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Effect of meal size on the postprandial metabolic response in Chinese giant salamander *Andrias davidianus* larvae

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ABSTRACT: The digestive physiological characteristics of Chinese giant salamander *Andrias davidianus* have not been reported in the existing literature, and improving our knowledge in this area could help in the artificial culture of the species. The effect of meal size on the specific dynamic action (SDA) of *A. davidianus* larvae was assessed in this study at a water temperature of 20°C. The Chinese giant salamander was fed by test diets at meal sizes of 0.5, 1, 2, 4, 8 and 12% of its body mass (4.41 ± 0.07 g), and the postprandial oxygen consumption rate (MO_2) was measured at 2 h intervals until the rate returned to its preprandial level. Peak MO_2 (MO_{2peak}) increased with meal size but levelled off at larger meal sizes within the studied range (8–12% body mass). The factorial metabolic scope increased from 1.27 to 2.11 when meal size increased from 0.5 to 12%. Time to reach MO_{2peak} was not affected by the relative meal size. The SDA duration increased from 8.89 to 47.33 h as the relative meal size increased from 0.5 to 12%. The amount of energy expended during SDA increased linearly with increasing meal size ($R^2 = 0.842$, $p < 0.001$, $n = 60$). There was no significant difference in the SDA coefficient among the different relative meal size groups. These data suggest that (1) *A. davidianus* larvae increase their energy demands during digestion by prolonging the SDA duration rather than increasing the MO_{2peak} as meal size increases, and (2) *A. davidianus* showed a smaller factorial metabolic scope in the process of digesting large meal sizes, which may be related to the limited MO_{2peak} of the species.

KEY WORDS: Ingestion · Metabolic rate · Specific dynamic action · *Andrias davidianus*

1. INTRODUCTION

The marked increase in the metabolic rate (MO_2) that occurs following feeding is commonly referred to as specific dynamic action (SDA). SDA represents the energetic expenditures associated with food capture and the handling, ingestion, digestion, absorption and assimilation of the various nutrients, such as proteins, fats and carbohydrates (Jobling 1981, Beamish & Trippel 1990, Brown & Cameron 1991, Secor 2009). SDA has been investigated in many animal taxa, such as crustaceans (Whiteley et al. 2001), fishes (Fu et al. 2006), amphibians (Secor et al. 2007), reptiles (Hopkins et al. 2004), birds (Green et al. 2006) and mammals (Lovatto et al. 2006). However, the majority of the SDA studies conducted in amphibians focused on anurans (Wang et al. 1995, Grayson et al. 2005, Secor et al. 2007), while little attention has been paid to species of Caudata (Feder et al. 1984, Secor 2001, Secor & Boehm 2006).

Intraspecific variations in SDA responses are attributed to differences in meal characteristics and envi-

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ronmental conditions (Secor et al. 2007). Previous studies on SDA in amphibians have found that meal size has a significant effect on SDA (Secor & Faulkner 2002, Secor & Boehm 2006, Secor et al. 2007, Timpone et al. 2020). Ingesting prey of different sizes requires adjustments to the physiological processes underlying meal digestion, such as gut evacuation, and has important ecological and energetic implications (Secor & Faulkner 2002, França et al. 2004, Timpone et al. 2020). The SDA duration and energy expended on SDA in amphibians, like other ectothermic animals, usually increase with increasing meal size (Secor & Boehm 2006, Secor et al. 2007). The peak MO_2 (MO_{2peak}) may increase linearly with meal size (Secor & Faulkner 2002, Timpone et al. 2020) or level off at higher meal sizes for some amphibians, such as the tiger salamander *Ambystoma tigrinum tigrinum* (Secor & Boehm 2006). Some studies have found that the SDA coefficient (SDA as a percentage of the ingested energy of a meal) did not change (Secor & Boehm 2006, Secor et al. 2007, Timpone et al. 2020) or increased with increasing meal size (Secor & Faulkner 2002, Secor et al. 2007). It has been suggested that the SDA response to meal size might be related to amphibian species (Secor et al. 2007, Timpone et al. 2020). Therefore, more studies on the effect of meal sizes on the postprandial metabolic response in different amphibian species are needed.

The Chinese giant salamander *Andrias davidianus* (Amphibia: Caudata) is currently the largest amphibian on our planet and is widely distributed throughout south-central China (Liang et al. 2019). The species normally inhabits rivers and streams and catches prey consisting of conspecifics, crabs, frogs, fishes, water shrews and invertebrates (Song 1994). The *A. davidianus* farming industry is developing rapidly in some provinces of China, such as Hunan and Shaanxi (Cunningham et al. 2016). However, some characteristics of the breeding regime, such as feeding frequency and meal size, need to be further optimized. Moreover, the species is Critically Endangered (IUCN 2019) because of habitat loss and the unsustainable overexploitation of wild individuals, such as through illegal poaching (Turvey et al. 2018). Limited data on the physiological characteristics of this species have been reported in the literature, such as electrical discharge and estradiol concentration (Olshanskii et al. 2016); SDA in *A. davidianus* has not been reported.

In this study, we selected *A. davidianus* as the experimental animal and investigated the effect of meal sizes on SDA under a range of meal sizes ranging from 0.5 to 12% of body mass. Our aim was to explore the digestive physiological characteristics of *A. davidianus* by measuring postprandial MO_{2peak}, the time to reach MO_{2peak}, the energy expended during SDA and the SDA coefficient at different meal sizes. Chironomid (Diptera: Chironomidae) larvae were used as the test diet, as it is the main food for *A. davidianus* larvae in the hatchery. We hope the present study can provide valuable information for the artificial culture of *A. davidianus.*

2. MATERIALS AND METHODS

2.1. Experimental animals

Andrias davidianus larvae (180 d after hatching, n = 200; Fig. 1) were obtained from the Zhujiangyuan Giant Salamander Culture Cooperative, Linwu County (25° 10′–25° 35′ N, 112° 20′–112° 47′ E), Hunan Province, China. The larvae had been fed with chironomid larvae in the breeding center. Prior to the experiment, the individuals were acclimated for 1 mo in a rearing system (L × W × H: 2 × 1 × 0.5 m). During the acclimation period, the temperature of the dechlorinated freshwater system was controlled at 20.0 ± 0.5°C, the dissolved oxygen level was maintained above 7 mg l^{-1} and the photoperiod was maintained at 14 h light:10 h dark. The water was continuously filtered, with 50% replaced each day. Every 2 d at 18:00 h, the salamanders were fed chironomid larvae to satiation.

2.2. Experimental protocol

In order to assist *A. davidianus* larvae with acclimating to the feeding environment, each individual was placed in a continuous-flow respirometer (for details, see Fu et al. 2005b) and fed to satiation with chironomid larvae every 2 d for 7 d. Our pilot experiment found that the maximum meal size of the species was approximately 12% of body mass under the experimental conditions. The SDA responses

Fig. 1. Chinese giant salamander *Andrias davidianus* larva

were measured at relative meal sizes of 0.5, 1, 2, 4, 8 and 12% of the body mass of each experimental salamander (methods of measurement are shown below). The group size for each meal size was 10 individuals. After 48 h of fasting, the larvae were removed from the respirometer chamber and weighed. The larvae were then returned to the respirometer chamber and acclimated for 24 h. This duration was determined by a pilot experiment and was enough for the larvae to recover to the pre-feeding metabolic rate. MO_2 was measured 10 times at 1 h intervals before feeding, and the mean of these measurements was defined as MO_{2rest}. Then, a prescribed quantity of chironomid larvae constituting the test diet was offered. Immediately after the salamanders finished the meal, the chambers were closed, and MO_2 was measured continuously at 2 h intervals for 50 h in all meal size groups until the postprandial metabolic rates returned to the pre-feeding rates.

To examine the effects of diurnal rhythm on the metabolic rate of *A. davidianus* under the experimental conditions, after a 24 h fast and measurement of their body masses, *A. davidianus* larvae (4.52 ± 0.17 g, n = 10) were placed in the respirometer chambers individually and allowed to acclimate to the experimental conditions for 48 h. Then, MO_2 was measured at a 2 h interval for 24 h under a 14 h light:10 h dark photoperiod.

Eight samples of 10 g chironomid larvae were taken from each trial and dried to constant mass at 70°C to analyze energy content using an oxygen bomb calorimeter (Model 1281, Parr Instrument Company). The average energy content of the samples (2.62 ± 0.03 kJ g^{-1} wet mass) was used as the energy content of the diet.

2.3. MO_2 measurements

MO_2 was measured in *A. davidianus* larvae by using a continuous-flow respirometer with 11 chambers (0.04 l) (see Fu et al. 2005b for details) under a 14 h light:10 h dark photoperiod. Ten chambers containing study animals were used as experimental chambers, and one empty chamber was used as a control chamber for calculation of background MO_2 (Pang et al. 2021). A feeding tube was mounted at the front of each respirometer chamber to allow the feeding of the *A. davidianus* individual in the chamber. Feces were siphoned by a tube mounted at the rear of each respirometer chamber (Fu et al. 2005a). The equation used for the calculation of MO_2 (mgO_2 kg^{-1} h^{-1}) was as follows (Fu et al. 2005b):

$$MO_2 = \Delta O_2 \times v/m \quad (1)$$

where ΔO_2 is the oxygen concentration difference (mgO_2 l^{-1}) between the experimental and blank chambers, v is the flow rate of water in the chamber (l h^{-1}) and m is the body weight of the experimental *A. davidianus* (kg). An oximeter (HQ30, Hach Company) was used for the measurement of the oxygen tension at the outlet of each chamber. Water flow rate through the chambers was calculated by the weight of water outflow collected from each chamber (Pang et al. 2021). The water temperature was 20.0 ± 1°C.

2.4. Parameters in SDA

We quantified the following parameters to describe the SDA process (for details, see Secor & Diamond 1997, Fu et al. 2006): MO_{2rest}, MO_{2peak}, time to MO_{2peak}, factorial metabolic scope, SDA duration, energy expended during SDA and the SDA coefficient.

2.5. Data analysis

Values are expressed as mean ± SE, and results were considered significant at $p < 0.05$. The effects of different meal sizes on all parameters were assessed using 1-way ANOVA. If the result was significant, Levene's test of homogeneity of variance was used. If the distribution was normal, ANCOVA was followed by the least significant difference (LSD) test; otherwise, the *t*-test was used. Nonlinear estimations between the relative meal sizes (% body mass) and SDA variables were also used when necessary. The software programs Excel (Microsoft Corporation) and SPSS 17.0 (IBM) were used for data analysis.

3. RESULTS

The average body mass and length of the experimental animals were 4.41 ± 0.07 g and 9.11 ± 0.06 cm, respectively (n = 60). There was no significant difference in body mass ($F_{5,59} = 0.920$, p = 0.476) or body length ($F_{5,59} = 0.482$, p = 0.788) among the different meal size groups (Table 1). MO_2 showed no significant change over the 24 h measurement period (ANOVA, $F = 0.342$, p = 0.974) and was not affected by the diurnal rhythm under the experimental conditions. Significant differences were not found in the MO_{2rest} values among the different meal size groups ($F_{5,59} = 0.126$, p = 0.413) (Table 1). MO_2 increased 2 h

Table 1. Effect of meal size on morphometric parameters and postprandial metabolic response in Chinese giant salamander *Andrias davidianus* larvae measured by several variables (mean ± SE). MO_{2rest}: resting metabolic rate; SDA: specific dynamic action. Values in each row without a common superscripted lowercase letter are significantly different ($p < 0.05$)

Variable	Meal size (% of body mass)					
	0.5	1	2	4	8	12
Sample number (n)	10	10	10	10	10	10
Body mass (g)	4.27 ± 0.19	4.35 ± 0.14	4.57 ± 0.18	4.37 ± 0.14	4.66 ± 0.19	4.26 ± 0.18
Body length (cm)	9.11 ± 0.18	9.09 ± 0.15	9.19 ± 0.66	9.26 ± 0.94	8.99 ± 0.13	9.04 ± 0.17
Meal size (% body mass)	0.46 ± 0.04^{f}	0.96 ± 0.05^{e}	2.30 ± 0.15^{d}	4.66 ± 0.35^{c}	7.88 ± 0.11^{b}	11.50 ± 0.63^{a}
Energy ingested (kJ kg^{-1})	11.98 ± 0.98^{f}	25.02 ± 1.26^{e}	60.38 ± 4.41^{d}	122.19 ± 9.19^{c}	206.58 ± 2.98^{b}	293.82 ± 16.56^{a}
MO_{2rest} (mgO_2 kg^{-1} h^{-1})	52.04 ± 1.87	50.39 ± 1.16	52.45 ± 1.51	50.60 ± 1.09	55.41 ± 3.05	53.25 ± 1.60
Time to peak metabolic rate (h)	3.77 ± 0.40	3.56 ± 0.44	4.47 ± 0.47	4.89 ± 0.48	4.00 ± 0.58	4.22 ± 0.52
Factorial metabolic scope	1.27 ± 0.05^{c}	1.48 ± 0.06^{c}	1.80 ± 0.64^{b}	1.95 ± 0.06^{ab}	1.92 ± 0.07^{ab}	2.11 ± 0.12^{a}
SDA coefficient (%)	6.00 ± 1.53	6.02 ± 0.82	8.10 ± 1.24	8.47 ± 0.40	6.81 ± 0.69	6.97 ± 0.61

after feeding, peaked 3–5 h post-feeding depending on the meal size and then slowly decreased to the pre-feeding level in all experimental groups (Fig. 2).

3.1. MO_{2peak}, factorial metabolic scope and time to MO_{2peak}

The MO_{2peak} significantly increased in the low meal size range (0.5, 1 and 2% meal sizes) ($p < 0.05$; Fig. 3). The MO_{2peak} of the 8 and 12% meal size groups was higher than those of 0.5, 1 and 2% meal size groups ($p < 0.05$; Fig. 3). However, there was no significant difference in MO_{2peak} between the 8 and 12% meal size groups.

There was no significant difference in the factorial metabolic scope between the 0.5 and 1% meal size groups. The factorial metabolic scopes of the 2, 4, 8 and 12% meal size groups were higher than those of 0.5 and 1% meal size groups ($p < 0.05$; Table 1). However, there was no significant difference between the factorial metabolic scope of the 4% meal size group and that of either 8 or 12% meal size groups (Table 1).

There was no significant change in the time to MO_{2peak} when the meal size increased from 0.5 to 12% (Table 1). The overall mean time to MO_{2peak} was 4.19 ± 0.20 h (n = 60).

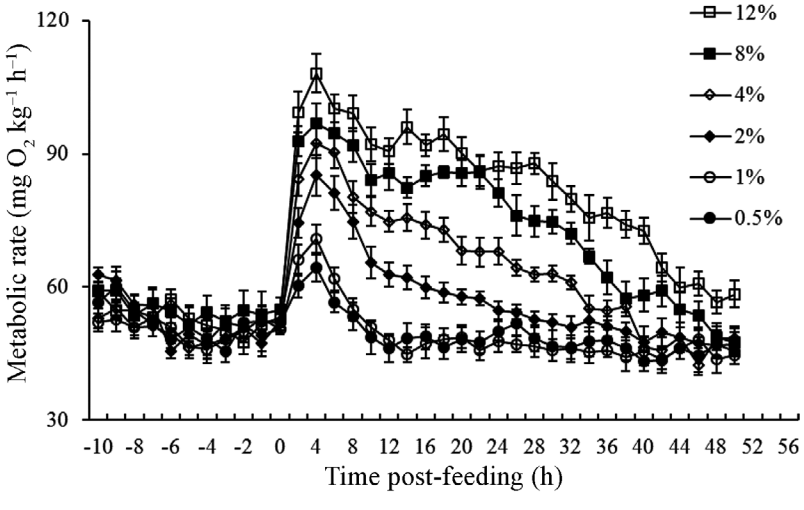

Fig. 2. Effect of meal size on the postprandial metabolic response in Chinese giant salamander *Andrias davidianus* larvae (mean ± SE)

3.2. Duration of SDA

There was no significant difference in the SDA duration between the 0.5 and 1% meal size groups ($p > 0.05$), both of which were shorter than the other meal size groups ($p < 0.05$; Fig. 4). There was no significant difference in the SDA duration between the 4 and 8% meal size groups ($p > 0.05$), both of which were shorter than the 12% meal size group ($p < 0.05$; Fig. 4).

3.3. Energy expended during SDA and the SDA coefficient

The energy expended during SDA markedly increased when the meal size increased from 0.5 to 12% (Fig. 5). There was no significant change in the SDA coefficient when the meal size increased from 0.5 to 12% (Table 1). The mean SDA coefficient in all experimental groups was 7.06 ± 0.40 (n = 60).

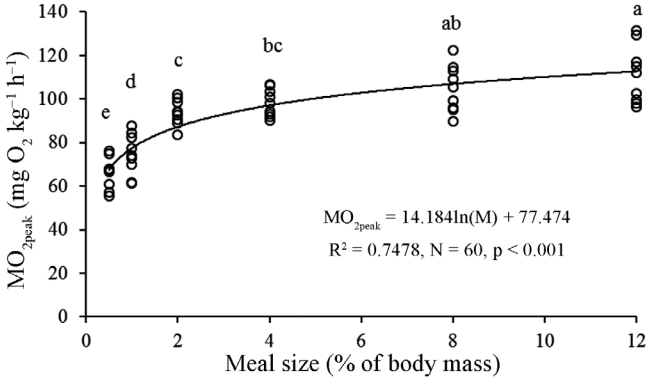

Fig. 3. Relationship between meal size (M) and peak oxygen consumption rate (MO_{2peak}) in Chinese giant salamander *Andrias davidianus* larvae. Values without a common lowercase letter are significantly different ($p < 0.05$)

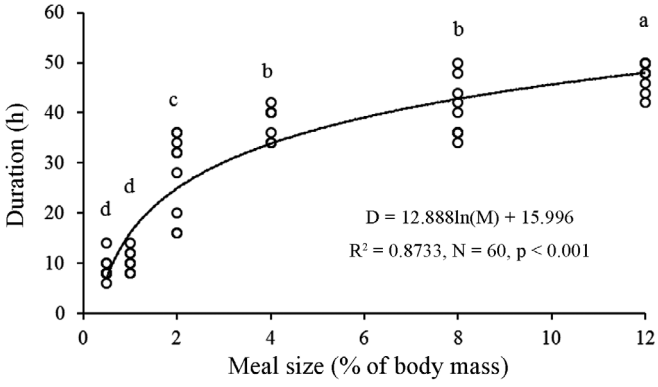

Fig. 4. Relationship between meal size (M) and specific dynamic action duration (D) in Chinese giant salamander *Andrias davidianus* larvae. Values without a common lowercase letter are significantly different ($p < 0.05$)

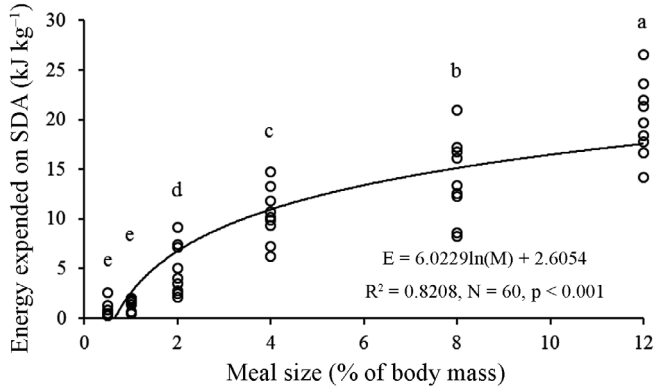

Fig. 5. Relationship between meal size (M) and the energy expended (E) on specific dynamic action (SDA) in Chinese giant salamander *Andrias davidianus* larvae. Values without a common lowercase letter are significantly different ($p < 0.05$)

4. DISCUSSION

4.1. Effect of meal size on MO_{2peak} in SDA

To date, there is no general consensus as to the effects of meal size on the MO_{2peak} of SDA for animals (Fu et al. 2006, Secor et al. 2007, Wang et al. 2012). Several studies on polar animals such as the Antarctic plunderfish *Harpagifer antarcticus* and limpet *Nacella concinna* found that there was no significant difference in MO_{2peak} among different meal sizes due to the animals' narrow metabolic scopes; the studied animals primarily relied on extending their digestive courses to meet their energy requirements (Boyce & Clarke 1997, Peck & Veal 2001). However, other studies have shown that MO_{2peak} increases linearly with increasing meal sizes in some fishes in Asia and amphibians in South America, such as the Chinese catfish *Silurus asotus* (Fu et al. 2006), marine toad *Bufo marinus* (Secor & Faulkner 2002) and Neotropical frog *Leptodactylus latrans* (Timpone et al. 2020), indicating that the postprandial metabolic increase is not limited by a ceiling associated with the cardiorespiratory gas transport capacity or the aerobic capacity of the gastrointestinal tract (Wang et al. 2001). The high MO_{2peak} may be conducive for rapid digestion of food in larger meal sizes and preparation for the next meal. In this study, MO_{2peak} increased logarithmically with meal size and plateaued in the large meal sizes (8–12% body mass) of *Andrias davidianus* larvae (Fig. 3). This trend suggests that the MO_{2peak} of *A. davidianus* does not increase linearly with increasing meal sizes, which is perhaps due to a limited metabolic capacity of the digestive system of *A. davidianus* larvae during the digestion of large meals. The limited MO_{2peak} of *A. davidianus* larvae may not be beneficial for the rapid digestion of food at larger meal sizes. Similar logarithmic relationships between meal size and MO_{2peak} have been found in animals such as the largemouth bass *Micropterus salmoides* (Beamish 1974), plaice *Pleuronectes platessa* (Jobling & Davies 1980), southern catfish *Silurus meridionalis* (Fu et al. 2005a) and water python *Liasis fuscus* (Bedford & Christian 2001).

The average factorial metabolic scope of amphibians is 3.43, as reviewed by Secor (2009), and the largest postprandial scopes (6.5–11.6 fold) are exhibited by 3 anuran species (*Bufo alverius*, *Ceratophrys ornata*, and *Pyxicephalus adspersus*) (Secor 2005). A previous study found that the factorial metabolic scope was 4.27 in the 12.5% relative meal for *Ambystoma tigrinum tigrinum* at 25°C (Secor & Boehm 2006). In this study, the factorial metabolic scope of

A. davidianus increased with meal size and levelled off at higher meal sizes within the studied range. The factorial metabolic scope was only 2.1 in the 12% relative meal size group, a value that was relatively lower than those obtained in other documented work on amphibian species (Secor & Faulkner 2002, Secor & Boehm 2006, Secor et al. 2007, Timpone et al. 2020). This result may be related to the limited MO_{2peak} of the species at larger meal sizes.

4.2. Effect of meal size on SDA duration

Changes in SDA duration with increasing meal size might be species-dependent (Secor & Faulkner 2002, Fu et al. 2006, Secor et al. 2007, Pang et al. 2009, Timpone et al. 2020). A previous study found that meal size did not have a significant effect on SDA duration in crucian carp *Carassius auratus* (Pang et al. 2009). Some amphibians did not show profoundly increased SDA duration in a high meal size range, such as the neotropical frog (Timpone et al. 2020), marine toad (Secor & Faulkner 2002) and tiger salamander (Secor & Boehm 2006). In this study, the SDA duration of *A. davidianus* increased with increasing meal size, implying that after ingesting a large meal, this species needs more time to complete digestion before the next feeding. *A. davidianus* usually prefer to hide in refuges such as rock crevices and caves after feeding. The prolonged duration of SDA in the high meal size range may be related to this habit of digesting. Similar results were also found in previously published studies (Fu et al. 2005a, 2006, Wang et al. 2012).

Amphibians usually have relatively long SDA durations (Secor 2009). Previous studies found that SDA durations vary from 1 to 9 d for amphibians digesting meals from 1 to 10% of their body mass (Wang et al. 1995, Secor et al. 2007). In this study, the minimum and maximum SDA durations determined for *A. davidianus* were approximately 9 h at a 0.5% meal size and 47 h at a 12% meal size, respectively; these durations were relatively shorter than those of other amphibians (Secor 2009). The results from this study suggested that feeding once every 2 d to satiation may be a suitable feeding frequency for *A. davidianus* larvae during artificial rearing. Many studies on amphibians have revealed that the digestion and assimilation of soft-bodied prey (earthworms, salamanders, grubs, earthworms and moth larvae) generated smaller SDA responses than the digestion of hard-bodied prey (beetle larvae, beetles and crickets); this difference could be attributed to the smaller effort required to break down and assimilate soft-bodied prey compared to that used to digest the hard chitinous exoskeletons of insect prey (Secor & Faulkner 2002, Secor & Boehm 2006, Secor et al. 2007, Secor 2009). Previous studies found that the SDA durations of the marine toad and tiger salamander were 5 and 6 d when the animals digested rodent and adult cricket meals equaling 10% of their body mass, respectively (Secor & Faulkner 2002, Secor & Boehm 2006). Therefore, the relatively short SDA duration of *A. davidianus* may be the result of the food (chironomid larvae) selected in this study being more easily ingested, digested and evacuated.

4.3. Effect of meal size on the SDA coefficient

The SDA coefficient of *A. davidianus* ranged from 6.0 to 8.5 in this study; these values are lower than that obtained for most amphibians (7.9–52.5%, average 23.3%; see reviews in Secor 2009). Priede (1985) suggested that natural selection allows animals to adopt specific strategies to maximize their energy income and expenditure ratios. The smaller SDA coefficient (average of 7.1%) obtained for *A. davidianus* indicates that the energy consumption required to digest food accounts for a small proportion of the food energy and that a larger proportion of food energy could be reserved for other activities such as growth and temperature regulation (Wang et al. 2012).

The relationships between SDA coefficients and meal sizes vary among different species (Secor & Faulkner 2002, Fu et al. 2005a, 2006, Secor et al. 2007, Wang et al. 2012, Timpone et al. 2020). Several studies have found that SDA coefficients decrease with increasing meal sizes (Boyce & Clarke 1997, Robertson et al. 2002, Fu et al. 2006, Wang et al. 2012). This may result from the energetic cost of processing a meal being fixed and independent of the meal size and the startup costs of processing a meal being similar at different meal sizes (Boyce & Clarke 1997, Robertson et al. 2002). In contrast, some work on python species found that the SDA coefficient increased with an increasing meal size (Soofiani & Hawkins 1982, Chakraborty et al. 1992, Secor & Diamond 1997, Secor & Faulkner 2002, Secor et al. 2007). A possible explanation for the disproportionately greater costs of digesting larger meals is the further upregulation of the function of the gastrointestinal tract of these species and the additional recruitment of intestinal nutrient transporters (and other cellular activities) with larger meals (Secor & Faulkner 2002, Secor et al. 2007). However, *A. david-*

ianus exhibited a characteristic curvilinear relationship between SDA and meal energy, and the SDA coefficient was not significantly altered with varying meal sizes in this study. Constant SDA coefficients at different meal sizes have been reported in most previously studied species, such as the common carp *Cyprinus carpio* (Chakraborty et al. 1992), southern catfish *S. meridionalis* (Fu et al. 2005a), black carp *Mylopharyngodon piceus* (Li et al. 2018), tiger salamander *A. tigrinum tigrinum* (Secor & Boehm 2006), Neotropical frog *L. latrans* (Timpone et al. 2020), fire-bellied toad *Bombina orientalis*, Great Plains toad *Bufo cognatus*, bubbling kassina *Kassina senegalensis* and American bullfrog *Rana catesbeiana* (Secor et al. 2007). These results suggested that these animals attained no net energetic gain by feeding on larger prey (Secor & Boehm 2006, Timpone et al. 2020).

5. CONCLUSIONS

Andrias davidianus larvae prolong digestion time to meet increased energy demands, as shown by the lower factorial metabolic scope of the species leading to MO_{2peak} values levelling off at large meal sizes. Moreover, *A. davidianus* larvae have a relatively small SDA coefficient that is not affected by meal size, contrary to that of other species. When fed chironomid larvae in this study, the SDA duration was approximately 48 h at the maximum meal size (12% body mass). The digestive physiological data of *A. davidianus* recorded for the first time in this study can provide an important reference, such as feeding frequency and meal size, for the artificial culture of the species.

Ethics approval. This study complied with the current law of the country in which it was performed and was approved by the Animal Care and Use Committee of the Key Laboratory of Animal Biology of Chongqing (permit number Zhao-20,151,010-01). The study was performed in strict accordance with the recommendations in the Guide for the Care and Use of Animals at the Key Laboratory of Animal Biology of Chongqing, China. All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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