



Insights Into Energy Accumulation and Allocation Strategy of Reproductive Migration of Black Amur Bream (*Megalobrama terminalis*) in the Pearl River Basin, China

OPEN ACCESS

Yaqiu Liu^{1,2,3}, Xinhui Li^{1,2,3}, Jie Li^{1,2,3*} and Yuefei Li^{1,2,3}

Edited by:

Chuanbo Guo,
Institute of Hydrobiology (CAS), China

Reviewed by:

Xiuming Li,
Chongqing Normal University, China
Xu Pang,
Southwest University, China
Yang Liu,
Chinese Academy of Fishery
Sciences, China

*Correspondence:

Jie Li
lijie1561@163.com

Specialty section:

This article was submitted to
Population, Community,
and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

Received: 04 January 2022

Accepted: 25 February 2022

Published: 26 April 2022

Citation:

Liu Y, Li X, Li J and Li Y (2022)
Insights Into Energy Accumulation
and Allocation Strategy
of Reproductive Migration of Black
Amur Bream (*Megalobrama
terminalis*) in the Pearl River Basin,
China. *Front. Ecol. Evol.* 10:848228.
doi: 10.3389/fevo.2022.848228

¹ Pearl River Fisheries Research Institute, Chinese Academy of Fishery Sciences, Guangzhou, China, ² Guangzhou Scientific Observing and Experimental Station of National Fisheries Resources and Environment, Guangzhou, China, ³ Key Laboratory of Aquatic Animal Immune Technology of Guangdong Province, Guangzhou, China

Energy allocation is an important component of the reproductive cycle, and as such, it will affect survival, migration, and reproductive success. To reduce the risk of reproductive migration failure and to optimally allocate a limited amount of energy, it is vital to first understand the trade-off between reproduction and somatic growth in migrating fish. In this study, we chose *Megalobrama terminalis*, an endemic species residing in the Pearl River basin with relatively high migratory potential, as a candidate to investigate energy accumulation and allocation strategy during reproductive migration. The analysis used a quantitative assessment of biochemical composition and energy density in somatic and visceral tissues of *M. terminalis* females during the reproductive cycle. The results indicated that stage III to stage IV of *M. terminalis* was the vital migration-launching period. The asynchrony of development was confirmed in energetic relationships in muscle and ovary. Specifically, there was a regulatory mechanism for allocating lipids to each tissue reasonably during the breeding migratory preparation period (stage III). The significant change in lipid content of the ovary is considered as a crucial physiological index, which reflects the readiness for breeding migration of *M. terminalis*. In addition, the negative energy density relationship between somatic and reproductive tissues indicated a trade-off between maximum metabolic ability and energy efficiency before migration launching in *M. terminalis*. The present findings provide effective information for initiating further research on the ecological adaptation of migrating fish species.

Keywords: reproduction, energy allocation, migration, *Megalobrama terminalis*, proximate composition

HIGHLIGHTS

- Current study is the first demonstration of energy accumulation and allocation strategy in *Megalobrama terminalis* during the breeding migration.
- The remarkable change of lipid content in ovary is considered as a crucial physiological index reflecting the readiness for breeding migration of *M. terminalis*.
- A regulatory mechanism to allocate the lipid of each tissue reasonably in the breeding migratory preparation period of *M. terminalis* has been found in our research.

INTRODUCTION

Almost half of all vertebrate species are fish, and they encompass a wide spectrum of physiological and ecological adaptations. Generally speaking, fish life-history theory predicts that organisms will balance their energy allocation among maintenance, storage, growth, migration, and reproduction to maximize their fitness (Roff, 1983). As a vital aspect of the life history, reproductive behavior is highly relevant to optimal energy accumulation and allocation (Alonso-Fernández and Saborido-Rey, 2012; Villegas-Ríos et al., 2014). Specifically, females are recognized as allocating more energy to gonad development than males (Saborido-Rey et al., 2004). In addition, fish reproductive migration is a highly energy-consuming activity. In the course of reproductive migration, fish are likely to face various risks, for example, less effective avoidance of predation and energy shortages. Therefore, fish regulate the types and levels of energy stored in various organs to meet the energy requirements of reproductive migration (Caudill et al., 2007). The previous research has indicated that body size, osmotic pressure regulation, swimming speed, and sexual maturity contribute to fish migratory preparation (McCormick et al., 1998; Saborido-Rey et al., 2004). Usually, the migrating fish with large body size and high fertility rates have a clear “profit” as concerning the consumption of energy during reproduction migration (Wysujack et al., 2010; Barneche et al., 2018). Moreover, it has been hypothesized that storing sufficient energy may be necessary for migratory fish reproduction migratory (Jonsson and Jonsson, 2003; Bureau et al., 2007).

Barbour (1985) proposed the hypothesis that fish need to reserve enough energy for migration during the migratory preparation period. Certain relevant research points supported this hypothesis (Thorpe et al., 1998). Nevertheless, the preparation period that differs among individuals within a population is considered discrepantly (Jonsson and Jonsson, 2003). Relevant research has indicated that individuals with higher energy initiated the migration earlier (Colombier et al., 2007). The contribution of energy molecules stored in different fish tissues is unevenly distributed during reproductive migration (Kiessling et al., 2004), although information related to the fish migratory preparation process is lacking. Energy density is identified as one of the most important indexes used to assess the stored energy capacity of fish, because it depends on the contents

carrying molecules such as proteins, fat, and carbohydrates (Mourente et al., 2002; Penney and Moffitt, 2014). In the recent years, energetics related to fish migration has become a focus in fish ecology (Penney and Moffitt, 2014; Thomas and Johan, 2018; Lennox et al., 2019; Tamarío et al., 2019). However, to the best of our knowledge, a very few studies have been conducted on the mechanism of energy reallocation in fish tissues in relation to digestion, growth, reproduction, and other major functions during the maturing process. Thus, the study of the biochemical composition of wild fish populations is an important approach for understanding the variation in energy allocation among life-history processes (Connell, 1975).

The black Amur bream (*Megalobrama terminalis*) is a migratory species inhabiting the lower reaches of the Pearl River. The species is regarded as a good candidate for studying the energy allocation of migratory fish (Chen et al., 2020). During spawning seasons, *M. terminalis* migrate nearly 250 km upstream from a drainage network to the spawning grounds (Luopangjiang and Qingpeitang). Owing to the continuous enhancement of human activities (e.g., water conservancy projects, waterway dredging, water pollution, and overfishing), serious decreases in wild populations of *M. terminalis* have been reported in the Pearl River basin during this decade (Li et al., 2014, 2018). In our previous research, it was demonstrated that the *M. terminalis* spawning migration occurs from late June to mid-July, a pattern that is different from historical records (Liu et al., 2021b). In the recent studies, *M. terminalis* was deemed to be an omnivorous fish with strong ecological adaptability (Liu et al., 2020, Liu et al., 2021b). The amount of energy allocated between growth and reproduction is deemed to be the critical factors for the survival and reproduction of *M. terminalis* in natural ecosystems. Related research suggests that there is a shift in the diet of black Amur bream during the gonad development period, with different food preferences of both immature and mature individuals (Xia et al., 2017, 2020). Further research has provided evidence that *M. terminalis* regulates activities of the gut microbiome and degradation enzymes to digest foods with higher nutrition to supply energy for the spawning migration (Liu et al., 2021a). However, the overall effect on variation in energy allocating during *M. terminalis* reproduction migratory has been difficult to evaluate.

To date, most previous research on *M. terminalis* has been related to larval resources, feeding habits, ecological investigation of spawning grounds, and digestive function (Tan et al., 2009; Wang et al., 2010; Xia et al., 2017; Liu et al., 2020), whereas a very few studies have reported the pattern of energy accumulation and reproductive investment for *M. terminalis* in the course of the reproduction cycle. To fill this knowledge gap, we attempted to investigate the utilization efficiency of energy storage, energetic trade-offs between somatic and reproductive growth and differences in energy accumulation, and allocation for gonadal maturation and spawning migration of *M. terminalis* females. A quantitative assessment method that involves biochemical composition and energy density was utilized to analyze somatic and visceral tissues of *M. terminalis* females in the spawning ground, the fattening ground, and migration routes during the

reproductive cycle. The aim was to characterize the process of energy accumulation and allocation during reproductive cycle of *M. terminalis*. In parallel, through analysis of fine-scale variation in proximate composition and energy content in the course of gonad development, the study aimed to provide data supporting further exploration of fitness in wild population of *M. terminalis*. Additionally, this study also collects data relevant to energetic ecology of fish migration.

MATERIALS AND METHODS

Ethics Approval

The methods that involve animals in this study were conducted in accordance with the Laboratory Animal Management Principles of China. All experimental protocols were approved by the Ethics Committee of the Pearl River Fisheries Research Institute, Chinese Academy of Fishery Sciences.

Fish Sampling

A total of 350 female specimens of black Amur bream from five localities were collected using circular cast nets (16 m diameter, mesh size 3 cm) in the Pearl River during 2019. The sampling variables that include date of collection, location, and environment information are provided in **Table 1**. According to the corresponding sampling sites and sampling times, sampling in sites S1–S2 was conducted from July 9 to 21. Sampling in sites S3–S5 was conducted from June 18 to July 8 to ensure the distinction between migratory and non-migratory *M. terminalis* (**Table 1**). The sampling sites are shown in **Figure 1**. For each sample, total body weight in g (W_t , measured to the nearest 1 g) and standard length (SL, to the nearest 1 mm), eviscerated weight (EW, to the nearest 1 g), and gonad and liver weights (GW and LW, respectively, to the nearest 0.01 g) were measured. The sex and stage of sexual maturity were identified for all individuals based on the morphological characteristics, as described by Nikolsky (1963): I = immature, II = developing, III = maturing, IV = mature, V = spawning and post-spawning. The gonadosomatic index ($GSI = 100 \times GW/EW$) was estimated as an indicator of the fish reproductive period. The hepatosomatic index ($HSI = 100 \times LW/EW$) and fatness ($K = 100 \times W_t/SL^3$) were measured as bioenergetic indices to evaluate fish conditions.

Histological Observations

Fish selected in different reproductive periods were anesthetized using MS-222 ($0.2 \text{ g L}^{-1} \text{ MS-222} + 0.2 \text{ g L}^{-1} \text{ NaHCO}_3$) and then stunned and quickly decapitated. For histological analysis, the left ovaries of fish were dissected out and fixed with Bouin's fixative for 24 h at 4°C and embedded in paraffin wax, and then, the tissues were cut to 5-mm thicknesses sections and stained with hematoxylin–eosin (H&E).

Biochemical Assays

To investigate the fish biochemical composition and energy density, 120 fish tissue samples were randomly selected for analysis. Each specimen was dissected, and organs and muscles

(without skin) were removed from a location posterior to the insertion of the dorsal fin. The liver and ovaries were taken from each fish stored in plastic bags on ice and frozen (-80°C) until processing. For biochemical analysis, each tissue of each sampled fish was homogenized and freeze-dried for 24 h at -80°C to a constant weight. The resulting dry tissue was cooled and weighed, and the moisture percentage was calculated as $(100 - \% \text{dry tissue})$. Determination of crude protein content was measured by the Kjeldahl method (Hach et al., 1985); determination of crude lipid content was measured by the chloroform–methanol extraction method (Folch et al., 1957); ash content was determined by the method of Penney and Moffitt (2014). The energy value was measured by a Phillipson Microbomb Calorimeter (Gentry Instruments Inc., Aiken, SC, United States). All biochemical analyses were performed in triplicate.

Statistical Analysis

The data were analyzed using STATISTICA 6.0 (StatSoft, Inc., Tulsa, OK, United States). The normality of the data and homogeneity of variance were assessed with the Kolmogorov–Smirnov test and Levene's test, respectively. The GSI, HSI, fatness, composition, and energy density were analyzed by one-way ANOVA to evaluate the differences among groups. All data were expressed as means \pm SD, and Tukey's *post-hoc* test was used as necessary. A *p*-value below 0.05 was used to determine statistical significance. Principal component analysis (PCA) was used to obtain principal coordinates and their visualization from the complex biochemical composition of the ovary. To better understand the relationship between biochemical content of the fish ovary and the habitat environment and biological indices associated with different groups, a redundancy analysis (RDA) was conducted. Here, we used the R implementation of the procedure (version 1.1.3).

RESULTS

Changes During Reproductive Migration

The biochemical composition changes in ovary of *M. terminalis* during the reproductive migration period are shown in **Figure 1**. The proportion of sexually mature (stages IV and V) individuals increased significantly in the main stem (S3, S4, and S5), whereas immature ovaries were dominant in the estuary (S1 and S2). The ovary of *M. terminalis* gradually matures during reproductive migration. Lipid constituents of the ovary of the black Amur bream rose from the ovary from S1 to S5, whereas water content showed an opposite pattern of variability (**Supplementary Figure 1**). To compare the similarity of proximate composition among different sample sites, PCA ordination revealed a clear separation of the proximate composition of the ovary between estuary and main stem populations. The proximate composition of ovary between the S1 and S2 groups on PCA scores showed greater similarity, separated from the proximate composition of the ovary in the S4 and S5 groups that formed a cluster (**Figure 2A**). Samples in the S3 group were located between non-migrating (S1, S2) and migrating populations (S4, S5)

TABLE 1 | Basic environmental information and biological information of gut microbial community pertaining for the different groups studied of *Megalobrama terminalis*.

		Estuary			Main stem	
		S1	S2	S3	S4	S5
Environmental information	Sample period	July 15 to 21	July 9 to 15	July 2 to 8	June 25 to July 1	June 18 to 24
	Temperature (°C)	28.7 ± 0.2	28.4 ± 0.4	28.8 ± 0.4	28.4 ± 0.3	28.7 ± 0.3
	Salinity (‰)	0.09 ± 0.03 ^b	0.05 ± 0.02 ^{ab}	0.01 ± 0.00 ^a	0.01 ± 0.00 ^a	0.01 ± 0.00 ^a
	pH	8.0 ± 0.1	7.9 ± 0.2	8.1 ± 0.2	8.2 ± 0.2	7.9 ± 0.2
	DO (mg/L)	6.7 ± 0.1 ^a	6.8 ± 0.2 ^{ab}	7.2 ± 0.1 ^b	7.7 ± 0.2 ^b	7.5 ± 0.2 ^{ab}
Biological information	<i>n</i>	50	50	50	50	50
	SL ± SD	182 ± 15.7 ^a	235 ± 21.2 ^{ab}	247 ± 16.4 ^b	271 ± 20.4 ^b	262 ± 16.1 ^b
	<i>W_t</i> ± SD	101.8 ± 19.1 ^a	259 ± 25.1 ^b	363 ± 22.5 ^c	403 ± 32.3 ^c	372 ± 23.1 ^c
	GSI (%)	0.7 ± 0.1 ^a	4.1 ± 1.3 ^b	6.9 ± 1.4 ^b	9.2 ± 2.3 ^b	6.6 ± 0.9 ^b
	HSI (%)	1.5 ± 0.12 ^a	2.5 ± 0.13 ^c	2.2 ± 0.12 ^{bc}	1.2 ± 0.10 ^a	1.0 ± 0.10 ^a
	K	1.8 ± 0.13 ^a	2.1 ± 0.20 ^{ab}	2.3 ± 0.22 ^b	2.4 ± 0.21 ^b	2.2 ± 0.14 ^b

Different superscript letters indicate significant differences in different groups, $p < 0.05$.

DO, dissolved oxygen; GSI, gonadosomatic index; HSI, hepatosomatic index; K, fatness; SL, standard length; W_t , body weight.

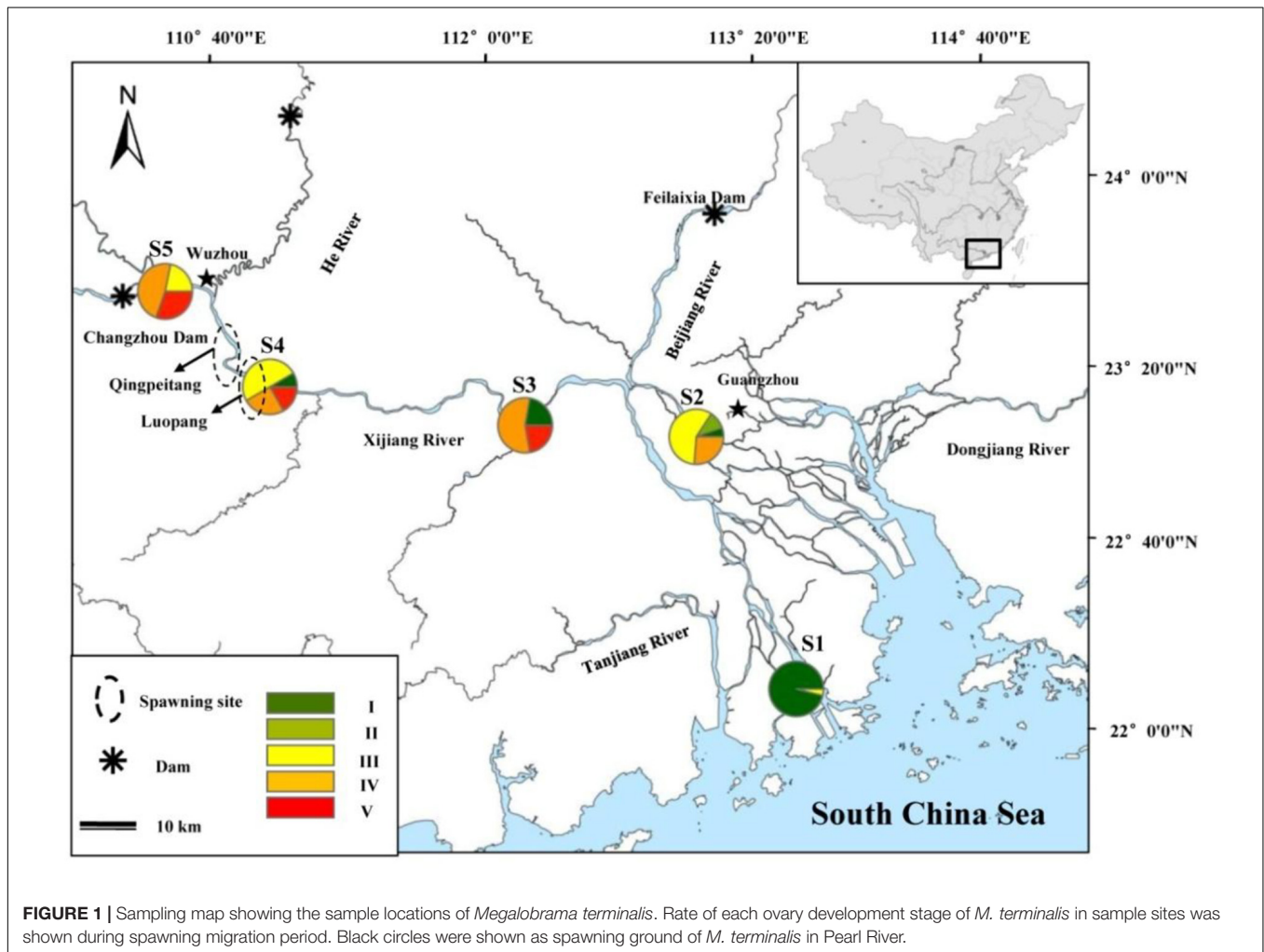
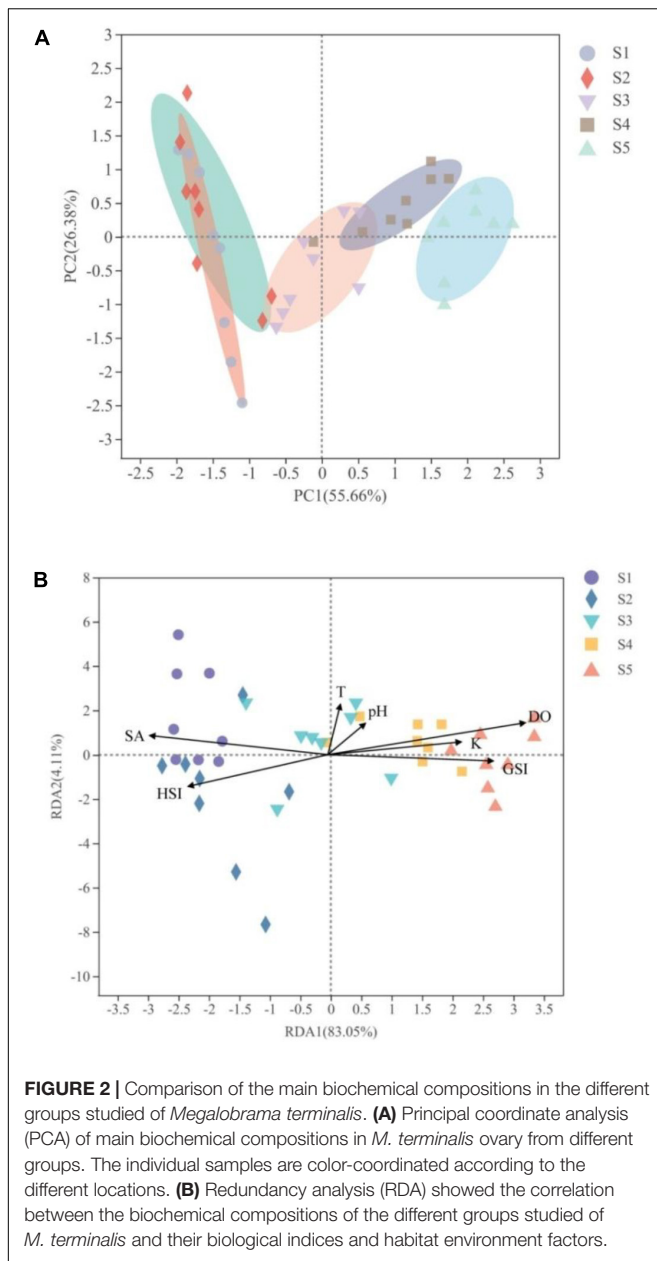


FIGURE 1 | Sampling map showing the sample locations of *Megalobrama terminalis*. Rate of each ovary development stage of *M. terminalis* in sample sites was shown during spawning migration period. Black circles were shown as spawning ground of *M. terminalis* in Pearl River.

(Figure 2A). The proximate composition of ovary in each group was closely related to their habitat and biological index (Figure 2B). The proximate composition of S4 and S5 groups

was more closely related to dissolved oxygen, fatness, and GSI. In contrast, the proximate composition of S1 and S2 was correlated with salinity and HSI.



Morphometry and Histology

The distribution of the morphometrical parameters across maturity stages is shown in **Figure 3**. It is clear that there were increases in length and weight from the immature stage to the mature stage (**Figures 3A,B**). Although this increase was gradual throughout the maturation for the somatic measurements, the GSI showed a sudden peak at stage IV (**Figure 3C**). However, HSI showed a peak at stage II and then gradually decreased (**Figure 3D**). Histological observations of the *M. terminalis* ovary during different developmental stages are shown in **Figure 4**. Oocytes varied markedly with ovary development, and the description of histological changes in *M. terminalis* is given shown in **Table 2**.

Proximate Composition: Variability in Different Tissues

Biochemical changes across different maturity stages in each tissue of female *M. terminalis* are presented in **Figure 5**. During sexual maturation, water contents in the ovary and liver decreased from stages I to III and then increased from stages III to V (**Figures 5A,C**). In the contrast, water content in muscle had no obvious changes from stages I to V (**Figure 5B**). For total ash, a slight downward trend was observed in ovary tissues from stages I and II (**Figure 5D**), whereas muscle and liver tissues remained practically unaffected (**Figures 5E,F**). Concerning protein content, this constituent increased in the ovary from stages I to III and dropped significantly in stage IV, which shows an opposite pattern compared to water content in ovary tissue (**Figure 5G**). In the muscle tissue, total protein content declined from stages III to V, whereas less variation was observed in the liver tissue during maturation (**Figures 5H,I**). Lipid content in the ovary and liver gradually went up from stages I to IV and then dropped off significantly in spawning and post-spawning (stage V) (**Figures 5J,L**). Similarly, lipid content in the muscle tissues increased and subsequently decreased during maturation with a maximum value in stage III (**Figure 5K**).

Energy Accumulation and Allocation

The weights of trunk, ovary, and liver were positively correlated with body mass from stages III to IV (**Figures 6A–C** and **Supplementary Table 1**). The rate of increase of ovary mass rose sharply from stages III to IV, whereas the rate of increase of trunk mass declined. The proportions of protein and lipid in muscle were positively correlated ($R^2 = 0.152$; $p < 0.01$) (**Figure 6D**), and the proportions of proteins and lipids were negatively related in the ovary and liver tissues from stages III to IV ($R_{ovary}^2 = 0.312$; $P_{ovary} < 0.01$; $R_{liver}^2 = 0.284$; $p_{liver} < 0.01$) (**Figures 6E,F**). The variation in energy density across maturity stages for each tissue is shown in **Figures 7A–C**. In the muscle, no significant change in energy density was perceived from stages I to V (**Figure 7A**). In contrast, there was a clear pattern related to reproduction, since maxima were observed in ovary and liver at female stage IV (**Figures 7B,C**), and there was a sharp drop reaching a minimum of energy density at stage V. Some statistically significant negative relationships were observed between ovary and muscle energy density from stages III to IV ($R^2 = 0.215$; $p < 0.01$) (**Figure 7D**). The muscle energy density decreased rapidly, whereas the ovary increased slowly in stage III. In contrast, energy density of muscle dropped slightly and ovarian energy density rose dramatically in stage IV. Ovary and liver energy density showed a positive relationship ($R^2 = 0.246$; $p < 0.01$) (**Figure 7E**). By contrast, muscle and liver energy density had a negative relationship from stages III to IV ($R^2 = 0.193$; $p < 0.05$) (**Figure 7F**).

DISCUSSION

In this study, we found that the ovary of migrating black Amur bream gradually matured during movement from the estuary (fattening ground) to the main stem (spawning ground) during the breeding season (**Figure 1**). Maturity stages III to IV of the

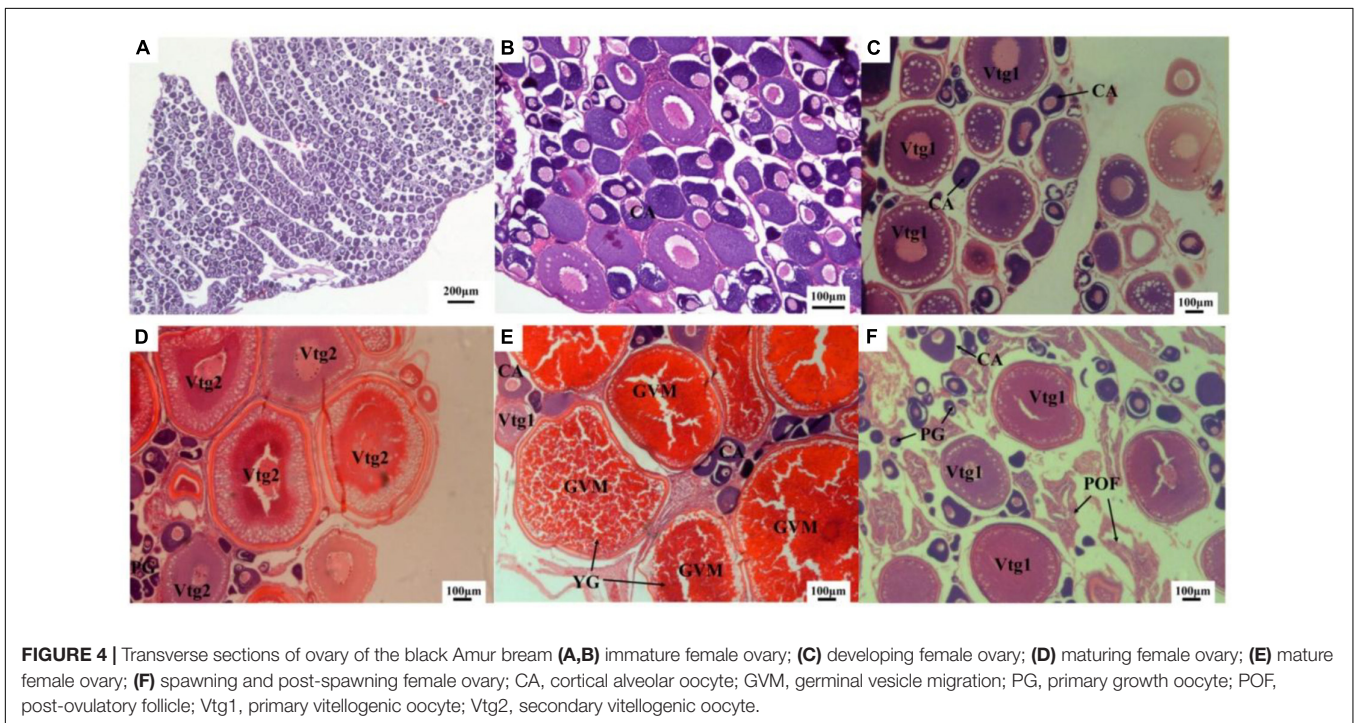
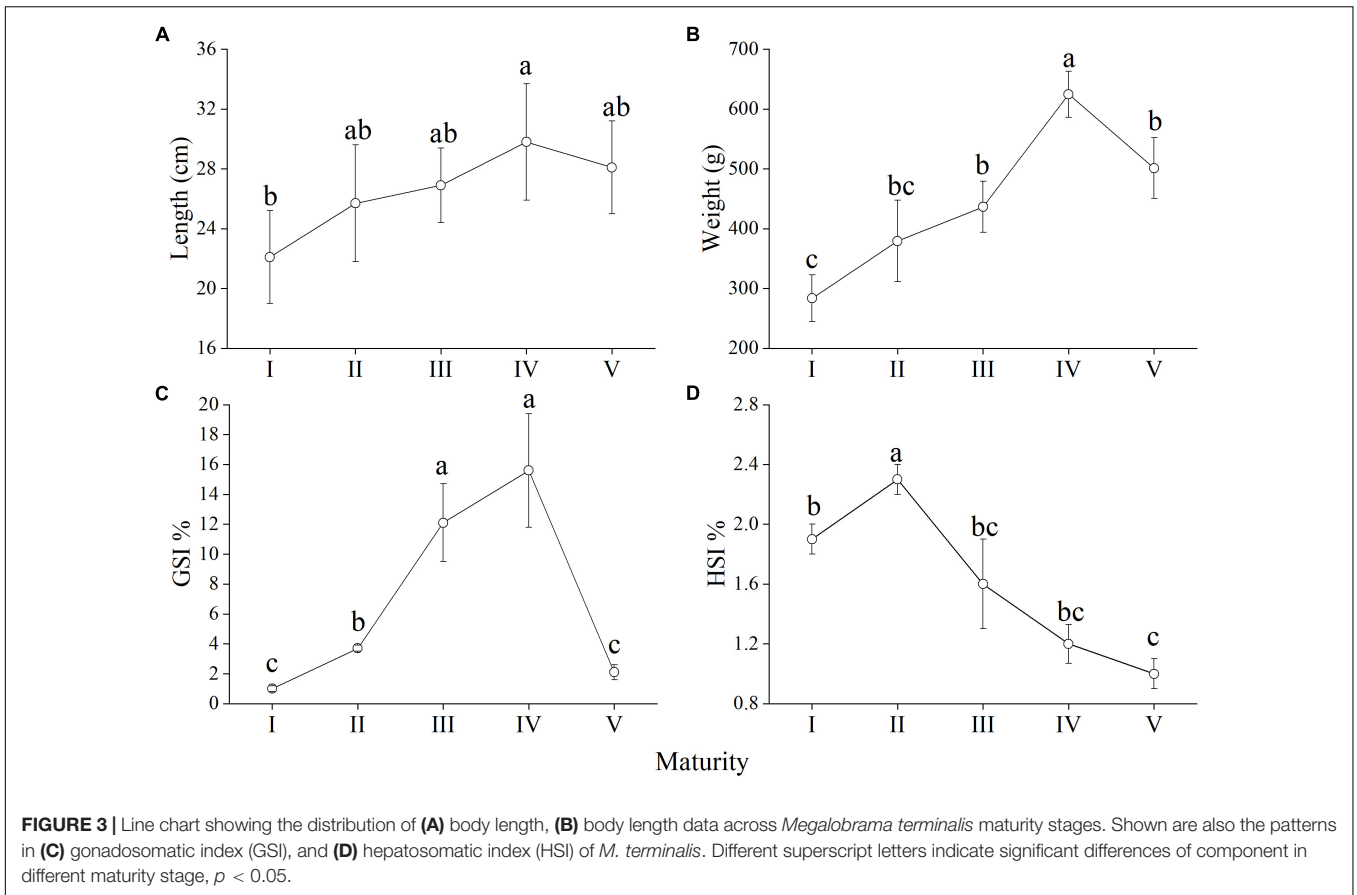
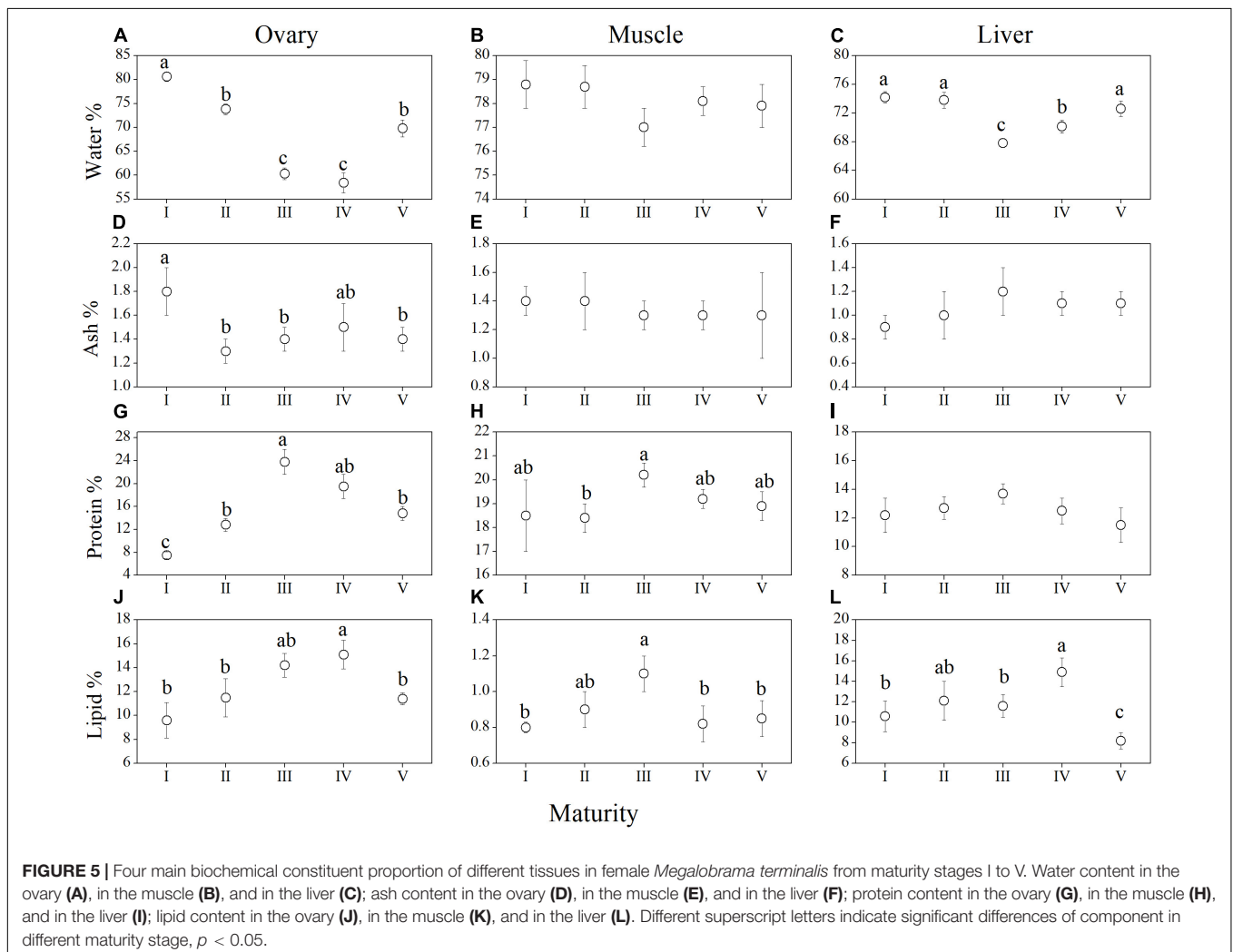


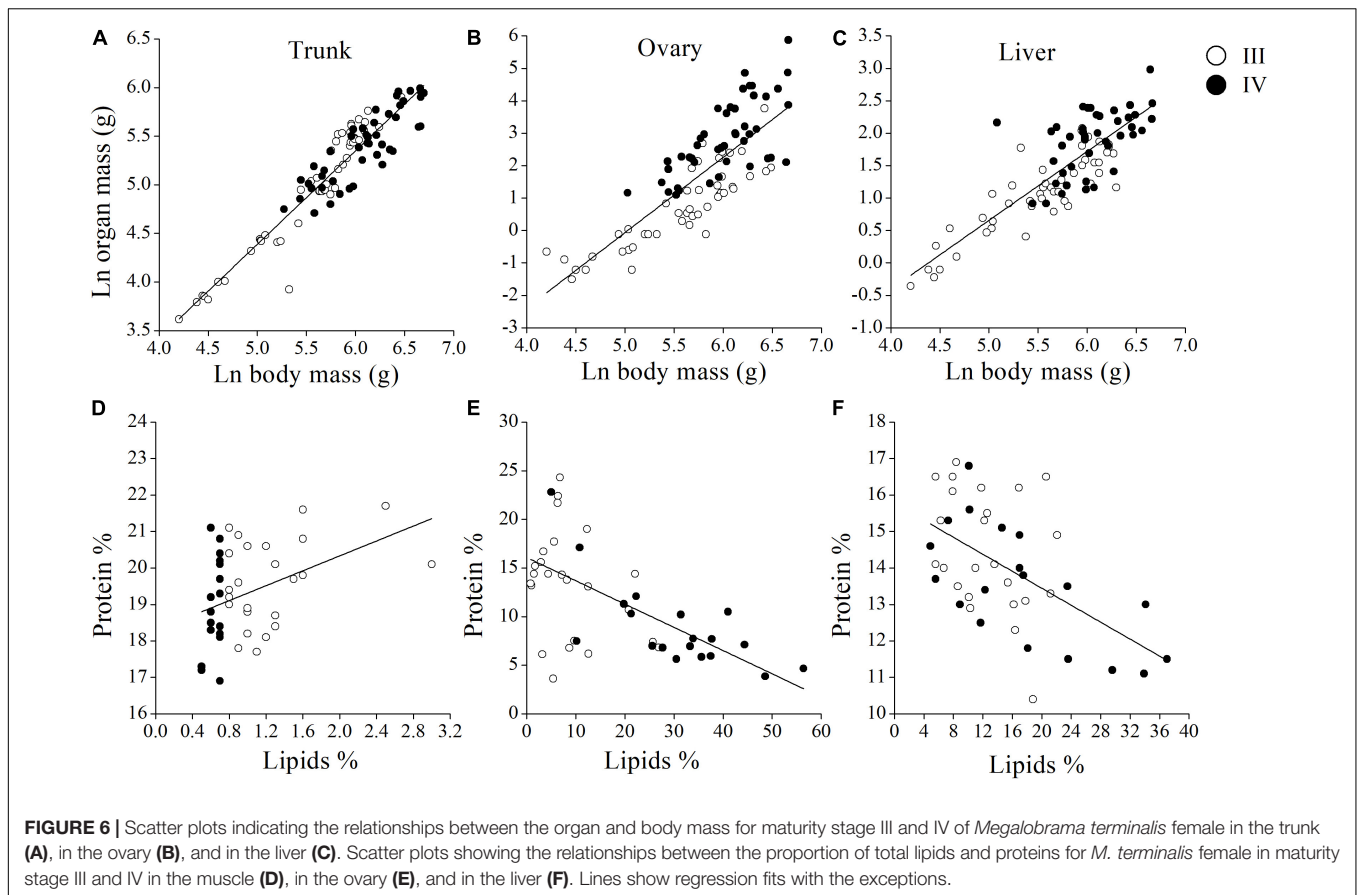
TABLE 2 | Histological descriptions of the stages in the reproductive cycle of female *Megalobrama terminalis*.

Stage	Description
I (Immature)	Small ovaries, often clear, blood vessels indistinct. Only oogonia and PG oocytes present.
II (Developing)	Enlarging ovaries, blood vessels becoming more distinct. PG, CA, and Vtg1 oocytes present.
III (Maturing)	The number of nucleolus increased and irregular deformation occurred close to the inner edge of the nuclear membrane. PG, CA, Vtg1, and Vtg2 oocytes present.
IV (Mature)	Large ovaries, blood vessels prominent. Individual oocytes visible macroscopically. Oocytes undergoing late GVM.
V (Spawning/post-spawning)	Flaccid ovaries, blood vessels prominent. Atresia (any stage) and POFs present. Some CA and/or vitellogenic (Vtg1, Vtg2) oocytes present.

black Amur bream were observed as a vital migration-launching period. Meanwhile, significant differences in environmental factors and biological indices were observed between estuary

and main stem populations, especially in salinity, dissolved oxygen, GSI, HSI, and fatness (**Table 1**). A clear separation of the proximate composition of the ovary was detected between estuary and main stem populations (**Figure 2A**). Secor (1999) indicated that not all individuals of migratory populations participated in the breeding migration. Non-migrating and migrating individuals demonstrated significant differences in maturity and energy reserves of fish reproductive organs. It is widely recognized that lipids and proteins are high energy substances for fish storage (Zaboukas et al., 2006; Sieiro et al., 2020). The recent study has illustrated that migratory individuals are evolving toward larger body size and higher fertility than non-migratory individuals (Burns and Bloom, 2020). In this study, we found that migrating population in the main stem had larger body size and higher GSI than that of non-migrating population (**Table 1**). The proximate composition of ovary in the groups S4 and S5 had a close relationship with biological indices, especially in fatness and GSI (**Figure 2B**). Lipid content in the ovary of the black Amur bream gradually increased from the estuary to the main stem, which indicates that migrating

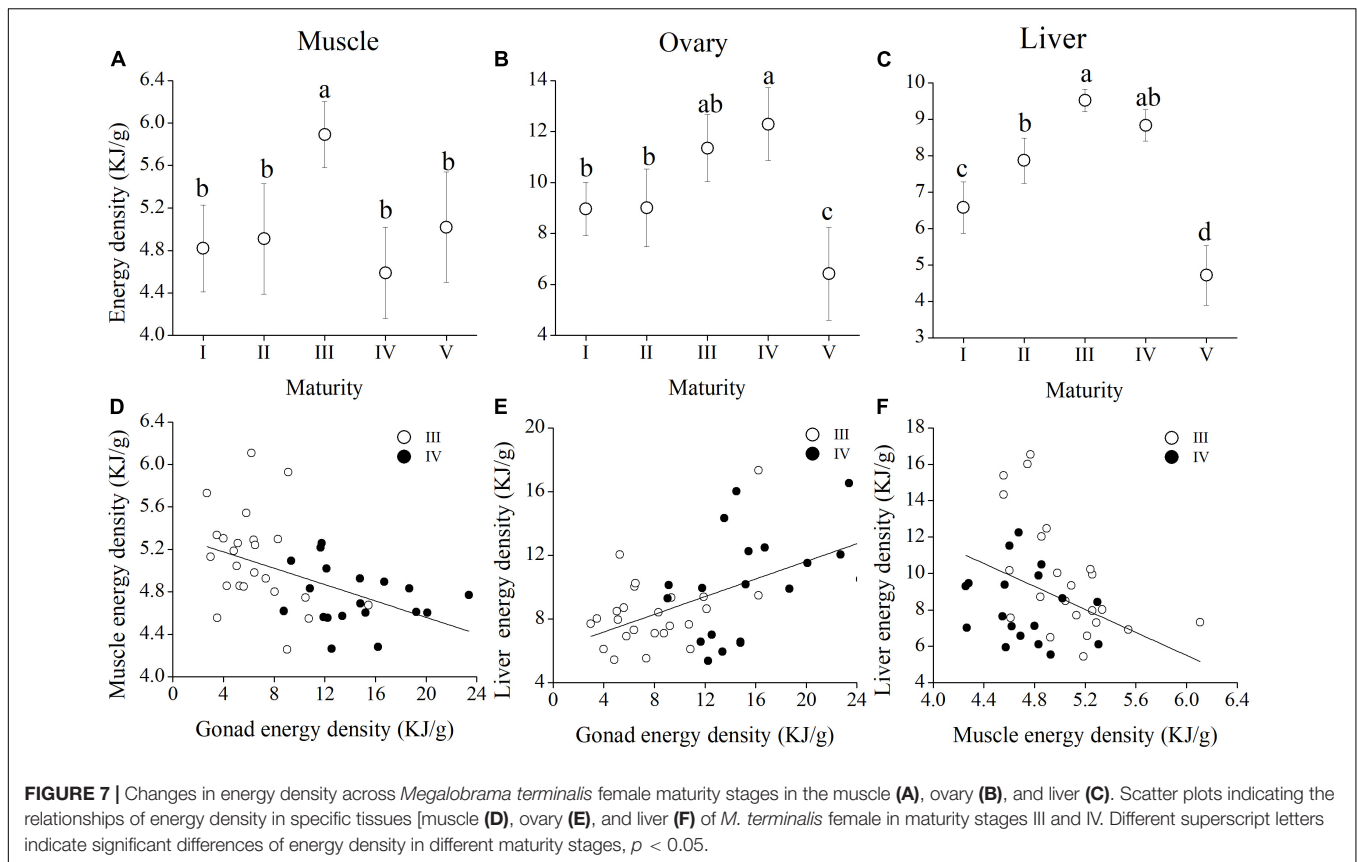




population stored more energy for ovary development. The high lipid content of tissues also signified the need for high energy biomolecules to perform the energy-consuming locomotion (Zaboukas et al., 2006). Relevant studies have pointed out that fish utilize lipids to regulate their energy expenditure for gonad development (Takama et al., 1985). Thus, the remarkable change in lipid content of the ovary might be considered as a crucial physiological index, which reflects the readiness for breeding migration of *M. terminalis*.

In order to make an effective assessment of *M. terminalis* ovary development, it is imperative to describe the process of energy accumulation and oocyte recruitment during ovary development. According to our study, it appears that *M. terminalis* follows a similar pattern of oocyte developmental stages as in most one-time spawning type fish species (Murua and Saborido-Rey, 2003; Costa et al., 2015). The variation tendency of the proximate composition in muscle and ovary tissues was due to increases in the protein content from stages I to III (Figures 5G,H). The protein content is essential to maintaining major body organic structure and function of migrating fish during reproductive migration (Lin et al., 2017; Serrat et al., 2019). In addition, somatic tissue is regarded as primarily location of fish energy reserves, and this is commonly determined by the protein content throughout reproduction (Lin et al., 2019). Lipid content in the ovary gradually increased during the migration-launching period, whereas that in the muscle slightly declined. This indicated that energetic investment of *M. terminalis* concentrated

on reproduction, whereas there was a more intense reduction in the lipid contents of the somatic tissues (Zaboukas et al., 2006). Furthermore, decreases in the lipid contents of fish somatic tissues are mainly devoted to supplying energy for reproductive migration (Doucett et al., 1999; Kiessling et al., 2004). During the migration-launching period, the accumulation of lipids in the ovary proceeds until the onset of vitellogenesis; this is interpreted as initiation of the synthesis of yolk-forming molecules. The production of abundant eggs during the relatively short period of reproduction is very energy intensive (Tocher, 2003). In the course of this period, the proportions of protein and lipid in the ovary showed a negative correlation, which suggests that lipids were more important than proteins in the *M. terminalis* ovary during advanced maturity stages. Studies present have shown that lipids are important in the ovaries of marine fish during maturity stages (Rosa et al., 2002; Serrat et al., 2019). Related research reveals that lipids predominate in the liver and ovary in the common octopus (Sieiro et al., 2006). Despite lipid content of somatic and reproductive tissue being of vital importance, the lipid content in tissues of *M. terminalis* rose to a certain level and remained stable instead of increasing blindly during the migratory reproductive preparation period (stage III). Relevant research has indicated that excessive lipids limited fish swimming speed during migration (Slotte et al., 2000). Consequently, lipids may have diverse effects in different tissues of the black Amur bream, and there may be a regulatory mechanism for allocating the lipids to each tissue to



reduce the risk of migration failure in the breeding migratory preparation period.

This study demonstrated that ovary mass gain is accelerated, while somatic mass grows more slowly during the vital migration-launching period. Relevant studies have indicated that the relationship between organ and body size can be applied to explain the allometric variation at the metabolic level (Oikawa and Itazawa, 1992). Some studies have manifested that the somatic tissues accumulated energy continuously until the physiologically maturing stage, whereas the reproductive organs had a drastic energy accumulation throughout the sexual maturation period (Lahti et al., 2001, 2002). The energy density in *M. terminalis* somatic tissues increased initially after declining owing to fluctuating contents of total protein and lipid during the maturation process. More specifically, the rise in the energy density of somatic tissues was due to the body growth of *M. terminalis* from stages I to III. Rapid body growth in fish results from intensive protein synthesis and low protein degradation (Houlihan et al., 1990; Sieiro et al., 2020). Owing to the high level of protein in the somatic tissues, the energy metabolism is mainly protein-based (Navarro et al., 2014). However, a negative energy relationship between somatic and reproductive tissues was observed in *M. terminalis* during the vital migration-launching period. The downtrend of energy density in somatic tissues after stage III was related to the decline of lipid content. The previous research has suggested that somatic tissues of migrating fish are applied to provide energy for the migration process (Kiessling et al., 2004). Moreover,

lipids are crucial energy substances with high energy efficiency in fish somatic tissues (Hinch et al., 2002). Higher variability of energy density in the ovary and liver was observed during a vital migration-launching phase due to enhanced lipid contents. This ascent of energy density in ovary associated with yolk accumulation in stage IV has been found in some fish species (Fernández et al., 2009; Wu et al., 2017). Specifically, rapid synthesis of yolk materials in the developing oocytes during the migration-launching phase is conducive to the energy substances being rapidly synthesized in the later physiological maturity stages (Alonso-Fernández and Saborido-Rey, 2012; Lin et al., 2017). Not all individuals in migratory fish populations participate in the migration (Secor, 1999). Non-migrating and migrating individuals presented obvious discrepancies in body size and lipid storage status. Our previous results suggested that lipid metabolism in migrating population was higher than that in non-migrating population, which provides a line of evidence for that *M. terminalis* consuming lipids to supply energy for spawning migration (Liu et al., 2021a). Similarly, it has been proposed that Atlantic salmon maturation was linked with growth rate and lipid metabolism (Herbinger and Friars, 1991). Barneche et al. (2018) revealed that larger females disproportionately reproduce more than smaller females whether measured by fecundity or by total reproductive energy. Larger females had a higher metabolic ability factor that is significant for fish survival, energy consumption, and migration (Priede, 1985; Hinch and Rand, 2000). The higher metabolic ability requires a more complex organizational structure, which inevitably leads to

higher energy consumption and lower energy efficiency (Weiner, 1993; Chappell et al., 1999; Hinch and Rand, 2000). In fact, energy accumulation is closely linked to the co-evolved life-history traits favored for optimal energetic allocation (Lin et al., 2017). Therefore, there may be a trade-off between maximum metabolic ability and energy efficiency before migration launching in the black Amur bream.

CONCLUSION

Above all, stages III to IV of the black Amur bream were observed as a crucial migration-launching period. The asynchrony of development was confirmed in energetic relationships in somatic and ovary tissues. In addition, the negative energy relationship between somatic and reproductive tissues clarified a trade-off between maximum metabolic ability and energy efficiency before the migration launching of *M. terminalis*. The lipid content displayed diverse effects in different tissues of *M. terminalis*, and there was a regulatory mechanism for allocating the lipid content of each tissue reasonably to reduce the risk of migration failure during the breeding migratory preparation period. The results demonstrated that there is a dependency between somatic and reproductive tissue growth in *M. terminalis* females during migratory preparation that serves to improve fitness. Finally, these findings illustrate that the high energy metabolism demands of reproduction of *M. terminalis* are regarded as a key factor driving the variation in energy accumulation and allocation. The findings facilitate further research on ecological adaptations of migrating fish during the reproductive cycle.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The methods involving animals in this study were conducted in accordance with the Laboratory Animal Management Principles

REFERENCES

- Alonso-Fernández, A., and Saborido-Rey, F. (2012). Relationship between energy allocation and reproductive strategy in *Trisopterus luscus*. *J. Exp. Mar. Biol. Ecol.* 416–417, 8–16. doi: 10.1016/j.jembe.2012.02.001
- Barbour, S. E. (1985). *Variation in Life History, Ecology and Resource Utilization by Arctic charr (Salvelinus alpinus L.) in Scotland*. [Ph.D thesis]. Edinburgh: University of Edinburgh.
- Barneche, D. R., Robertson, D. R., White, C. R., and Marshall, D. J. (2018). Fish reproductive–energy output increases disproportionately with body size. *Science* 360, 642–645. doi: 10.1126/science.aao6868
- Bureau, D., Colombier, S. B. D., Bolliet, V., Lambert, P., and Bardonnnet, A. (2007). Energy and migratory behavior in glass eels (*Anguilla Anguilla*). *Physiol. Behav.* 92, 684–690.
- Burns, M. D., and Bloom, D. D. (2020). Migratory lineages rapidly evolve larger body sizes than non- migratory relatives in ray- finned fishes. *Proc. Royal Soc. B* 287:20192615. doi: 10.1098/rspb.2019.2615

of China. All experimental protocols were approved by the Ethics Committee of the Pearl River Fisheries Research Institute, Chinese Academy of Fishery Sciences. Written informed consent was obtained from the owners for the participation of their animals in this study.

AUTHOR CONTRIBUTIONS

YaL: conceptualization, data curation, and writing—original draft. XL: funding acquisition. JL: funding acquisition and supervision. YuL: formal analysis, writing, reviewing, and editing. All authors contributed to the article and approved the submitted version.

FUNDING

This study was funded by Guangdong Basic and Applied Basic Research Foundation, grant number: 2019B1515120064; National Key R&D Program of China, grant numbers: 2018YFD0900902 and 2018YFD0900903; Open Fund of Key Lab of Freshwater Biodiversity Conservation, Ministry of Agriculture and Rural Affairs of China, grant number: LFBC1006; Open Fund Project of Fishery Resources and Environmental Science Experimental Station of The Upper-Middle Reaches of Yangtze River Ministry of Agriculture, grant number: 0202020017.

ACKNOWLEDGMENTS

We are grateful to Weitao Chen and Shuli Zhu for assistances in collecting specimens. We thank LetPub (www.letpub.com) for its linguistic assistance during the preparation of this manuscript.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.848228/full#supplementary-material>

- Caudill, C. C., Daigle, W. R., Keefer, M. L., Boggs, C. T., Jepson, M. A., Burke, B. J., et al. (2007). Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition–dependent mortality? *Can. J. Fish Aquat. Sci.* 64, 979–995. doi: 10.1139/f07-065
- Chappell, M., Bech, C., and Buttemer, W. (1999). The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. *J. Exp. Biol.* 202, 2269–2279. doi: 10.1242/jeb.202.17.2269
- Chen, W., Li, C., Chen, F., Li, Y., Yang, J., Li, J., et al. (2020). Phylogeographic analyses of a migratory freshwater fish (*Megalobrama terminalis*) reveal a shallow genetic structure and pronounced effects of sea-level changes. *Gene* 737:144478. doi: 10.1016/j.gene.2020.144478
- Colombier, S. B. D., Bolliet, V., Lambert, P., and Bardonnnet, A. (2007). Energy and migratory behavior in glass eels (*Anguilla anguilla*). *Physiol. Behav.* 92, 684–690. doi: 10.1016/j.physbeh.2007.05.013
- Connell, J. J. (1975). *Control of Fish Quality*. Farnham: Fishing News Books Ltd.

- Costa, E. F., Dias, J. F., and Murua, H. (2015). Reproductive strategy and fecundity of the keystone species *Paralanchurus brasiliensis* (Teleostei, Sciaenidae): an image processing techniques application. *Environ. Biol. Fish.* 98, 2093–2108. doi: 10.1007/s10641-015-0432-2
- Doucett, R. R., Booth, R. K., Power, G., and McKinley, R. S. (1999). Effects of the spawning migration on the nutritional status of anadromous Atlantic salmon (*Salmo salar*): insights from stable isotope analysis. *Can. J. Fish. Aquat. Sci.* 56, 2172–2180. doi: 10.1139/f99-147
- Fernández, D. A., Lattuca, M. E., Boy, C. C., Pérez, A. F., Ceballos, S. G., Vanella, F. A., et al. (2009). Energy density of sub-Antarctic fishes from the Beagle Channel. *Fish. Physiol. Biochem.* 35, 181–188. doi: 10.1007/s10695-008-9234-1
- Folch, J. M., Lees, M., and Sloane-Stanley, G. H. (1957). A simple method for the isolation and purification of total lipid from animal tissue. *J. Biol. Chem.* A 226, 497–509. doi: 10.1016/s0021-9258(18)64849-5
- Hach, C. C., Scott, V. B., and Kopelove, A. B. (1985). A powerful Kjeldahl nitrogen method using peroxymonosulfuric acid. *J. Agric. Food. Chem.* 33, 1117–1123. doi: 10.1021/jf00066a025
- Herbinger, C. M., and Friars, G. W. (1991). Correlation between condition factor and total lipid content in Atlantic salmon, *salmo salar* L. *Aquat. Fish. Mana.* 22, 527–529. doi: 10.1111/j.1365-2109.1991.tb00766.x
- Hinch, S. G., and Rand, P. S. (2000). Optimal swim speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. *Can. J. Fish. Aquat. Sci.* 57, 2470–2478. doi: 10.1139/f00-238
- Hinch, S. G., Standen Emily, M., Healey Michael, C., and Farrell Anthony, P. (2002). Swimming patterns and behaviour of upriver-migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada. *Hydrobiologia* 483, 147–160. doi: 10.1007/978-94-017-0771-8_17
- Houlihan, D. F., McMillan, D. N., Agnisola, C., Genoino, I. T., and Foti, L. (1990). Protein synthesis and growth in *Octopus vulgaris*. *Mar. Biol.* 106, 251–259.
- Jonsson, N., and Jonsson, B. (2003). Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. *Can. J. Fish. Aquat. Sci.* 60, 506–516. doi: 10.1139/f03-042
- Kiessling, A., Lindahl-Kiessling, K., and Kiessling, K. (2004). Energy utilization and metabolism in spawning migrating early start sockeye salmon (*Oncorhynchus nerka*): the migratory paradox. *Can. J. Fish. Aquat. Sci.* 61, 452–465. doi: 10.1139/f04-006
- Lahti, K., Huusknen, H., Laurila, A., and Piironen, J. (2002). Metabolic rate and aggressiveness between brown trout populations. *Func. Ecol.* 16, 167–174. doi: 10.1046/j.1365-2435.2002.00618.x
- Lahti, K., Laurila, A., Enberg, K., and Piironen, J. (2001). Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. *Anim. Behav.* 62, 935–944. doi: 10.1006/anie.2001.1821
- Lennox, R. J., Paukert, C. P., Aarestrup, K., Auger-Méthé, M., Baumgartner, L., Birnie-Gauvin, K., et al. (2019). One Hundred Pressing Questions on the Future of Global Fish Migration Science, Conservation, and Policy. *Front. Ecol. Evol.* 7:286. doi: 10.3389/fevo.2019.00286
- Li, Y., Li, C., Zhu, S., Yang, J., Xia, Y., and Li, X. (2018). Exploitation status of *Megalobrama terminalis* based on analysis of SBR and YPR models in Xijiang river. *Acta Hydrobiol. Sin.* 42, 975–983.
- Li, Y., Li, X., Yang, J., Sovan, L., Shuai, F., and Li, J. (2014). Effect of Pearl River closed fishing on *Megalobrama terminalis* recruitment stock. *J. Fish. China.* 38, 503–509.
- Lin, D., Chen, X., Wei, Y., and Chen, Y. (2017). The energy accumulation of somatic tissue and reproductive organs in post-recruit female *Illex argentines* and the relationship with sea surface oceanography. *Fish. Res.* 185, 102–114. doi: 10.1016/j.fishres.2016.09.023
- Lin, D., Han, F., Xuan, S., and Chen, X. (2019). Fatty acid composition and the evidence for mixed income-capital breeding in female Argentinean short-fin squid *Illex argentinus*. *Mar. Biol.* 166, 90.
- Liu, Y., Chen, W., Li, Y., Li, J., and Li, X. (2020). Growth and ontogenetic development of digestive functionality in black Amur bream (*Megalobrama terminalis*). *Aquat. Res.* 51, 3593–3601. doi: 10.1111/are.14697
- Liu, Y., Li, X., Li, Y., Li, J., and Zhu, S. (2021b). Reproductive biology and strategy of black Amur bream (*Megalobrama terminalis*) of Xijiang River. *J. Lake Sci.* 33, 232–241. doi: 10.18307/2021.0117
- Liu, Y., Li, X., Li, J., and Chen, W. (2021a). The gut microbiome composition and degradation enzymes activity of black Amur bream (*Megalobrama terminalis*) in response to breeding migratory behavior. *Ecol. Evol.* 11, 5150–5163. doi: 10.1002/ece3.7407
- McCormick, S. D., Hansen, L. P., Quinn, T. P., and Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 55, 77–92. doi: 10.1139/d98-011
- Mourete, G., Megina, C., and Díaz-Salvago, E. (2002). Lipids in female northern bluefin tuna (*Thunnus thynnus thynnus* L.) during sexual maturation. *Fish. Physiol. Biochem.* 24, 351–363.
- Murua, H., and Saborido-Rey, F. (2003). Female reproductive strategies of marine fish of the North Atlantic. *J. Northw. Atl. Fish. Sci.* 33, 23–31. doi: 10.2960/j.v33.a2
- Navarro, J. C., Monroig, Ó, and Sykes, A. V. (2014). “Nutrition as a key factor for cephalopod aquaculture,” in *Cephalopod Culture*, eds J. Iglesias, L. Fuentes, and R. Villanueva (Netherlands: Springer), 77–95. doi: 10.1007/978-94-017-8648-5_5
- Nikolsky, G. (1963). *The Ecology of Fishes*. London: Academic Press.
- Oikawa, S., and Itazawa, Y. (1992). Relationship between metabolic rate *in vitro* and body mass in a marine teleost, porgy *pagrus major*. *Fish. Physiol. Biochem.* 10, 177–182. doi: 10.1007/BF00004511
- Penney, Z. L., and Moffitt, C. M. (2014). Proximate Composition and Energy Density of Stream-Maturing Adult Steelhead during Upstream Migration, Sexual Maturity, and Kelt Emigration. *Tran. Am. Fish. Soc.* 143, 399–413. doi: 10.1080/00028487.2013.862184
- Priede, I. (1985). “Metabolic scope in fishes,” in *Fish Energetics*, eds Tytler P., Calow P. (Dordrecht: Springer), 33–64. doi: 10.1007/978-94-011-7918-8_2
- Roff, D. A. (1983). An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.* 40, 1395–1404. doi: 10.1139/f83-161
- Rosa, R., Nunes, M. L., and Sousa Reis, C. (2002). Seasonal changes in the biochemical composition of *Octopus vulgaris*, Cuvier, 1797, from three areas of the Portuguese coast. *Bull. Mar. Sci.* 71, 739–751.
- Saborido-Rey, F., Garabana, D., Stransky, C., Melnikov, S., and Shibanov, V. (2004). Review of the population structure and ecology of *S. mentella* in the Irminger sea and adjacent waters. *Rev. Fish Biol. Fish.* 14, 455–479. doi: 10.1007/s11160-005-3585-9
- Secor, D. H. (1999). Specifying divergent migrations in the concept of stock: the contingent hypothesis. *Fish. Res.* 43, 13–34. doi: 10.1016/s0165-7836(99)00064-8
- Serrat, A., Saborido-Rey, F., García Fernández, C., Muñoz Frigola, M., Lloret Romanach, J., Thorsen, A., et al. (2019). New insights in oocyte dynamics shed light on the complexities associated with fish reproductive strategies. *Sci. Rep.* 9:18411. doi: 10.1038/s41598-019-54672-3
- Sieiro, P., Aubourg, S. P., and Rocha, F. (2006). Seasonal study of the lipid composition in different tissues of the common octopus (*Octopus vulgaris*). *Eur. J. Lipid Sci. Tech.* 108, 479–487. doi: 10.1002/ejlt.200500322
- Sieiro, P., Otero, J., and Aubourg, S. P. (2020). Biochemical Composition and Energy Strategy Along the Reproductive Cycle of Female *Octopus vulgaris* in Galician Waters (NW Spain). *Front. Physiol.* 11:760. doi: 10.3389/fphys.2020.00760
- Slotte, A., Johannessen, A., and Kjesbu, O. S. (2000). Effects of fish size on spawning time in Norwegian spring-spawning herring. *J. Fish Biol.* 56, 295–310. doi: 10.1111/j.1095-8649.2000.tb02107.x
- Takama, K., Love, R. M., and Smith, G. L. (1985). Selectivity in mobilisation of stored fatty acids by maturing cod, *Gadus morhua* L. *Comp. Biochem. Physiol. B.* 80, 713–718. doi: 10.1016/0305-0491(85)90450-x
- Tamarío, C., Sunde, J., Petersson, E., Tibblin, P., and Forsman, A. (2019). Ecological and Evolutionary Consequences of Environmental Change and Management Actions for Migrating Fish. *Front. Ecol. Evol.* 7:271. doi: 10.3389/fevo.2019.00271
- Tan, X., Li, X., Lin, J., Zhou, D., Gao, X., and Li, J. (2009). Ecological differentiation between two breeding populations of *Megalobrama terminalis* in the Pearl River based on hydro-acoustic research. *Acta Ecol. Sin.* 29, 1756–1762.
- Thomas, A., and Johan, B. (2018). Ecology of animal migration. *Cur. Biol.* 28, 968–972. doi: 10.1016/j.cub.2018.04.043
- Thorpe, J. E., Mangel, M., Metcalfe, N. B., and Huntingford, F. A. (1998). Modelling the proximate basis of salmonid life-history variation, with application to

- Atlantic salmon, *Salmo salar* L. *Evol. Ecol.* 12, 581–599. doi: 10.1023/a:1022351814644
- Tocher, D. (2003). Metabolism and functions of lipids and fatty acids in teleost fish. *Rev. Fish. Sci.* 11, 107–184. doi: 10.1080/713610925
- Villegas-Ríos, D., Alonso-Fernández, A., Domínguez-Petit, R., and Saborido-Rey, F. (2014). Energy allocation and reproductive investment in a temperate protogynous hermaphrodite, the ballan wrasse *Labrus bergylta*. *J. Sea Res.* 86, 76–85. doi: 10.1016/j.seares.2013.11.010
- Wang, C., Li, X. H., Lai, Z. N., Tan, X., Li, J., Li, Y., et al. (2010). The study on community structure difference of phytoplankton in two *Megalobrama terminalis* spawning grounds of Xijiang River. *Guan. Agri. Sci.* 37, 156–160.
- Weiner, J. (1993). Physiological limits to sustainable energy budgets in birds and mammals: ecological implications. *Trends Ecol Evol.* 7, 384–388. doi: 10.1016/0169-5347(92)90009-Z
- Wu, L., Tang, W., and Zhang, Y. (2017). Research on the differences of anadromous migratory distance between *Coilia mystus* and *Coilia nasus* based on the transfer process of body lipid. *J. Fish. Chin.* 41, 212–220.
- Wysujack, K., Greenberg, L. A., Bergman, E., and Olsson, I. C. (2010). The role of the environment in partial migration: food availability affects the adoption of a migratory tactic in brown trout *Salmo trutta*. *Ecol. Freshw. Fish.* 18, 52–59. doi: 10.1111/j.1600-0633.2008.00322.x
- Xia, Y., Li, J., Li, Y., Zhu, S., Huang, Y., Wu, Z., et al. (2017). Small-subunit ribosomal DNA sequencing analysis of dietary shifts during gonad maturation in wild black Amur bream (*Megalobrama terminalis*) in the lower reaches of the Pearl River. *Fish. Sci.* 83, 955–965. doi: 10.1007/s12562-017-1123-z
- Xia, Y., Li, Y., Zhu, S., Li, J., Li, S., and Li, X. (2020). Individual dietary specialization reduces intraspecific competition, rather than feeding activity, in black amur bream (*Megalobrama terminalis*). *Sci. rep.* 10:17961. doi: 10.1038/s41598-020-74997-8
- Zaboukas, N., Miliou, H., Megalofonou, P., and Moraitou-Apostolopoulou, M. (2006). Biochemical composition of the Atlantic bonito *Sarda sarda* from the Aegean Sea (eastern Mediterranean Sea) in different stages of sexual maturity. *J. Fish. Biol.* 69, 347–362. doi: 10.1111/j.1095-8649.2006.01090.x

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's Note: All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Copyright © 2022 Liu, Li, Li and Li. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.