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Allometric growth in larval and juvenile blackhead seabream *Acanthopagrus schlegelii* (Bleeker, 1854) (Peciformes: Sparidae)

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ABSTRACT

Allometric growth in larvae and juvenile blackhead seabream *Acanthopagrus schlegelii* (Bleeker, 1854) was studied. In the larval head, snout length, snout-gill slit distance, interocular distance and mouth width showed positive allometric growth, while eye diameter and head height showed negative allometric growth. In the head of juveniles, interocular distance and mouth width showed negative allometric growth, while all other organs showed positive allometric growth. In larval body, body thickness showed positive allometric growth, while all other body parts showed negative allometric growth. In the juvenile body, caudal peduncle length, caudal peduncle height and body thickness showed positive allometric growth, while head length, body height, trunk length and tail length showed negative allometric growth. All of the larval swimming structures (the dorsal fins, pectoral fins, pelvic fins, anal fins and caudal fins) showed positive allometric growth. The rapid development of key organs in the blackhead seabream after the initiation of exogenous nutrition allows for a significant increase in viability with minimal metabolic loss. The information generated through this study can provide a framework for understanding how blackhead seabream responds developmentally to challenging external pressures during their early life.

Keywords: Allometric growth, Blackhead seabream, Early development, Juveniles, Larvae

Introduction

Blackhead seabream *Acanthopagrus schlegelii* (Bleeker, 1854) (Peciformes, Sparidae), is a warm water fish, widely distributed in rocky coastal habitats of China, Japan and Korea (Shi *et al.,* 2012). It is a suitable candidate species for aquaculture because of its fast growth rate, disease resistance, farming potential (Jeong *et al.,* 2007) and consumer preference due to good taste and nutritional value (Xue *et al.,* 2008). Due to its aquaculture importance, seed production technology was developed in China (Xue *et al.,* 2008). Many studies have focused on feeding, nutrition and diseases of blackhead seabream (Ma *et al.,* 2008; Wang *et al.,* 2008). However, the mechanisms of allometric growth and organ development in this species remain unknown.

Allometric growth is common in the biological world (Niklas, 1994). It depicts the relative growth rate among various parts of an organism, or the association(s) among various physical attributes (Wold *et al.,* 2008). Various early functional organs in fish generally follow an allometric pattern (Choo and Liew, 2006; Katsanevakis *et al.,* 2007). Organs closely related to viability grow rapidly (Katsanevakis *et al.,* 2007) and once the rapidly-growing organ is functional, its growth rate plateaus or gradually decreases (Snik *et al.,*1997; Herbing, 2001).

Information gained by understanding the allometric growth pattern of cultivable fishes is of particular importance for nursery aquaculture. This study on the allometric growth of blackhead seabream larvae and juveniles will be helpful in understanding the developmental characteristics of important functional organs and to explore the various challenges and demands at different growth stages.

Materials and methods

Experimental material

Fertilised eggs of blackhead seabream were obtained by hastening parturition at the Lingshui Base of Hainan Tropical Aquatic Research and Development Centre, South China Sea Fisheries Research Institute, Sanya, China. All experiments were performed *in situ* using Fiber Reinforced Plastic Containers (FRPC). Fertilised eggs

were acclimatised gradually to 27.5^{0}C for 20 min and thereafter transferred to 500 l fiber glass incubator. At two days post-hatching (DPH), larvae (2.90±0.17 mm average total length TL) were transferred to three nursery tanks, each of 2500 l capacity, at a stocking density 60 larvae l^{-1}. Nursery tanks were filled with filtered seawater (5 µm pore size). The inlet valve was adjusted such that the daily flow rate was twice the capacity of the tank. The light cycle was 14 h of 2000 lumens and 10 h of darkness. Salinity and water temperature of the experimental tanks were, 33±0.8‰ and 29.0±1.0^{0}C respectively. The nursery tanks were supplied with mild aeration through air compressor air stones.

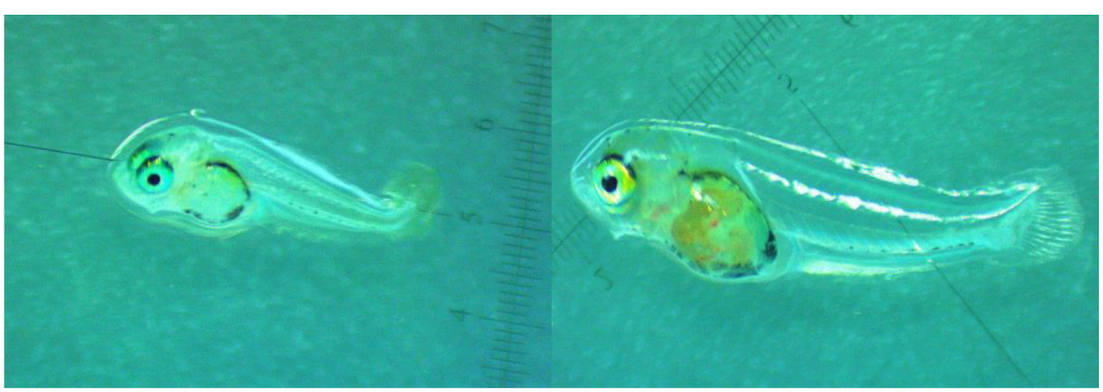
From 2 DPH, the larvae were fed with *Brachionus rotundiformis* at a density of 10-20 ind ml^{-1} until 9 DPH (4.50±0.10 mm TL). At 7 DPH (4.03±0.11 mm TL), mixed copepods (mostly *Calanus sinicus*) were given at a density of 20-30 ind ml^{-1}. On 18 DPH (9.65±0.63 mm TL), *B. rotundiformis* was replaced with *Artemia salina* at a density of 50-60 ind ml^{-1}. This feeding regime continued until the end of the experiment. To add extra nutrients, *B. rotundiformis*, copepods and *A. salina* were enriched with S.presso (INVE Aquaculture, Salt Lake City, UT, USA) for 12 h before feeding. To ensure sufficient live food availability, green water environment was used for the larvae and juveniles. *Nannocholoropsis* sp. (Qingdao Hongbang Biotechnology Co., Ltd.) along with *B. rotundiformis* were supplied. The drain filters were cleaned daily to prevent outlet blockage and to remove excess bait, excreta and dead larvae or juveniles by siphoning.

Measurement of body parts

Ten larvae or juveniles were collected from rearing tanks at 10:00 hrs daily from 1 to 7 DPH; every other day from 9 to 21 DPH and every third day from 24 to 39 DPH (total 20 sampling events). Collected individuals were anesthetised using 40 mg l^{-1} Aqui-S® (AQUI-S New Zealand Ltd., New Zealand). Anesthetised larvae were then examined under SZ40 stereomicroscope (Olympus Corporation, Tokyo, Japan) equipped with a digital camera (Canon EOS 600D, Japan) and the morphology of the external structures were assessed and photographed (Fig.1). Deformities could be observed directly under the microscope and deformed samples were removed to ensure accuracy of analysis. For all normally-developing larvae and juveniles, Auto CAD 2014 (Autodesk Inc, USA) was used to measure the head region (snout length, snout-gill slit distance, eye diameter, head height, interocular distance and mouth width), the body (head length, body height, trunk length, tail length, caudal peduncle length, caudal peduncle height and body thickness) and the swimming structures (dorsal fins, pelvic fins, pectoral fins, anal fins and caudal fins), from photos. All measurements were taken parallel or perpendicular to the horizontal axis of the fish. The scale used was accurate to 0.01 mm. After photography, all samples were fixed in 10% neutral formalin solution and stored in darkness.

Data processing

The relationship between total length and age can be expressed by the mathematical model $y = ae^{bx}$, where x is DPH, y is the total length at the given age, a is the intercept on the y-axis and b is the growth rate (Zhuang *et al.,* 2009). The allometric growth model for fish is described by the power function $y = ax^b$, where x is the total length of the fish, y is the length of an organ, a is the intercept on the y-axis and b is the allometric growth index (Wold *et al.,* 2008). In the allometric growth model, when b = 1, growth is constant; when b> 1, the given organ is growing rapidly (positive allometric growth); when b<1, the given organ is growing slowly (negative allometric growth). In fish, the formation of a functional stomach marks the transition from larva to juvenile (Stroband and Kroon, 1981). Here, the larvae began to develop a stomach gland at 17 DPH.



(a) (b)

Fig. 1. Blackhead (a) seabream larvae and (b) juveniles

Different growth stages can be expressed by different growth equations, *e.g.* $y = a_1x^{b1}$ and $y = a_2x^{b2}$. For each pair of growth equations, the Student's *t*-test in SPSS 19.0 (International Business Machines Corporation, USA) was used to determine whether b1 and b2 were significantly different ($p<0.05$). Non-linear regression parameters were fitted to each of the two models (SPSS 19.0). Next, a segmentation regression model was added to determine the maximum coefficients (R^2) and the minimum residual sum of squares as the curve-fitting standard (EXCEL 2016, Microsoft Corporation, USA).

Results

Relationship between total length and age

The exponential equation describing the relationship between total length and age in the blackhead seabream larvae and juveniles was $y = 2.6599e^{0.063x}$ (R^2=0.974) (Fig. 2). The average length of larvae at 1 DPH was 2.86±0.00 mm; after 39 days of growth, the average length increased to 25.79±4.67 mm, with an average growth rate of 0.588 mm per day.

Growth in larval and juvenile blackhead seabream

Growth in the head

In larvae and juveniles, the snout length, snout-gill slit distance, eye diameter, head height, eye cross and mouth width increased allometrically, relative to total length (Table 1). In larvae (<17 DPH), the allometric growth indices (b value) of the head region ranged from 0.538 to 2.322 (snout length 2.322, snout-gill slit distance 1.355, eye diameter 0.825, head height 0.538, eye cross 2.136 and mouth width 1.497). All six indices were significantly different from 1 ($p<0.05$). Snout length, snout-gill slit distance, eye cross and mouth width showed positive allometric growth, while eye diameter and head height showed negative allometric growth. In juveniles (>17 DPH), the allometric growth indices varied from 0.878 to 1.338 (snout length 1.338, snout-gill slit distance 1.130, eye diameter 1.120, head height 1.262, eye cross 0.878 and mouth width 0.904). Again, all size indices were significantly different from 1 (p for all indices <0.05). Snout length, snout–gill slit distance, eye diameter and head height showed positive allometric growth while eye cross and mouth width showed negative allometric growth. Thus, in the heads of larvae, snout length, snout-gill slit distance, eye cross and mouth width grew rapidly. Snout length and snout-gill slit distance continued to grow rapidly in juveniles, as did eye diameter and head height. However, the rate of increase in eye cross and mouth width had slowed down. At the transition between larva and juvenile (17 DPH), the average total length was 9.08±0.59 mm and our analyses suggested a concurrent significant shift in the rate of change of eye diameter, head height, eye cross and mouth width ($p<0.05$).

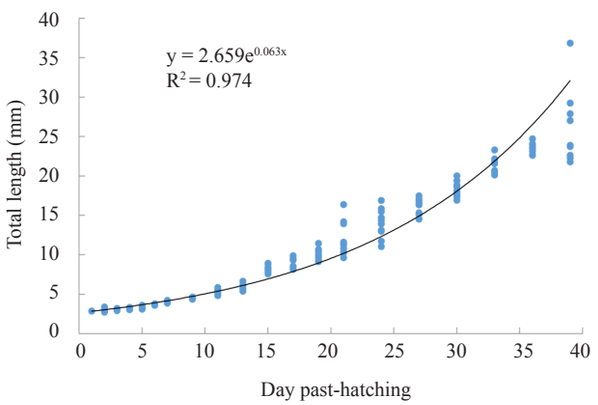


Fig. 2. Total length of blackhead seabream larvae and juveniles as a function of age (from 1 to 39 days post-hatch)

Growth in the body

In both larvae and juveniles, head length, body height, trunk length, tail length, caudal peduncle length, caudal peduncle height and body thickness all displayed allometric growth (Table 2). In the larvae (<17 DPH), the allometric growth index of body thickness was 2.515 ($p<0.05$), indicating positive allometric growth. The growth indices of all body parts measured were significantly less than 1 ($p<0.05$), indicating negative allometric growth (head length 0.541, body height 0.696, trunk length 0.376, tail length 0.716, caudal peduncle length 0.992 and caudal peduncle height 0.952). In the juveniles (>17 DPH), the allometric growth indices of head length, body height, trunk length and tail length were all significantly less than 1 (p for all indices <0.05), indicating negative allometric growth (head length 0.824, body height 0.906, trunk length 0.839 and tail length 0.886). In juveniles (>17 DPH), the caudal peduncle length, caudal peduncle height and body thickness were all significantly greater than one ($p<0.05$), indicating positive allometric growth (caudal peduncle length 1.009; caudal peduncle height: 1.027 and body thickness: 1.001). Therefore, in the blackhead seabream, head length, body height, trunk length and tail length grew slowly during the larval and juvenile stages, while body thickness grew rapidly. The caudal peduncle length and caudal peduncle height increased slowly in the larvae, but rapidly in the juveniles. At the transition between larva and juvenile (17 DPH), our analysis suggested a significant shift in the rate of change in caudal peduncle length and caudal peduncle height ($p<0.05$).

Table 1. Growth equations of the head parts of blackhead seabream larvae and juveniles

Larvae/Juveniles	Parameter	Growth equation	b value
Larvae	Snout length	$y = 0.0021x^{2.322}$ $R^2 = 0.908$	2.322 ($p<0.05$)
	Snout-gill slit distance	$y = 0.0475x^{1.355}$ $R^2 = 0.976$	1.355 ($p<0.05$)
	Eye diameter	$y = 0.0805x^{0.825}$ $R^2 = 0.941$	0.825 ($p<0.05$)
	Head height	$y = 0.2777x^{0.538}$ $R^2 = 0.985$	0.538 ($p<0.05$)
	Eye cross	$y = 0.0402x^{2.136}$ $R^2 = 0.996$	2.136 ($p<0.05$)
	Mouth width	$y = 0.0488x^{1.497}$ $R^2 = 0.989$	1.497 ($p<0.05$)
juvenile	Snout length	$y = 0.0147x^{1.338}$ $R^2 = 0.989$	1.338 ($p<0.05$)
	Snout–gill slit distance	$y = 0.0724x^{1.130}$ $R^2 = 0.983$	1.130 ($p<0.05$)
	Eye diameter	$y = 0.0364x^{1.120}$ $R^2 = 0.983$	1.120 ($p<0.05$)
	Head height	$y = 0.0604x^{1.262}$ $R^2 = 0.900$	1.262 ($p<0.05$)
	Eye cross	$y = 0.4219x^{0.878}$ $R^2 = 0.985$	0.878 ($p<0.05$)
	Mouth width	$y = 0.2464x^{0.904}$ $R^2 = 0.986$	0.904 ($p<0.05$)

Table 2. Growth equations of the body parts of blackhead seabream larvae and juveniles

Larvae/Juveniles	Parameter	Growth equation	b value
Larvae	Head length	$y = 0.492x^{0.541}$ $R^2 = 0.995$	0.541 ($p<0.05$)
	Body height	$y = 0.2796x^{0.696}$ $R^2 = 0.996$	0.696 ($p<0.05$)
	Trunk length	$y = 0.7448x^{0.376}$ $R^2 = 0.975$	0.376 ($p<0.05$)
	Tail length	$y = 0.2764x^{0.716}$ $R^2 = 0.993$	0.716 ($p<0.05$)
	Caudal peduncle length	$y = 0.1231x^{0.992}$ $R^2 = 0.998$	0.992 ($p<0.05$)
	Caudal peduncle height	$y = 0.1296x^{0.952}$ $R^2 = 0.997$	0.952 $P<0.05$)
	Body thickness	$y = 0.0194x^{2.515}$ $R^2 = 0.997$	2.515 ($P<0.05$)
Juvenile	Head length	$y = 0.2595x^{0.824}$ $R^2 = 0.974$	0.824 ($P<0.05$)
	Body height	$y = 0.1703x^{0.906}$ $R^2 = 0.972$	0.906 ($p<0.05$)
	Trunk length	$y = 0.2591x^{0.839}$ $R^2 = 0.978$	0.839 ($p<0.05$)
	Tail length	$y = 0.1846x^{0.886}$ $R^2 = 0.971$	0.886 ($p<0.05$)
	Caudal peduncle length	$y = 0.1178x^{1.009}$ $R^2 = 0.977$	1.009 ($p<0.05$)
	Caudal peduncle height	$y = 0.1074x^{1.027}$ $R^2 = 0.979$	1.027 ($p<0.05$)
	Body thickness	$y = 0.2546x^{1.001}$ $R^2 = 0.978$	1.001 ($p<0.05$)

Growth of swimming structures

The primary external swimming structures in larvae and juveniles are the dorsal fins, pectoral fins, pelvic fins, anal fin and caudal fin (Table 3). These fins are critical to advancing, balancing and guiding (Fukuhara, 1992). In the larval stage (<17 DPH), the allometric growth indices of all the fins were significantly greater than one (p for all indices <0.05), indicating positive allometric growth (dorsal fins 1.177, pectoral fins 1.589, pelvic fins 2.564, anal fin 1.150 and caudal fin 2.285). In the juvenile stage (>17 DPH), the allometric growth indices of the dorsal fin, pectoral fin and pelvic fin were significantly less than one ($p<0.05$), indicating negative allometric growth (dorsal fins 0.828, pectoral fin 0.725 and pelvic fin 0.932). The allometric growth indices of the anal fin and caudal fin were significantly greater than one ($p<0.05$), indicating positive allometric growth (anal fin 1.154 and caudal fin 1.132), which indicated that the dorsal fin, pectoral fin, pelvic fins, anal fin and caudal fin grew rapidly in larvae. In juveniles, the anal fin and caudal fins continued to grow rapidly, but the growth of the dorsal fin, pectoral fin and pelvic fins became slow. At the transition between larva and juvenile (17 DPH), our analysis suggested a significant shift in the rate of growth of the dorsal fins, pectoral fins and pelvic fins (p for all <0.05).

Discussion

As fish grown for aquaculture are protected from predators, the coordination between the biological characteristics of the breed and the breeding environment is the primary avenue to improve yield (Boglione *et al.,* 2013, 2014; Lee-Montero *et al.,* 2015). Nutrient supply, water quality, light intensity, water volume and stocking density all have profound impacts on farming success (Ma *et al.,* 2015; Sun *et al.* 2015; Yoseda *et al.,* 2008), as do challenges including skeletal malformations, improper nutrition, toxins, immune deficiencies, mechanical shocks and parasites (Ho and Lin, 2005; Ching *et al.,* 2012). Therefore, the developmental patterns of farmed fish are of great practical significance for accurate regulation

Table 3. Growth equations of the swimming structures of blackhead seabream larvae and juveniles

Larvae/Juveniles	Swimming structure	Growth equation	b value
Larvae	Dorsal fins	$y = 0.1895x1.177$ $R^2 = 0.835$	1.177 ($p<0.05$)
	Pectoral fins	$y = 0.1138x1.589$ $R^2 = 0.968$	1.589 ($p<0.05$)
	Pelvic fins	$y = 0.0238x2.564$ $R^2 = 0.998$	2.564 ($p<0.05$)
	Anal fins	$y = 0.0757x1.150$ $R^2 = 0.990$	1.150 ($p<0.05$)
	Caudal fins	$y = 0.0337x2.285$ $R^2 = 0.977$	2.285 ($p<0.05$)
Juvenile	Dorsal fins	$y = 0.3734x0.828$ $R^2 = 0.995$	0.828 ($p<0.05$)
	Pectoral fins	$y = 0.716x0.725$ $R^2 = 0.987$	0.725 ($p<0.05$)
	Pelvic fins	$y = 0.3126x0.932$ $R^2 = 0.986$	0.932 ($P<0.05$)
	Anal fins	$y = 0.0738x1.154$ $R^2 = 0.990$	1.154 ($p<0.05$)
	Caudal fins	$y = 0.3731x1.132$ $R^2 = 0.988$	1.132 ($p<0.05$)

of the feeding environment and for high-tech feeding programmes (Prestinicola *et al.,* 2013). In fish, allometric growth is a mechanism of self-protection found in early development during cell differentiation and organ formation (Wold *et al.,* 2008). That is, developmental priority is given to important functional organs, such as those related to nutritional intake and predator avoidance (Solomon *et al.,* 2017). Allometric growth has previously been described in several fish, including *Chaetodipterus faber* (Barros *et al.,* 2015), *Platax orbicularis* (Barros *et al.,* 2015), *Chelon labrosus* (Khemis *et al.,* 2013) and six species of ponyfish (Deyrestani *et al.,* 2015). Consistent with these studies, data here show that the blackhead seabream selectively prioritises the development of vital organs for a short period of time, after which growth plateaus or slows down. This implies that for optimal performance and to conserve metabolic energy, rapid growth is carefully restricted to the shortest possible period.

Development of the head

In marine fish, skull structure and fin development vary by species; some form within the egg envelopes (Leis, 2015), while others form after hatching and develop rapidly (Koumoundouros *et al.,* 1997; 2000). After hatching, the eye of some larvae were not coloured and the larvae were without opened (formed) mouths; the formation (opening) of the mouth is often accompanied by the colouration of the eyes (Sarasquete *et al.,* 1995; Micale *et al.,* 2006). During the early period of development, vision and chemoreceptors play important roles in feeding and avoiding predation (Yufera 2011). Inconsistent with *Acipenser schrenckii* (Ma *et al.,* 2007) and *Acipenser baeri* (Zhuang *et al.,* 2009), the development of eyes of the blackhead seabream was slow in the larvae but rapid in juveniles. The inter-ocular distance increased rapidly during the larval stage and slowly during the juvenile stage, suggesting that rapid eye growth is critical for feeding ability and predation avoidance (Yufera, 2011). After the mouth opens, the larvae continue to consume the yolk sac nutrients and must also feed exogenously to meet developmental requirements (Yufera, 2011). The larval maxilla and mandibles grow to allow the capture and ingestion of larger, higher-energy foods. As the blackhead seabream larval yolk sac was depleted at 2 to 3 DPH, there was a need for exogenous feeding immediately (Pena and Dumas, 2009). At 17 DPH, there was a significant change in the rate of increase in eye diameter, head height, inter-ocular distance and mouth width. The rapid growth in the larval stage and the slow growth in the juvenile stage suggested that blackhead seabream mouth was almost fully developed at 17 DPH. Our results indicated that eye diameter, head height, interocular distance and mouth width were preferentially developed in larvae.

Development of the body parts

During the early ontogeny of fish larvae, the muscles, bones and digestive system develop along a central axis, forming the trunk (Gisbert and Doroshov, 2006). The trunk is connected to the head anteriorly and the tail posteriorly, acting as a hub in the swimming fish (Barlow, 1986). As the formation of a functional stomach marks the transition from larval stage to juvenile stage of some fish, 17 DPH characterised as the transition point of blackhead seabream, when the pyloric sphincter developed (Stroband and Kroon, 1981). The length of the trunk of the blackhead seabream larvae increased slowly, while body thickness increased rapidly. This discrepancy was probably related to the development of the digestive system. The folded digestive tract and the developing liver and kidney occupied a major part of the body cavity, stretching the three-dimensional structure of the trunk. In juveniles, trunk length and body height continued to increase slowly, indicating that the juvenile digestive tract still required rapid development to absorb adequate nutrition. In contrast, the length of the blackhead seabream tail grew slowly in both larvae and juveniles, consistent with results obtained in a previous study of the golden pompano (Yang *et al.,* 2017).

Development of the swimming structures

The early developmental processes of the swimming related structures of several fish have previously been published, including that of *Sparus aurata, Dentex dentex, Diplodus sargus* (Koumoundouros *et al.,* 1997; 1999; 2001) and *Pagros major* (Matsuoka, 1987). In these species, the caudal fins develop and ossify first, indicating that the caudal fins were of primary importance during early fish development (Koumoundouros *et al.,* 1997; 1999). In the blackhead seabream, the dorsal fins, pectoral fins and pelvic fins grew rapidly in larvae but slower in juveniles, suggesting that these fins were almost completely developed in juveniles and were able to reach the required level. In juveniles, slower growth helps to keep fin size synchronised with body growth (Árnason *et al.,* 2009). In blackhead seabream, the pectoral fins grew rapidly during the larval stage and slowly during the juvenile stage, indicating that pectoral fin function improved during larval and juvenile development (Webb and Weihs, 1986). The dorsal fin and pelvic fins also grew rapidly during the larval stage and slowly during the juvenile stage, suggesting that these fins replaced the simple folds of yolk sac in the larval stage and that growth was mostly completed during the larval stage. The comprehensive analysis conducted on the main swimming structures of the blackhead seabream indicated that the swimming structures of this fish improved and that athletic ability increased during the larval phase.

The results of the present investigation of allometric growth of blackhead seabream will help improve the rearing efficiency, optimise feeding schemes and promote the development of blackhead sea bream breeding programmes.

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