}10^{c}$	$22{\cdot}92 \pm 1{\cdot}20^{c}$
	5 days	$5{\cdot}63 \pm 0{\cdot}13^{b}$	$5{\cdot}58 \pm 0{\cdot}10^{c}$				
H_D (mm)	2 days	$1{\cdot}00 \pm 0{\cdot}09^{a}$	$1{\cdot}61 \pm 0{\cdot}10^{a}$	$1{\cdot}95 \pm 0{\cdot}10^{a}$	$3{\cdot}01 \pm 0{\cdot}10^{a}$	$5{\cdot}52 \pm 0{\cdot}13^{a}$	$10{\cdot}94 \pm 0{\cdot}24^{a}$
	3 days	$0{\cdot}99 \pm 0{\cdot}07^{a}$	$1{\cdot}58 \pm 0{\cdot}09^{a}$	$1{\cdot}89 \pm 0{\cdot}10^{b}$	$2{\cdot}76 \pm 0{\cdot}07^{b}$	$4{\cdot}64 \pm 0{\cdot}10^{b}$	$9{\cdot}57 \pm 0{\cdot}18^{b}$
	4 days	$0{\cdot}81 \pm 0{\cdot}05^{b}$	$1{\cdot}37 \pm 0{\cdot}06^{b}$	$1{\cdot}71 \pm 0{\cdot}07^{c}$	$2{\cdot}42 \pm 0{\cdot}05^{c}$	$4{\cdot}07 \pm 0{\cdot}09^{c}$	$8{\cdot}38 \pm 0{\cdot}12^{c}$
	5 days	$0{\cdot}71 \pm 0{\cdot}02^{c}$	$0{\cdot}67 \pm 0{\cdot}05^{c}$				
B_D (mm)	2 days	$1{\cdot}25 \pm 0{\cdot}10^{a}$	$2{\cdot}12 \pm 0{\cdot}10^{a}$	$2{\cdot}69 \pm 0{\cdot}13^{a}$	$3{\cdot}52 \pm 0{\cdot}18^{a}$	$5{\cdot}83 \pm 0{\cdot}15^{a}$	$13{\cdot}85 \pm 0{\cdot}25^{a}$
	3 days	$1{\cdot}17 \pm 0{\cdot}08^{a}$	$1{\cdot}88 \pm 0{\cdot}08^{b}$	$2{\cdot}55 \pm 0{\cdot}08^{b}$	$3{\cdot}22 \pm 0{\cdot}16^{b}$	$5{\cdot}06 \pm 0{\cdot}15^{b}$	$11{\cdot}70 \pm 0{\cdot}19^{b}$
	4 days	$1{\cdot}01 \pm 0{\cdot}11^{b}$	$1{\cdot}63 \pm 0{\cdot}09^{c}$	$2{\cdot}17 \pm 0{\cdot}10^{c}$	$2{\cdot}90 \pm 0{\cdot}18^{c}$	$4{\cdot}49 \pm 0{\cdot}17^{c}$	$10{\cdot}02 \pm 0{\cdot}18^{c}$
	5 days	$0{\cdot}86 \pm 0{\cdot}03^{c}$	$0{\cdot}80 \pm 0{\cdot}04^{d}$				
E_D (mm)	2 days	$0{\cdot}54 \pm 0{\cdot}03^{a}$	$0{\cdot}77 \pm 0{\cdot}03^{a}$	$0{\cdot}92 \pm 0{\cdot}04^{a}$	$1{\cdot}28 \pm 0{\cdot}04^{a}$	$1{\cdot}62 \pm 0{\cdot}06^{a}$	$2{\cdot}30 \pm 0{\cdot}06^{a}$
	3 days	$0{\cdot}51 \pm 0{\cdot}03^{b}$	$0{\cdot}72 \pm 0{\cdot}03^{b}$	$0{\cdot}90 \pm 0{\cdot}05^{a}$	$1{\cdot}18 \pm 0{\cdot}04^{b}$	$1{\cdot}48 \pm 0{\cdot}05^{b}$	$2{\cdot}01 \pm 0{\cdot}04^{b}$
	4 days	$0{\cdot}45 \pm 0{\cdot}02^{c}$	$0{\cdot}66 \pm 0{\cdot}03^{c}$	$0{\cdot}81 \pm 0{\cdot}03^{b}$	$1{\cdot}09 \pm 0{\cdot}04^{c}$	$1{\cdot}32 \pm 0{\cdot}04^{c}$	$1{\cdot}75 \pm 0{\cdot}03^{c}$
	5 days	$0{\cdot}37 \pm 0{\cdot}02^{d}$	$0{\cdot}37 \pm 0{\cdot}03^{d}$				
M_H (mm)	2 days	$0{\cdot}52 \pm 0{\cdot}08^{a}$	$0{\cdot}80 \pm 0{\cdot}09^{a}$	$1{\cdot}03 \pm 0{\cdot}07^{a}$	$1{\cdot}79 \pm 0{\cdot}13^{a}$	$2{\cdot}94 \pm 0{\cdot}14^{a}$	$7{\cdot}41 \pm 0{\cdot}22^{a}$
	3 days	$0{\cdot}49 \pm 0{\cdot}06^{b}$	$0{\cdot}76 \pm 0{\cdot}06^{b}$	$0{\cdot}99 \pm 0{\cdot}07^{a}$	$1{\cdot}60 \pm 0{\cdot}11^{b}$	$2{\cdot}60 \pm 0{\cdot}13^{b}$	$6{\cdot}35 \pm 0{\cdot}19^{b}$
	4 days	$0{\cdot}44 \pm 0{\cdot}05^{c}$	$0{\cdot}67 \pm 0{\cdot}08^{c}$	$0{\cdot}87 \pm 0{\cdot}07^{b}$	$1{\cdot}32 \pm 0{\cdot}10^{c}$	$2{\cdot}07 \pm 0{\cdot}08^{c}$	$5{\cdot}25 \pm 0{\cdot}15^{c}$
	5 days	$0{\cdot}38 \pm 0{\cdot}04^{d}$	$0{\cdot}37 \pm 0{\cdot}03^{d}$				
M_D (mm)	2 days	$0{\cdot}69 \pm 0{\cdot}07^{a}$	$0{\cdot}93 \pm 0{\cdot}09^{a}$	$1{\cdot}05 \pm 0{\cdot}09^{a}$	$1{\cdot}57 \pm 0{\cdot}08^{a}$	$2{\cdot}35 \pm 0{\cdot}10^{a}$	$4{\cdot}75 \pm 0{\cdot}15^{a}$
	3 days	$0{\cdot}65 \pm 0{\cdot}05^{a}$	$0{\cdot}89 \pm 0{\cdot}06^{a}$	$1{\cdot}05 \pm 0{\cdot}10^{a}$	$1{\cdot}45 \pm 0{\cdot}07^{b}$	$2{\cdot}04 \pm 0{\cdot}10^{b}$	$4{\cdot}15 \pm 0{\cdot}12^{b}$
	4 days	$0{\cdot}55 \pm 0{\cdot}05^{b}$	$0{\cdot}78 \pm 0{\cdot}05^{b}$	$0{\cdot}96 \pm 0{\cdot}07^{b}$	$1{\cdot}27 \pm 0{\cdot}05^{c}$	$1{\cdot}83 \pm 0{\cdot}09^{c}$	$3{\cdot}60 \pm 0{\cdot}11^{c}$
	5 days	$0{\cdot}52 \pm 0{\cdot}03^{b}$	$0{\cdot}49 \pm 0{\cdot}02^{c}$				

M, body mass; L_T, total length; H_D, head depth; B_D, body depth; E_D, eye diameter; M_H, musculature height; M_D, mouth diameter.

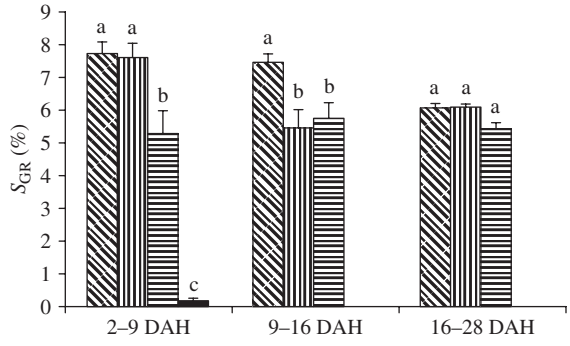

FIG. 3. Specific growth rates (S_{GR}, at 2–9, 9–16 and 16–28 days after hatch, DAH) of *Siniperca scherzeri* larvae under different initial feeding times: 2 (▨), 3 (▥), 4 (▤) and 5 (■) days. Values are means ± S.D. Means sharing different lowercase letters are significantly different ($P < 0{\cdot}05$).

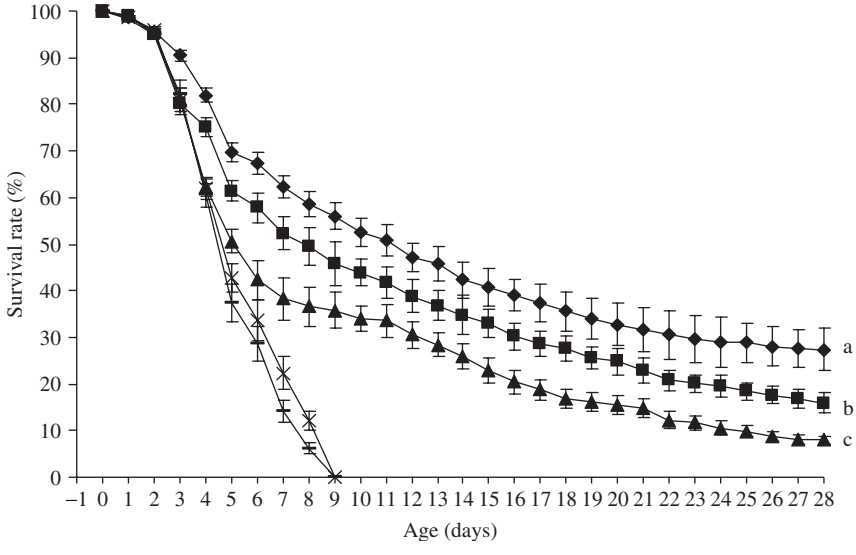

FIG. 4. Survival rate of *Siniperca scherzeri* larvae under different: initial feeding times: 2 (◆), 3 (■), 4 (▲) and 5(×) days and starved control (▬). Values are means ± S.D. Means sharing different lower case letters are significantly different ($P < 0{\cdot}05$).

DISCUSSION

The yolk volume (1·461 mm^3) of newly hatched *S. scherzeri* larva is much larger than that of many other species at the time of hatching, *e.g.* European sea bass *Dicentrarchus labrax* (L.) 0·219 mm^3, lined sole *Achirus lineatus* (L.) 0·22 mm^3, bay anchovy *Anchoa mitchilli* (Valenciennes) 0·15 mm^3, sea bream *Archosargus rhomboidalis* (L.) 0·34 mm^3 (Houde, 1974) and Asian sea bass *Lates calcarifer* (Bloch) 0·107 mm^3 (Kailasam *et al*., 2007). Larvae of some fish species are not able to initiate first feeding until yolk exhaustion (Houde, 1974), and some even start first feeding several days after yolk exhaustion (Gisbert & Williot, 1997; Gisbert *et al*., 2004).

Siniperca scherzeri larvae, however, could initiate first feeding at 2 DAH when the yolk sac was still visible. Fish larvae depend largely on yolk reserves to supply the energy for developing the feeding ability and physiological mechanisms before first feeding. In many fish species, larvae show a mixed nutrition period before yolk-sac exhaustion. This period and the time of first feeding of fish larvae are different for each species and influenced by many factors, such as egg quality, yolk-sac volume and temperature (Shan *et al*., 2008). Large egg size and yolk can support more nutrition reserves, which allow more time to initiate feeding before the onset of irreversible starvation (Blaxter & Hempel, 1963). *Siniperca scherzeri* larvae, however, have a fertilized egg diameter of 1·8–2·0 mm which is larger than the Atlantic herring *Clupea harengus* L. (1·2–1·7 mm) (Blaxter & Hempel, 1963; McGurk, 1984), Japanese flounder *Paralichthys olivaceus* (Temminck & Schlegel) (0·91 mm) (Yamashita & Aoyama, 1986) and *Pelteobagrus vachellii* (Richardson) (1·7 mm) (Ma *et al*., 2006), but the first-feeding time is very early and the tolerance to hunger seems comparatively low in this species. Moreover, *S. scherzeri* larvae have only 3 days of mixed feeding time at 23° C and render the larvae vulnerable to starvation. Hence, *S. scherzeri* larvae must successfully establish exogenous feeding as early as possible or suffer starvation soon after yolk reserve exhaustion. It is likely that the main reason for the early feeding activity of *S. scherzeri* is related to the life history of this freshwater species. It has been established that, in general, freshwater species have a direct ontogeny, and at hatching they have more developed fry than marine species which can initiate feeding long before the yolk sac is depleted. Marine species like *C. harengus* and *P. olivaceus* have poorly developed larvae at hatching as well as an indirect ontogeny (Blaxter & Hempel, 1963; McGurk, 1984; Yamashita & Aoyama, 1986).

Complete yolk absorption of *S. scherzeri* larvae was noticed at 5 DAH. The time of complete yolk absorption is different in fishes and time span from yolk exhaustion to starvation is water temperature dependent and species specific (Dou *et al*., 2005). When temperature increased from 7·5 to 9·2° C, the first-feeding time of *C. harengus* changed from 6 to 3 DAH (Yin & Blaxter, 1987), and in *P. olivaceus*, when temperature increased from 12 to 21° C, the first-feeding time moved up 5 days (Seikai *et al*., 1986; Dou *et al*., 2005). Analysis of the information available for 25 species (Shan *et al*., 2008), showed that the first-feeding time in most fish larvae occurs 1–3 DAH at 22–28° C, while at 6–21° C, fish larvae begin their first feeding at 6–7 DAH. In the present study with a temperature of 23° C, *S. scherzeri* larvae initiated first feeding at 2 DAH, therefore corresponding with the above.

Most fish larvae mainly initiate first feeding by eating zooplankton. Larvae of the *Siniperca* genus, however, generally prey on other fish larvae when they first start feeding and this is uncommon in most common carnivorous fishes (Wu, 1987). This first feeding on other fish larvae could be a kind of natural selection in its life history, and its carnivorous feeding habit relates to morphometric, ecological and physiological characteristics of the species.

In the present study, the first feeding rate of *S. scherzeri* was 33·33% which was comparatively low. Fish larvae feeding ontogeny corresponds with the functional development of sensory, buccal and swimming organs (Shan *et al*., 2008). In early life history, those organs related to feeding cannot develop simultaneously in larvae. The lower initial feeding rate could also be due to other factors such as culture conditions, prey size, prey density and learning of feeding behaviour. The feeding

rate on 3 DAH, however, was very high (Fig. 2), indicating that the organs used for feeding by most larvae were well developed.

The P_{NR} is related to species, yolk-sac duration, nutritional condition of broodstock and temperature (Lasker *et al*., 1970; Rogers & Westin, 1981; Shan *et al*., 2008). It is especially related to temperature, becoming shorter when temperature increases. *Paralichthys olivaceus* took 2·0–3·7 days from yolk exhaustion to P_{NR} at 15–21° C (Dou *et al*., 2005); *C. harengus* took 3–5 days from yolk exhaustion to P_{NR} at 7·5–13·1° C (Blaxter & Hempel, 1963; Yin & Blaxter, 1987). The P_{NR} of *S. scherzeri* larvae occurred between 4 and 5 days after hatching at 23° C, range ± 1·0° C. In some species, this period is only ≤1 day, *e.g. A. rhomboidali*s and *A. lineatus* (Houde, 1974). Some cold temperature species could establish first feeding a longer time after the yolk exhaustion, such as Atlantic salmon *Salmo salar* L. (Koss & Bromage, 1990) and Siberian sturgeon *Acipenser baerii* Brandt (Gisbert & Williot, 1997). The duration from commencement of feeding to the time of P_{NR} is considered as the time of recoverable starvation and is an index of the ability to resist fasting (Hunter, 1981; Yamashita & Aoyama, 1986). The optimal duration was regarded as 1 day for *S. scherzeri*, because >80% of larvae began to feed at 3 DAH and P_{NR} occurred between 4 and 5 DAH (Fig. 2). The time span is relatively short compared to that of *C. harengus* (Blaxter & Ehrlich, 1974; Yin, 1991), tench *Tinca tinca* (L.) (Ling *et al*., 2003) and *Ancherythroculter nigrocauda* Yih & Wu (Xiong *et al*., 2006). Hence, the ability of *S. scherzeri* larvae to withstand starvation was lower than for the above species.

Siniperca scherzeri larvae showed inferior growth performance when first feeding was initiated at 4 and 5 DAH. Similarly, in other species, such as *A. lineatus*, *A. rhomboidalis* (Houde, 1974), Malabar grouper *Epinephelus malabaricus* (Bloch & Schneider) (Yoseda *et al*., 2006*a*), coral trout grouper *Plectropomus leopardus* (Lacépède) (Yoseda *et al*., 2006*b*) and *L. calcarifer* (Kailasam *et al*., 2007), the larval growth and survival were all influenced by delaying the first feeding time. The inferior growth and survival of larvae under delayed feeding should be attributed to starvation caused by the delayed feeding. As starvation causes the arrest of normal tissue synthesis, growth reduction with increasing degrees of starvation is to be expected (Xiong *et al*., 2006). The differences observed in the morphometric characters of fish larvae in this study suggests that the first feeding should be started at 2 DAH for better growth and survival and any further delay in first feeding leads to poor growth. Moreover, from the present results, the yolk in *S. scherzeri* larvae is available up to 4 DAH, suggesting energy from the yolk alone might not be sufficient and exogenous feed must be supplied to meet the nutritional requirements for larval development. Although the morphometric characters of larvae first-fed at 2 days were significantly higher than in 3 and 4 day treatments from 16 DAH to the end of the experiment, interestingly the S_{GR} from 16 to 28 DAH did not show significant differences among treatments (Fig. 3), indicating that there was a kind of compensatory growth mechanism in this period.

Survival rate of fish larvae is influenced by nutrients stored in the yolk sac, temperature, feed density, prey types and time of initial feeding (Houde, 1974; Ware, 1975; Hodson & Blunt, 1986). The nutritional value of the food, particularly the quantity and size of the prey fish larvae, have been shown to affect the growth and survival of *S. scherzeri* larvae, and the prey organisms used in the present experiment proved to be feasible in practice (Xia *et al*., 2006). In the present study, a higher survival rate

was recorded when the larvae initiated feeding at 2 days compared to 3 and 4 day first-fed larvae, which was similar to results for *L. calcarifer* larvae (Kailasam *et al*., 2007). Delayed initial feeding around P_{NR} or later would compromise the feeding ability due to morphological and histological deformities induced by early starvation (Gwak & Tanaka, 1999; Dou *et al*., 2002). This is in agreement with the present study where the *S. scherzeri* larvae first fed at 5 days (P_{NR}) resulted in total mortality and deformed shape and organs on 9 DAH. Dou *et al*. (2005) and Shan *et al*. (2008) reported the successful initial feeding before P_{NR} was critically important for *P. olivaceus* larvae and rock bream *Oplegnathus fasciatus* (Temminck & Schlegel) larvae survival respectively, and this was the case in the present experiment.

Due to the high commercial value of *S. scherzeri* in aquaculture, seed culture of this fish is becoming more and more popular in China. Delayed initial feeding, however, is a bottleneck for seed production, resulting in high mortality and poor growth performance of *S. scherzeri* larvae during the early life stages. Hence, the present study, sacrificing many *S. scherzeri* larvae by withholding food, was necessary to determine the optimal first feeding time in order to enhance larval growth and survival in seed culture. On animal welfare and ethical grounds, there are also technical problems in saving small larvae after sampling and measuring, and most died in the present study. It is suggested that larval sampling techniques to avoid large-scale mortality should be developed for future studies.

The authors are very grateful to three anonymous reviewers for their valuable comments to improve the manuscript. The authors also thank the Assistant Editor S. Blaber and T. Chung for improving the English, and. Z. Lixin, the manager of Qichun Fishery for his equipment assistance. This research is funded by Key Technology R&D Programme of Hubei Province titled as 'High quality and efficiency technology and demonstration of spotted mandarin fish culture' (the accession number: 2006AA201B05).

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