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The effects of temperature and dissolved oxygen on the growth, survival and oxidative capacity of newly hatched hybrid yellow catfish larvae (*Tachysurus fulvidraco*♀ × *Pseudobagrus vachellii*♂)

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ABSTRACT

Demand for yellow catfish fry, an economically important farmed fish in China, has increased dramatically. Newly hatched larvae are highly sensitive to changes in environmental conditions, with water temperature (*T*) and dissolved oxygen (*DO*) being two important factors that affect their early development. We investigate optimal *T* (between 19.0 and 33.0 °C) and *DO* (between 2.0 and 12.0 mg L^{-1}) concentrations on growth and antioxidant enzyme activity of newly hatched hybrid yellow catfish larvae (*Tachysurus fulvidraco* × *Pseudobagrus vachellii*) using a central composite design. We use a response surface method to optimize the response variables for survival (S) and growth, and the reduction of oxidative stress, over a 50-day experimental duration. *T* has a significant effect on specific growth rate (SGR), hepatic malondialdehyde (MDA) content, and superoxide dismutase (SOD) and catalase (CAT) activities ($P < 0.05$). *DO* concentration has a significant effect on SGR, S, hepatic MDA content, and SOD and CAT activities ($P < 0.05$). *T* and *DO* also have significant second order effects on SGR, S, SOD, and CAT activities ($P < 0.05$). Increased *DO* at low *T* stimulates SOD and CAT activities and alleviates oxidative damage. Adjusted R^2 values for SGR, S, CAT, SOD, and MDA models are 0.734, 0.937, 0.916, 0.894 and 0.826, respectively. A combination of 26.8 °C and 7.3 mg L^{-1} represents optimal rearing conditions, in that larval growth and antioxidant ability is improved. Results show that *T* and *DO* during larviculture of yellow catfish have important implications for aquaculture.

1. Introduction

Fish are among the most primitive and large vertebrates living in water. Except a few large, deep-sea species, most are unable to produce or maintain stable endogenous heat. As their gill and body surfaces constantly exchange heat with their ambient environment, they are also unable to maintain a constant body temperature different from that of their environment (Fu et al., 2018; Junior et al., 2019). When temperature changes, fish can reduce stress by heat-regulating behaviors such as tolerance, resistance or preference (Pederzoli and Mola, 2016).

Water temperature (*T*) is an important factor affecting the early development of fish (Rombough, 1997), within certain ranges of which they can adapt. While an increase in *T* (within a specified range) can accelerate fish embryo development (Qiang et al., 2019), shorten incubation time, and promote the first-feeding of newly hatched larvae, beyond that range (when too high or low), malformation, and stagnation of development or even embryonic death, can occur (Jonsson and Jonsson, 2014; Imsland et al., 2019). *T* also greatly impacts the normal development of fish eggs and larvae (Bian, 2016). During early development, low *T* reduced the hatching rate of lumpfish (*Cyclopterus lumpus*), the survival of hatched larvae, and resulted in an increased rate of deformities (Imsland et al., 2019). At *T* exceeding 32.0 °C or lower than

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22.0 °C, the growth and survival of genetically improved farmed tilapia (GIFT, *Oreochromis niloticus*) larvae was significantly reduced compared with fish reared at 27.5 °C (Qiang et al., 2011). High *T* also influence oxygen dissolution rates in water (Madaro et al., 2018), the population structure and quantity of plankton (Shin et al., 2019), and the rate of propagation of pathogenic microorganisms (Du et al., 2008), all of which indirectly affect fish survival.

Most oviparous fish undergo a transition from endogenous to exogenous nutrition during larval development. Newly hatched larvae rely on the yolk sac to provide nutrients and reduce oxygen consumption (Wang et al., 2010). As the feeding organs develop and the yolk sac is absorbed, fish start to depend on exogenous nutrition. During this developmental stage fish need to be exposed to suitable *T* and have a sufficient supply of oxygen. Adverse environmental conditions such as unfavorable *T* and hypoxia may lead to an increase in reactive oxygen species (ROS) in newly hatched larvae, resulting in the gradual consumption of antioxidant enzymes. Without sufficient antioxidant enzymes, the active oxygen in cells cannot be removed and ROS production increases. Peroxidation of lipids, proteins and DNA, often leads to oxidative damage and death in newly hatched larvae (Klein et al., 2017).

Under normal conditions, ROS are degraded by the antioxidant system to maintain the health of the body. This antioxidant system includes the enzymes superoxide dismutase (SOD) and catalase (CAT). Klein et al. (2017) found that when the Antarctic fish *Notothenia coriiceps* was exposed to water at 4 °C for 6 days, SOD activity in the liver and brain tissue decreased, and lipid peroxidation increased. This increase in oxidative damage to the tissues was the result of thermal stress. Lushchak and Bagnyukova (2006) found that elevated *T* helped to stimulate the antioxidant response of goldfish (*Carassius auratus*). Within a short period of time SOD and CAT activities increased, and after 4 h enzyme activity decreased once the fish were exposed to normal temperatures. The SOD and CAT activities of Nile tilapia increased with increasing *T* (20–32 °C) (Abdel-Tawwab and Wafeek, 2017). However, when the ambient *T* exceeded the suitable *T* range (25–32 °C) for olive flounder *Paralichthys olivaceus*, the specific growth rate, survival and antioxidant enzyme activity, decreased (Xu et al., 2010).

Dissolved oxygen (*DO*) in water mainly comes from oxygen dissolved from the air and that produced by algal photosynthesis. In aquatic environments, the *DO* content of water bodies may be influenced by physical, chemical or biological factors, which often vary seasonally or diurnally. This may have an important impact on fish growth and survival (Pollock et al., 2007). Fish growth requires extremely high energy consumption. Studies of various species have reported significant positive linear correlations between oxygen consumption in fish and growth rate (Carter and Brafield, 1992; Xie and Sun, 1992). When there is sufficient *DO* in the environment, fish can expend more energy on growth. Metabolism rates of fish increase dramatically in aquatic environments supersaturated with *DO*, or in hypoxic conditions. In these conditions fish may produce excessive reactive oxygen free radicals, causing damage to cells and tissues, and changing the balance of the oxidant-antioxidant system, thereby affecting fish behavior and growth (Filho et al., 2005). Accordingly, the study of growth, survival and antioxidant capacity of fish under different *T* and *DO* conditions, is of pure and applied scientific value.

Yellow catfish are an economically important freshwater fish, the demand for which in China has increased rapidly in recent years. This species occurs mainly in China's rivers and lakes, especially in the middle and lower reaches of the Yangtze River. Described as delicious and nutritious, with tender flesh and no intermuscular thorns, their reputation as nourishing and medicinally valuable has contributed to their increased domestic and international demand. With the continuous expansion of artificial breeding of yellow catfish, the demand for fry production has also risen.

Our research team began breeding hybrid yellow catfish (*Tachysurus fulvidraco* ♀ × *Pseudobagrus vachellii* ♂) in 2014, since which time we have made steady progress solving difficulties associated with their artificial breeding. We previously reported a *T* of 26.0 °C and *DO* of 8.3 mg L^{-1} led to the best fertilization and hatching, and lowest deformity rates (Qiang et al., 2019). Herein we focus on identifying the optimum *T* and *DO* requirements of newly hatched larvae, and the effect of these factors on antioxidant capacity. This information will help improve the growth and survival of newly hatched larvae and reduce oxidative stress.

2. Materials and methods

2.1. Experimental fish

Newly hatched hybrid yellow catfish larvae were used to investigate the effects of *T* and *DO* on growth and antioxidant enzyme activities. Healthy, 3 year-old *Pseudobagrus vachellii* ♂ (*P. vachellii*, about 270 g) and *Tachysurus fulvidraco* ♀ (*T. fulvidraco*, about 120 g), both wild strains from Pearl River, were selected as parents. About 6000 eggs were placed in a culture dish, to which 0.4 mL of semen was added, followed by 20 mL of water, then gentle stirring for 2 min to stimulate fertilization. After mixing, the artificially inseminated eggs were de-bonded using an 8% concentration of yellow mud suspended in water, for 5 min (Qiang et al., 2019). Fertilized eggs were held in an incubator at water temperature 26.5 °C ± 0.3 and *DO* 8.0 mg L^{-1} ± 0.5 until hatching. Newly hatched larvae (body weight: 0.002 g ± 0.001; body length: 0.51 cm ± 0.01) were collected for experimentation after 75 h, by which stage the larvae had exhausted their yolk-sac as a source of nutrition. Experimental fish were placed in a holding tank and acclimated to initial feeding for 4 d.

2.2. Experimental design

The experiment used a two-factor central composite design (CCD), with *T* (19–33 °C) and *DO* (2.0–12.0 mg L^{-1}) as experimental factors. *DO* was controlled by adjusting the rate of nitrogen or oxygen charged into the water. *T* was controlled using an electronic constant temperature rod (range: 18–36 °C, ± 0.3 °C). Real-time readings were made using a *DO* meter (Hach LDO101, Loveland, USA, measuring range 0.1–20.0 mg L^{-1}). Each experimental factor had five coding levels: −a, −1, 0, 1, a (Table 1); the central combination was repeated five times to estimate the pure error. Thus, there were a total of 13 experimental combinations (4 axial, 4 factorial, and 5 central). All runs were arranged in random order to eliminate systematic error. The experimental data were framed as means of three replicates for each axial and factorial point. Response variables were specific growth rate (SGR), survival (S), liver malondialdehyde (MDA) content, and SOD and CAT activities. The specific coding levels and actual value combination are detailed in Table 1.

2.3. Rearing management

The experiment was conducted in 39 × 400 L plastic tanks, to which 300 L of tap water had been added and aerated for 3 days prior to experimentation. *T* acclimation was carried out gradually, ensuring that temperature rise and fall did not exceed 2 °C per day. *T* used in experimental treatments were 19.0 °C, 21.1 °C, 26.0 °C, 30.9 °C and 33.0 °C. The corresponding *DO* levels were normalized. Each tank had 100 newly hatched larvae of initial weight 0.01 g (±0.002 g) (3900 fish in total). There were no significant differences in body weight between the experimental groups (ANOVA, $P > 0.05$) at the start of the experiment. Fish were fed the equivalent of 15%–20% their body weight (crude protein 38.5%; crude fat 7.5%), and this amount was continuously adjusted once a week during the experiment. One third of the total volume of water in each tank was changed every 3 days. The *T* difference before and after changing water in experimental tanks did not exceed 0.5 °C. Tanks were held at the natural photoperiod. Concentrations of

Table 1
Experimental design of temperature (*T*)-dissolved oxygen (*DO*) combinations and response observations (Mean ± SD).

Run	Coded *T*	Coded *DO*	Actual *T* (°C)	Actual *DO* (mg L^{-1})	Specific growth rate (% d^{-1})	Survival (%)	Catalase [U (mg prot)$^{-1}$]	Superoxide dismutase [U (mg prot)$^{-1}$]	Malondialdehyde (mmol mg^{-1})
1	a	0	33.0	7.1	0.97 ± 0.11	68.0 ± 5.6	45.43 ± 3.21	2.75 ± 0.13	0.32 ± 0.02
2	0	0	26.0	7.1	1.24 ± 0.09	92.0 ± 4.7	75.33 ± 4.23	3.46 ± 0.34	0.25 ± 0.01
3	0	−a	26.0	2.2	0.79 ± 0.07	57.0 ± 3.6	89.59 ± 7.31	2.43 ± 0.17	0.36 ± 0.08
4	0	0	26.0	7.1	1.41 ± 0.10	86.0 ± 7.1	69.47 ± 8.33	3.54 ± 0.28	0.21 ± 0.05
5	−1	−1	21.1	3.6	0.56 ± 0.04	59.0 ± 4.5	93.72 ± 6.72	2.01 ± 0.14	0.38 ± 0.04
6	−a	0	19.0	7.1	0.43 ± 0.02	52.0 ± 6.2	71.28 ± 5.61	2.26 ± 0.29	0.42 ± 0.02
7	0	0	26.0	7.1	0.95 ± 0.08	85.0 ± 4.1	71.36 ± 5.82	3.27 ± 0.51	0.27 ± 0.03
8	0	a	26.0	12.0	0.74 ± 0.06	22.0 ± 1.6	81.22 ± 9.14	3.34 ± 0.46	0.19 ± 0.04
9	0	0	26.0	7.1	1.15 ± 0.11	93.0 ± 5.8	65.81 ± 7.03	3.56 ± 0.12	0.24 ± 0.02
10	1	1	30.9	10.6	1.27 ± 0.09	43.0 ± 7.1	62.34 ± 5.52	3.41 ± 0.19	0.27 ± 0.03
11	0	0	26.0	7.1	1.22 ± 0.12	86.0 ± 5.0	72.94 ± 4.18	3.29 ± 0.31	0.22 ± 0.02
12	−1	1	21.1	10.6	0.51 ± 0.04	51.0 ± 6.2	65.11 ± 6.19	2.75 ± 0.42	0.31 ± 0.04
13	1	−1	30.9	3.6	1.13 ± 0.14	79.0 ± 9.3	62.62 ± 4.03	2.97 ± 0.22	0.28 ± 0.03

Note: a = star arm, and |a| = 1.41421 for this experimental design.

NO_2^- (<0.01 mg L^{-1}), NO_3^- (<1.5 mg L^{-1}), and total ammonia nitrogen (0.05 mg L^{-1}) were maintained during experimentation.

2.4. Determination of response variables

Fish were held in experimental tanks for 50 days, at the end of which time they were fasted for 24 h prior to sampling. The body weight of 15 randomly selected fish from each experimental group was measured. SGR was measured using the equation, SGR (% d^{-1}) = [($\ln W_2 - \ln W_1$)/($t_2 - t_1$)] × 100, where W_1 and W_2 represent fish body weight (g) at the start (t_1) and end (t_2) of experimentation, respectively. Percentage S was measured by: S (%) = (number of fish harvested/number of fish stocked) × 100.

Five fish were randomly sampled from each tank for analysis of antioxidant indices. About 0.05 g of liver tissue was removed from each fish and immediately frozen in liquid nitrogen, then stored at −70 °C until analysis. Prior to analysis the liver sample was thawed and rinsed with pre-cooled physiological saline, then blot dried on filter paper, then weighed. Samples were homogenized with 4 times the volume (W/V) of pre-cooled physiological saline, and the crude enzyme solution was stored at 4 °C. Antioxidant measurements were completed within 24 h. The protein was subjected to the Folin-phenol reagent method (Lowry et al., 1951). The thiobarbituric acid (TBA) method was used to determine the change of MDA content in liver tissue, to evaluate the degree of lipid peroxidation. Thiobarbituric acid was condensed with the product MDA in lipid peroxidation to form a red product, which was colorimetrically measured at 532 nm. The activity of SOD was determined using the xanthine oxidase method. Activity was defined as the SOD activity unit (U) corresponding to a 50% inhibition of SOD per milligram of tissue protein in 1 mL of reaction solution. CAT activity was determined by colorimetric method. One unit of CAT activity was defined as the amount of decomposing 1 μmol H_2O_2 per mg protein per second, expressed as U (mg protein)$^{-1}$. Reaction results were measured using a BioTek Eon™ microplate spectrophotometer (BioTek, USA). The kits for experiment were purchased from Nanjing Jiancheng Biotechnology Co., Ltd. (Nanjing, China).

2.5. Data processing and model building

Experimental data were expressed as means ± standard deviations (SD), and processed using Statistica 8.0 software. The quadratic polynomial regression model of the response regarding the factors was as follows:

$$\hat{Y} = b_0 + b_1 T + b_2 DO + b_3 T \times DO + b_4 T^2 + b_5 DO^2$$

where $\hat{Y}$ is the prediction of responses (SGR, S, MDA, SOD, and CAT); b_0 is constant, b_1, b_2, b_3, b_4, and b_5 are regression coefficients. Results were considered significant at $P < 0.05$, and highly significant at $P < 0.01$. Parameters in the regression equation were estimated by the least squares method.

3. Results

3.1. Effects of T and DO on SGR of hybrid yellow catfish

Effects of *T* and *DO* on SGR of newly hatched hybrid yellow catfish larvae are shown in Table 1. Regression fitting was performed on the data using the least squares method. The model $P = 0.0094$ (Table 2) indicated that the regression model was highly significant, and the lack of fit term $P = 0.4934$, indicated that the fitted model was valid. The primary effect of *T* and second order effects of *T* and *DO* had a significant effect on SGR ($P < 0.05$). *DO* had no significant effect on SGR, and *T* and *DO* had no interaction effect on SGR ($P > 0.05$). The quadratic regression equation was:

$$\text{SGR} = -6.317 + 0.486T + 0.142DO + 0.003T \times DO - 0.009T^2 - 0.015DO^2$$
(adjusted $R^2 = 0.734$)

The response surface plot for *T*, *DO* and SGR is shown in Fig. 1. Using this set of dynamic maps, the interaction of experimental factors on the growth of newly hatched larvae was evaluated. Under experimental conditions, as *T* and *DO* increased, SGR increased initially and then decreased. When *T* was 29.1 °C and *DO* was 7.4 mg L^{-1}, the SGR of newly hatched larvae was 1.28% d^{-1}. When the *DO* was 7.0 mg L^{-1}, the low *T* environment (19.0 °C) had a more obvious inhibitory effect on the growth of the newly hatched larvae than a high *T* environment (33.0 °C) ($P < 0.05$).

3.2. Effects of T and DO on S of hybrid yellow catfish

The effects of *T* and *DO* on S of newly hatched yellow catfish are detailed in Table 1. The model $P < 0.01$ indicated that the regression model was highly significant (Table 3), and the lack of fit term $P = 0.1219$ indicated that the fitted model was valid. The second order

Table 2
Analysis of regression coefficients of coded model terms for specific growth rate.

Factor	Coefficient Estimate	Standard Error	95% CI Low	95% CI High	*P*-value
Intercept	1.194	0.074	1.019	1.369	
T	0.262	0.058	0.124	0.400	0.0028
DO	0.002	0.058	−0.136	0.140	0.9682
T × *DO*	0.048	0.083	−0.148	0.243	0.5829
T^2	−0.213	0.063	−0.361	−0.065	0.0113
DO^2	−0.181	0.063	−0.329	−0.033	0.0234
Model					0.0094

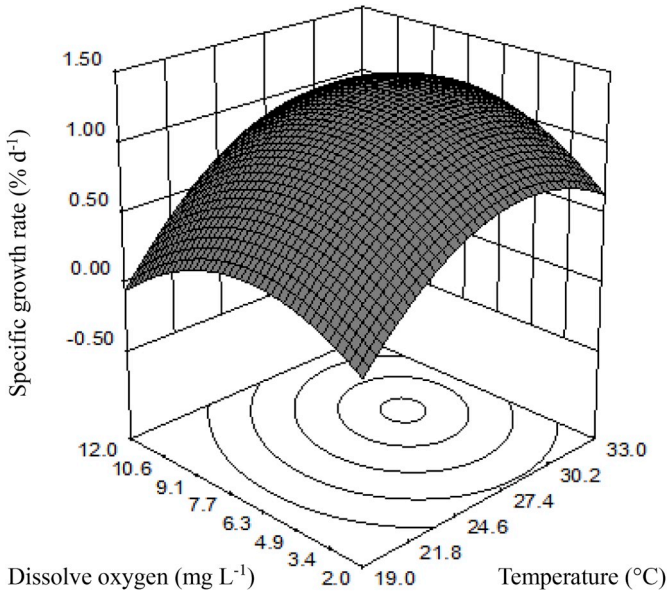

Fig. 1. Response surface plot for the effects of temperature and dissolved oxygen on the specific growth rate of newly hatched hybrid yellow catfish (*Tachysurus fulvidraco* ♀ × *Pseudobagrus vachellii* ♂) larvae.

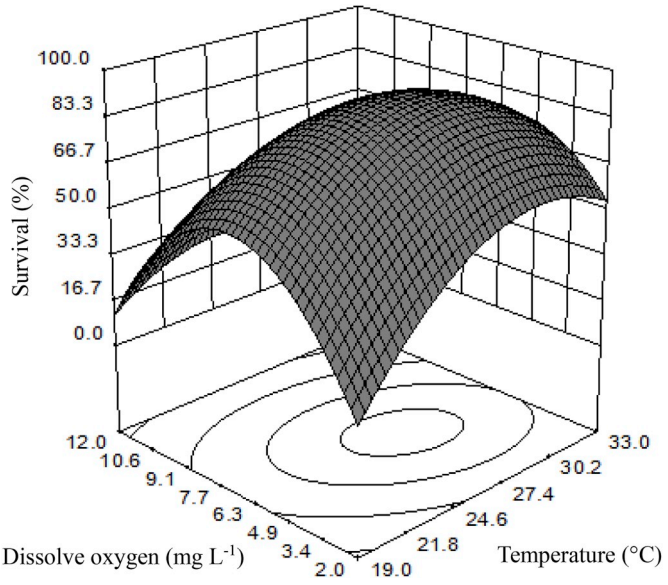

Fig. 2. Response surface plot for the effects of temperature and dissolved oxygen on the survival of newly hatched hybrid yellow catfish (*Tachysurus fulvidraco* ♀ × *Pseudobagrus vachellii* ♂) larvae.

effects of *T* and the primary and secondary effects of *DO* had a significant effect on S ($P < 0.01$). The primary effect of *T* had no significant effect on S ($P > 0.05$), but the interaction between *T* and *DO* had a significant effect on S ($P < 0.05$). The quadratic regression equation describing *T*, *DO*, and S was:

$$S = -415.698 + 29.593T + 34.028DO - 0.414T \times DO - 0.496T^2 - 1.875DO^2 \text{ (adjusted } R^2 = 0.937)$$

The response surface plot of *T*, *DO*, and S is shown in Fig. 2. Under the experimental conditions, when *T* and *DO* increased, S increased initially and then decreased. When *T* was 27.3 °C and *DO* was 6.1 mg L^{-1}, S was high, reaching 91.2%, with a reliability of 0.965. When *T* was 33 °C and *DO* was 12 mg L^{-1}, the S of newly hatched larvae was less than 15%. When *T* was 33 °C and *DO* levels were high (>10.0 mg L^{-1}), the S of newly hatched larvae was significantly lower compared with S at low *DO* levels (<3.0 mg L^{-1}). Results indicate a combination of high *T* and high *DO* are not conducive to S of newly hatched larvae.

3.3. Effects of T and DO on hepatic CAT activity in hybrid yellow catfish

Levels of hepatic CAT in newly hatched hybrid yellow catfish (Table 1) were subjected to regression fitting using the least squares method. The regression model was highly significant ($P = 0.0002$) (Table 4), with the lack of fit $P = 0.4785$, indicating that the fitted model was valid. The primary and second order effects of *T* and *DO* had a significant effect on CAT levels ($P < 0.01$), and the interaction between *T* and *DO* was also significant ($P < 0.01$). The quadratic regression model

Table 3
Analysis of regression coefficients of coded model terms for survival.

Factor	Coefficient Estimate	Standard Error	95% CILow	95% CI High	*P*-value
Intercept	88.940	2.453	83.140	94.740	
T	4.208	1.939	−0.378	8.793	0.0666
DO	−11.637	1.939	−16.223	−7.052	0.0005
$T \times DO$	−7.100	2.742	−13.585	−0.615	0.0360
T^2	−12.158	2.080	−17.075	−7.240	0.0006
DO^2	−22.508	2.080	−27.425	−17.590	<0.0001
Model					<0.0001

Table 4
Analysis of regression coefficients of coded model terms for catalase activity.

Factor	Coefficient Estimate	Standard Error	95% CI Low	95% CI High	*P*-value
Intercept	70.982	1.612	67.171	74.793	
T	−8.803	1.274	−11.816	−5.791	0.0002
DO	−5.091	1.274	−8.104	−2.078	0.0052
$T \times DO$	7.083	1.802	2.822	11.343	0.0057
T^2	−6.547	1.366	−9.778	−3.316	0.0020
DO^2	6.978	1.366	3.747	10.209	0.0014
Model					0.0002

for *T*, *DO*, and CAT was:

$$CAT = 52.561 + 9.184T - 20.461DO + 0.413T \times DO - 0.267T^2 + 0.7581DO^2 \text{ (adjusted } R^2 = 0.916)$$

The response surface plots for *T*, *DO*, and CAT are shown in Fig. 3. Under the experimental conditions, as *T* and *DO* increased, there was a corresponding increase in CAT activity at first, and then a decrease. When *DO* levels were low, high *T* had a more significant inhibitory effect on CAT activity compared with at low *T*. When the *T* was 26.0 °C, low *DO* and high *DO* levels helped stimulate CAT activity.

3.4. Effects of T and DO on hepatic SOD activity in hybrid yellow catfish

Levels of SOD activity in newly hatched hybrid yellow catfish are detailed in Table 1. The regression model was highly significant ($P = 0.0004$) (Table 5), with the lack of fit $P = 0.2276$ indicating that the fitted model was valid. The primary and second order effects of *T* and *DO* had a significant effect on SOD activity ($P < 0.01$), but the interaction between *T* and *DO* was not significant ($P > 0.05$). The quadratic regression model for *T*, *DO*, and SOD was:

$$SOD = -12.629 + 1.017T + 0.495DO - 0.004T \times DO - 0.018D^2 - 0.021DO^2 \text{ (adjusted } R^2 = 0.894)$$

Under the experimental conditions, when *DO* was 7.0 mg L^{-1} and *T* was 19.0–28.0 °C, hepatic SOD activity increased with the increase in *T*. When the *T* was higher than 28.0 °C, SOD activity decreased significantly (Fig. 4). When *T* was 26.0 °C, the activity of SOD at a *DO*

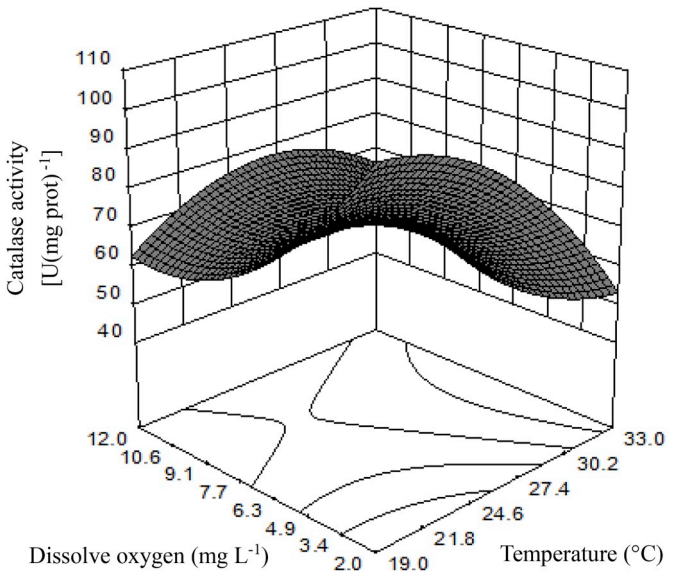

Fig. 3. Response surface plot for the effects of temperature and dissolved oxygen on the catalase activity of newly hatched hybrid yellow catfish (*Tachysurus fulvidraco* ♀ × *Pseudobagrus vachellii* ♂) larvae.

Table 5
Analysis of regression coefficients of coded model terms for superoxide dismutase activity.

Factor	Coefficient Estimate	Standard Error	95% CI Low	95% CI High	*P*-value
Intercept	3.424	0.076	3.245	3.603	
T	0.289	0.060	0.148	0.430	0.0019
DO	0.308	0.060	0.167	0.450	0.0013
$T \times DO$	−0.075	0.085	−0.275	0.125	0.4043
T^2	−0.437	0.064	−0.589	−0.285	0.0002
DO^2	−0.247	0.064	−0.399	−0.095	0.0063
Model					0.0004

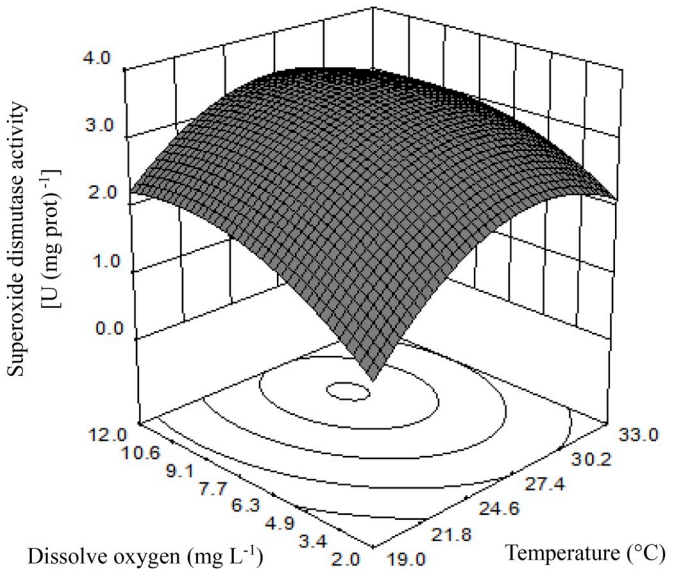

Fig. 4. Response surface plot for the effects of temperature and dissolved oxygen on the superoxide dismutase activity of newly hatched hybrid yellow catfish (*Tachysurus fulvidraco* ♀ × *Pseudobagrus vachellii* ♂) larvae.

8.5 mg L^{-1} was significantly higher than when *DO* was 2.0 mg L^{-1}. At a *T* of 26.4 °C and a *DO* of 10.6 mg L^{-1}, hepatic SOD activity was 3.55 U (mg protein)$^{-1}$, and the reliability was 0.996.

3.5. Effects of T and DO on hepatic MDA content in hybrid yellow catfish

The MDA content in livers of newly hatched hybrid yellow catfish, and the model fit and results of significance testing, are presented in Table 6. The regression model was significant ($P = 0.023$), with the lack of fit not being significant ($P = 0.2477$), indicating that the model was valid. The primary effect of *T* and *DO* and the second order effect of *T* had significant effects on MDA content ($P < 0.05$). The second order effect of *DO* and the interaction between *T* and *DO* had no significant effect on MDA content ($P > 0.05$). The quadratic regression model for *T*, *DO*, and MDA content was:

$$\text{MDA} = 2.466 - 0.147T - 0.052DO + 0.001T \times DO + 0.003T^2 + 0.001DO^2$$

(adjusted $R^2 = 0.826$)

Under experimental conditions, when *DO* was 7.0 mg L^{-1}, the hepatic MDA content of newly hatched larvae at both low (19 °C) and high (33 °C) *T* was significantly elevated compared with the level of hepatic MDA content at 26 °C (Fig. 5). At a temperature of 26 °C, the hepatic MDA content at high *DO* (12.0 mg L^{-1}) was low compared with hepatic MDA content at low *DO* (2 mg L^{-1}). As *DO* in water increased, the hepatic MDA content in hybrid yellow catfish decreased.

3.6. Optimization of response variables

Using the method of Montgomery (2005), the maximization of growth, S and antioxidant capacity of newly hatched yellow catfish larvae were simultaneously optimized. The optimal combination of *T* and *DO* was 26.8 °C and 7.3 mg L^{-1}, respectively. The predictive value for SGR was 1.23% d^{-1}, and S was 88.57%. The activity of hepatic CAT, SOD and the level of MDA, were 69.30 U (mg protein)$^{-1}$, 3.47 U (mg protein)$^{-1}$, and 0.23 mmol mg^{-1}, respectively, with a reliability of 0.78.

4. Discussion

4.1. Effect of T on the growth and S of newly hatched larvae of hybrid yellow catfish

T is one of the most important environmental factors to affect fish survival and growth, with changes in it (within limits) promoting growth and development (Nytrø et al., 2014). As a regulator, *T* mainly controls fish metabolic rates, affecting the enzyme activity of physiological and biochemical processes, and influencing fish behavior and growth (Miegel et al., 2010).

Fish are poikilotherms and grow faster at higher *T*, within suitable *T* ranges. Growth rates of GIFT tilapia increased significantly as *T* increased from 20.0 to 30.0 °C (Qiang et al., 2012a). Lumpfish grew faster at water *T* of 13 °C and 16 °C compared to 4 °C (Nytrø et al., 2014). We report the growth of newly hatched yellow catfish larvae to be higher at 29.1 °C than at 33 °C, at *DO* 7.4 mg L^{-1}. These differences may

Table 6
Analysis of regression coefficients of coded model terms for malondialdehyde content.

Factor	Coefficient Estimate	Standard Error	95% CI Low	95% CI High	*P*-value
Intercept	0.238	0.013	0.208	0.268	
T	−0.035	0.010	−0.059	−0.011	0.0106
DO	−0.040	0.010	−0.064	−0.016	0.0057
$T \times DO$	0.015	0.014	−0.019	0.049	0.3323
T^2	0.063	0.011	0.037	0.089	0.0007
DO^2	0.015	0.011	−0.010	0.041	0.2021
Model					0.0023

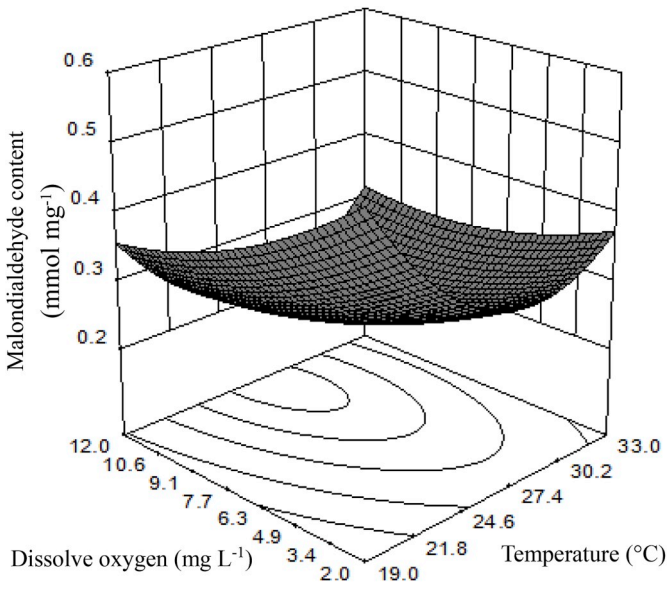

Fig. 5. Response surface plot for the effects of temperature and dissolved oxygen on the malondialdehyde content of newly hatched hybrid yellow catfish (*Tachysurus fulvidraco* ♀ × *Pseudobagrus vachellii* ♂) larvae.

be attributed to the oxygen- and capacity-limited thermal tolerance of newly hatched larvae (Pörtner et al., 2017). When temperatures approach limiting values, constraints on the capacity of an aquatic animal to supply oxygen to tissues to meet demand cause a progressive decline in growth performance (Pörtner and Knust, 2007).

In previous studies, the SGR and feed conversion rate (dietary lipid level 9.2%) of yellow catfish juveniles at 27.5 °C was significantly higher than at 20 °C and 34 °C. Fish of different sizes may have different optimum *T* requirements: the optimal *T* for growth of turbot *Scophthalmus maximus* changed with body size (Arnason et al., 2009); the optimum *T* for growth of turbot at 1 g, 10 g, 100 g, and 1000 g, was 22.5 °C, 20.8 °C, 19.1 °C, and 17.5 °C, respectively; the optimal *T* for growth of lumpfish also decreased with increasing fish size, with lumpfish weighing 11.0–20.0 g growing best at 15.7 °C, and with fish of 20.0–40.0 g growing best at 16.1 °C, 100.0–110.0 g at 13.1 °C, and 120.0–200.0 g at 8.9 °C (Nytrø et al., 2014). At an optimal *T*, less energy is required to sustain life and more energy is available for growth. When *T* rises above a certain critical value, this stresses larvae and slows growth rate. Excessive *T* may disrupt metabolism (Mueller et al., 2015). Similar results were found in this study.

In the early stages of larval growth and development, organ systems and physiological functions are being formed, and these processes are very sensitive to changes in environmental factors (Imsland et al., 2019). In high *T* environments, fish experience decreased *DO*, resulting in increased metabolism, leading to increased oxygen demand. Fish are prone to hypoxia and even death. Biologically active substances in fish, such as proteins and enzymes, may be deactivated at high *T*. Therefore, at high *T* (29.1 °C) the growth of newly hatched larvae may accelerate, but the metabolic burden may increase. This is not conducive to the timely transport of harmful substances, leading to an increase in mortality. However, a low *T* environment (19 °C) inhibits larval growth and development. Low *T* may decrease immunity, change osmotic pressure, increase oxygen consumption, and reduce the secretion of neurohormones, such as enzymes, leading to adverse effects (Cheng et al., 2017, 2018).

4.2. Effects of DO levels on growth and S of newly hatched larvae of hybrid yellow catfish

During fry culture, especially in high-density rearing conditions, increased *DO* results in higher growth rate. The *DO* in water is generally increased by filling with pure oxygen (Foss et al., 2003). With increased *DO*, the growth rate of European sea bass *Dicentrarchus labrax* (Thetmeyer et al., 1999) and piapara *Leporinus elongatus* (Wilhelm Filho et al., 2005) increased significantly. Within a certain range, fish actively feed at higher *DO*, and the efficiency of nutrient use is also high. Higher *DO* may promote the conversion of proteins, lipids and other nutrients into energy for growth (Welker et al., 2013). In the current study, at 26.0 °C and $DO < 7\ mg\ L^{-1}$, the SGR of newly hatched larvae increased with an increase in *DO*, although this increase was not statistically significant compared with the SGR of larvae at a *DO* of $2\ mg\ L^{-1}$. This may be attributed to the short culture period used in this experiment. It is also possible that the 2–12 $mg\ L^{-1}$ range in *DO* used in the experiment was insufficient to cause large changes in the growth of newly hatched larvae. There were no significant differences in the growth and food conversion rates for rainbow trout (*Oncorhynchus mykiss*) held at different *DO* levels: low (65%), normal (100%), and supersaturated (130%) (Caldwell and Hinshaw, 1994). Person-Le Ruyet (2002) also reported no statistically significant differences in growth, feeding rate and food conversion rates of turbot held at *DO* levels of 147% and 223%, although there was a trend for increases related to increased body mass.

A low *DO* ($2\ mg\ L^{-1}$) significantly inhibited S of newly hatched larvae. Periodic hypoxia and continuous hypoxia in water are common phenomena in aquaculture. Fish have a complete physiological response to hypoxic conditions, including increased respiratory efficiency, enhanced blood oxygen affinity (Silkin and Silkina, 2005), increased blood oxygen circulation rate (Gamperl and Farrell, 2004), and an altered metabolic rate and reduced energy consumption (Hochachka, 1997). During early development, some newly hatched larvae may exhibit adaptive regulation. These larvae can adapt to environmental hypoxia, and have no resulting inhibitory effects on growth. However, if larvae fail to adapt to hypoxic conditions, the stress response may result in decreased food intake, slower organ development and possible damage, and an increased mortality rate (Bernet et al., 2001). Excessive *DO* in water may also cause a strong stress response in fish, often accompanied by excessive production of ROS, causing liver damage. In the current study, when *T* was 26.0 °C, the S (<30%) of newly hatched larvae at a high *DO* ($12\ mg\ L^{-1}$) was significantly lower compared with S (>80%) at normal *DO*.

4.3. Effect of T on antioxidant activity in newly hatched hybrid yellow catfish larvae

Changes in antioxidant enzyme activity reflect the physiological status of fish under different environmental conditions, and can be used as an important physiological indicator. SOD and CAT are important antioxidant enzymes that enable organisms to cope with oxidative damage. The antioxidant system response mechanism of fish is specific to different tissues and organs. For example, with an increase in *T* the SOD activity in the brain and kidney of goldfish was four times higher compared with fish held at average *T*. Initially the activities of SOD and CAT in muscle tissue of goldfish decreased, but levels then increased with exposure to stress over time (Lushchak and Bagnyukova, 2006). However, SOD activity in the brain and liver tissues of an Antarctic fish (*Notothenia coriiceps*) decreased with increasing *T* (Klein et al., 2017). In the current study, the activities of hepatic SOD and CAT in newly hatched yellow catfish larvae increased at first, but then decreased with increasing *T*. This may have occurred because within an appropriate *T* range the oxygen consumption rate of fish increased as ambient *T* increased, leading to an increase in production of ROS also. The increase in SOD and CAT activities may be a response to changes in metabolism, thereby mitigating oxidative damage. The high *T* (33.0 °C) used in the experiment on newly hatched yellow catfish larvae exceeded the optimal range (26.0–28.0 °C) for this species, and this may have inhibited metabolism, resulting in the accumulation of oxygen free radicals generated by the redox reaction. When antioxidant enzymes

resist oxidative damage in cells, the activity levels are reduced (Yu, 1994). Once *T* exceeded a suitable range for olive flounder larvae (25.0–32.0 °C), the SGR, S, and antioxidant enzyme activity also decreased (Xu et al., 2010).

MDA is the final product of lipid peroxidation, which reflects the extent of oxidative damage in fish. After stimulation at a low water *T* of 5 °C, the amount of MDA in the liver of North Sea eelpout (*Zoarces viviparus*) increased significantly (Heise et al., 2006). A low *T* treatment (16 °C) also significantly increased the MDA content in GIFT livers (Qiang et al., 2012b). In the current study, low *T* also stimulated an increase in the hepatic MDA content of newly hatched yellow catfish larvae. At low *T*, fish metabolism accelerates, and ROS and lipid peroxidation is enhanced. However, when *T* exceeds an appropriate range for newly hatched larvae, the increase in *T* and oxygen consumption inhibits antioxidant enzyme activity. As a result, excessive levels of ROS cannot be removed, resulting in a large accumulation of MDA and increased oxidative damage.

4.4. Effect of DO levels on the antioxidant capacity of newly hatched hybrid yellow catfish larvae

In anoxic environments, aquatic animals accumulate electrons and use the remaining oxygen to form ROS, which may result in high ROS levels (Janssens, 2000). Endogenous antioxidant systems can reduce the effects of ROS and alleviate cellular oxidative stress. Our study revealed SOD activity was inhibited in a low *DO* environment, but CAT activity increased significantly. CAT can convert H_2O_2 into water, reduce H_2O_2 and lipid peroxides (such as MDA), and alleviate MDA accumulation in tissue. In hypoxic conditions, the SOD activities in the brain, liver and gill tissues of the common carp *Cyprinus carpio* (Lushchak et al., 2005) increased significantly, however the SOD and CAT activities in goldfish plasma were significantly reduced (Sun et al., 2012). High levels of *DO* may help to improve the oxidative parameters to cope with hyperoxia stress, and to alleviate damage to tissue cell membranes. Ritola et al. (2002) reported supersaturated *DO* can stimulate the SOD and CAT activities of rainbow trout. Lygen et al. (2000) also found that treatment of Atlantic salmon (*Salmo salar*) with 140–150% supersaturated *DO* for several weeks increased both SOD and CAT activities in the liver. In the current study, high *DO* effectively stimulated the activity of both SOD and CAT in newly hatched yellow catfish larvae, and reduced the oxidative damage caused by MDA. Interestingly, the high *DO* environment had a significant inhibitory effect on S of newly hatched larvae. The high *DO* environment affected the antioxidant capacity of newly hatched larvae, and may change energy metabolism and exercise capacity, which may affect S. We also found that increasing the *DO* at high *T* can alleviate oxidative damage in fish. Due to oxygen limited thermal tolerance, hyperoxia may stimulate the activities of SOD and CAT and alleviate thermal stress in newly hatched yellow catfish larvae (Pörtner et al., 2006; Pörtner et al., 2017).

4.5. Second order effects and interaction effects of T and DO on growth and antioxidant capacity of newly hatched hybrid yellow catfish larvae

The quadratic regression model revealed the second order effects of *T* and *DO* to be significant on the growth, S, and hepatic SOD and CAT activities of newly hatched yellow catfish larvae. The second order effect of *T* on hepatic MDA content was also significant. These results indicate a peak for each response variable existed, which is significant for aquaculture production. When *T* and *DO* deviated from optimal values, growth and antioxidant capacity of newly hatched yellow catfish larvae decreased in a curvilinear manner. To ensure the best production efficiency, *T* and *DO* should be held at optimal levels during larval production. We report the interaction between *T* and *DO* had an effect on S and on CAT activity in hybrid yellow catfish larvae. At different *T*, *DO* had different effects on fish. When *DO* was high (>10 mg L^{-1}), larval S was greatest at 25 °C, while at low *DO* (<4 mg L^{-1}), the S of larvae was optimal at 28 °C. These differences may be attributed to the adaptive response of newly hatched larvae to *T* and *DO*, and to the antioxidant response. Further study is needed to understand the effects of pH, culture density, and photoperiod time and intensity on the culture of newly hatched larvae.

5. Conclusion

High growth and S are important to ensure efficient production of yellow catfish fry. In this study, the effects of *T* and *DO* on the growth, S and hepatic antioxidant capacity of newly hatched yellow catfish larvae were analyzed using RSM and CCD. The models of SGR, S, hepatic CAT activity, SOD activity, and hepatic MDA content, had adjusted R^2 values of 0.734, 0.937, 0.916, 0.894, and 0.826, respectively. At an optimal combination of *T* and *DO* of 26.8 °C/7.3 mg L^{-1}, the predictive values for larval growth, S, hepatic CAT activity, SOD activity, and hepatic MDA content, were 1.23% d^{-1}, 88.57%, 69.30 U (mg protein)$^{-1}$, 3.47 U (mg protein)$^{-1}$, and 0.23 mmol mg^{-1}, respectively. The optimal rearing environment helps promote the growth and S of newly hatched larvae, and enhances antioxidant capacity. To maximize efficiency for yellow catfish fry production, *T* and *DO* should be maintained at optimal values.

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Authors' contributions

Xu Pao conceived and designed the experiment, Liang Ming and Liang Cong carried out fertilization and incubation of hybrid yellow catfish, and Qiang Jun and Zhong Chun Yi measured growth and analyzed the database and built models. He Jie, Bao Jing Wen and Li Hong Xia measured SOD, CAT, and MDA. Qiang Jun and Zhong Chun Yi wrote the paper with contributions from all other authors. All authors have read and approved the final version of the manuscript.

Declaration of competing interest

None.

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Appendix A. Supplementary data

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