

## Article

# Allometric Growth Patterns and Ontogenetic Development during Early Larval Stages of *Schizothorax waltoni* Regan and *Percocypris retrodorslis* in Southwest China

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**Abstract:** Due to a sharp decline in resources, *Schizothorax waltoni* Regan and *Percocypris retrodorslis* have been listed as wildlife under second-class protection in China. Under culture conditions, the early development and allometric growth patterns of *S. waltoni* and *P. retrodorslis* were researched from the hatching stage to 60 DPHs (days post-hatching), and a sampling of ten to fifteen larvae was made every day, followed by measurements with Axio Vision 4.8 software (Carl Zeiss AG, Jena, Germany). Morphological indicators included the anal fin length, the body depth, the body depth at the anus level, the caudal fin length, the dorsal fin length, the eye diameter, the head length, the head depth, the pectoral fin length, the tail length, the trunk length, the snout length, the total length, and the ventral fin length. Based on the morphology development of *S. waltoni* Regan and *P. retrodorslis*, four periods of larval growth were identified: pre-flexion larvae at 0–14 DPHs and 0–16 DPHs; flexion larvae at 14–23 DPHs and 16–26 DPHs, post-flexion larvae at 23–50 DPHs and 26–52 DPHs, and the juvenile stage. In newly hatched larvae, most organs and body parts were not differentiated, and they successively developed within 26 DPHs. The depletion of the yolk sac was observed at 23 DPHs and 25 DPHs. Allometric growth mainly occurs in the head and tail regions, indicating that body parts related to feeding and swimming behaviors were more important than the other parts. In addition, the growth pattern shows that the development of organs gives priority to the functions of gill respiration, sensation, exogenous feeding, and swimming. The inflection points of body part growth patterns only appeared before 40 DAH, so future studies should concentrate focus on developing the best feeding from the first feeding to 40 DAH. These outcomes were discussed with regard to the ontogeny of the functional morphology in relation to ecology and aquaculture. It is expected that this research can provide valuable perspectives in species conservation.

**Keywords:** morphology; *Schizothorax waltoni* Regan; *Percocypris retrodorslis*; larval development; growth coefficient



**Citation:** Xu, B.; Li, D.; Wei, K.; Zhu, X.; Xu, J.; Ma, B. Allometric Growth Patterns and Ontogenetic Development during Early Larval Stages of *Schizothorax waltoni* Regan and *Percocypris retrodorslis* in Southwest China. *Water* **2023**, *15*, 824. <https://doi.org/10.3390/w15040824>

Academic Editor: Jan Kubečka

Received: 16 January 2023

Revised: 15 February 2023

Accepted: 17 February 2023

Published: 20 February 2023



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## 1. Introduction

The early-stage ontogeny of most fishes is characterized by extensive variability expressed in the morphology and function of many organs and systems. The physiological and behavioral abilities during the early growth stages are determined by these variations. From the perspectives of structure and function, morphogenesis is controlled by genetic and environmental elements and induces shape changes and sudden or gradual variations in various morphological characteristics. Starvation, predation, and other factors are considered to be some of the main regulating factors for larval survival, affecting the recruitment and intensity of wild populations and seed quality under culture conditions [1,2]. Because most functional systems of fishes are incomplete while hatching, morphogenesis is intense at the early stages of development. Morphological variations during this period transform the newly hatched larvae into juvenile or advanced fry forms in a short time, indicating that

the development function improves survival, which is an ordinary characteristic among teleost fish [3]. An accurate evaluation of the nutritional status, growth rate, and change rule of the early stages of the larvae and juveniles will help to find and control the factors that affect the early survival rate and growth rate of these fish so as to improve their growth and survival rate [4]. These facts relate to the relevant changes in the association between developing larvae and environmental conditions and the increase in fish size, which is caused by differential relative development patterns defined as allometry [4–6].

Allometry is an ordinary characteristic during early larval growth, guaranteeing that the organs used for the most significant functions are developed first, followed by the growth of organs with a lower survival priority [7–10]. Studying the allometric growth of fish at the early stage is one of the most important parts of studying the early life history of fish, which is of great significance to fish classification and species conservation [7]. Determining relative growth patterns during early growth stages is conducive to the management of fishery resources and fish farming through promoting normal development patterns in some conditions and improving feeding methods in the case of examined abnormal larval growth. *Schizothorax waltoni* Regan, 1905, which belongs to *Schizothorax* Heckel of Cyprinidae, is mainly distributed in the trunk and tributaries of the Xigaze to the Milin section of the Yarlung Zangbo River. This species is an omnivorous fish, and it mainly feeds on benthic invertebrates and algae [11,12]. *Percocypris retrodorslis*, which belongs to *Percocypris* of Cyprinidae, is mainly distributed in the Lancang River and Nujiang River systems; it is a carnivorous fish mainly feeding on small fish, but it also eats crustaceans, insects, and other larvae [13,14]. These two species of fish live in rivers originating from Tibet. At present, the phenomenon of overfishing is still relatively serious [15], especially in some populated and economically developed areas, such as the middle reaches of the main stream of the Yarlung Zangbo River and Lancang River, which have been overfished with a miniaturized catch, indicating that fish resources have begun to decline, as well as highlighting the urgency to strengthen the management of fishery resources [11]. Due to the sharp decline in resources, they have been listed as wildlife under second-class protection in China [16]. So far, data on the early life history of *S. waltoni* and *P. retrodorslis* are extremely limited. The present study has aimed to illustrate the early morphological development and allometric growth patterns of *S. waltoni* and *P. retrodorslis* larvae and juvenile specimens from their hatching up to 60 days post-hatching (DPHs) under controlled conditions, so as to understand the adaptations of the priorities during early development and improve artificial rearing technology.

## 2. Materials and Methods

### 2.1. Source and Culture Conditions of the Larvae

In this study, the fertilized eggs of parent fish were bred by the research group. The parent fish were caught in natural waters and transported by air to the Wolong Base of Aquatic Institute of Sichuan Academy of Agricultural Sciences for breeding. Twenty females and twenty males were kept in ponds (10 m long, 4 m deep and 1.5 m high). Each pond provided filtered karst water (100 L/min) from the intake. The culture conditions were as follows:  $15 \pm 1$  °C (water temperature),  $6.93 \pm 0.25$  mg/L (concentration of water dissolved oxygen), and pH  $8.08 \pm 0.09$ . The *Limnodrilus* and special feed for salmon (0.8 # salmon feed produced by Chengdu Gran Company, 58% protein content, sediment feed) were fed together. The feeding amount was 2–6% of the fish weight, twice a day.

The total length of the female *S. waltoni* was 464–628 mm, with a weight of 749–1874 g, while the total length of the males was 352–524 mm, with a body weight of 386–1125 g. The total length of the female *P. retrodorslis* was 504–940 mm, with a weight of 1540–9300 g, while the total length of the male fish was 350–409 mm, with a weight of 460–750 g. All the females were over 8 years old and the males were over 4 years old. Carp pituitary (PG), a luteinizing hormone-releasing hormone analogue (LRH-A<sub>2</sub>), and human chorionic gonadotropin (HCG) were used to induce artificial breeding. The drugs were injected into the abdominal cavities of the fish twice. *S. waltoni* drugs used for the first injection of females

contained HCG (300–500 IU/kg) and LRH-A<sub>2</sub> (2–5 µg/kg), and drugs for the second injection consisted of HCG (800–1000 IU/kg), LRH-A<sub>2</sub> (4–7 µg/kg), and PG (5–6 mg/kg). *P. retrodorslis* drugs used for the first injection of females included PG (5 mg/kg), LRH-A<sub>2</sub> (2–5 µg/kg), and HCG (100–300 IU/kg), while the second injection of drugs consisted of PG (10 mg/kg), LRH-A<sub>2</sub> (5–10 µg/kg), and HCG (1000–2000 IU/kg). Male fish were injected only once, and the dose was half that of the female fish. The first and second needles were separated by 24 h, and the fertilized eggs were obtained by artificial dry fertilization. More than 50,000 fertilized eggs were obtained. We observed the embryo development through microscopic examination and picked out the white eggs. The hatching rates were as high as 95% in both species.

Incubation water was filtered with karst cave water introduced upstream with a constant water temperature of  $15 \pm 1$  °C during the test. The water temperature was near optimal for larvae growth and survival [11–14]. The water was filled with oxygen using an air pump, and the dissolved oxygen was maintained above 7.0 mg/L. The incubation basin was a round, glass, fiber-reinforced plastic basin with a diameter of 1.2 m and a water depth of 0.2 m (volume 226 L), and 5–20 incubation basins were used (about 10,000 larvae per container). With the growth of the fish fry, the density of the larvae was gradually decreased from 50 specimens/L to 10 specimens/L. Each seedling basin was provided with filtered karst water (100 L/h) from the top, and the drainage hole was located at the bottom of the center of the seedling basin. Then, the drainage hole was covered with a mesh with a diameter of 300 µm to prevent the loss of the larvae. It was cultured in running water for 24 h and aerated daily. The larvae were acquired by artificial spawning held under controlled conditions (15 °C, 12L:12D photoperiod). The placement of newly hatched larvae was made in a circulating water system. The culture conditions were as follows:  $15 \pm 1$  °C (water temperature),  $7.02 \pm 0.13$  mg/L (concentration of water dissolved oxygen), 12L:12D (artificial lighting), and 500 lux (illumination strength at the water surface) [10].

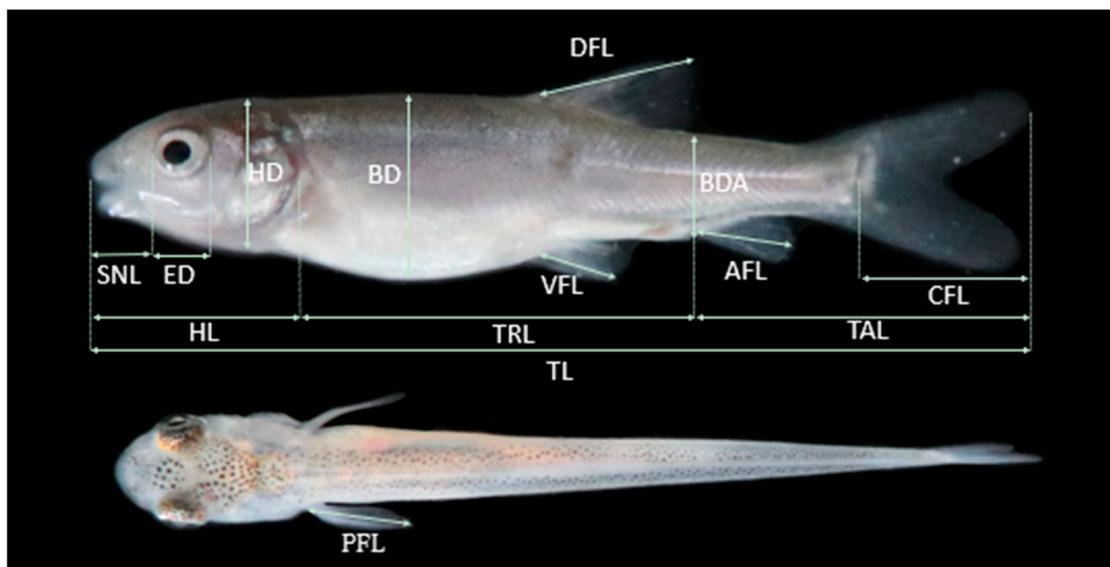
## 2.2. Feeding Management

The feeding of larvae started at 5 DPHs. At first, the feeding was basically carried out with rotifers (*Brachionus plicatilis*), improved with *Chlorella* sp., and the concentration was about 30,000 cells/mL. Rotifers were provided three times a day. Exogenous feeding generally conforms to the whole pigmentation in the eyes, as representatively shown for other fish larvae [17,18]. The larvae from the mouth opening were fed with rotifers at a density of 4 rotifers/mL until 8 DPHs. *Artemia nauplii* (Tianjin Red Sun Aquaculture, Tianjin, China) was fed from 9 DPHs to 23 DPHs with a density of 5 nauplii/mL. Juvenile *Artemia* were fed to the larvae from 24 DPHs until 60 DPHs with a density of 0.1 juvenile/mL. The survival rates of both larvae exceeded 90%.

## 2.3. Morphological and Morphometric Features of Larval Developmental Stages

The larvae from every rearing tank were sampled (before feeding in the morning,  $n = 10$ –15) each day from 0 DPHs to 60 DPHs [8,10]. The larvae were observed with the Olympus SZ61 (Olympus Co., Ltd., Tokyo, Japan) and photographed using a digital camera (EOS 6D; Canon, Tokyo, Japan). The sampled larvae were euthanized with a dose of MS-222 (Sigma-Aldrich, Shanghai, China; dose: 50 mg/L). A total of 955 *S. waltoni* larvae and 671 *P. retrodorslis* larvae were sampled. Each specimen was classified into one of the four ontogenetic periods according to Kendall et al. (1984), i.e., pre-flexion, flexion, post-flexion, and juvenile larvae periods [19]. These development characteristics were considered to be achieved when at least 50% of the specimens represented this particular stage ( $n = 50$ –100). On every digital photograph, some body ratios in relation to ingestion and movement were measured to the nearest 0.01 mm. These indicators included the following: the anal fin length (AFL), the body depth (BD), the body depth at the anus level (BDA), the caudal fin length (CFL), the dorsal fin length (DFL), the head length (HL), the head depth (HD), the eye diameter (ED), the pectoral fin length (PFL), the tail length (TAL), the trunk length (TRL), the total length (TL), the snout length (SNL), and the ventral fin

length (VFL) (Figure 1). Among them, the pectoral fin differentiated after the hatching stage, and it was measured since the age of 0 days, while the other fins were measured separately after the differentiation. The fin length refers to the linear distance from the starting point of the outer base of each fin to the end of the longest fin.



**Figure 1.** Schematic diagram of morphological and metric indicators in the larvae. AFL, anal fin length; BD, body depth; BDA, body depth at anus level; CFL, caudal fin length; DFL, dorsal fin length; HL, head length; HD, head depth; ED, eye diameter; PFL, pectoral fin length; SNL, snout length; TAL, tail length; TRL, trunk length; TL, total length; VFL, ventral fin length.

#### 2.4. Allometric Growth

Calculations of the allometric development of 13 morphometric characters were made from hatching until 60 DPHs. The significant differences were determined by the *t*-test using SPSS 22.0 (SPSS Inc., Chicago, IL, USA). The allometric development was shown as function:  $Y = aX^b$ , where dependent variable *Y* is the morphometrically measured characteristic, and independent variable *X* refers to the total length, *a* stands for the nodal increment, and *b* refers to the development parameter [6]. If *b* = 1, the development showed isometric growth; if *b* was greater than 1, the allometric development was positive growth; and if *b* was less than 1, the allometric development showed negative growth [6]. In addition, growth curves were calculated on the basis of van Snik et al. [5]. A statistical comparison of growth parameters was made with a *t* test for  $\alpha = 0.05$ . The morphological parameter data were then sorted according to the growth of *x*, standing for the TL. The regression lines were calculated for a minimum value of *X* until an alteration value of *X*; however, for an alteration value of *X* until a maximum value of *X*, an alteration value of *X* changed iteratively from a minimum value of *X* + 2 to a maximum value of *X* – 2, and a *t* test was also used to review whether the development parameters (minimum value of *X* to an alteration value of *X*) and (an alteration value of *X* to a maximum value of *X*) varied greatly ( $\alpha = 0.05$ ) [5,17,20,21]. The intermediate value of *X* that iteratively displayed the largest *t*-value referred to the inflexion point.

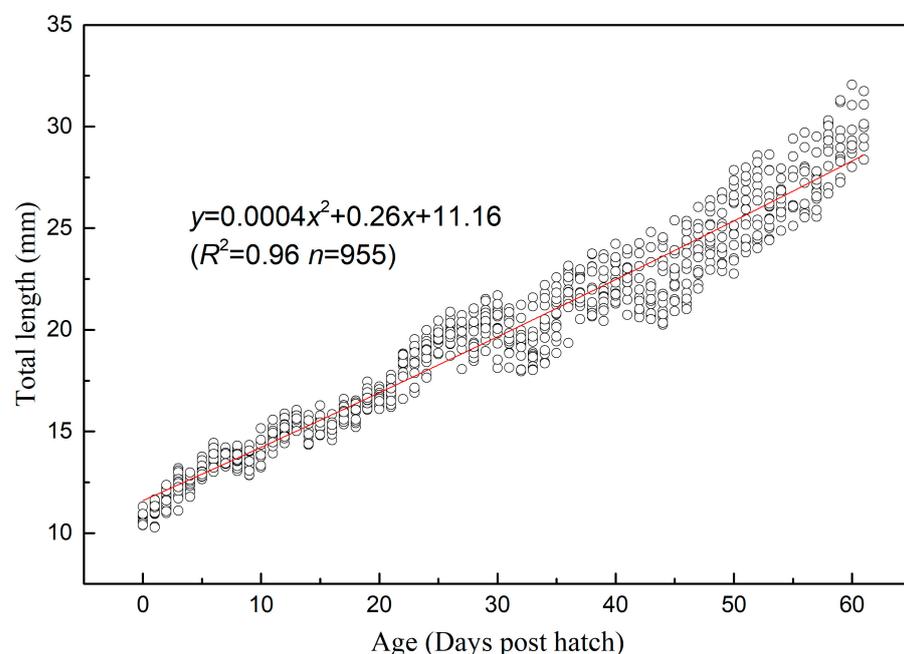
Statistical analysis was conducted with SPSS22.0 and Microsoft Excel (Microsoft, Washington, DC, USA). Origin Pro 9.0 (Origin Lab, Northampton, MA, USA). was adopted to create all figures.

### 3. Results

#### 3.1. Ontogenetic Development

##### 3.1.1. Ontogenetic Development of *Schizothorax waltoni*

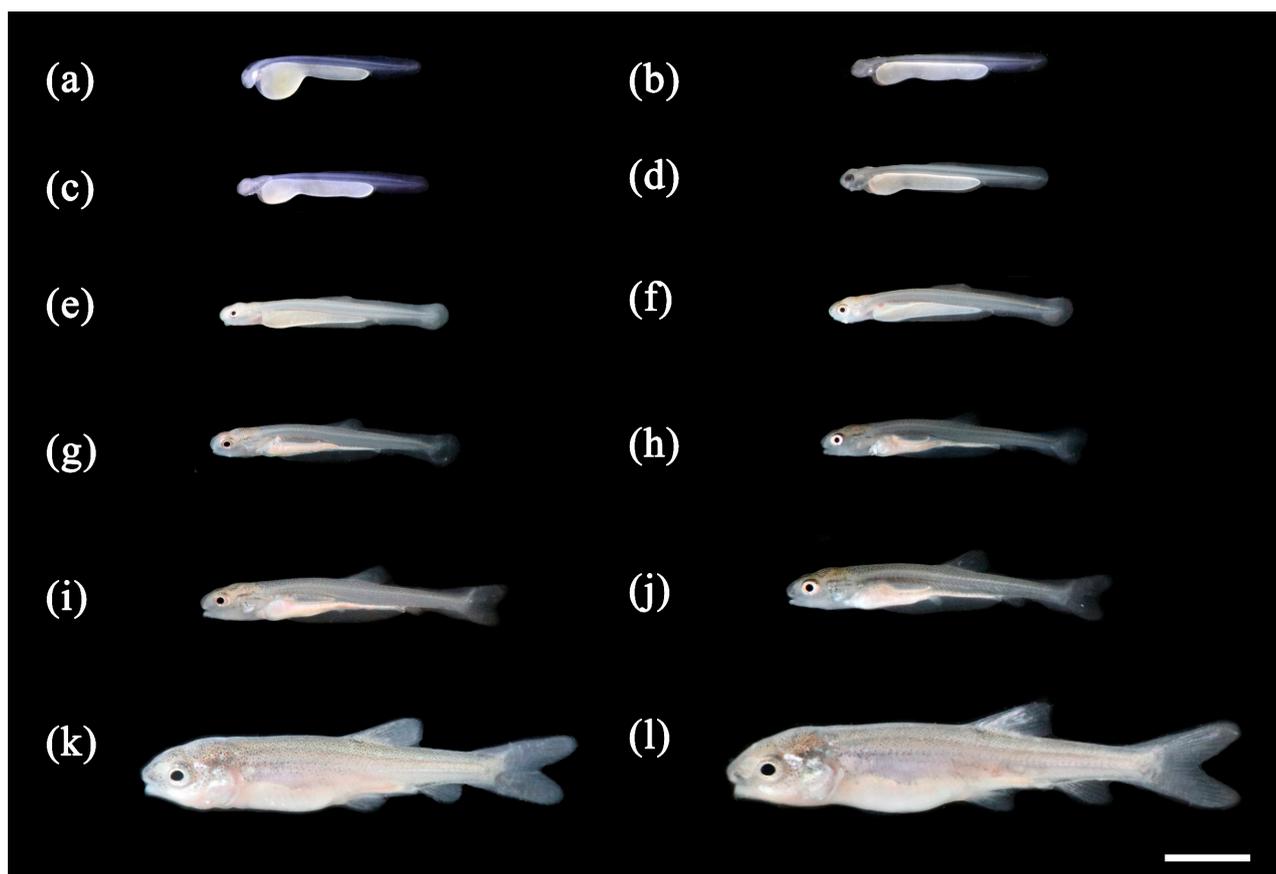
There was a second-order polynomial increase in the TL of *S. waltoni* from hatching to 60 DPHs ( $R^2 = 0.96$ ) (Figure 2). The TL of the *S. waltoni* increased by 19.39 mm (the average total length was 10.71 and 30.10 mm at 0 DPHs and 60 DPHs, respectively,  $n = 955$ ) (Figure 2). Larvae pre-flexion lasted from hatching to 14 DPHs. The larvae at 0 DPHs had large eyes without pigment (Figure 3a). We could observe light red chromatophores in the heart and yolk veins of the larvae, but no red chromatophores were observed in the heads, trunks, or tails. The pectoral fins were small behind the otoliths. The front part of the yolks were oval and the back parts were slender. The larvae laid on their sides on the bottom of the water and their tails swung two–four times per minute. Melanin appeared in the eyes at 1 DPHs (Figure 3b). At 2 DPHs, the eyes were filled with melanin and the branchial arches appeared (Figure 3c). At 4 DPHs, the mouths were opened, and the yolks decreased and became slender (Figure 3d). At the same time, movement capacity was enhanced. At 8 DPHs, there was more melanin on the dorsa and the abdomens of the larvae, and the yolks were further reduced (Figure 3e). Furthermore, the dorsal fins started to differentiate, while the larvae could only swim for a short time. At 11 DPHs, the first bladder chambers appeared (Figure 3f). The flexion larval stage lasted from 14 DPHs to 23 DPHs. At 16 DPHs, the dorsal fin strips appeared and the anal fins began to differentiate (Figure 3g). At 18 DPHs, the ventral fin primordia appeared (Figure 3h). At 23 DPH, the fin strips of the anal fins appeared, with the complete absorption of the yolk sacs (Figure 3i). The post-flexion larval stage duration lasted from 23 DPHs to 50 DPHs. At 25 DPHs, the second bladder chambers appeared (Figure 3j). At 50 DPHs, the fin folds of the larvae were completely absorbed (Figure 3k), and then the larvae entered the juvenile stage (Figures 3l and 4).



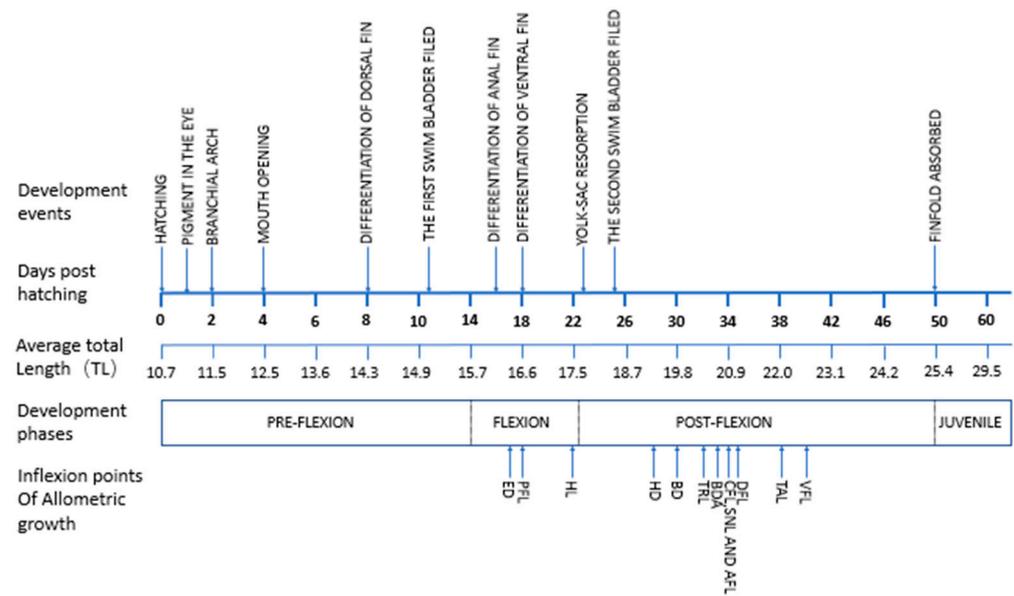
**Figure 2.** The correlation relationship between days post-hatch and total length of *S. waltoni* Regan during larval and juvenile periods.

### 3.1.2. Ontogenetic Development of *Percocypris retrodorslis*

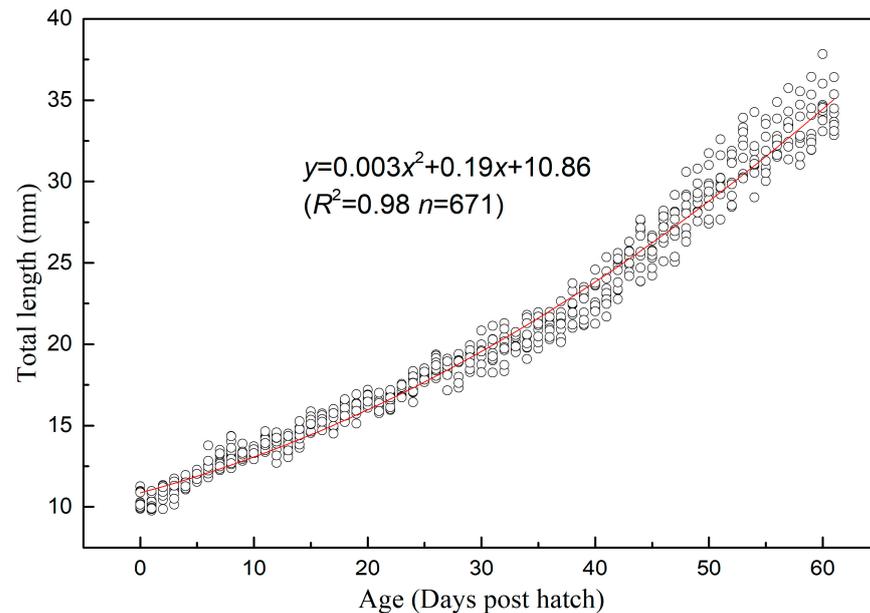
Growth of *P. retrodorslis* larvae followed a second-order polynomial curve, too (Figure 5). Until 60 DPHs, the TLs of the *P. retrodorslis* increased by 24.45 mm (the average total lengths were 10.29 and 34.74 mm at 0 DPHs and 60 DPHs, respectively;  $n = 671$ ) (Figure 5). The pre-flexion larval stage lasted from hatching to 16 DPHs. The newly hatched larvae had large eyes without pigment (Figure 6a). The front parts of the yolks were oval and the back parts were slender. The larvae laid on their sides on the bottom of the water with their tails swinging three–five times per minute. Melanin appeared in the eyes at 1 DPHs (Figure 6b). At 3 DPHs, the eyes were filled with melanin and the branchial arches appeared, and the yolks became long and columnar (Figure 6c). At 5 DPHs, the mouths were opened and movement ability was enhanced (Figure 6d). At 8 DPHs, there was more melanin on the heads and bodies of the larvae, with the yolks further reduced (Figure 6e). Furthermore, the dorsal fins started to differentiate. At 14 DPHs, the first bladder chambers appeared (Figure 6f). The flexion larval stage lasted from 16 DPHs to 26 DPHs. At 18 DPH, the anal fins began to differentiate (Figure 6g). At 25 DPHs, the ventral fin primordia appeared, with the depletion of yolk sacs. The post-flexion larval stage lasted from 26 DPHs to 52 DPHs. At 26 DPHs, the second bladder chambers appeared (Figure 6h). At 52 DPHs, the fin folds of the larvae were completely absorbed (Figure 6i), and then the larvae entered the juvenile stage (Figures 6k and 7).



**Figure 3.** Morphological development of *S. waltoni* Regan during larval and juvenile periods. Larvae at 0 DPHs, 10.71 mm TL (a); 1 DPHs, 11.20 mm TL (b); 2 DPHs, 11.59 mm TL (c); 4 DPHs, 12.57 mm TL (d); 8 DPHs, 13.81 mm TL (e); 11 DPHs, 14.78 mm TL (f); 16 DPHs, 15.17 mm TL (g); 18 DPHs, 16.01 mm TL (h); 23 DPHs, 18.35 mm TL (i); 25 DPHs, 19.65 mm TL (j); 50 DPHs, 25.41 mm TL (k); 60 DPHs, 30.10 mm TL (l). Scale bars = 5 mm.



**Figure 4.** Major growth events of *S. waltoni* during larval and juvenile periods. AFL, anal fin length; BD, body depth; BDA, body depth at anus level; CFL, caudal fin length; DFL, dorsal fin length; HL, head length; HD, head depth; ED, eye diameter; PFL, pectoral fin length; SNL, snout length; TAL, tail length; TRL, trunk length; TL, total length; VFL, ventral fin length.

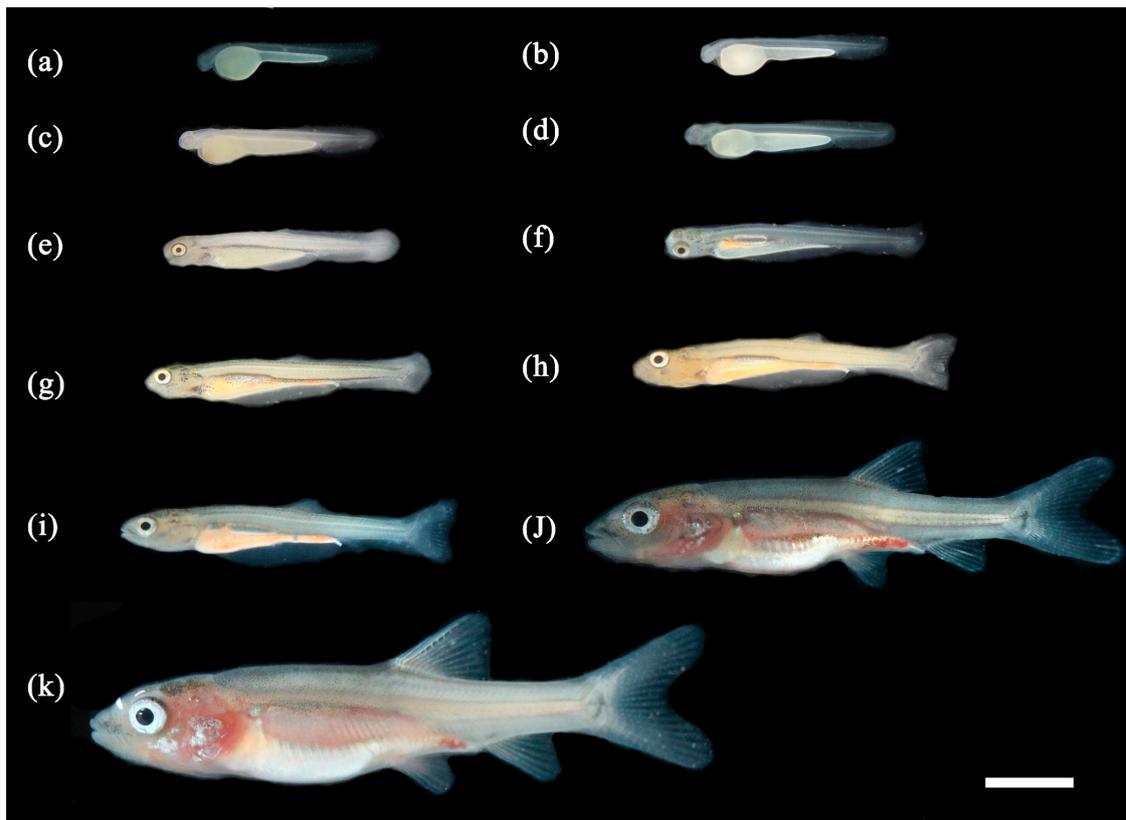


**Figure 5.** The correlation relationship between days post-hatch and total length of *P. retrodorsalis* during larval and juvenile periods.

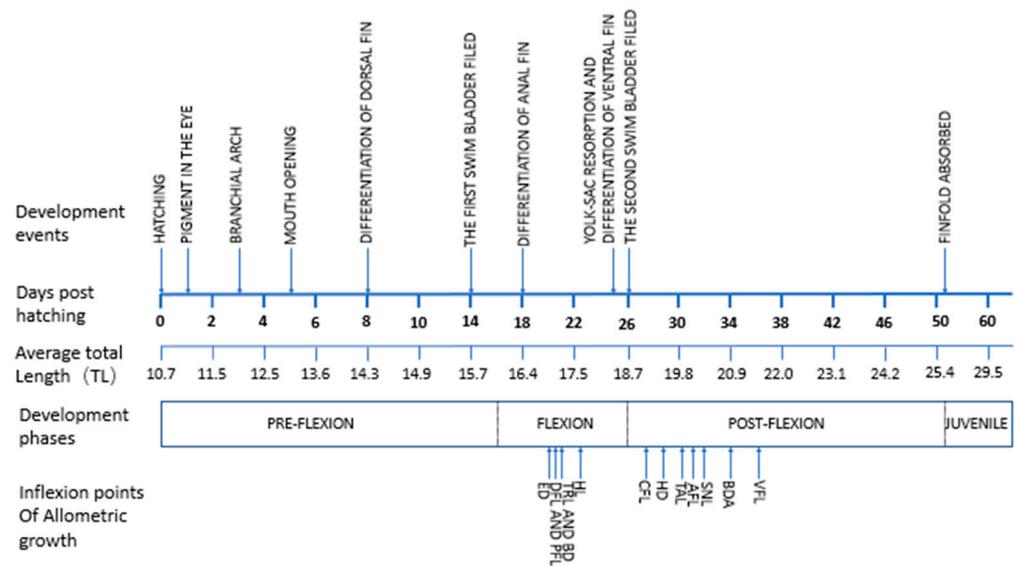
### 3.2. Allometric Growth Pattern

#### 3.2.1. Allometric Growth Pattern of *Schizothorax waltoni*

Twelve of the thirteen morphometric characters that were measured followed a positive allometric growth trend after hatching, except the trunk length (TRL), throughout the study period (Figure 8, Table 1). All the inflexion points were noted during the flexion phase and post-flexion phase.



**Figure 6.** Morphological development of *P. retrodorslis* during larval and juvenile periods. Larvae at 0 DPHs, 10.29 mm TL (a); 1 DPHs, 10.43 mm TL (b); 3 DPHs, 11.04 mm TL (c); 5 DPHs, 11.79 mm TL (d); 8 DPHs, 13.15 mm TL (e); 14 DPHs, 14.48 mm TL (f); 18 DPHs, 15.96 mm TL (g); 25 DPHs, 18.05 mm TL (h); 26 DPHs, 18.63 mm TL (i); 51 DPHs, 30.07 mm TL (j); 60 DPHs, 34.74 mm TL (k). Scale bars = 5 mm.



**Figure 7.** Major growth events of *P. retrodorslis* during larval and juvenile periods. AFL, anal fin length; BD, body depth; BDA, body depth at anus level; CFL, caudal fin length; DFL, dorsal fin length; HL, head length; HD, head depth; ED, eye diameter; PFL, pectoral fin length; SNL, snout length; TAL, tail length; TRL, trunk length; TL, total length; VFL, ventral fin length.

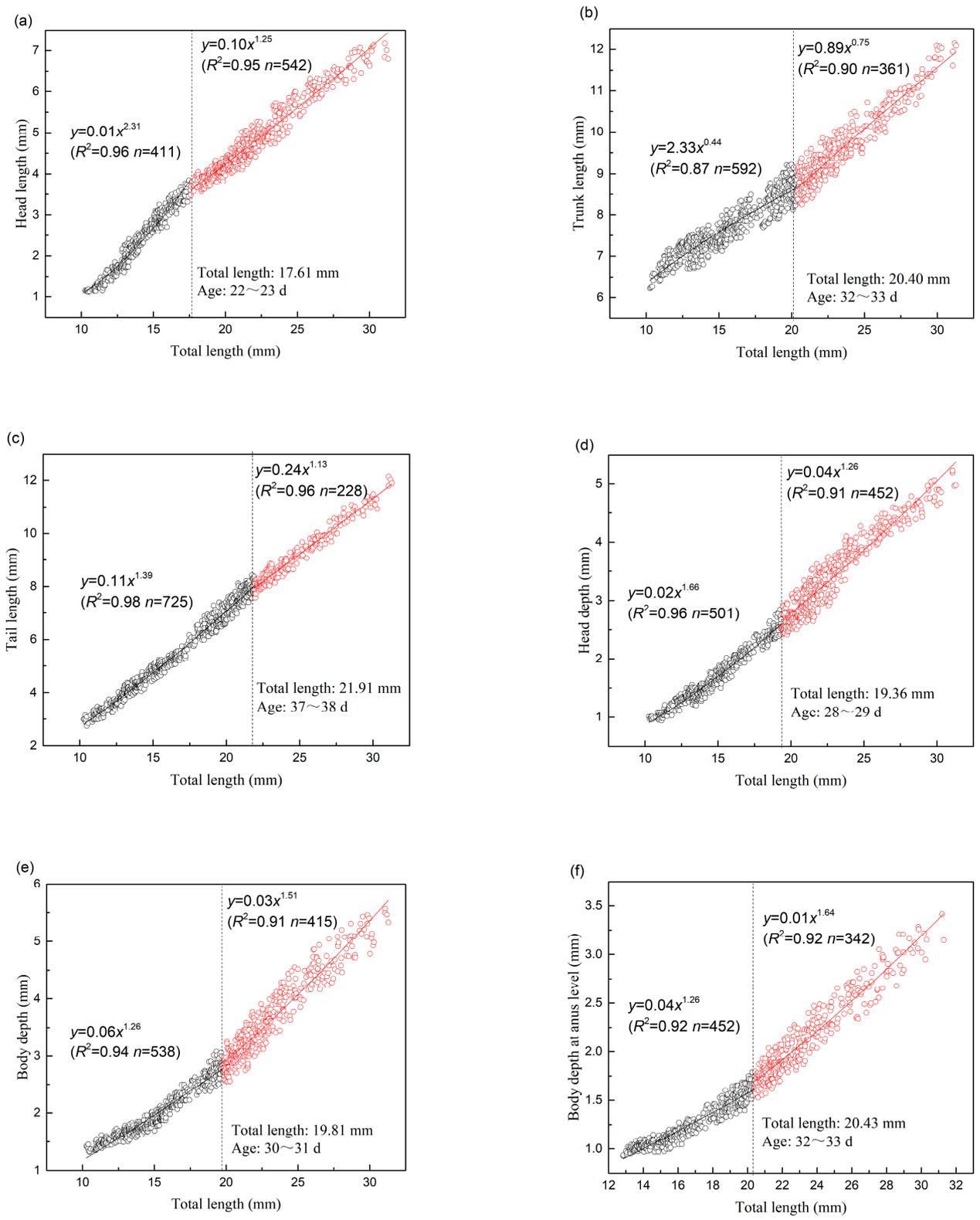


Figure 8. Cont.

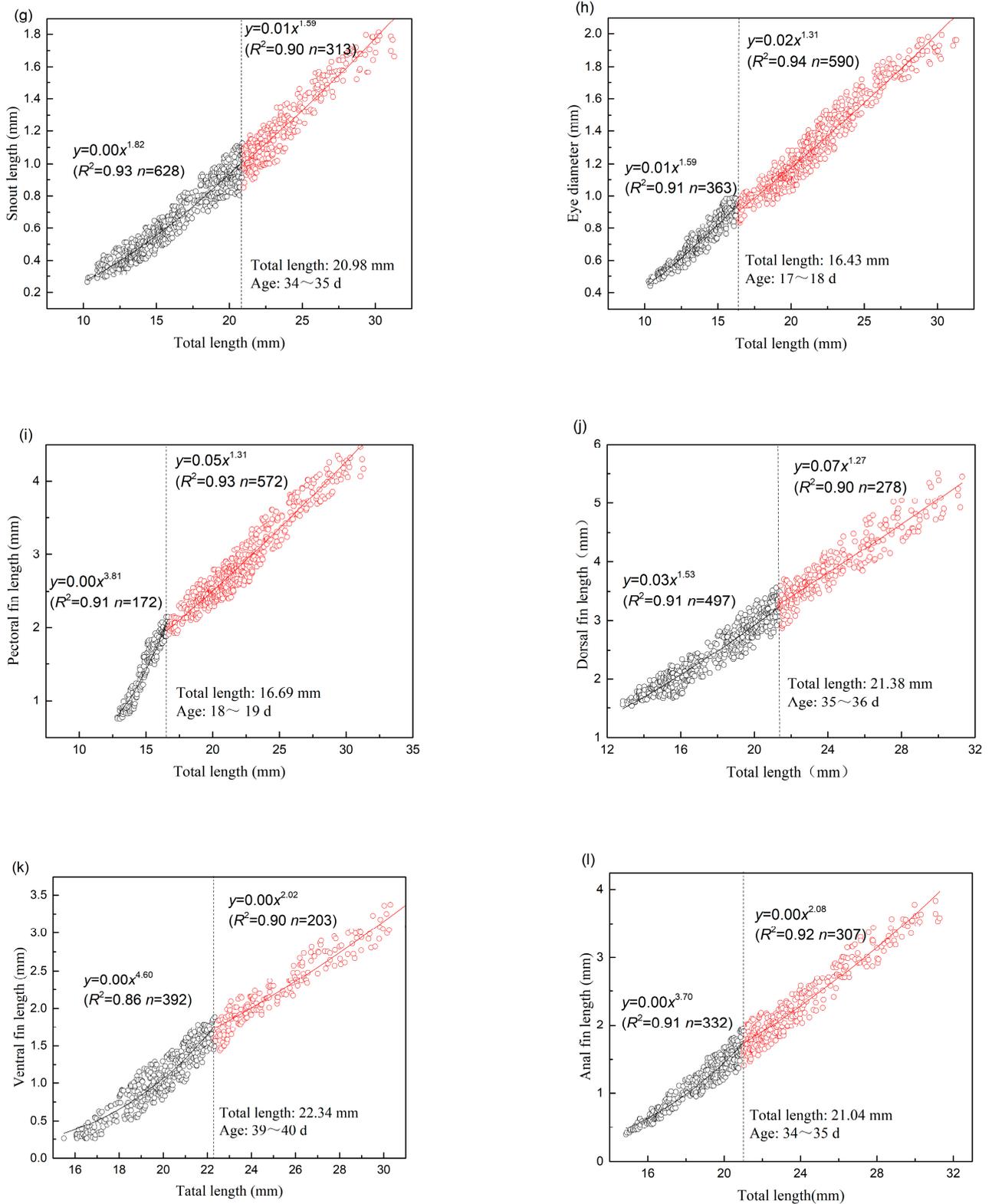
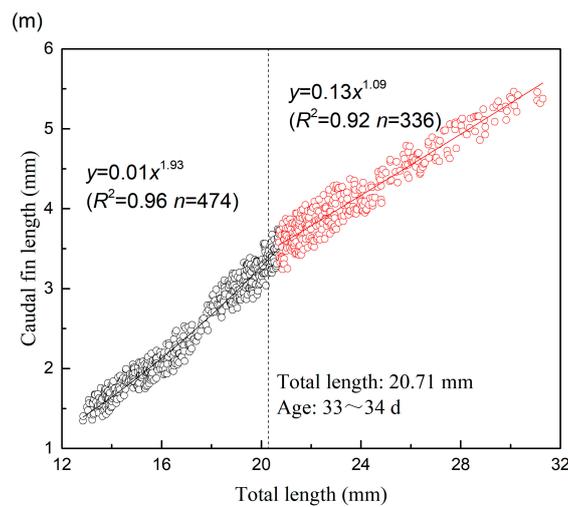


Figure 8. Cont.



**Figure 8.** Allometric growth curve and equations of *S. waltoni* during larval and juvenile periods. (a) Head length; (b) Trunk length; (c) Tail length; (d) Head depth; (e) Body depth; (f) Body depth at anus level; (g) Snout length; (h) Eye diameter; (i) Pectoral length; (j) Dorsal fin length; (k) Ventral fin length; (l) Anal fin length; (m) Caudal fin length. The line of dashes represents the body length and age of the inflexion point.

**Table 1.** Regression parameters for allometric growth of *S. waltoni* larvae.

Character	SL: Inflexion Point (mm)	Before Inflexion Point					After Inflexion Point				
		n	b	a	R <sup>2</sup>	p Value	n	b	a	R <sup>2</sup>	p Value
HL	17.61	411	2.313	0.005	0.955	0.022	542	1.252	0.098	0.947	0.039
TRL	20.40	592	0.436	2.327	0.865	0.019	361	0.752	0.894	0.899	0.045
TAL	21.91	725	1.387	0.11	0.982	0.041	228	1.127	0.244	0.964	0.039
HD	19.36	501	1.664	0.018	0.962	0.008	452	1.264	0.038	0.906	0.041
BD	19.81	538	1.261	0.064	0.941	0.011	415	1.506	0.032	0.905	0.046
BDA	20.43	452	1.263	0.036	0.916	0.004	342	1.642	0.012	0.916	0.014
SNL	20.98	628	1.823	0.004	0.927	0.004	313	1.591	0.008	0.895	0.006
ED	16.43	363	1.594	0.011	0.907	0.002	590	1.311	0.023	0.935	0.005
PFL	16.69	172	3.813	0.000	0.907	0.016	572	1.312	0.049	0.932	0.021
DFL	21.38	497	1.531	0.030	0.908	0.026	278	1.272	0.067	0.903	0.041
VFL	22.34	392	4.603	0.000	0.857	0.024	203	2.019	0.003	0.902	0.021
AFL	21.04	332	3.700	0.000	0.905	0.014	307	2.084	0.003	0.919	0.027
CFL	20.71	474	1.934	0.010	0.961	0.017	336	1.092	0.128	0.915	0.024

The HL (Figure 8a), HD (Figure 8d), SNL (Figure 8g), and ED (Figure 8h) showed positive allometric growth trends in relation to TL ( $b_1 = 2.31$ ,  $b_1 = 1.66$ ,  $b_1 = 1.82$  and  $b_1 = 1.59$ , respectively;  $b_1$  is the b-value before the inflexion point) prior to the inflexion point (17.61 mm, 19.36 mm, 20.98 mm, and 16.43 mm TLs, respectively), and then continued to showed positive but decreased allometric growth trends ( $b_2 = 1.25$ ,  $b_2 = 1.26$ ,  $b_2 = 1.59$ , and  $b_2 = 1.31$ , respectively;  $b_2$  is the b-value after the inflexion point) to 60 DPH (Figure 2a). The growth pattern of the TAL (Figure 8c) was positive allometric ( $b_1 = 1.39$ ) prior to its inflexion point (21.91 mm TL), and then isometric allometric afterwards ( $b_2 = 1.13$ ). The TRL (Figure 8b) displayed negative allometric development ( $b_1 = 0.44$ ) prior to the inflexion point (20.40 mm TLs), and then continued to show negative but increased allometric growth ( $b_2 = 0.75$ ). The BD (Figure 8e) and BDA (Figure 8f) showed positive allometric growth (both  $b_1 = 1.26$ ) prior to the inflexion point (19.81 mm and 20.43 mm TLs), and continued to show positive but increased allometric growth ( $b_2 = 1.51$  and  $b_2 = 1.64$ , respectively).

The PFL (Figure 8i), DFL (Figure 8j), VFL (Figure 8k), and AFL (Figure 8l) all showed positive allometric growth patterns ( $b_1 = 3.81$ ,  $b_1 = 1.53$ ,  $b_1 = 4.80$ , and  $b_1 = 3.80$ , re-

spectively) prior to the inflexion point (16.69 mm, 21.38 mm, 22.34 mm, and 21.04 mm TLs, respectively), and then continued to show positive but decreased allometric growth ( $b_2 = 1.31$ ,  $b_2 = 1.27$ ,  $b_2 = 2.02$ , and  $b_2 = 2.08$ , respectively). The growth pattern of the CFL (Figure 8m) was positive allometric ( $b_1 = 1.93$ ) prior to its inflexion point (20.71 mm TL), then isometric allometric afterwards ( $b_2 = 1.09$ ).

### 3.2.2. Allometric Growth Pattern of *Percocypris retrodorslis*

Twelve of thirteen morphometric characters were measured after a positive allometric growth after hatching, except the trunk length (TRL), throughout the studied period, too (Figure 9, Table 2). Thus, all the inflexion points were noted during the flexion phase and post-flexion phase, too.

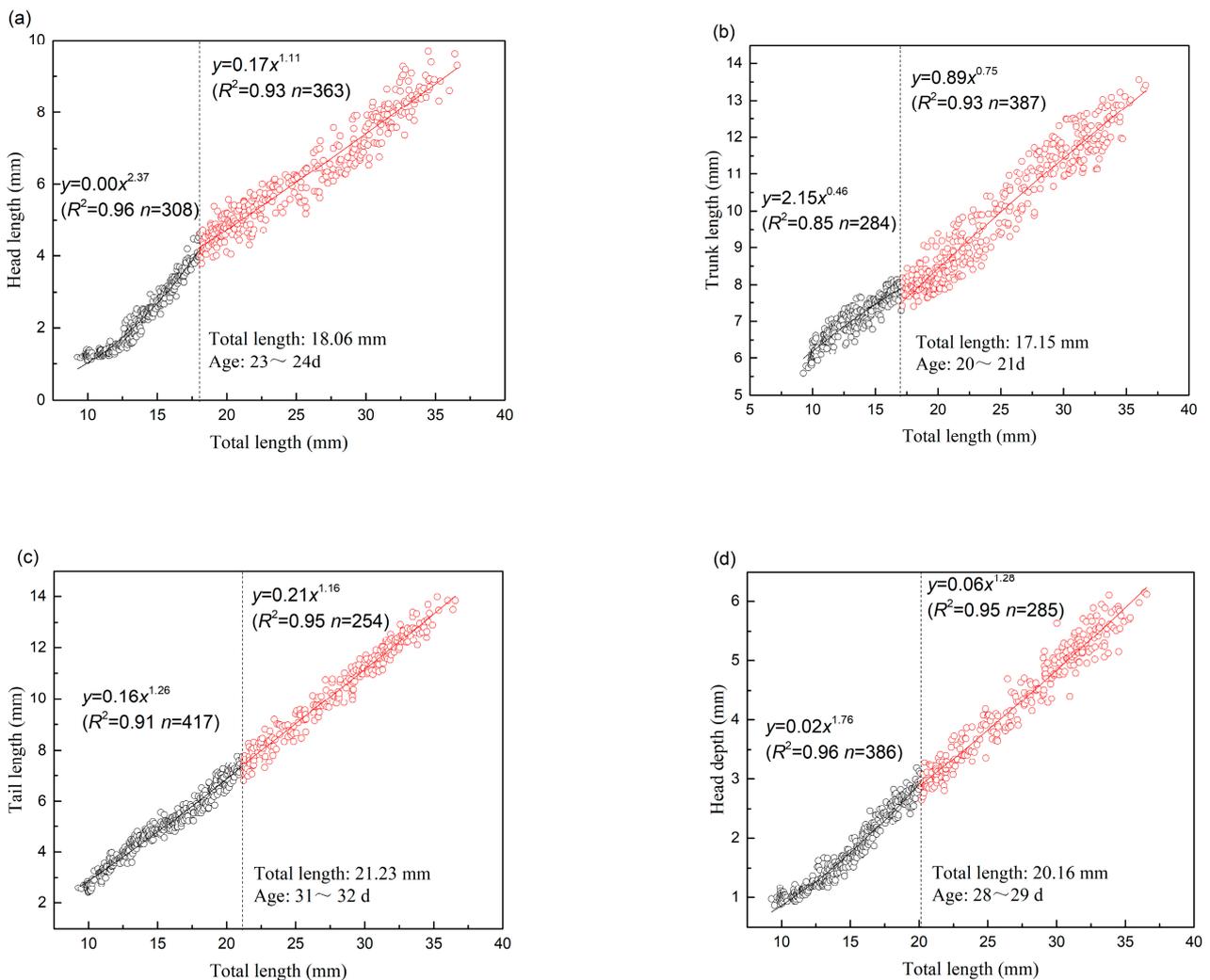


Figure 9. Cont.

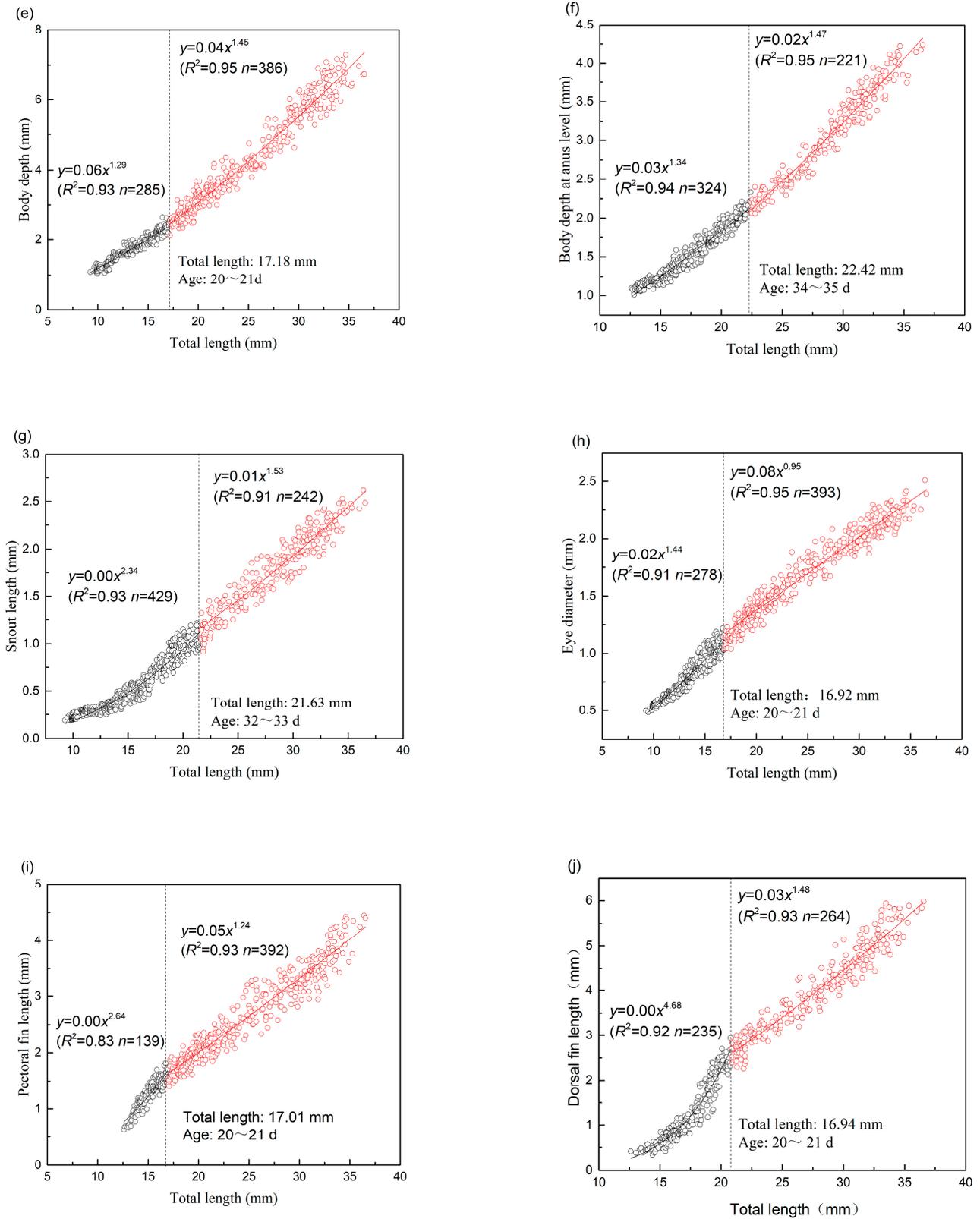
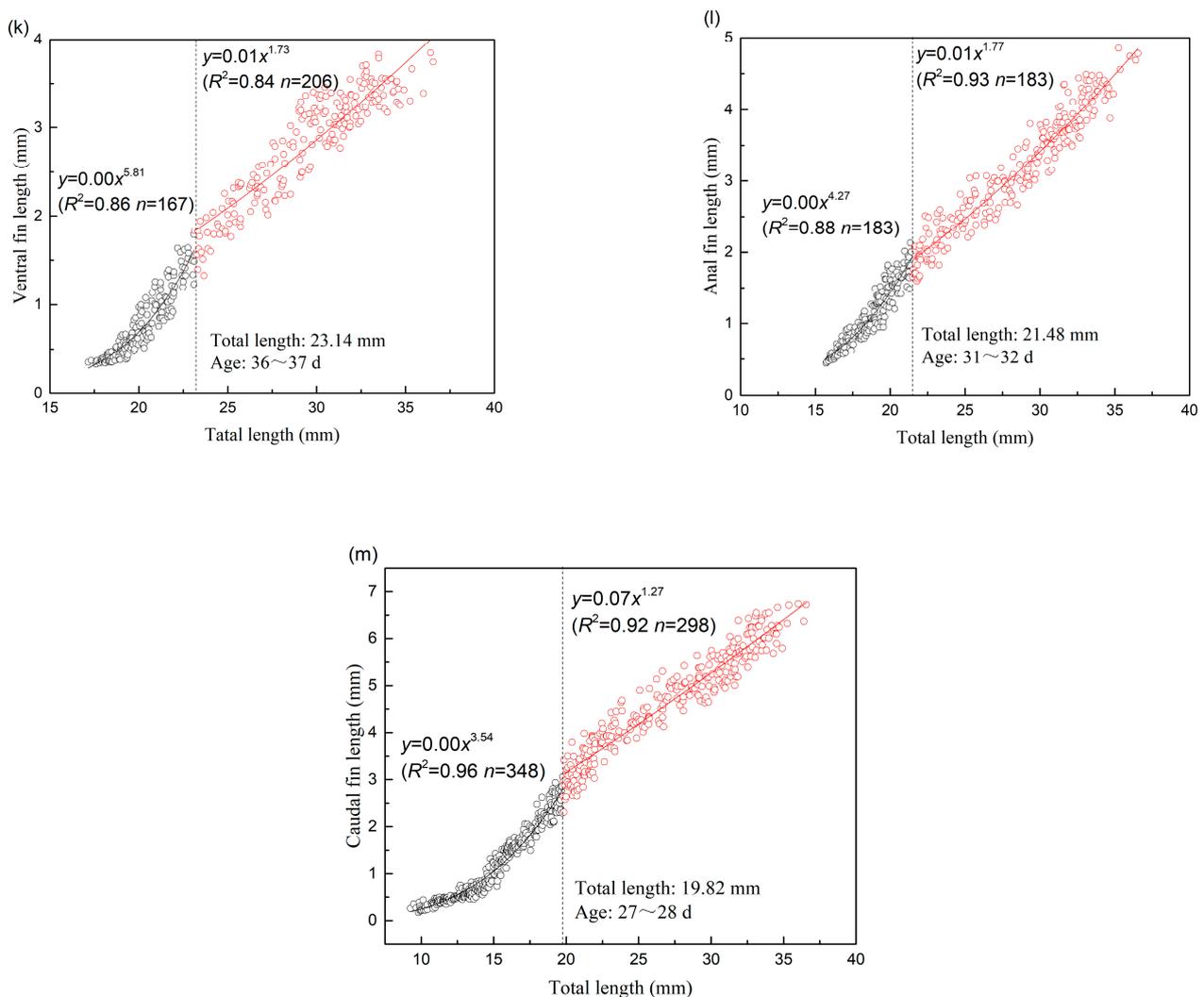


Figure 9. Cont.



**Figure 9.** Allometric growth curve and equations of *P. retrodorslis* during larval and juvenile periods. (a) Head length; (b) Trunk length; (c) Tail length; (d) Head depth; (e) Body depth; (f) Body depth at anus level; (g) Snout length; (h) Eye diameter; (i) Pectoral length; (j) Dorsal fin length; (k) Ventral fin length; (l) Anal fin length; (m) Caudal fin length. The line of dashes represents the body length and age of the inflection point.

The HL (Figure 9a), TAL (Figure 9c), and ED (Figure 9h) showed positive allometric growth trends in relation to TL ( $b_1 = 2.37$ ,  $b_1 = 1.26$ , and  $b_1 = 1.44$ , respectively) prior to the inflexion point (18.06 mm, 21.23 mm, and 16.92 mm TL), and then showed isometric allometric growth trends ( $b_2 = 1.11$ ,  $b_2 = 1.16$ , and  $b_2 = 0.95$ ). The growth patterns of the HD (Figure 9d) and SNL (Figure 9g) were positively allometric ( $b_1 = 1.76$  and  $b_1 = 2.34$ ) prior to the inflection point (20.16 mm and 21.63 mm TLs), and then continued to show positive but decreased allometric development ( $b_2 = 1.28$  and  $b_2 = 1.53$ ). The TRL (Figure 9b) showed negative allometric development ( $b_1 = 0.46$ ) prior to the inflexion point (17.15 mm TL), and then continued to show negative but increased allometric development ( $b_2 = 0.75$ ). The BD (Figure 9e) and BDA (Figure 9f) showed positive allometric development ( $b_1 = 1.29$  and  $b_1 = 1.34$ ) prior to the inflexion point (17.18 mm and 22.42 mm TLs), and then continued to show positive but increased allometric development ( $b_2 = 1.45$  and  $b_2 = 1.47$ ).

The PFL (Figure 9i), DFL (Figure 9j), VFL (Figure 9k), AFL (Figure 9l), and CFL (Figure 2m) all showed positive allometric growth patterns ( $b_1 = 2.64$ ,  $b_1 = 4.68$ ,  $b_1 = 5.81$ ,  $b_1 = 4.27$ , and  $b_1 = 3.54$ ) prior to the inflexion point (17.01 mm, 16.94 mm, 23.14 mm, 21.48 mm, and 19.82 mm TL, respectively), and then continued to show positive but

decreased allometric growth patterns ( $b_2 = 1.24$ ,  $b_2 = 1.48$ ,  $b_2 = 1.73$ ,  $b_2 = 1.77$ , and  $b_2 = 1.27$ , respectively).

**Table 2.** Regression parameters for allometric growth of *P. retrodorslis*.

Character	TL: Inflection Point (mm)	Before Inflexion Point					After Inflexion Point				
		n	b	a	R <sup>2</sup>	p Value	n	b	a	R <sup>2</sup>	p Value
HL	18.06	308	2.374	0.004	0.960	0.033	363	1.106	0.172	0.929	0.015
TRL	17.15	284	0.458	2.155	0.846	0.022	387	0.750	0.893	0.926	0.038
TAL	21.23	417	1.256	0.160	0.905	0.016	254	1.156	0.214	0.946	0.011
HD	20.16	386	1.757	0.015	0.958	0.016	285	1.283	0.061	0.950	0.045
BD	17.18	285	1.293	0.060	0.925	0.011	386	1.446	0.040	0.954	0.037
BDA	22.42	324	1.336	0.033	0.940	0.006	221	1.472	0.022	0.948	0.017
SNL	21.63	429	2.344	0.000	0.927	0.005	242	1.529	0.011	0.906	0.015
ED	16.92	278	1.440	0.019	0.905	0.003	393	0.945	0.081	0.947	0.007
PFL	17.01	139	2.644	0.001	0.827	0.013	392	1.242	0.049	0.926	0.042
DFL	16.94	235	4.678	0.000	0.915	0.017	264	1.479	0.029	0.927	0.035
VFL	23.14	167	5.816	0.000	0.859	0.019	206	1.727	0.008	0.836	0.039
AFL	21.48	183	4.274	0.000	0.883	0.021	183	1.774	0.008	0.928	0.044
CFL	19.82	348	3.538	0.000	0.956	0.025	298	1.266	0.071	0.916	0.046

#### 4. Discussion

Allometric development pattern is an ordinary approach and core element during the early growth of fishes, since key data on ecological and biological requirements and functional performance of fishes [19–24] are limited. During this period, the following conditions were found in the larvae: the appearance of pigment, eye development, mouth opening, bladder expansion, the differentiation of fins, removal of blockage, ingestion from the digestive tract, and the digestion of the first batch of exogenous feed.

After hatching, the larvae of *S. waltoni* and *P. retrodorslis* in this study were relatively large (total lengths of 10.71 mm and 10.29 mm, respectively) compared to other cyprinids larvae, such as *Horadandia atukori* [25] (2.3–2.6 mm), *Chela dadiburjori* [26] (2.4–2.6 mm), *Leuciscus leuciscus* [27] (an average total length of 7.47 mm), *Leuciscus cephalus* [28] (an average total length of 6.68 mm), and *Gobiocypris rarus* [23] (4–5 mm). The study of *Scomber scombrus* L. showed that temperature had a great impact on the growth and development stage of the larvae [29]. We only compared the early development of these fishes at the suitable temperature. The pigment in the eyes of *S. waltoni* and *P. retrodorslis* larvae appeared at 1 DPHs, just like *Aphyocypris chinensis* [30]. In contrast, the pigment of *H. atukori*, *C. dadiburjori*, *L. leuciscus*, and *G. rarus* larvae appears before hatching. The mouth opening time of *S. waltoni* (4 DPHs) and *P. retrodorslis* (5 DPHs) was, at post-flexion stage, the same as *G. rarus* (1 DPHs), and *L. leuciscus* (1 DPHs). The first swim bladders of *S. waltoni* (11 DPHs) and *P. retrodorslis* (14 DPHs) filled at the post-flexion stage, which is the same as *G. rarus* (1 DPHs), *L. leuciscus* (1 DPHs), *H. atukorali* (age not recorded), and *C. dadiburjori* (age not recorded). The yolk-sac resorption of *S. waltoni* (23 DPHs) and *P. retrodorslis* (25 DPHs) was, at the flexion stage, the same as *G. rarus* (4 DPHs) and *L. leuciscus* (4 DPHs). The second swim bladder of *S. waltoni* (25 DPHs) and *P. retrodorslis* (26 DPHs) filled at the flexion stage, which is the same as *G. rarus* (10 d), *L. leuciscus* (10 d), and *H. atukorali*. However, the second swim bladder of *A. chinensis* filled at the post-flexion stage. The dorsal fin of *S. waltoni* (8 DPHs) and *P. retrodorslis* (8 DPHs) differentiated at the post-flexion stage, while *G. rarus* (6 DPHs), *L. leuciscus* (4 DPHs), *H. atukorali*, and *C. dadiburjori* all filled at the flexion stage. The anal fin of *S. waltoni* (16 DPHs) and *P. retrodorslis* (18 DPHs) differentiated at the flexion stage, which is the same as *G. rarus* (8 DPHs) and *L. leuciscus* (9 DPHs). The exception is that *C. dadiburjori* differentiated at the post-flexion stage. The ventral fin of *S. waltoni* (18 DPHs) and *P. retrodorslis* (25 DPHs) differentiated at the post-flexion stage, which is the same as *G. rarus* (10 DPHs) and *L. leuciscus* (10 DPHs). It should be mentioned that the observation results of the early development of these fishes are basically similar to the

morphological model described in this study. However, in terms of the relative time of individual events and structure formation, there are differences between species in their responses to different biological and abiotic factors (such as diet, temperature, etc.). Feeding conditions or genetic elements may help to effectively interpret these diversities. Larger newly hatched larvae have larger yolk sacs, which can provide energy for the metabolism of larvae, help to protect from enemies, establish external feeding, and ensure a higher survival rate of larvae in harsh environments.

The growth coefficient of the larvae shows that the growth of body parts was different at each development phase, supporting the hypothesis that for improving the survival probability, the ontogenetic priority changed during development [3,31]. From the initial development state at hatching, the differentiation process occurs in the endogenous nutrition stage to guarantee the smooth transition to exogenous nutrition. Based on Osse et al. [31], during endogenous nutrition, the positive allometry of the head length and tail length reflected the early preferential development of organs and systems associated with important functions (including eating and swimming). Similarly, this also indicated that morphogenesis at this stage is more intense. In the head part, the early differentiation and growth of the sensory system (photoreceptor and olfactory), nervous system (mainly refers to the midbrain and hindbrain), and ingestion system (structures of oral, maxillary, and mandibular) can help to increase the likelihood of prey detection and feeding [6,32]. In the tail part, the rapid development of the tail helped to enhance the swimming capacity and avoid predators [6]; this adaptability also helped to decrease and improve the energy cost of the larvae [4,31]. It has also been reported that ontogenetic behavior changes are consistent with bone development [33].

According to our results, the development stage of *S. waltoni* and *P. retrodorslis* was found to change the individual genetic priority. Four periods of larval growth were recognized: pre-flexion larvae at 0–14 DPHs and 0–16 DPHs; flexion larvae at 14–23 DPHs and 16–26 DPHs; post-flexion larvae at 23–50 DPHs and 26–52 DPHs; and the juvenile stage. The early development characteristics of the larvae of both species were mainly concentrated in the pre-flexion phase and the flexion phase, while the inflection points were focused in the flexion stage and the post-flexion stage. The inflection point of the eye diameter of the two kinds of larvae was the first to arise. This can promote the full development of the eyes, so as to improve the ability of early larvae to eat food and escape from the enemy. However, there are also exceptions. The eye diameter of the Japanese lamprey grew at an isometric speed, because it lives in a dark environment and does not rely on the eyes to find food [34]. After 60 days of growth, the total length of the juveniles of the *P. retrodorslis* was larger than that of the juveniles of the *S. waltoni*. The inflection point ages of the tail lengths, the ventral fin lengths, the dorsal fin lengths, and the anal fin lengths of *P. retrodorslis* larvae were measured sooner, and the growth index ( $b$ ) was greater than that of the *S. waltoni* larvae, indicating that *P. retrodorslis* larvae can help to improve swimming ability sooner. At the same time, although the trunk lengths of the two species of fish were negative, allometric growth was observed before and after the inflection point, but the body depths and body depths at the anus level showed positive allometric growth before and after the inflection point. This is consistent with the results of *Sebastes schlegelii* [35] and *Oplegnathus fasciatus* [36]. After the inflection point, the growth speed of the body lengths, body heights and anal body heights of the two species of fish was faster than that before the inflection point. We believe that the total lengths and yolk sacs of these two kinds of fishes in cold water were larger, and the development of the digestive systems was relatively lagged in this study. Then, the digestive organs and swim bladders at the trunk began to differentiate before the inflection point, and then the viscus of the larvae and the juveniles continued to develop. The trunk lengths can meet the needs of viscus development, showing negative allometric growth. However, the body heights were not adequate for this need, so they showed positive allometric growth, and the growth rate was faster after the inflection point.

There were 3 morphometric characteristics of *S. waltoni* that showed the inflection points during the flexion stage, while 10 morphometric characteristics showed the inflection points during the post-flexion stage. Then, six morphometric characteristics of *P. retrodorsalis* showed inflection points during the flexion stage, and seven morphometric characteristics showed the inflection points during the post-flexion stage, which may be associated with their feeding habits. Before the inflection point, it was preferred to improve the feeding and swimming abilities by driving the development of the tail and head segments. After the inflection point, the growth coefficient significantly decreased, indicating that the growth priority changed. This growth pattern has also been found in the larvae of various teleost populations [8,37,38]. The allometric development pattern during early fish ontogeny was probably determined by genes. In the flexion stage, there was a variation in the development parameters of larvae (including the head, trunk, and tail segments) [19]. An increase in the development parameter of the head segment was found, possibly because of the respiratory system. The development parameter of the trunk segment displayed negative allometry. Although the allometry of the trunk segment in the flexion phase was negative, the BD and BDA showed positive allometry because of the inflation of the airbladder and the development of the digestive tract. In spotted sea bass, the growth of the coiling of digestive tract and mucosal folds began in this phase [21]. These changes, as well as the increase in enzyme activity, enhanced digestive ability [38]. Similarly, the tail segment displayed negative allometric development, which can help to improve swimming ability and, together with the development of SNLs, can allow for a larger prey intake [39]. In the post-flexion stage, the development parameters of the larvae (including the head, trunk, and tail segments) were significantly reduced. The lengths of the pectoral fins, dorsal fins, ventral fins, anal fins, and caudal fins of most of the fish showed positive allometric growth before the inflection point, positive allometric growth, or isometric growth, with a slightly lower growth coefficient after the inflection point, as evidenced by our research results. The exception is that the pectoral fin length of *Lates calarifer* was isometric growth before the inflection point, and the caudal fin length of *Lates calarifer* was of negative allometric growth before the inflection point [40]; the caudal fin length of the spotted knifejaw was of negative allometric growth after the inflection point [41]; the caudal fin length of the golden pompano was negative allometric growth before the inflection point [42]; and the growth coefficient of ventral fin length of chum salmon after the inflection point was greater than that before the inflection point [43]. In addition, with the disappearance of the fin folds and the continued growth of fins, variations in the swimming patterns of other teleost larvae have also been reported [22,44,45]. We believe that this is associated with a change in the swimming style and the juvenile type. We speculate that this is closely related to the size of the fish and its living environment. The response of larvae and juveniles to environmental pressure was different at different stages of development. During the period from hatching to the disappearance of yolk sacs, the larvae transformed from the endogenous nutrition stage to the exogenous nutrition stage, and the head organs showed positive allometry [21]. It is therefore necessary to improve the feeding and respiratory abilities as soon as possible. The larvae also helped to strengthen their ability to escape enemies and prey, and the rapid growth of swimming organs helped to fulfill this request.

*S. waltoni* and *P. retrodorsalis* are mainly distributed in the plateau valley of southwest China. In this area, the air is dry and thin, with strong solar radiation. The water source is mainly meltwater from snow-capped mountains. The surface runoff brings less nutrients, which is not suitable for the growth and reproduction of plankton [11,12]. In the natural breeding season, the water temperature is low and the food is poor, which has a profound impact on the morphology and physiological metabolism of fish. Based on the developmental features and environmental adaptability of larval fishes, in the production of artificial breeding, it is necessary to provide the environmental conditions required to promote the growth pattern in the early stages, and appropriate initial feeding should give priority to the development of important organs so as to effectively acquire exogenous nutrients that are integral in order to survive the early dangerous period and avoid death [46]. During the

natural reproduction stage of wild fish, it is greatly ecologically significant to protect their spawning grounds and create a good environment for hatching and early development.

## 5. Conclusions

We found that significant allometric growth occurred in the preferentially developed organs associated with ingestion, respiration, and swimming capacity, which was strongly linked to the changes in functional requirements. These led to the emergence of inflection points and changes in the growth of body parts. These changes were also related to dense morphometric growth and organ changes. The growth pattern changed from allometric to isometric, which is very common in larvae and juveniles. It is expected that this research can provide valuable perspectives in species conservation.

**Author Contributions:** B.X. analyzed data and wrote the first draft; D.L. guided and supervised the research; K.W. gave great help in revising the manuscript; X.Z. and J.X. assisted in breeding and observation; B.M. helped in data handling and result analysis. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was supported by the National Freshwater Aquatic Germplasm Resource Center (FGRC18537).

**Data Availability Statement:** Not applicable.

**Acknowledgments:** The authors thank Fisheries Research Institute of Sichuan Academy of Agricultural Sciences for providing the test site and device.

**Conflicts of Interest:** The authors declare no conflict of interest.

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