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Water Temperature Affects the Ontogenetic Development of Yellowtail Amberjack *Seriola lalandi dorsalis* (Gill 1863)

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Abstract

The effect of temperature on survival, growth, jaw deformity, and point of no return (PNR) after food deprivation in newly hatched yellowtail amberjack Seriola lalandi dorsalis larvae were studied in experimental conditions. The performance of fed and un-fed yellowtail amberjack larvae were tested at 21, 23 and 25˚C for 24 days. In the fed treatment, fish survivals at 21 and 23˚C were significantly higher than that at 25˚C by 24 day post hatch (DPH). Fish length and dry weight at 25˚C were significantly higher than those reared at 21 and 23˚C. Temperature significantly affects the feeding incidence of fish larvae from 3 DPH to 5 DPH. In the unfed treatment, fish larvae reached PNR at 5, 6 and 8 DPH at 25, 23 and 21˚C, respectively. Higher temperatures increased fish ontogenetic development, but decreased the time to reach PNR. The high rate of jaw deformity occurred at high temperature by 24 DPH. Our results indicate that rearing temperature is a key factor affecting the ontogenetic development of yellowtail amberjack larvae and the optimum temperature for the first feeding larval is 21-23˚C. Temperatures above 25˚C are likely to cause mortality of yellowtail amberjack larvae in the first 10 DPH.

Keywords

Temperature; Yellowtail amberjack larvae; Growth; Survival; PNR; Jaw malformation

Introduction

Temperature is important for development of fish larvae because it can regulate metabolism and feeding behaviour [1,2]. Temperature directly influences the size of fish larvae at hatching, yolk absorption, growth, survival, feeding success and digestion [3-9]. In many cases, high mortality and abnormality of fish larvae are attributed to unsuitable temperature in the rearing system [10-13]. Within the temperature range of fish tolerance, the increase of temperature accelerates ontogenetic development, but a high temperature may reduce fish survival rates at the same time [14]. During ontogenetic development, the size at metamorphosis tends to increase at low temperature [15,16]. In contrast, at high temperatures, yolk-sac absorption of fish larvae is faster resulting in a shorter endogenous feeding period [9,17,18]. Within the range of optimal temperatures, food intake of fish usually increases with temperature increment, but falls dramatically at the low end of optimal temperatures [19]. Therefore, choosing appropriate temperature for rearing fish larvae is essential to achieve fast growth and high survival in finfish hatcheries.

In larval fish rearing, fish mortality in the early stage is closely related to food supply under favourable conditions because fish development depends on adequate nutrition uptake [20-23]. However, temperature can influence the duration of endogenous feeding and the ability of fish larvae to tolerate food deprivation because temperature directly regulates the rate of yolk absorption [24,25]. After yolk sac is depleted, fish larvae will rely on food from exogenous sources only. Therefore, the time at first feeding in fish larvae is crucial for their growth and survival.

Furthermore, when larvae are deprived of food after yolk-sac absorption, some fish may permanently lose their ability to feed from an external source [20,24]. Blaxter and Hempel [20] were the first to define the term of point-of-no-return (PNR) for herring as being 50% of larvae losing their ability of normal feeding after a period of food deprivation. This definition is also termed as “irreversible starvation” in larval fish biology [20]. During the onset of exogenous feeding, fish mortality is likely to occur if the provision of first feeding is beyond the PNR [20]. For this reason, it is necessary to examine the PNR at various temperatures for a newly introduced fish species in aquaculture.

Jaw malformation is another factor not only causing low fish survival but also reducing the market value of marine fish species [26,27]. Jaw malformations have been reported to be associated with poor nutrition [27-31] and environmental factors [27,32-34]. Lein et al. [10] suggested that temperature

can be a primary rearing condition influencing jaw development because organ development and differentiation in fish are temperature-dependent. At low temperature, significant deformities of gill-cover and skeleton in gilt-head sea bream Sparus aurata [35] and cranial deformities in European sea bass, Dicentrarchus labrax [36] have been reported.

The yellowtail amberjack (Seriola lalandi dorsalis) belongs to the Carangidae family and is widely distributed throughout warm–temperate waters of the northern hemisphere. It has been introduced as a new species for aquaculture due to its fast growth, high flesh quality and suitability for cage culture for 20s. However, low survival and unreliable fingerling quality have greatly hindered the fingerling production of yellowtail amberjack in China. Up to present, the impact of temperature on survival and growth of yellowtail amberjack in the early stage is not known for this species. It is unclear if temperature could affect deformity in yellowtail amberjack, though jaw malformation has been a serious problem in the larval rearing of yellowtail kingfish [27,36], a Seriola lalandi subspecies distributing in the Southern Hemisphere waters. It is therefore necessary to examine the relationship between temperature and jaw deformity during the early stage of larval fish rearing. The objective of this study was to understand the impact of temperatures on the ontogenetic development of yellowtail amberjack. Specifically, we examined survival, growth and development of fish larvae at different temperatures. We further quantified the time required for fish larvae to reach the point of no return after yolk absorption and jaw malformation at different temperatures. The results of this study would provide insights into the understanding of role of temperature in regulating fish survival and the development of management strategies to improve production efficiency in finfish hatcheries.

Materials and Methods

Ethical approval

In this study, the handle of fish was carried out in strict accordance with the recommendation in the Animal Welfare of Chinese Academy of Fishery Sciences Animal Welfare Committee. The protocol, species and number of animals used in this study were approved by the South China Sea Fisheries Research Institute Animal Welfare Committee (Approved Number: A201601A01).

Experimental design and larval fish rearing

Fertilized eggs were obtained from a local hatchery in Lingshui Town, Hainan Province, China and transported to the Tropical Aquaculture Research and Development Centre, South China Sea Fisheries Research Institute, Chinese Academy of Fishery Sciences. Upon arrival, all larvae hatched in 500 L fibreglass incubators at 23.5˚C. The experimental design included three temperatures 21, 23 and 25˚C with three replicates. A total of nine tanks were used in the temperature experiment. After hatching, the larvae were stocked into the 500 L fibreglass rearing tanks at a density of 60 larvae/L per tank. All rearing tanks were supplied with filtered seawater with a 6 µm filter in a flow-through system at a daily water exchange rate of 300% tank volume. Two air stones were used in each tank to maintain dissolved oxygen at saturation and to homogenize the distribution of microalgae, rotifers and Artemia nauplii. Light intensity at 2400 lx and a photoperiod of 14 h light and 10 h dark was used. Salinity was maintained at 36‰ throughout the experiment.

Rotifers (Brachionus plicatilis) were fed to the 3 days post hatching (DPH) larvae until 13 DPH at 10 rotifers/ml. The rotifers fed with microalgae (Nannocholoropsis sp.) were enriched with DHA Selco (INVE Aquaculture) for 12 h before adding into fish rearing tanks. Instant microalgae (Nannocholoropsis sp.) were also added into the larval rearing tanks as food for rotifers, and to create a green background for fish larvae. Artemia nauplii were enriched with DHA Selco (INVE Aquaculture) before they were introduced into the larval rearing tanks from 9 to 24 DPH at 5 Artemia/mL.

Fish sampling, growth and dry weight measurements

Upon egg arrival, 50 eggs were randomly collected in triplicate from the incubating tanks to measure the egg diameters. The average egg diameter was 1.40 ± 0.03 mm (n=50). Fish larvae were daily collected in triplicate from the rearing tanks from hatching to 6 DPH. Subsequently, the specimens were collected on 8, 11, 15, 19 and 24 DPH. Standard length, feeding incidence, and yolk sac size were measured on 10 fish per tank under a dissecting microscope on each sampling day. Ten fish from each tank were used to determine dry weight, and the larvae were first washed with distilled water before body weight analysis. Fish were dried in an oven at 60 ˚C for 48 h to obtain dry weight.

Mortality rates were recorded daily by counting dead fish on the bottom of each tank. Growth was determined by the absolute growth rate (AGR) in mm/day and by the specific growth rate (SGR) as %/day using the following equations [37].

$$AGR=(SLf–SLi)/\Delta t,$$

$$SGR=100\ (LnSLf–LnSLi)/\Delta t,$$

Where SLf and SLi were the final and initial fish standard length (mm), respectively, and Δt was the time between sampling intervals. The volume of yolk sac (YSV, mm^3) was calculated using the formula for an ellipsoidal volume: $YSV=\pi/6 \times L \times H2$, where L was the major axis and H the minor axis of the yolk sac [20]. The feeding incidences were calculated by the following formula:

$$Feeding\ incidence=100 \times N1/N0,$$

Where N0 is the number of fish larvae, and N1 is the number of larvae with food in the gut [10].

Point of no return (PNR)

At each temperature, a total of 30,000 fish larvae were deprived of food and kept in a 500 L tank. All other rearing conditions were the same as those in the feeding experiment. Starting from 6 h after yolk sac exhaustion, 20 starved larvae

were daily taken from the unfed tank and transferred into a 4 L beaker in triplicate to test the time required to reach the PNR. Larvae were provided with rotifers stained with neutral red (10 µL/mL) for 30 min at a density of 20 rotifers/ml. The fish gut was examined under a microscope after fish were feeding for 2 h. The percentage of feeding larvae that had been deprived of food for a given number of days was calculated in respect to the total number of larvae tested. The PNR was defined as a threshold time when 50% of the larvae were still alive but was unable to eat, despite food availability [20].

Jaw deformity analysis

At the end of the temperature trial, 50 larvae were randomly selected from each tank to examine jaw deformity. The jaw malformation was scored using the method by Battaglene and Cobcroft [32]. In brief, the "0" score stands for normal jaw; "0.5" for very minor malformation; "1" stands for minor malformation; "2" for moderate malformation; and "3" for severe malformation.

Statistical analysis

All data were expressed as mean ± SD, and tested using one-way ANOVA (PASW Statistics 18.0). When a significant treatment effect was found, Tukey's test was performed for multiple range comparisons (P<0.05). The relationship between standard length (SL) and dry weight (DW) were calculated by the power regression DW=a × SLb (PASW Statistics 18.0). Values of the exponent b provide information on fish growth. When b=3, the increase in weight was isometric. When the value of b was >3, the weight increase was allometric (positive if b>3, negative if b<3) [38].

Results

Fish survival, growth, feeding and yolk depletion

Fish survival was significantly affected by temperature (P<0.05, **Figure 1A**). The final survival of fish larvae decreased with the increasing of temperature **(Figure 1)** and the decreasing of survival followed a linear regression of y= –7.9428x + 29.719 (r2=0.9989, **Figure 1A**). At the end of this experiment, the highest survival was observed in fish reared at 21˚C and lowest survival was observed at 25˚C (P<0.05). Temperature significantly affected the growth of yellowtail amberjack larvae (P<0.05, **Figure 1B-1D**). Fish length increased from 4.18 ± 0.06 mm at hatching (0 DPH) to 8.3 ± 0.5 mm at 21˚C, 9.8 ± 0.4 mm at 23˚C, and 13.8 ± 1.9 mm at 25˚C by 24 DPH, respectively. But before 11 DPH, no differences were observed between temperature treatments (P>0.05, **Figure 1B**). On 15 DPH, the standard length of fish at 25˚C was significantly higher than at other temperatures (P<0.05). On 24 DPH, fish at 25˚C were still bigger than those at 21˚C and 23˚C (P<0.05) and fish at 23˚C were larger than those cultured at 21˚C environment (P<0.05). The absolute and specific growth rates of yellowtail amberjack were significantly affected by rearing temperature (P<0.05). Within the rearing temperature of 21-25˚C, the increment of temperature increased both absolute and specific growth rates of fish larvae **(Figure 1C and 1D)**. Larvae in the 25˚C treatment exhibited the highest absolute (0.38 ± 0.07 mm/day) and specific growth rate (4.8 ± 0.60%/day). Furthermore, the absolute and specific growth rates of larvae at 25˚C were almost two folds greater than the larvae at 21˚C.

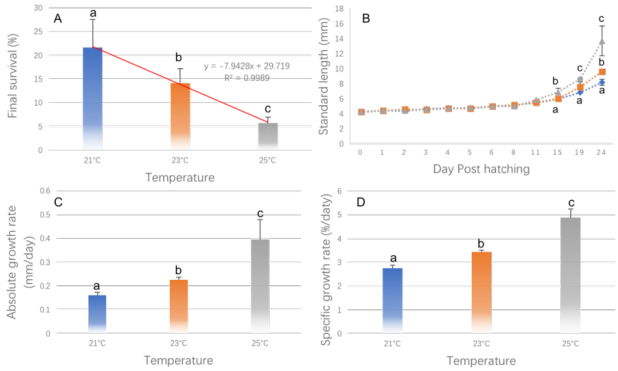

Figure 1 Final survival (A), standard length (B), absolute growth rate (C), and specific growth rate (D) of yellowtail amberjack larvae cultured at 21˚C (■), 23˚C (■) and 25˚C (■). Mean ± SD (n=3) with different superscript letter is significantly different in multiple comparisons (P<0.05).

In this study, the standard length (x) and dry weight (y) relationships of yellowtail amberjack larvae were quantified by the regression equation of y=a × xb. The length-weight relationships of fish culture at 21, 23 and 25 ˚C can be expressed at y21=6E-05 × 4.78 (r2=0.96), y23=4E-05 × 5.02 (r2=0.95) and y25=6E-05 × 4.79 (r2=0.98), respectively **(Figure 2)**. The b values were 4.78–5.02, where a ranged from 4.0 × 10^{-5} to 6.0 × 10^{-5}. The maximum b was observed at 23˚C.

The volume of yolk sac in yellowtail amberjack larvae was 0.49 ± 0.09 mm^3 at 8 h after hatch and decreased to 0.009 ± 0.00 mm3 at 80 h after hatch. Yolk-sac depletion was not significantly affected by the rearing temperatures (P>0.05, **Figure 3A**) and a rapid depletion was found between 8 h and 18 h. Feeding incidences of fish larvae were significantly affected by the rearing temperature from 2 DPH to 5 DPH (P>0.05, **Figure 3B**). The feeding incidence of fish larvae in 21˚C group was significantly lower than those observed in 23 and 25˚C (P<0.05) between 3 DPH and 5 DPH. Starting from 6 DPH, the feeding incidences of fish larvae were not significantly affected by the rearing temperature (P>0.05).

The time for fish larvae to reach the PNR depended on the rearing temperatures **(Figure 3D)**. The PNR at 25, 23 and 21˚C occurred on 5, 6 and 8 DPH, respectively. The average of feeding incidences at 21, 23 and 25˚C was 4.46 ± 1.88% in starved fish and no significant differences were found between these treatments (P>0.05). On 5 DPH, feeding incidence in fish at 25˚C was significantly higher than that at 21˚C (P<0.05). The peaks of feeding incidence at 21 and 23˚C occurred on 6 and 5 DPH, respectively.

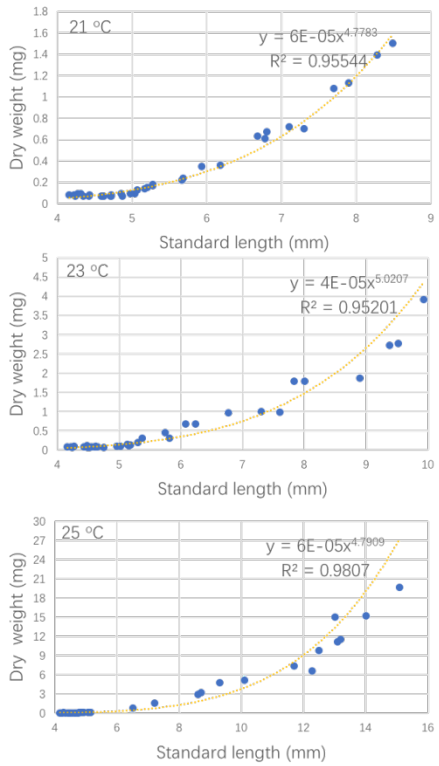

Figure 2 The relationship between standard length and dry weight of yellowtail amberjack larvae cultured at 21, 23 and 25˚C (n=36). A total of 1080 fish larvae were measured in this study.

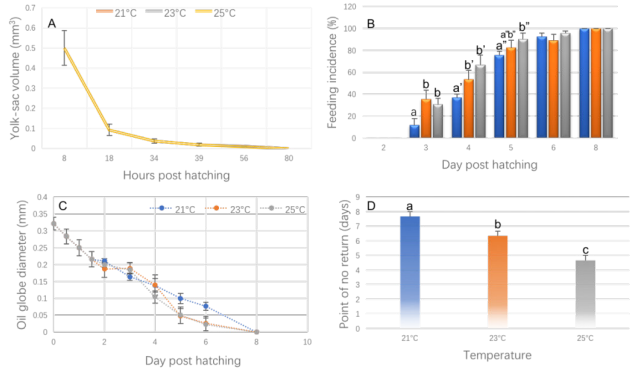

Figure 3 Yolk-sac volume (A), feeding incidence (B), oil globe diameter (C) and point of no return (C) of yellowtail amberjack larvae cultured at 21˚C (■), 23˚C (■) and 25˚C (■). Mean ± SD (n=3) with different superscript letter is significantly different in multiple comparisons (P<0.05).

Jaw deformities

Temperature significantly affected the jaw malformation of yellowtail amberjack larvae **(Figure 4)**. In this study, category 0.5 jaw malformations were 15.06%, 50.33% and 33.31% in 21, 23 and 25˚C, respectively **(Figure 4)**. In 25˚C group, significantly higher category 1, 2 and 3 malformations were observed. In calculating the final malformation percentage, we excluded category 0.5, as most of malformations in this category was minor which cannot significantly affect fish feeding. Jaw malformation of fish larvae increased with the increasing of rearing temperature. By the end of this experiment, the highest jaw malformation was observed in 25˚C group, and the lowest jaw malformation was recorded in the 21˚C rearing group (P<0.05).

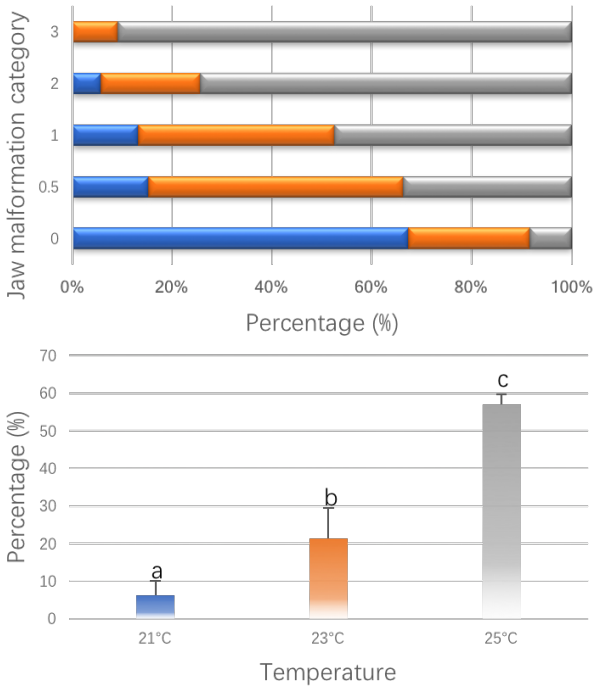

Figure 4 Jaw malformation category and jaw malformation rate of yellowtail amberjack larvae cultured at 21˚C (■), 23˚C (■) and 25˚C (■). Mean ± SD (n=3) with different superscript letter is significantly different in multiple comparisons (P<0.05). A total of 450 fish larvae were examined for jaw malformations.

Discussion

Previous studies suggest that the temperature range of 17-24˚C suits larvae of most temperate fish species [39-41]. Moran [42] reported that 18-24˚C should be suitable for egg incubation and the first feeding yellowtail kingfish larvae. This present study scrutinised the influence of temperature on ontogeny of yellowtail amberjack during early life. Water temperature significantly affected growth, survival and jaw deformities of yellowtail amberjack larvae. Importantly, rearing temperature not only affected the time of yolk sac depletion, but also changed the window for the period when the initial feeding should start for the first feeding larvae.

Increasingly more evidence indicates that high fish mortality is associated with food availability when fish start first feeding [43-48]. Previous studies indicate that PNR is closely related to

temperature, as low temperature extends the time for larvae to reach the PNR and high temperature shows the opposite [18,20,49]. In the present study, a similar trend was observed where high temperature shortened the time for PNR. Dou et al. [18] suggested that the insufficient time for the first feeding larvae to learn to take food before the onset of irreversible starvation (PNR) might be the potential cause for the mortality. Since higher temperature reduced the time for PNR, larvae of yellowtail amberjack have less time to find their feeding capability. This may explain why massive mortality rates occur earlier under higher temperature in the present study.

The effects of temperature on fish growth, food intake and metabolic activity are usually concurrent [50]. In the present study, the growth of newly hatched amberjack was not temperature dependent in their first 12 days of life. However, fish growth was visibly affected by temperatures after 15 DPH, and growth was accelerated when temperature elevated from 21 to 25˚C. Previous studies have demonstrated that higher temperature can lead to increasing of metabolism, feeding and food assimilation in fish larvae such as Australian snapper Pagrus auratus [8], striped trumpeter Latris lineata [51], brown sole Pseudopleuronectes herzensteini [15], Atlantic halibut Hippoglossus hippoglossus [10] and yellowtail kingfish Serilola lalandi lalandi [41]. In yellowtail amberjack, the positive relationship between temperature and growth may be attributed to the improved digestive function of larvae after 15 DPH as Chen et al. [52] reported that the goblet cells and gastric glands present in the gut of yellowtail kingfish larvae after 15 DPH. However, this need further verify in this species.

The impact of temperature on fish growth could be detected from the length – weight regression equation that is to evaluate the impact of environmental variables on growth [53]. In the regression equation of length-weight relationship, the exponent b is a measure of relative logarithmic growth rates between length and weight, and the b value represents the increments of weight over length in the same period [54]. The range of b values for marine fish larvae in previous studies was 2.7 to 4.5 [53,55]. In the present result, the b value was 4.78 at 21˚C, 5.02 at 23˚C and 4.79 at 25˚C, suggesting that weight gain of larvae at 21, 23 and 25˚C is faster than other fish species.

The size of the yolk sac volume decreases as fish grow [10]. In the present study, yolk depletion was rapid from 8 to 18 h and the time of yolk sac exhaustion was 56-80 h after hatching. Despite temperature differences, the rate of yolk decline in yellowtail amberjack was not different between treatments. These results were similar to our previous studies on Seriola lalandi lalandi (unpublished data). Similarly, the rate of yolk utilization haddock was not temperature dependent in the temperature range tested [56].

Ambient water temperature can be a significant factor influencing the success of initial feeding in fish larvae [57]. Brett [5] suggested that the amount of food intake is concomitant with the temperature increase and peaks before reaching the supra-optimal temperature. In the present study, the feeding incidence was significantly affected by temperature in the first five days after hatching. A higher feeding incidence was observed in 23˚C and 25˚C group suggesting these two temperatures may stimulate the feeding of fish larvae in their early life.

Temperature is a key factor determining the tolerance of food deprivation in fish larvae since it directly affects fish metabolism, yolk absorption, feeding activity and food conversion efficiency [24,25,41]. Evidence indicates that mortality was strongly temperature-dependent in the larvae and juveniles of the Asian catfish, Pangasianodon hypophthalmus [58]. Similarly, high temperature caused poor digestion and high mortality in Japanese flounder larvae Paralichthys olivaceus [18]. In the present study, temperature increment lead to low fish survival especially in the first 10 days after hatching, though mortality was relative stable after 10 DPH. Similar mortality patterns were also found in striped trumpeter Latris lineata as its massive mortality occurred during the initial feeding period [59].

Jaw malformation is a major concern in fish culture because it affects fingerling quality for further growout [36,60,61]. Extreme temperatures and salinities can contribute to jaw malformation [62-64]. In the present study, the rate of jaw malformation in fish larvae increased with temperature rise. This result supports the early finding that jaw malformations are associated with environmental temperature [10,65] and increasing of rearing temperature could lead to high deformity in fish larvae [64]. It has been suggested that temperature can indirectly affect larval ontogeny by alteration of nutritional requirement of fish at different temperatures [66]. The increased fish metabolism at high temperature will lead to a high demand of energy and nutrition supply [67] and interrupt the balance between nutrient requirement and food intake leading to larval malnutrition [29,68,69]. These could explain the appearance of high jaw deformity rate at higher rearing temperature, though the mechanism warrants further exploration.

Conclusion

The present study demonstrated that temperature affected ontogenetic development of yellowtail amberjack larvae. At 25˚C fish larvae had lower survival but higher growth rate, suggesting that this temperature is not suitable for early larval rearing. The optimum temperature for amberjack larvae should be 21-23˚C since fish showed higher survival and low jaw deformity at this range. Consequently, we recommend that it is potential to use lower temperature in fish early development stage and a comparatively higher temperature in a later stage to achieve better production yield. The timing of temperature changes, however, requires further investigation.

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