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THE EFFECT OF EXHAUSTIVE EXERCISE TRAINING AND FASTING ON POST-EXERCISE OXYGEN CONSUMPTION RATE IN SOUTHERN CATFISH (*SILURUS MERIDIONALIS CHEN*)*

CAO Zhen-Dong and FU Shi-Jian

(Laboratory of Evolutionary Physiology and Behaviour, Chongqing Key Laboratory of Animal Sciences, Chongqing Normal University, Chongqing 400047, China)

Abstract: To test whether training and fasting have significant effects on maintenance energy expenditure and anaerobic metabolism, the resting oxygen consumption rate (VO_{2rest}) and post-exercise VO_2 (EPOC) in southern catfish (*Silurus meridionalis* Chen) fed on maintenance rations (1.5% body mass per day) or fasted during 15d of exhaustive exercise training (5 min chasing) and a subsequent 5d without training was investigated at 25℃. Two groups kept under the same conditions without exercise training acted as feeding and fasting controls. The VO_{2rest} values of both feeding and fasting controls decreased significantly during the experiment ($P < 0.05$), while those of the feeding and fasting training groups were significantly increased after 15d of training ($P < 0.05$). VO_{2rest} of both training groups decreased significantly to control levels after training was stopped. The VO_{2peak} values of both feeding and fasting controls decreased significantly during the experiment ($P < 0.05$), while those of the feeding and fasting training groups were unchanged after 15d of training. VO_{2peak} of both training groups decreased significantly to control levels after training was stopped. There were no significant differences in excess post-exercise VO_2 (EPOC) between any training and control groups. It is suggested that: (1) VO_{2rest} and VO_{2peak} were significantly improved by exercise training compared with the control groups, but returned to their previous values 5d after stopping training; (2) post-exercise VO_2 recovered faster in training groups compared with control groups, and this trait persisted 5d after stopping training; (3) training had similar physiological effects on feeding and fasting southern catfish, except that VO_{2rest} was more sensitive to training in the fasting group.

Key words: Excess post-exercise oxygen consumption (EPOC); Exhaustive exercise training; VO_{2rest}; *Silurus meridionalis* Chen

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Exercise training protocols may be categorized as endurance (aerobic) or sprint (anaerobic). It is reasonable to assume that these two training regimens modify the physiology and biochemistry of fish differently, and may reflect differences in aerobic and anaerobic capacity[1]. Endurance-trained fish show elevated critical swim speeds[2], increased fatigue resistance[3], increased density of myonuclei fibres and mitochondrial in fast muscle[4, 5]. All that indicates a high demand for oxygen in training fish which might meet by the blood supply and with the required oxygen and metabolite supply of muscle tissue. As a sequence, energetics parameters such as rest and the maximal oxygen consumption (VO_2) in training fish would be larger. However, in zebrafish larvae, endurance training did not provoke any improvement at the level of total oxygen transport in the blood[6], and the effects of endurance training on VO_{2rest} and VO_{2max} are controversial in other fishes, which probably due to differences in training intensity and training duration. Given for this, exhaustive exercise training (sprint to exhaustion) can be a more useful model for the study

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Corresponding author: Cao Zhen-Dong (1949—), male, professor; major in fish ecology; E-mail: z.d.cao@hotmail.com

of training effects in fish. However, it is surprising that, despite the high proportion of white muscle in fish, anaerobic sprint training has been under-investigated compared with endurance training [1, 7].

Excess post-exercise VO_2 (EPOC) is represented by elevated VO_2 following exhaustive exercise. It reflects the increased quantity of oxygen required to restore tissue and cellular stores of oxygen and high-energy phosphates, biochemical imbalances in metabolites such as lactate and glycogen, and other functions such as ionic and osmotic balance [8]. The magnitude of EPOC is closely related to the anaerobic capacity of animals, while VO_{2peak} (and the rate of decrease of VO_2) during recovery might be limited by their aerobic capacity to some extent [9, 10]. According to Kieffer [11], it is an ideal "model system to study rate limiting factors in exercise performance and recovery in fish". So, we consider it may be an ideal model to investigate the training effect of fishes.

The southern catfish (*Silurus meridionalis* Chen) is a warm-water sedentary forager. Several studies of the energetics of this fish have been documented in our laboratory [12—14]. In a previous experiment, we found that this species was easily acclimatized to stress. It could eat "normally" 6h after exhaustive exercise (chasing for 5 min) in a pilot trial. Thus, the effect of exhaustive exercise training on VO_{2rest} and post-exercise VO_2 were investigated using juvenile southern catfish as a model. The main aim of this study was to determine whether training affected VO_{2rest} and the post-exercise VO_2 curve.

Nutritional history and status have profound effects on the physiology and energetics parameters of fish. Fasting is not the only stress that fish might meet in their natural environment, but it is often used in research [11]. When facing fasting, fish might be down-regulated its aerobic and anaerobic performance for saving of energy, thus VO_{2rest} and the post-exercise VO_2 may decrease. It could be more interesting to find how it is going with EPOC when fish facing fasting and training concurrently. So, the second aim of this study was to investigate the influence of fasting and feeding regimens on EPOC and its interaction with training.

1 Materials and methods

1.1 Experiment animals

Juvenile fish were obtained from a local live market and acclimated in a rearing system 4 weeks before the experiment. The temperature of the dechlorinated freshwater was maintained at 25.0 ±1.0℃ and the oxygen content was kept above 7 mg·O_2/L. During this period, the fish were fed maintenance rations (1.5% body mass per day) of cutlets of freshly killed loach (*Misgumus anguillicaudatus*). A 14h light: 10h dark photoperiod was used to simulate the natural light cycle throughout the experiment.

1.2 Experimental protocol and operation

After acclimation, 40 fish of similar weight (21.37 ±0.36 g) were selected and acclimated for another week at 25.0 ±1.0℃ in a flow-through respirometer modified from the design of Fu, *et al* [13, 14]. The fish received food at 1.5% body mass at 20:00 each day. They were weighed after acclimation and divided into four groups randomly (10 fish in each group). Two groups continued to receive the maintenance rations. One of these feeding groups was chased to exhaustion (5 min) at 8:00 and referred to as the feeding training group. The other feeding groups served as feeding control group (one fish in the feeding control group died during the experiment). The remaining two groups were fasted during the experiment; one was an exhaustive exercise training group (fasting training group) and the other group served as fasting control group. The method of exhaustive exercise training was fully described by Fu, *et al* [15, 16]. VO_2 was measured at 07:00 and 18:00 daily, and the mean value was regarded as the resting oxygen consumption rate (VO_{2rest}). After 15d of training, the fish were held in the chamber for another 5d without training (the feeding regimen was unchanged). Post-exercise VO_2 was recorded for 30 min at the beginning of training (feeding and fasting training groups only), after 15d of training (all four groups), and at the end of the experiment; that is, 5d after stopping training (all four groups). The fish were held in an experimental chamber (0.1 L) and a chamber without a fish acted as a control for background oxygen consumption. The follow-

ing formula was used to calculate VO_2 (mgO_2 /kg · h):

$$VO_2 = \Delta O_2 \times v / m \quad (1)$$

where ΔO_2 is the measured difference in oxygen concentration (mg · O_2 /L) between the experimental chamber and the control chamber, v (L/h) is the velocity of flow in the chamber, and m is the body mass of the test fish (kg). The dissolved oxygen concentration was measured at the outlet of the chamber using an oxymeter (HQ20; Hach Company, Loveland, Colorado, USA). The flow rate of water through the respirometer chamber was measured by collecting the water outflow from each tube over 1 min [13]. Fish were placed into the respirometer chamber immediately after exercise, and their post-exercise VO_2 was measured at 2, 3, 4, 5, 10, 15, 20, 25, and 30 min after transfer. The flow rate was about 0.3 L/min, and a 99% exchange of water could be achieved over about 1.5 min in the 0.1 L chamber [17].

1.3 Data analysis

The effects of fasting and training on body weight and VO_2 were compared using t-test. The comparison between training and control, and those between feeding and fasting were tested by independent t-test, while those between 15d training and 5d without training were tested by dependent t-test. P values lower than 0.05 were considered statistically significant and all data were presented as mean ± SE. STATISTICA 4.5 (StatSoft Inc.) was used for data analysis.

2 Results

The body masses of both feeding groups (feeding control group and feeding training group) did not change significantly during the experiment, while those of the fasting groups (fasting control group: $t = 3.194$, $P = 0.011$, fasting training group: $t = 4.682$, $P = 0.001$) were significantly decreased after 15d of fasting (Tab. 1). Thus, the body masses of fasting control group ($t = -3.111$, $P = 0.014$) and fasting training group ($t = -3.949$, $P = 0.003$) were significantly lower than those of feeding control group and feeding training group after 15d of training.

Tab. 1　Effect of treatment on post-exercise VO_2 in southern catfish (mean ±SE)

	Initial	15d				5d			
		Feeding control	Feeding training	Fasting control	Fasting training	Feeding control	Feeding training	Fasting control	Fasting training
Number	20	9	10	10	10	9	10	10	10
Weight (g)	21.9 ±0.5	22.5 ±0.4	22.3 ±0.9	19.4 ±0.7*^	18.9 ±0.4*^	22.6 ±0.5	23.2 ±0.7	19.1 ±0.7*^	18.8 ±0.5*^
VO_{2rest}, (mg/kg · h)	93.3 ±2.6	82.0 ±4.8	103.8 ±4.3*$	82.3 ±3.7	115.4 ±4.1*$	79.3 ±3.7*	79.6 ±5.4*#	77.6 ±4.9*	80.6 ±4.8*#
VO_{2peak}, (mg/kg · h)	508.2 ±15.0	396.7 ±14.0*	519.9 ±10.6$	446.8 ±17.9*	515.4 ±23.4$	420.8 ±13.2*	431.4 ±12.9*#	424.8 ±22.0*	425.6 ±14.2*#
EPOC, (mg/kg)	105.5 ±4.7	99.3 ±3.2	100.8 ±6.0	93.3 ±4.5	86.2 ±7.4*	111.7 ±3.6	104.9 ±6.1	102.0 ±8.0	89.0 ±6.4*
VO_{2peak} /VO_{2rest}	5.51 ±.20	4.97 ±0.36	5.09 ±0.24	5.50 ±0.26	4.47 ±0.13*$^	5.42 ±0.35	5.62 ±0.37	5.65 ±0.42	5.43 ±0.37#

*: significantly different from initial value

#: value at the end of the experiment was significantly different from that after 15d of exercise training

$: value of training group was significantly different from that of control group in the same sample time

^: value of feeding group was significantly different from that of fasting group in the same sample time

The VO_{2rest} values of both feeding ($t = -23.157$, $P = 0.050$) and fasting training ($t = 3.585$, $P = 0.005$) groups after 15d of training increased significantly compared with the initial values. VO_{2rest} of both fasting ($t = -5.417$, $P < 0.001$) and feeding ($t = -2.730$, $P = 0.029$) training groups were significantly higher than that of control groups after 15d of training. The VO_{2rest} values of both feeding ($t = 4.630$, $P = 0.001$) and fasting ($t = 4.822$, $P = 0.001$) training groups decreased significantly 5d after stopping training ($P < 0.05$). As a result, there were no significant differences in VO_{2rest} between any groups at the end of the experiment. However, all VO_{2rest} values at the end of the experiment were significantly lower than the ini-

tial values (t = 3.785 - 5.359, P = 0.001 - 0.004).

For all fish, VO_2 increased immediately after transferred to chamber and then slowly returned to a stable level after exercise (Fig. 1). The VO_2 curves exhibited profound differences among treatments and sample times. The VO_{2peak} values of the training groups (feeding training group and fasting training group) changed insignificantly, while those of the control groups (feeding control group (t = 5.682, P < 0.001) and fasting control group (t = 3.572, P = 0.006) decreased significantly after 15d of training. Thus, the VO_{2peak} values of both training groups (fasting: t = 3.536, P = 0.007; feeding: t = 4.495, P < 0.001) were significantly higher than those of control groups after 15d of training. After 5d without training, the VO_{2peak} values of both training groups decreased significantly (fasting: t = 3.642, P = 0.007; feeding: t = 5.082, P < 0.001). Thus, there was no significant difference in VO_{2peak} between any groups at the end of the experiment. However, all values at the end of the experiment were significantly lower than the initial VO_{2peak} (t = 2.179 - 3.747, P = 0.006 - 0.050).

There were no significant differences in EPOC between any training and control groups or feeding and fasting groups, but EPOC of fasting training groups after 15d training (t = 3.267, P = 0.011) and 5d stop training (t = 3.777, P = 0.005) were significantly lower that that of initial value. VO_{2peak}/VO_{2rest} of fasting training group decreased significantly (t = 5.124, P = 0.001) after 15d training and significantly increased (t = -2.490, P = 0.038) after 5d without training, thus VO_{2peak}/VO_{2rest} of fasting training group after 15d training was significantly lower than those of fasting control (t = -2.640, P = 0.030), feeding training groups (t = -2.280, P = 0.050).

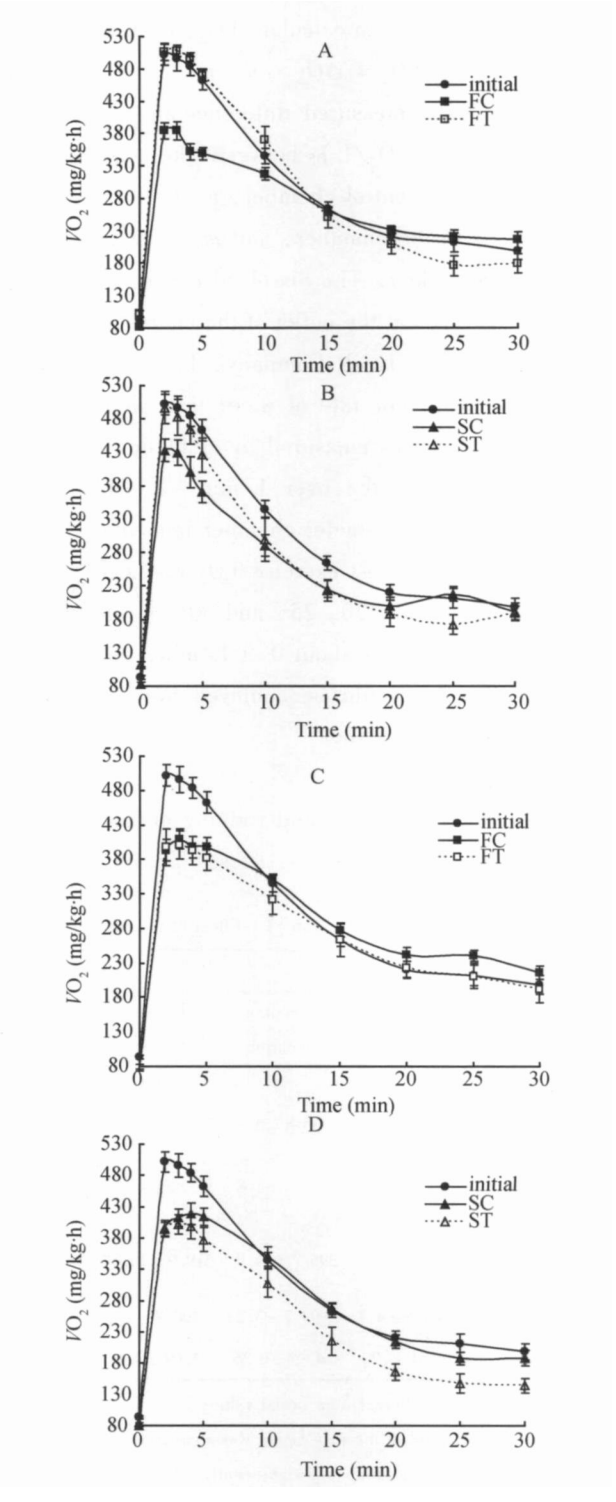

Fig. 1 Post-exercise VO_2 curve of southern catfish after 15d of exercise training (A and B) and 5d after stopping training (C and D)
FC: feeding control group; FT: feeding training group; SC group: fasting control group; ST: fasting training group

3 Discussion

3.1 Effect of exhaustive exercise training on VO_{2rest} and post-exercise VO_2

This study showed that VO_{2rest} and post-exercise VO_2 were significantly affected by the experimental treatment. Decreases of VO_{2peak} and VO_{2rest} during an experiment have been documented in a lizard (*Amphibolurus nuchalis*) [18]. This might be due to the effect of captivity on experiment animals. The fish used in this study were acclimated for 4 weeks in a rearing system before the experiment, but the captivity effect might have still been profound, since the conditions in the

rearing system were different to those of the respirometer. Compared with the control groups, 15d of training elicited a 15%—30% increase in VO_{2peak}. There was no previous documented research on the effect of anaerobic training on VO_{2peak} in a fish species. However, elevated VO_{2peak} was found in endurance-trained fish and lizards [18, 19]. This was perhaps due to improved oxygen extraction in the tissues [20], increased blood hemoglobin concentration [21], and increased heart size [19]. The effect of anaerobic training on VO_{2rest} in fish had not been previously documented. VO_{2rest} in trained fish increased by 25%—40% in this study. The effects of endurance training on VO_{2rest} in fish were controversial. Endurance training elicited increased VO_{2rest} in zebrafish (*Danio rerio*) [22], but decreased VO_{2rest} in rainbow trout (*Salmo gairdner*) [23]. This might be related to training regimen, training intensity, training duration, the species used, and even the experimental design. Researchers paid little attention to the stability of this training effect. The present study found that the difference between control and training groups elicited by 15d of training was completely eliminated 5d after stopping training. This suggested that the effect of training on VO_{2rest} and VO_{2peak} was relatively unstable.

It has been found that anaerobic training increases resting white muscle glycogen and post-exercise lactate levels in fish [1]. Since EPOC reflects the increased quantity of oxygen required to restore tissue and cellular stores of oxygen and high-energy phosphates, and biochemical imbalances in metabolites such as lactate and glycogen [8], EPOC should increase after exercise training. No data on anaerobic effects on EPOC are available, but an early study on the effect of aerobic training on EPOC found that it increased three times compared with that in untrained fish [19]. In this study, EPOC did not differ significantly among experiment treatments, even though the VO_{2peak} and VO_2 values of trained fish were much higher than those of untrained fish in the first several minutes of recovery. This was partly due to the lower VO_2 in the prolonged phase of recovery of trained fish, as a result of the rapid turnover of ATP, creatine phosphate (PCr), lactate, and glycogen in anaerobically trained fish [1]. Also, the stress-related response might be lower in trained fish since their plasma catecholamine and cortisol levels were lower than in untrained fish [23, 24]. In southern catfish, such a stress-related response might account more than 40% of EPOC under exhaustive exercise treatment [16]. In addition, most related studies have measured post-exercise VO_2 over 30—45 min (it appeared that the recovery process was largely finished during this period of time), but the prolonged phase of EPOC such as restoration of white muscle glycogen and clearance of lactate (which might mostly be affected by exercise training) might not end at 40 min [11]. Thus, EPOC in trained fish might be underestimated compared with the control group.

The results of this study suggested that training might have more effects on aerobic capacity than anaerobic capacity. Improved ventilation with training led to higher VO_{2peak} and a faster recovery rate. The post-exercise VO_2 profile was markedly altered by training, but the total energy expenditure elicited by exhaustive exercise was not changed. The effect of training on aerobic capacity was relatively unstable and disappeared 5d after stopping training. It was worth mentioning that VO_2 in the trained fish was still higher than that in the controls at the end of the experiment (5d after stopping training). It suggested that the recovery rates of the training groups remained higher than those of the control groups even 5d after stopping training.

3.2 Influence of fasting on training effect

It has been shown that starvation influences a number of physiological (e.g. energy reserves) and biochemical (e.g. enzyme levels) factors in fish [25, 26]. It could also alter post-exercise VO_2 with training. It is believed that muscle glycogen may decrease markedly during fasting [11, 27], and decreased glycogen levels can set limits to burst performance and post-exhaustive VO_2. According to a previous study [28], fasting had profound effects on body metabolites and energetics in southern catfish, so it was interesting that the effect of training was similar in feeding and fasting groups in this study; i.e., VO_{2rest} and VO_{2peak} were significantly higher and VO_2 decreased faster in trained fish than in the controls after 15d of training. The training effect in both disappeared 5d after stopping training. VO_{2rest} was larger in the fasting training group than in the feeding

training group, but this difference disappeared 5d after stopping training. This suggested that the difference was elicited by the interaction of training and fasting. One explanation might be that energy and metabolites were needed for restoration of depleted metabolites such as ATP, PCr and glycogen, and clearance of lactate. Such energy and metabolites could come from ingested food in the feeding group, but they could only come from body deposits and decomposition in the fasting group. The energy expenditure might be higher in the latter situation.

4 Conclusion

Exhaustive exercise leads to higher routine energy expenditure, aerobic capacity, and recovery rate. There were no significant differences in the effects of training between feeding and fasting groups with regard to aerobic capacity, but the routine energy expenditure of the fasting training group was larger than that of the feeding training group. The effect of training on aerobic capacity, and hence the post-exercise $\dot{V}O_2$ profile, was unstable, while the effect on recovery rate may be more stable.

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力竭性运动锻炼和饥饿对南方鲇运动后过量耗氧的影响*

曹振东　付世建

(重庆师范大学,重庆师范大学进化生理与行为学实验室,重庆市动物生物学重点实验室,重庆　400047)

摘要:为了检验力竭性运动锻炼和饥饿是否对南方鲇 *Silurus meridonalis* Chen维持能量消耗和无氧代谢能力产生影响,在 25℃条件下测定了维持日粮 (1.5% body mass per day)和饥饿条件下南方鲇 15d力竭性锻炼 (5min chasing)和随后 5d恢复过程静止代谢率 (VO_{2rest}) 和运动后过量耗氧 (Excess post-exercise VO_2, EPOC)的变化。另外两组非锻炼组分别作为摄食和饥饿对照组。实验过程中摄食和饥饿对照组 VO_{2rest}显著下降 ($P<0.05$),而摄食和饥饿对照组经过 15d的锻炼显著上升 ($P<0.05$)。经过 5d的恢复 2锻炼组 VO_{2rest}显著下降与对照组无显著差异。摄食和饥饿对照组力竭运动后代谢率峰值 (VO_{2peak})在实验过程中显著下降 ($P<0.05$),而摄食和饥饿锻炼组经过 15d没有显著变化。锻炼取消后 2锻炼组 VO_{2peak}显著下降至对照组水平。各锻炼组和对照组间过量耗氧均无显著差异。实验提示:(1) 锻炼导致 VO_{2rest}和 VO_{2peak}显著提高,但影响可塑性大,5d恢复期后影响消失;(2)锻炼导致力竭运动后代谢恢复速率加快,5d恢复期后锻炼影响依然存在;(3)对饥饿和摄食组,锻炼的生理影响相似,但饥饿组 VO_{2rest}对锻炼更为敏感。

关键词:运动后过量耗氧 (EPOC);力竭性运动锻炼;静止代谢率;南方鲇