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Early development and the point of no return in pikeperch (*Sander lucioperca* L.) larvae*

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Abstract The objectives of the present study were to evaluate the yolk-sac and oil globule absorption and point of no return (PNR) of pikeperch (*Sander lucioperca* L.) larvae. Artificial propagation of pikeperch was performed at (15±2)°C. Yolk-sac absorption, oil globule absorption, larval growth and the first initial feeding rate were observed to analyze the early growth and to determine the PNR of pikeperch larvae. The total length of newly hatched (0 day after hatching, DAH) pikeperch larvae was (4.25±0.22) mm and the volume of the yolk-sac and the oil globule was (0.30±0.12) mm^3 and (5.14±2.28) 10^{-2} mm^3 respectively. The yolk-sac and the oil globule were exhausted at 11 DAH and 14 DAH, respectively. Pikeperch larvae began feeding at 8 DAH with an initial feeding rate about 10.0%. From 9 to 14 DAH, the initial feeding rate increased rapidly, and reached its highest (about 82.7%) at 14 DAH. It declined thereafter, 48.9% at 15 DAH and 35.6% at 16 DAH, thus the pikeperch larvae reached PNR by 15–16 DAH. The appropriate first feeding time for the pikeperch larvae is 11–12 DAH, when the initial feeding rate is higher than half of the maximum initial feeding rate.

Keyword: growth; initial feeding rate; pikeperch (*Sander lucioperca*) larvae; Point of No Return

1 INTRODUCTION

Pikeperch (*Sander lucioperca* L.) is an economically important Percidae species and is distributed throughout the basins of the Aral Sea, Black Sea, Caspian Sea and Baltic Sea in Europe, and the basins of the Ili River and the Rtysh Tixche River in China. This species is euryhaline, with a wide range of optimal temperature (0–30°C) and is a valuable aquaculture species and sport fish due to its tender meat (Schulz et al., 2007; Wang et al., 2009). Historically, the pikeperch market mainly relied on commercial fishing efforts, which resulted in a sharp decline in wild populations (Dil, 2008). To meet the need of the pikeperch market, intensive aquaculture of pikeperch has been increased in the Netherlands, Denmark, Finland, France and China (Li and Li, 1996; Fontaine, 2009; FAO, 2011). During the last decade, studies have focused on the influence of temperature on growth and gonad development (Lappalainen et al., 2009; Hermelink et al., 2011; Hermelink et al., 2013), the effect of different hormones on spawning (Rónyai, 2007; Křišťan et al., 2013; Falahatkar and Poursaeid, 2014), and the impact of diet on the pikeperch larval digestive system (Nyina-Wamwiza et al., 2005; Kowalska et al., 2012). The major limitation of pikeperch aquaculture has been the inadequate supply of fingerlings, which is primarily the result of a high mortality during the larval stage (Mélard et al., 1996; Ruuhijärvi and Hyvärinen, 1996). In China, pikeperch eggs are hatched in tanks. After hatching, larvae are bred in the

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same containers during the first two weeks, and then are transferred into ponds for further culture (Li and Li, 1996). Due to the long and irregular hatching time of pikeperch larvae and simultaneous low temperature in early spring, when plankton organisms rarely form a high density, the initial ingestion time and palatable food supply in their ponds are hard to match, which leads to the low survival rate of pikeperch larvae.

Early larvae go through three developmental stages (Yin, 1995): stage 1, the endogenous nourishment stage, stage 2, the mixed nourishment stage and stage 3 the exogenous nourishment stage. At the onset of exogenous feeding, fish larvae face death from starvation if the first feeding is delayed after the PNR, which is the threshold time point when initially starved larvae lose their capability to recover from starvation, even if they are later fed ad libitum (Blaxter and Hempel, 1963). This critical point is often used as an index to experimentally quantify 'nutritional vulnerability' or 'nutritional flexibility' (Sulkin, 1978). The principal objectives of the present study have been to evaluate the timing of yolk and oil globule absorption, the initial feeding rate and the PNR of pikeperch larvae, and to provide aquaculture guidelines on the initial feeding time for pikeperch larvae.

2 MATERIAL AND METHOD

2.1 Obtaining experimental larvae

The larvae were provided by Suzhou Shajiabang East Lake Modern Fishery Science and Technology Development Co. Ltd. The broodstock were injected with luteinizing hormone-releasing hormone analogue (LHRHa) plus domperidone hormone (DOM) (Ningbo, Renjian Pharmaceutical Co. Ltd.), with male fish receiving half the dose of female fish. Following hormone injection, broodstock were placed in a tank (4 m×2 m×1 m) with 1 female:1 male paired matching. The parent fish spawned on a round nest composed of palm. After spawning, fertilized eggs were taken every day and embryonic development was observed under a microscope. Prior to hatching, fertilized eggs were transferred to a polyvinyl chloride tank (50 cm×35 cm×30 cm). Each set of fertilized eggs were only from a single broodstock pair.

2.2 Method of cultivation

The larvae were reared in similar polyvinyl chloride tanks. During the experiment, water temperature was maintained at (15±2)°C. The larvae were divided into two groups. One group served as a control group and another group was a starvation group. All the groups were investigated in triplicate under identical conditions. The stocking density of each group was basically the same (100 ind./L). Aeration was supplied continuously and 1/3 of the water was changed every two days. The pH was 8.0±0.5 and the ammonia nitrogen remained under 0.03 mg/L. Light conditions followed the natural diurnal cycle. The control group were fed with rotifers (*Brachionus diversicornis* and *Brachionus quadridentatus*), of which density were kept at about 30 ind./mL, three times per day. The rotifers were enriched from the culture pond by a plankton net (mesh size 0.03–0.04 mm). The starvation groups were not fed and the water was filtered through a plankton net to ensure that there was no occurrence of dietary items in the water.

2.3 Morphometric characters of the larvae

The experimental larvae hatched on March 20, 2015, considered as 0 day after hatching. Every day, 15 fish were taken from each tank of the control group and of the starvation group. After being anesthetized with MS-222 (50 mg/L), and the main characteristics of early larval development were observed by optical microscopy (Olympus). A stereomicroscope (Ji Fei company, XTL-500) and a micro camera (Yichuang Corporation, MY310), were used to measure growth trait data, including yolk-sac long-diameter (R), yolk-sac short-diameter (r), oil globule diameter (d), total length (L), accurate to 0.01 mm. Yolk-sac volume (V_Y) and the oil globule volume (V_{og}) were calculated as follows:

$$V_{og}=4/3\cdot\pi\cdot(d/2)^3.$$

The larval oil globule and yolk-sac were combined into an ellipsoid, so yolk-sac volume was equal to the yolk-sac total volume minus the oil globule volume.

$$V_Y=4/3\cdot\pi\cdot(r/2)^2\cdot R/2-V_{og}.$$

The growth rate of larvae is expressed as the specific growth rate (SGR) using the following equation: $SGR=100(\ln L_{ta}-\ln L_{tb})\cdot t^{-1}$, where t was the time between t_a and t_b.

2.4 Initial feeding rate and PNR

Each morning at 10:00 starting from 0 DAH, 15 larvae from each tank of the starvation groups were transferred into a glass cylinder and fed with rotifers. After 2 hours, the larvae were removed, anesthetized with MS-222 (50 mg/L), then examined with a

stereomicroscope to identify the presence of rotifers in their intestine. Initial feeding rate is expressed using the following equation:

Initial feeding rate=(number of larvae with rotifers in the fish intestine/ the total number of larvae)×100%.

The method to determine PNR has been adopted from Blaxter and Yin (Blaxter and Hempel, 1963; Yin and Blaxter, 1987; Yin, 1991a). After hatching, the initial feeding rate of starved larvae was determined daily. PNR was defined as the time when the initial feeding rate of the starved larvae dropped to half of the highest initial feeding rate. The experiment terminated when no starved larvae could initiate feeding.

2.5 Statistical analysis

All statistical analysis was conducted with the Statistical Product and Service Solutions 17.0. The data followed a normal distribution (Shapiro-Wilk test) to ensure that assumptions used by *t*-test were satisfied. Larval growth and SGR were tested by independent-samples *t*-test. The results are expressed as mean±SD (standard deviation) of the data, and *P* value less than 0.05 is considered statistically significant.

3 RESULT

3.1 Developmental characteristics of larvae

After hatching, the pikeperch larvae developed rapidly in morphology and experienced significant changes in their digestive system. The main morphological development characteristics were as follows.

0 DAH: the larva was straight and the whole body was transparent; the oil globule was in front of the light yellow yolk-sac (Fig.1a).

1 DAH: the larval incipient intestine was formed at the end of their yolk-sac, which was a slender fuzzy line (Fig.1b).

2 DAH: larval sarcomere was visible and the larva possessed an open mouth (Fig.1c).

3 DAH: the larval gut was visible. The fan-shaped pectoral fin bud was formed. The black pigment in their eyes increased, the auditory vesicle was present, and the anus was closed (Fig.1d).

4 DAH: intestinal secretions were observed in the intestinal tract, which was followed by intestinal peristalsis (Fig.1e).

5 DAH: the intestine began to widen and the bowel wall was smooth (Fig.1f).

6 DAH: intestinal peristalsis had begun; the intestinal wall was slightly folded, and the anus was open with intestinal secretions being discharged (Fig.1g).

7 DAH: the anterior part of the intestine differentiated into the early stage of the stomach.

8 DAH: the intestinal fold increased; the intestinal valve appeared; the intestine differentiated into the anterior and the posterior intestine, and intestinal peristalsis was visible. A few larvae began feeding, suggesting that the larvae went into the mixed feeding stage (Fig.1h).

9 DAH: the bladder began to inflate, which looked slightly like the back projection, and the larvae began to swim horizontally (Fig.1i).

10 DAH: larvae jaws moved, with enlargement of the anterior mid gut and constriction of the hindgut; black pigment fills the eyeball (Fig.1j).

11 DAH: yolk-sac absorption was completed; the oil globule remained; the upper and lower jaws were active.

12 DAH: the digestive tract was full of food; the oil globule was oval (Fig.1k).

14 DAH: oil globule disappeared, and the larvae began to enter the exogenous feeding stage.

16 DAH: some larvae possessed twisted spines (Fig.1l).

18 DAH: all starved larvae had died.

3.2 The change during larval growth

The total length of newly hatched (0 DAH) pikeperch larvae was (4.25±0.22) mm. On 14 DAH, The larval total length in the control group and the starvation group was (6.05±0.14) mm and (5.92± 0.10) mm, respectively. Following the exhaustion of the yolk-sac and oil globule from 14 DAH, growth difference appeared between the control group and the starvation group ($P<0.001$) (Fig.2).

As shown in Fig.3. From 0 to 8 DAH (endogenous feeding stage), the larval SGR in the control groups was (3.74±0.39)% and in the starvation groups (3.57±0.30)% ($P>0.05$). From 8 to 14 DAH (mixed feeding stage), the SGR in the control groups ((0.89±0.09)%) was significantly higher than that in the starvation groups ((0.53±0.06)%) ($P<0.05$). During 14–16 DAH (exogenous feeding stage), the larvae of the starvation group demonstrated declining SGR ((2.22±0.85)%), while the larval SGR in the control groups was (3.57±0.31)%.

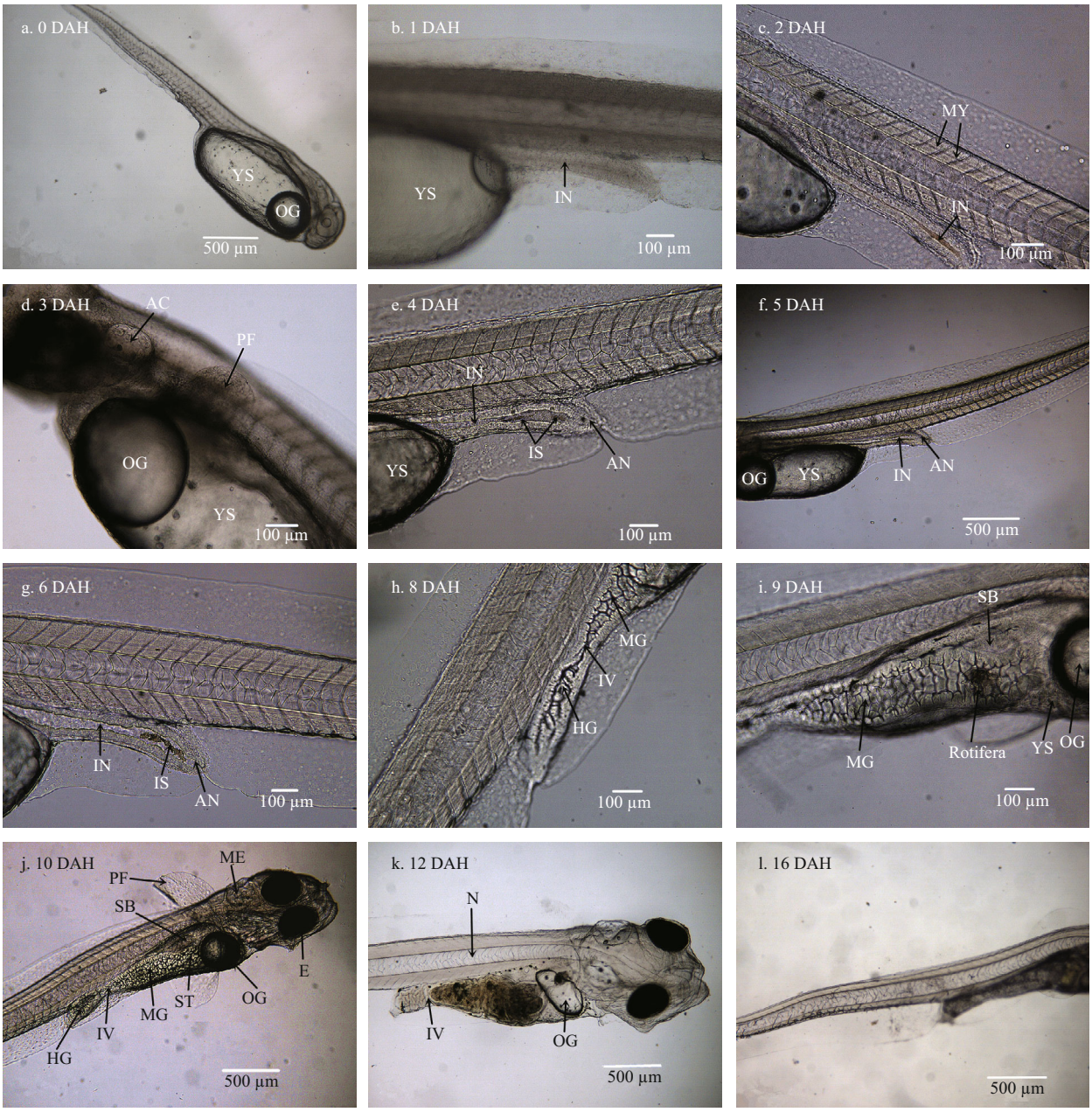

Fig.1 The growth characteristics of pikeperch (*Sander lucioperca* L.) larvae

AC: auditory capsule; AN: anus; HG: hindgut; IN: incipient intestine; IS: intestinal secretions; IV: intestinal valve; MG: mid gut; MY: myomere; N: notochord; OG: oil globule; PF: pectoral fin; SB: swim bladder; ST: stomach; YS: yolk-sac.

3.3 The change of the yolk-sac and the oil globule

The newly hatched pikeperch larvae had a large oval yolk-sac (V_Y=(0.30±0.12) mm^3) and a spherical-shaped oil globule (V_{og}=(5.14±2.28) 10^{-2} mm^3). There was no significant difference (P>0.05) in the V_Y and V_{og} between the control and the starvation groups from 0 to 14 DAH. Complete depletion of the yolk-sac and the oil globule were respectively noticed at 11 DAH and 14 DAH, in both the control and the starved groups (Table 1).

3.4 The initial feeding rate and PNR

Pikeperch larvae began feeding at 8 DAH, and the initial feeding rate was approximately 10%. Over the next 6 days, the initial feeding rate increased rapidly, peaking at 82.7% at 14 DAH. By 15 DAH, the initial feeding rate decreased to 48.9% and 35.6% in 16 DAH (Fig.4). Between 15 DAH to 16 DAH, the initial feeding rate dropped to about half of the highest initial feeding rate (82.7%), and this time point should be considered as the Point of No Return.

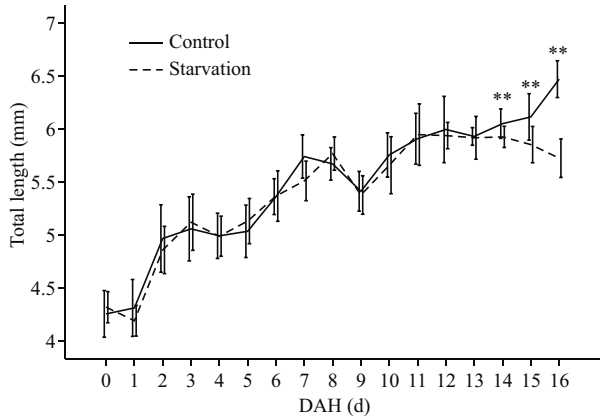

Fig.2 The comparison of total length between control and starved groups of pikeperch (*Sander lucioperca*) larvae during 0–16 DAH

Data are expressed as mean±SD and bars represent standard deviations of the means (n=15). ** indicates significant difference (P<0.01) among different groups.

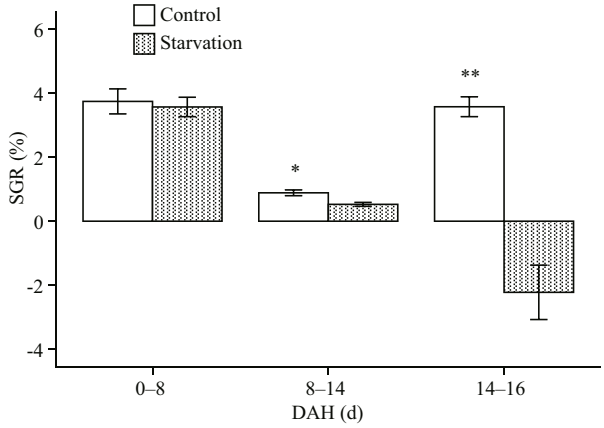

Fig.3 The comparison of change in SGR in control and starved groups of pikeperch (*Sander lucioperca*) larvae during 0–16 DAH

Data are expressed as mean±SD and bars represent standard deviations of the means (n=3). * indicates significant difference (P<0.05) and ** indicates significant difference (P<0.01) among different groups.

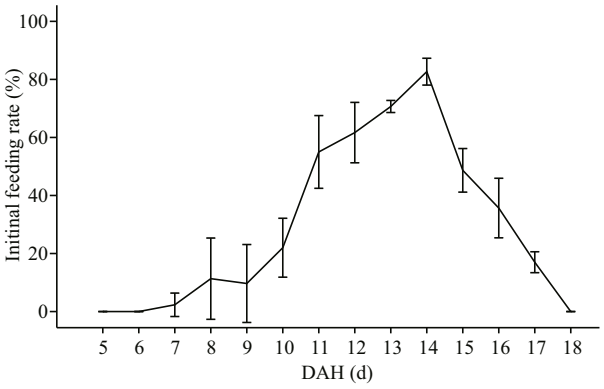

Fig.4 Initial feeding rate of pikeperch (*Sander lucioperca*) larvae

Data are expressed as mean±SD and bars represent standard deviations of the means (n=3).

Table 1 Yolk-sac and oil globule depletion in pikeperch (*Sander lucioperca*) larvae of control and starved groups

DAH (d)	Volume of yolk-sac (mm³)		Volume of oil globule (10^{-2} mm³)	
	Control	Starvation	Control	Starvation
0	0.30±0.12	0.26±0.08	5.14±2.28	5.26±2.03
1	0.31±0.16	0.29±0.11	4.88±1.28	5.62±1.06
2	0.26±0.15	0.20±0.05	5.70±2.93	5.75±1.09
3	0.19±0.08	0.16±0.06	3.93±0.59	4.11±0.86
4	0.15±0.06	0.14±0.03	3.28±0.61	3.69±0.89
5	0.11±0.04	0.11±0.03	3.40±0.72	3.44±0.79
6	0.07±0.02	0.06±0.02	3.46±0.90	3.14±0.90
7	0.05±0.01	0.05±0.02	3.15±0.74	3.04±0.48
8	0.06±0.02	0.04±0.03	2.44±0.79	2.53±0.92
9	0.05±0.02	0.05±0.02	2.29±0.68	2.10±0.79
10	0.01±0.01	0.03±0.02	2.01±1.04	1.80±0.57
11	0	0	1.34±0.37	1.64±0.53
12	0	0	1.22±0.62	1.23±0.35
13	0	0	0.55±0.38	0.50±0.37
14	0	0	0	0
15	0	0	0	0

Data are expressed as mean±SD (n=15).

4 DISCUSSION

4.1 The growth of pikeperch larvae

Farris suggested that larvae can be divided into three stages: the rapid growth stage immediately following hatching, the slow growth stage around yolk-sac exhaustion and the negative growth stage following a failure to establish exogenous feeding (Farris, 1959). Based on our study, early growth of pikeperch larvae can be divided into three such stages: stage 1 (the endogenous feeding stage) is from 0 DAH to 8 DAH when the larvae were initially fed. During this stage, larval development is manifested mainly in the feeding organs, such as mouth and intestine. Larvae depend largely on yolk sources before feeding ability and physiological mechanism become fully developed. Stage 2 (the mixed feeding stage) is from 8 DAH to 14 DAH when the oil globule was exhausted. During this stage, the larval bladder begins to inflate, upper and lower jaws are active. Larval swimming and feeding ability are further improved.

The beginning of the exogenous feeding facilitates the establishment of the larval movement patterns, especially cruising pattern (Yin and Blaxter, 1989). Stage 3 (the exogenous feeding stage) begins from the exhaustion of the oil globule (after 14 DAH). In stage 1, we found no significant difference in larval SGR between the control and the starvation group. After first feeding, SGR of the feeding larvae was significantly higher than that of the starved larvae. After depletion of endogenous nutrients, negative growth appeared in the starved larvae. Our results show that starvation hindered pikeperch larval growth after the endogenous feeding stage. This change is an adaptation phenomenon to improve the feeding rate and survival rate (Yin and Blaxter, 1986; Yin, 1991b).

4.2 Changes the yolk-sac and the oil globule

The V_Y of newly hatched pikeperch larvae was (0.30±0.12) mm^3 similar to *Pomoxis nigromaculatus* ((0.34±0.05) mm^3) (Qin, 2014), *Dicentrarchus labrax* (0.30 mm^3) (Rønnestad et al., 1998), and much larger than many other species, such as *Lates calcarifer* (0.107 mm^3) (Kailasam et al., 2007) and *Clupea harengus* (0.182 mm^3) (Yin, 1991b). The endogenous feeding of pikeperch larvae utilizes the yolk-sac and the oil globule. We found no significant differences in the depletion of either the yolk-sac or the oil globule, between the control and the starvation groups. At (15±2)°C, the pikeperch larval mixed feeding period lasted for 6 days (8–14 DAH), much longer than that of many other species such as *Siniperca scherzeri* (3 days, 23°C) (Zhang et al., 2009), *Trachinotus ovatus* (1 day, (28±1)°C) (Ma et al., 2014), and *Paralichthys olivaceus* (0.4 day, 14.6°C) (Dou et al., 2005). Large yolk-sacs and longer mixed feeding stages can support more nutrition reserves, which allow more time to initiate feeding before the onset of irreversible starvation (Blaxter and Hempel, 1963; Qiu et al., 2014). Of course, the time of complete yolk-sac absorption is temperature-dependent and species-specific (Dou et al., 2005) and to a large extent it depends on temperature (Snyder, 1976). Future studies should focus on the relation between temperature and the depletion of the yolk-sac and the oil globule.

During the mixed feeding stage, we found the yolk-sac was exhausted on 11 DAH and the oil globule became the main source in the later part of mixed feeding. This suggests that fats are utilized by pikeperch larvae less effectively and that the yolk-sac is the first and the most important source of energy (Palińska-Żarska et al., 2014), similar to in *Lota lota* larvae (Palińska-Żarska et al., 2014) and *Lutjanus campechanus* larvae (Williams et al., 2004). The presence of oil globules in some species, which could be retained for a period of time after yolk-sac exhaustion, may provide extra energy reserves and withstand starvation (Mookerji and Rao, 1999). In some teleost fishes, most of the lipids are confined to the oil globule. The size of the oil globule remains constant during embryogenesis but is reduced following yolk depletion (Silversand et al., 1996). There are two major roles for the oil globule in pikeperch larvae. Energy derived from lipid catabolism is used as energy for swimming (Rønnestad et al., 1998). The oil globule also increases larval buoyancy and allows the larvae to achieve a vertical position in the water to facilitate feeding (Hunt et al., 1996; Williams et al., 2004; Palińska-Żarska et al., 2014).

4.3 The initial feeding rate and PNR

According to the duration of highest initial feeding rate, larvae can be divided into two types. Type A larvae start to feed at a low initial feeding rate followed by a rapid increase and then a successively rapid decrease, similar to *Pagrosomus major* (Bao et al., 1998) and *Acipenser sinensis* (Chai et al., 2011). Type B larvae possess a low initial feeding rate which rapidly increases and is maintained for a period of time, similar to *Paralichthys olivaceus* (Dou et al., 2005) and *Gadus morhua* (Overton et al., 2010). The duration of the highest feeding rate is proportional to the larval resistance to starvation. Pikeperch larvae can be classified as a Type A. Our results show that pikeperch larvae reached a maximum initial feeding rate at 14 DAH which decreased rapidly within 24 hours. Moreover, oil globule exhaustion was completed on 14 DAH, and shortly thereafter larvae entered the PNR (15–16 DAH). If there is no food, the pikeperch larvae can withstand starvation for only 1–2 days at (15±2)°C. *Paralichthys olivaceus* larvae took 2–3.7 days from yolk exhaustion to PNR at 15–21°C (Dou et al., 2005); *Clupea harengus* larvae took 3–5 days from yolk exhaustion to PNR at 7.5–13.1°C (Blaxter and Hempel, 1963; Yin and Blaxter, 1987); *Miichthys miiuy* larvae took 2 days from yolk exhaustion to PNR at 24°C (Shan et al., 2009). The ability of pikeperch larvae to withstand starvation was weaker than other species and highlights the need to identify the critical initial feeding time to maximize aquaculture efforts.

5 CONCLUSION

This study has shown that at (15±2)°C, the appropriate first feeding time for pikeperch larvae is 11–12 DAH, when the initial feeding rate is higher than half of the maximum initial feeding rate. If the first feeding is later than 15 DAH, the pikeperch larvae have entered the PNR, which will result in mortality.

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