The Status of Silver Carp Resources and Their Complementary Mechanism in the Yangtze River

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The global climate and environmental variability can induce fish adaptive strategy change and form a corresponding complementary mechanism subsequently. Because of climate fluctuation, human activities, and water conservancy projects, it has been reported that natural fish resources of the silver carp have been declining in a wavy trend from 1950. However, few studies have explored the potential effects of determining the relationship between the adult fish and fish larvae. Using the field survey method, this study analyzed the fisheries resource status of the adult silver carp and its early life stage in the Yangtze River. Results indicated that different geographic populations showed significant habitat dependence, and the adult silver carp tends to choose habitats with slow water flow, rich biological bait, and less human interference. What is more, its distribution pattern has regional and seasonal differences obviously. Additionally, redundancy analysis on the fish larvae showed that water temperature and water flow are the two most important factors influencing the fish larvae blooming. According to the generalized additive model (GAM), the hydrological factors that significantly influence the larvae abundance are water temperature, transparency, daily increasing rate of water level, and discharge ($p < 0.05$). Combining the historical and present research data, the results indicated that river and lake connected habitat is essential for the silver carp recruitment and migration. Future studies should focus on the complementary mechanism of silver carp both in the natural habitat and invasion waters. It is suggested that the spawning habitat should be well protected during the channel project and economic belt construction along the Yangtze River.

Keywords: *Hypophthalmichthys molitrix*, complementary mechanism, the Yangtze River, climate change, habitat selection, fish larvae

INTRODUCTION

The most significant change in the global climate and environment is global warming (Zandalinas et al., 2021). A global hydrological water temperature modeling framework predicts the global daily river discharge and water temperature under future climate conditions (van Vliet et al., 2013; Huang et al., 2021). The results showed that the global mean river water temperatures are predicted to increase 0.8–1.6°C, and the future mean water temperature increase in the Yangtze River is expected

to be up to 1.8°C for the period 2071–2100 (Rodriguez-Dominguez et al., 2019; Yue et al., 2021). Global warming is a critical concern in spawning ecology of fishes, especially in freshwater (Huang et al., 2021). Researchers have indicated that elevated temperatures shorten the spawning period of silver carp in the Pearl River (Shuai et al., 2018). Consequently, global warming is expected to impact the reproductive function of fish, which has implications for wild population dynamics and diversity (Rodriguez-Dominguez et al., 2019). The Yangtze River is the longest river in China, which has an elevation varying from 5,000 to 0 m above the sea level. High drop and altitude difference lead to different characteristics of water temperature distribution in the Yangtze River (Chen et al., 2020). Because discrete ecosystem in rivers limited fish to follow optimal temperature conditions for spawning migration, the impact of warming was likely to be stronger and stronger especially for fish species in freshwater (Schmidt et al., 2020).

Fish spawning migration patterns are regulated by essential factors such as hydrographic parameters and spawning population stocks (Song et al., 2019). It is well known that construction and operation of the Three Gorges Dam (TGD) have brought changes to the hydraulics and water quality in the middle and lower reach of the Yangtze River (Liu et al., 2019). Consequently, spawning habitats for these fish species have been deteriorated, and thus their populations, such as the silver carp, have decreased (Zhang et al., 2021). Silver carp (*Hypophthalmichthys molitrix*) is one of the four majorly farmed carps in China (Li et al., 1984), which is a native fish species in the Yangtze River and its resource dynamics can serve as an indicator for the ecosystem (Fu et al., 2003). The Yangtze River is the main place where the germplasm resources have occurred for the silver carp in China (Fu et al., 2003; Fang et al., 2021). According to field surveys, the percentage of the silver carp both in the larval catch and the adult catch has sharply reduced from the 1960s (Wang et al., 2019). Silver carp was artificially bred in 1958 successfully and transported to other countries overboard. Some of them have formed new local populations because of changes in habitat such as water temperature, water flow, and river dynamics. Since 2011, the TGD has been discharging water to make artificial floods into the downstream areas and induced the spawning of four major Chinese carps successfully (Tao et al., 2017).

Fishes cannot live without water, and therefore they are directly affected by the ongoing changes in the aquatic ecosystems. Sexual maturation and successful reproduction are the key processes for species survival and evolution (Servili et al., 2020). In fish, it is largely dependent on specific environmental factors that control or modulate sexual maturation and spawning (Servili et al., 2020). Thus, the ongoing rapid environmental changes directly interfere with reproductive processes and may jeopardize spawning success and fish larvae survival (Rogers et al., 2019). It is well known that dam construction can reduce connectivity of rivers, fragment watersheds, affect fish assemblages by interrupting fish migration, and reduce species diversity (Fu et al., 2003). It also causes direct changes in water depth (WD), flow velocity, and hydrological processes, which result in downstream river channel erosion, physical habitat unfitness, and water quality deterioration. The artificial

embankments and dams on surrounding habitats also have resulted in a significant disturbance for the river ecosystem (Addy and Wilkinson, 2021).

As the silver carp resource of Chinese indigenous population showed a declining trend, the strategy of 10-year fishing ban on the Yangtze River has been implemented from January 2020 (Chen et al., 2020). Fish in the early life history refers to the period from fertilization to embryonic and larval stages and then to juvenile stage. It has been proven that the early resources of silver carp in the Yangtze River are under enormous threat (Liu et al., 2004). Overfishing is the most direct reason for the decline in fishery resources, which not only damages the diversity of fish but also destroys the resources of parent fish and juvenile fish, which makes the fish community smaller and younger (Sokta et al., 2020). Large scales of water conservancy construction also have a significant impact on the river ecosystem. It locked the migration pathway and destroyed the spawning grounds and nursery grounds of fish (Yao et al., 2015). Besides, land reclamation and water pollution also lead to the destruction of fish habitat and directly reduced the fish resources (Chen et al., 2017). At present, because of the 10-year strategy of banning fishing, it is necessary to assess the natural process of fish survival, growth, and reproduction both in the adult and larval stages. In this study, we described the major findings of a long-term research program on the fisheries resources survey of the silver carp and provided its possible complementary mechanism in the Yangtze River. Addressing the historical data, the current status of silver carps, the complementary mechanism, and possible management strategies were discussed for encountering the changing climate.

MATERIALS AND METHODS

Field Sampling Site

The sampled river section is alongside the lower reach of the Yangtze River. The survey period is from 2016 to 2019. Sampling and study area were in four sections, namely, Hukou (HK), Anqing (AQ), Dangtu (DT), and Changshu (CS). Three sampling sites were set in each section for the larval fish, namely, the right bank (R), the left bank (L), and the middle site (M). Two survey sites were set in each section for the adult fish of silver carp survey (shown in magnified graph, **Figure 1**).

Adult Fish Survey

Environmental factors were tested in each sampling site including the following content. Water temperature (WT, °C), dissolved oxygen (DO, mg·L^{-1}), and pH were recorded using a multiparametric probe (WTW Multi 340i, MultiLine, Germany). Water transparency (WTP) was measured using a secchi disk. Current velocity (CV, m·s^{-1}) was measured using a flow meter Digital Flow Meter 23090 (KC Denmark A/S, Silkeborg, Denmark). Average WD (m) was measured using a depth sounder (S48-1X, Maikeyi, Beijing, China).

The fishing net includes stick-nets and multi-mesh gill nets. Among them, the length of a single stick-net is 75 m, the height of the net is 5 m, the mesh size of the block net is 3.5 cm, and the capsule mesh size of the bag net is 1 cm. The length and height of a single multi-mesh gill net are 100 and 2 m, and

FIGURE 1 | Sampling site details in the Yangtze River.
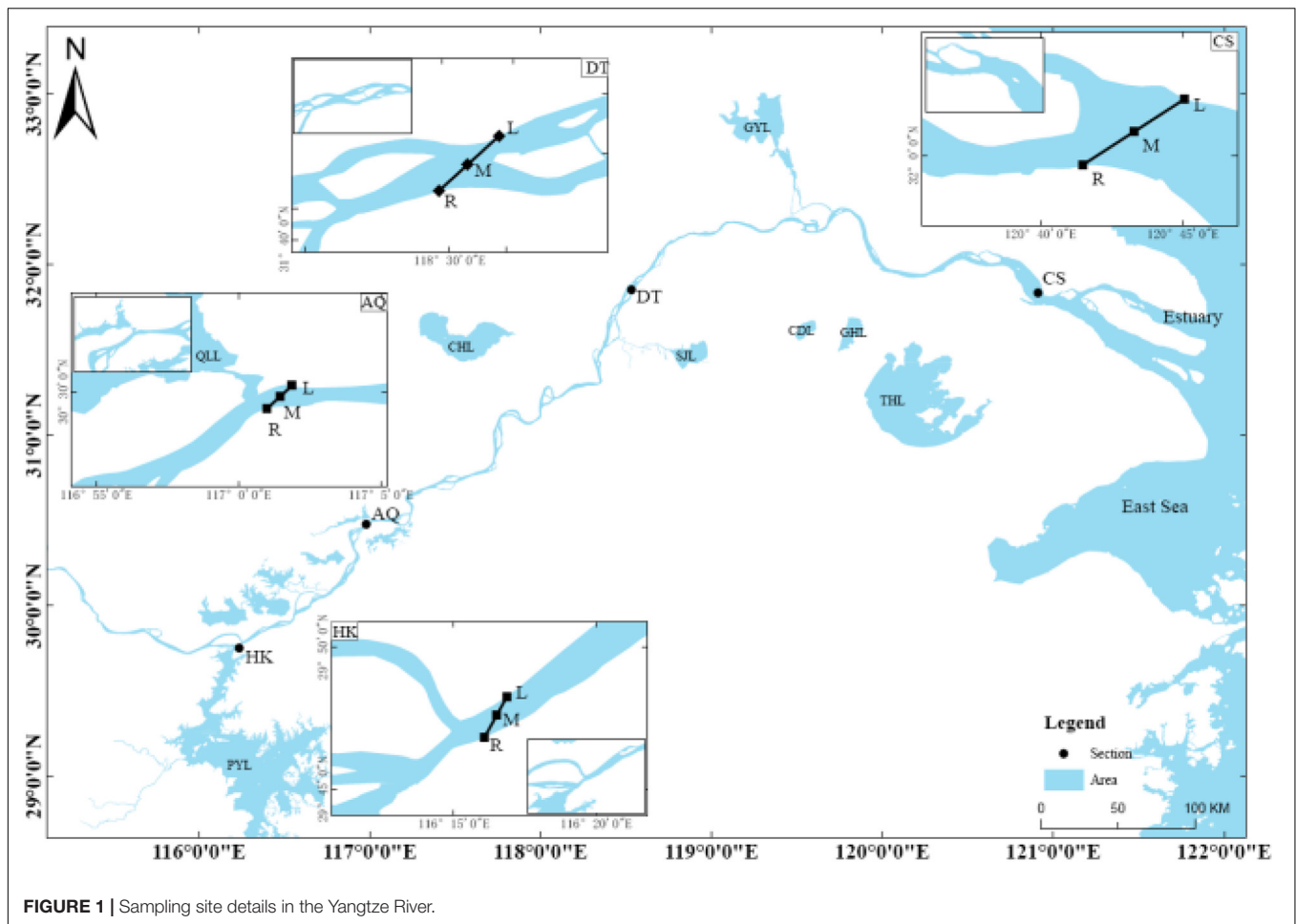
the mesh sizes are 2, 4, 6, 8, 10, and 14 cm, respectively. The investigation period was from January 2016 to December 2019; during the investigation, the multi-mesh gill nets were lowered to the designated investigation waters before 5:00 p.m., and the nets were closed before 8:00 a.m. on the next day. For each catch, the body length (BL) and weight were measured, and the biological characteristics were determined for the sampled sliver carp.

Fish Resource Estimation

According to the annual average catch per unit effort (CPUE), the total number of fishing vessels and the annual fishing days of a single vessel, the proportion of weight and individual number in each section, and the average annual catch weight and numbers were estimated. Annual average natural resources in the sampled sections were estimated using FISAT II medium length stock analysis method. Among them, the limit BL is $L\infty = 1,047.2$ mm and $k = 0.1603$, and the relationship between BL and body weight is $W = aL^b$ ($a = 0.000040413$, $b = 2.7546$; $R^2 = 0.8652$). The natural mortality estimation module was used in FISAT II and Pauley empirical formula was used to estimate the natural mortality of silver carp (Wang et al., 2019). The fishing mortality coefficient (FMC) of the maximum BL group is 0.5 as the initial value, do repeat calculation using iterative method, until the given

FMC value and the weighted average value of the fishing death coefficient of each BL group converge, then the final FMC value can be determined.

Larval Fish Survey

Sampling was conducted daily during the fish spawning season. Sampling sites were set to ensure that they typified the four designated sections in terms of the larval fish development (Cao et al., 2007). The sampling process has been described as follows (Ren et al., 2016). Briefly, larval fish were collected using an ichthyologic trap net (0.5 mm mesh size and 4.9 m² area of the net mouth). A flow meter (Digital Flow Meter 23090, Denmark) was tied in the net mouth to measure the water flow volume. The sampling process was conducted for about 5 min on the spot using a traditional fishing boat against the current. Sampling time was set at every morning (08:00–11:00 a.m.) during the fish spawning season (May–August) during 2016–2019. The net was deployed about 20 m along the river bank side of the sampling sections. Larval fish sampling was conducted upstream using a traditional fish boat at a speed of 2 km/h. For each sample, after cleaning vegetation and foreign matters, ichthyoplankton were collected and then preserved in 75% ethanol for later classification and identification. At all sampling sections, WT,

TABLE 1 | Catch statistics of the sliver carp in each section.

Sections	CPUE (Kg)	Fishing boats	Capture days	Annual catch weight (kg)	Annual catch number (tail)	The body length range (cm)
HK	18.31	118	180	4088.29	22,372	1.2–66.8
AQ	12.92	126	180	2213.71	11,888	1.1–58.2
DT	10.84	180	180	4145.62	23,616	2.3–76.2
CS	7.78	293	180	5124.67	26,723	2.6–87.6

CPUE, catch per unit effort; HK, Hukou; AQ, Anqing; DT, Dangtu; CS, Changshu.

WF, and WTP were simultaneously measured, respectively. Daily water level and discharge were acquired from the Changjiang Hydrological Network.[1]

Early Resource Occurrence Quantity

The calculation method of larval fish density refers to the previous method (Cheng et al., 2013; Ren et al., 2016). According to the number of fish larvae collected, the sampling time, the difference between the beginning and end of the flow meter, and the active net area are calculated according to the following formula: $Q_i = (0.3 \times C_i \times a_i)/t_i$, $D_i = \frac{N_i}{Q_i \times t_i}$, where Q_i is the flow through the net mouth during the i time period (m³/s), C_i is the flow difference during the i time period in the flow meter, and a is the net port area of active gear (m²), 0.3 is the constant of the flow meter, and t is the time of collecting the fish larvae (s). D_i is the density of fish larvae collected during the i time period (ind./m³) and N_i is the number of fish larvae collected in the i time period (ind.).

The coefficient of comparison is between the average density of fertilized eggs in the sampling section and the density of fertilized eggs in fixed point. $C = \sum \frac{\bar{d}}{d_i}$, where d_i is the fish fry density at fixed sampling points and $\bar{d}$ is the average density of the fish fry at each sampling site in the cross-section.

Fertilized eggs runoff during collection period is $M_i = D_i \times Q_i \times C_i$, where M_i is the number of eggs passing through the section of the river during the i time period, D_i is the density of eggs collected during the i time period, and Q_i is the cross-section flow during the i time of collection.

Fertilized eggs runoff during non-collection period is $M_{i\ i+1} = (M_i/t_i + M_{i+1}/t_{i+1})t_{i\ i+1}/2$, where $M_{i,\ i+1}$ is the fertilized eggs runoff during collection interval of the $i,\ i+1$ time and $t_{i,\ i+1}$ is the collection time interval of the $i,\ i+1$ time period. The total runoff of eggs collected in the river section is $M = \sum M_i + \sum M_{i,i+1}$.

Data Processing and Analysis

The density of fish larvae was calculated as the fish larvae number per 100 m³ of the filtered water. The detrended correspondence analysis (DCA) and distance-based redundancy analysis (db-RDA) (length of gradient < 3, suit for lineal model, otherwise using unimodal model) were used to unravel the variables explaining the differences in larval fish assemblages (Pan et al., 2015). Statistical significance was set at $P = 0.05$. GAM was used to analyze hydrological factors on the abundance of fish larvae

(Daskalov, 1999). The smoothing splines (cubic spline) were used to represent the non-linear effect of predictors. The maximum degree of smoothing was set at 6 to avoid unrealistic patterns in the explanatory variables and to reduce over-fitting. According to the Akaike information criterion (AIC), the optimal number of nodes and the optimal model are determined (Akaike, 1973). As the original data are relatively discrete, the larval fish density and water environmental factors are processed using log (x+1) to meet the normal distribution of the analyzed data and using Monte-Carlo permutation test to sieve environmental factors (Pan et al., 2015). SPSS 19.0 and Excel 2016 were used for data analysis and drawing graphs, and Pearson correlation test was used for correlation analysis.

Ethical Statement

All sampling procedures were reviewed and approved according to the Regulations for the Administration of Affairs Concerning Experimental Animals, as approved and authorized by the State Council of the People's Republic of China.

RESULTS

Adult Silver Carp Resources in the Lower Reach of the Yangtze River

During the survey period from 2016 to 2019, according to the annual average CPUE in each river section, results showed that the annual average catch weight, the average annual catch number, and the BL range in the HK, AQ, DT, and CS sections were different (**Table 1**). Further analysis showed that the BL range of silver carp in the lower reach of the Yangtze River was 31.9–876 mm, and the average BL was 283.52 mm, of which 100–300 mm was the dominant BL group, accounting for 51.27%. The weight range of silver carp is 65.02–6,500 g, and the average weight is 700.99 g, of which 200–400 g group is the dominant weight group, accounting for 57.89%, and the average weight is 387.61 g (**Figure 2**).

The cumulative fishing mortality, annual total resources, and annual total tail of silver carp in HK, AQ, DT, and CS show significant river section differences (**Table 2**). The cumulative mortality of fishing in the HK section is significantly lower than that in other sections, and the difference between the other three river sections is not obvious. The average annual fishery resources and tail in each river section are CS > DT > HK > AQ. Interestingly, the total fishery resources of CS section are significantly higher than those of other sections.

FIGURE 2 | Body weight range ratio in different sections.
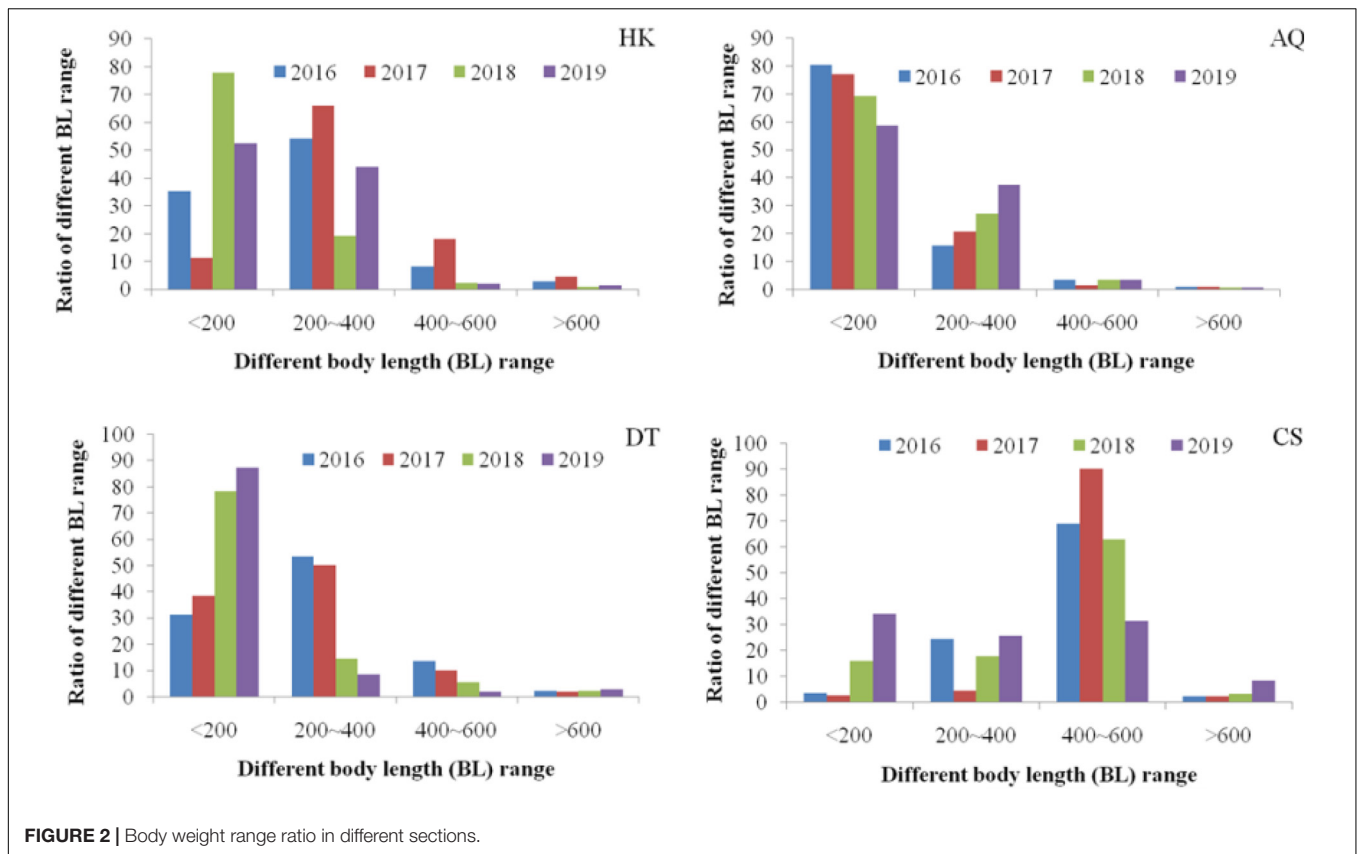
Fish Larvae of Silver Carp in the Lower Reach of the Yangtze River

A total of 1,139 silver carp larvae were collected during 226 days of field survey in HK section from 2016 to 2019. A total of 224 fertilized eggs were collected at different stages, including tail bud-emergence stage, blast cyst stage, and early gastrula stage. During the investigation period, the fish larvae and fertilized eggs of silver carp showed an increasing trend year by year. According to above mentioned methods, the estimated runoff of silver carp in the early life history passing through the HK section from 2016 to 2019 is 5.08×10^8, 5.69×10^8, 6.72×10^8, and 7.32×10^8, respectively. A total of 826 silver carp larvae and 126 fertilized eggs were collected, from 2016 to 2019, during 312 days of field survey in the AQ section. During the investigation period, the variation of fish larvae and fertilized eggs of silver carp showed a fluctuating trend annually. According to the number of larvae and fertilized eggs collected, the runoff of

silver carp larvae passing through the AQ section from 2016 to 2019 is estimated to be 8.08×10^8, 9.69×10^8, 9.72×10^8, and 10.32×10^8, respectively. However, only 36 silver carp larvae and 2 fertilized eggs were collected during 236 days of field survey in DT and CS sections during the investigation period. By the same estimating method, the runoff passing through the DT and CS sections can be ignored.

Distribution Patterns of the Adult Fish

During the investigation period, different BL groups of silver carp showed different distribution patterns in the sampled sections (**Figure 2**). Silver carps of different BL groups in the HK section showed a downward trend year by year. The juvenile silver carp in the below 200 mm BL group in the AQ section were significantly higher than those in other BL groups and showed a downward trend year by year. The silver carp in the 200–400 mm BL group showed an upward trend yearly, and the interannual distribution in the 400–600 mm and above 600 mm BL groups has no significant difference. The ratio of juvenile silver carp in the below 200 mm BL group in the DT section showed an obvious upward trend year by year, while the 200–400 and 400–600 mm BL groups showed a downward trend. The ratio of juvenile silver carp in the below 200 mm BL group and adult silver carp in the above 600 mm BL group in the CS river section is small and showed an obvious upward trend year by year. The 400–600 mm BL group has an absolute advantage in the surveyed section, but the resources showed a downward trend year by year.

TABLE 2 | Total resources and catch tail of the sliver carp.

Sections	The cumulative fishing mortality (%)	Annual total resources(t)	Annual total tail (tail)
HK	4.11	371.74	102,604
AQ	6.72	235.22	83,978
DT	5.77	640.69	66,973
CS	5.51	2612.65	226,142

Silver carp of different BL groups also have obvious seasonal differences between the investigated sections. Seasonal variations in the adult fish in different sections are shown in **Figure 3**. During spring, autumn, and winter, the above 600 mm BL group of silver carp in the CS section was significantly higher than that in other sections. The 400–600 mm BL group in each section in summer was obviously high. In autumn, the silver carp in the below 200 mm BL group was dominant in the HK, AQ, and DT sections, but the ratio in the CS section was lowest. In winter, the ratio of juvenile silver carp in the HK and AQ sections in the below 200 mm BL group was high, and the proportion of adult silver carp (400–600 mm and >600 mm BL group) in the DT and CS sections was high. The results showed that in the river-lake connected sections such as HK and AQ, the proportion of juvenile silver carp in the below 200 mm BL group was significantly higher than that in other investigated sections.

Change Patterns of the Larval Fish and Influential Factors

During the survey time, as for the larval fish results, the highest abundance of larval fish and fertilized eggs appeared in the HK and AQ sections. Comparing the average abundance of larval fish in each sampling section exhibited the trend as HK > AQ >> DT > CS. Interestingly, the highest abundance of the larval fish appeared in the HK section, and the lowest abundance appeared in the CS section, which was almost never sampled. Furthermore, the larval fish and fertilized eggs were continuously sampled

from early June to early August, and peaked in early July. The GAM results showed that the hydrological factors significantly influence the abundance of fish larvae (**Figure 4**; $P < 0.05$). In the HK and AQ sections, the contribution orders were the daily increasing rate of water level, WTP, water temperature, and the daily increasing rate of discharge (**Table 3**, $P < 0.05$). Among them, the total deviation interpretation rate by the optimized GAM was 67.2 and 83.7%, respectively. Results revealed the concrete influence of hydrological conditions on the abundance of the larval carps (**Figure 4**).

DISCUSSION

Importance of Adult Silver Carp and Early Resource Research

The silver carp is a type of semi-migratory fish species between rivers and lakes, and it grows up, matures in floodplain lakes, and spawns in rivers (often triggered by increasing temperature and rising water levels). Due to overfishing, water pollution, habitat loss, and hydroelectric engineering such as the TGD, the natural resources of the four Chinese carps have declined considerably during the past decades. Studies showed that the closer to the dam, the more obvious the effect is. Most studies on the complementary mechanism of the silver carp focused in the up and middle reaches, and the lower reach of the Yangtze River has often been ignored. Some studies have indicated that the recruit population contribution has shifted from the middle reaches
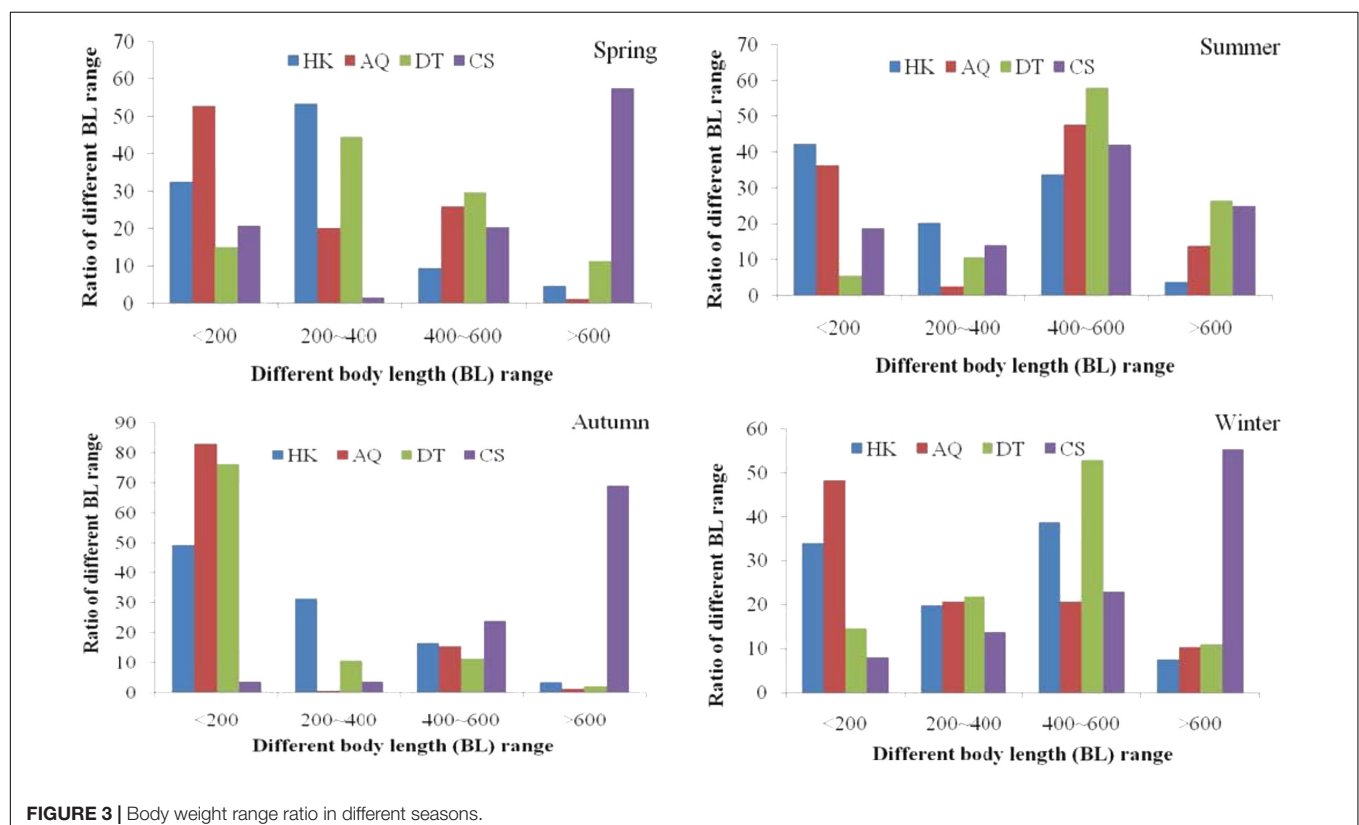

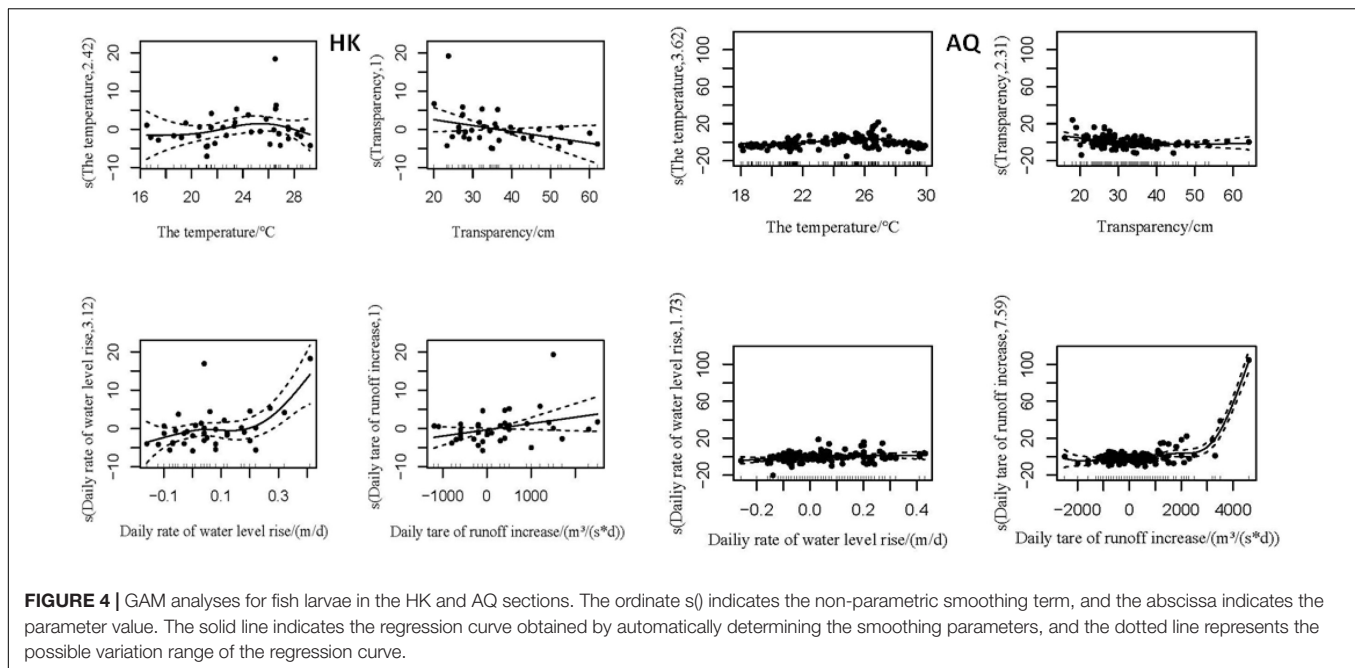**FIGURE 3 |** Body weight range ratio in different seasons.

FIGURE 4 | GAM analyses for fish larvae in the HK and AQ sections. The ordinate s() indicates the non-parametric smoothing term, and the abscissa indicates the parameter value. The solid line indicates the regression curve obtained by automatically determining the smoothing parameters, and the dotted line represents the possible variation range of the regression curve.

TABLE 3 | Deviation interpretation rate of environmental factors for the GAM model.

Dependent variable (Ichthyoplankton density)	Water temperature	Water transparency	Water level	Water runoff	Total deviation interpretation rate
HK	27.6%	49.5%	49.6%	29.4%	67.2%
AQ	16.8%	26.3%	31.6%	74.2%	83.7%
DT	–	–	–	–	–
CS	–	–	–	–	–

The optimal model was selected according to Akaike information criterion (AIC) criterion. The correction determination coefficient of the prediction model was set above 0.5 (R-sp > 0.5), significant correlation was set at the 0.05 level (P < 0.05). WT, water temperature; WT, water transparency; WL, daily rise of water level; WR, daily rise of water runoff.

to the lower reaches. In this case, studies on the complement mechanism of the silver carp in the lower reach of the Yangtze River became even more important. Furthermore, the hatching of fertilized eggs and the development of fish larvae were transferred by the downstream drift and subsequently juvenile fish were moved into nursery areas and grown up, and such biological process probably happens in the lower reaches. For this reason, clarifying the growth and death characteristics of silver carp in the early life stage and its supplementary contribution to the adult population will provide a scientific and basic data support for the protection of silver carp resources in the Yangtze River.

Habitat Characteristics and Resource Distribution

The field survey results showed that the closer the section is to the estuary, the fewer the larvae silver carp is, and the bigger BL group gradually increased. Adult silver carps can swim freely and have strong control ability in water. What is more, the adult silver carps tend to choose habitats with slow water flow, rich biological bait, and less human interference. In the lower reach of the Yangtze River from HK to the estuary, there are many sandbars,

developed water network, distributed thousands of bays, and rich bait biological sources along the river. This kind of habitat is an important feeding ground for the silver carp (Shuai et al., 2018). Results in this study found that adult silver carps were widely distributed in the investigated sections. In the section with sandbar habitat, such as HK, AQ, DT, and CS, the distribution density of the adult fish was high, and the distribution of BL group was rich. Interestingly, the adult silver carp resources are highest in the CS section. The CS section is wide, with obvious river diversion, and has the characteristics of rising and falling tides. Some studies have shown that the tide can significantly promote the enrichment of plankton, which are the main feed resource for the silver carps. Therefore, comparing with other sections, the CS section has more abundant bait organisms and is more suitable for the fish growth. Another important reason for more big silver carps in this section may be the numerous and effective stock enhancement in the lower reaches of the Yangtze River in recent years.

The spatial heterogeneity of the fish larvae is mainly affected by the hydrological situation and the topography of the water area. The sandbars obviously existed in the HK and AQ sections and divided water flow into two or more streams. This habitat

usually can form the "vortex water," which is necessary for the silver carp spawning behavior. Based on the study result, it can be speculated that the spawning ground are distributed in Jiangzhou, Longping, and Qizhou waters, which contain many sandbars, with eddies or bends in the river center (unpublished data). There is no spawning ground found below AQ section. The main reason is that after silver carp spawning, the life history stages of drifting and first feed must be completed in the early development stage; the drifting distance from AQ to the estuary cannot meet the developmental needs of the silver carp from the fertilized eggs to the initial feed stage (Shuai et al., 2018). The HK section is connected to the Poyang Lake, which is the river-lake connected section in the lower reach of the Yangtze River, and the AQ section is a relatively stable bifurcated river with many complex beaches. This complex ecosystem with the characteristics of connecting river and lake (RL) can provide good nursing and feeding places for silver carps.

Spatial-Temporal Dynamics and Affecting Factors

Silver carp has the migratory habit between river and its connected water body, and its distribution pattern has obviously seasonal differences (Zhang et al., 2021). Because the adult fish may choose the complex section for winter migration, in spring, it was found that the ratio of the adult fish with a lower BL was higher in the HK and AQ sections. Summer is the spawning season, the WT and the WL begin to rise in the river, and under the accelerating current, the adult fish begin spawning. For this reason, the number of middle and high BL groups increased generally in the HK and AQ sections. After the spawning period, the hatched fish larvae successively entered Poyang Lake or Wanhe River for nursing and feeding. However, the CS section has a little salinity and is not fit for the hatched fish larvae. Therefore, the ratio of the below 200 mm BL group was lowest in the CS section. It can be seen that the seasonal distribution characteristics of adult silver carp are closely related to their reproductive biological characteristics and river-specific habitat.

Drifting development extensively exists in the early stage of river fish species, and its growth and development is also affected by abiotic and biological factors (Nagrodski et al., 2012). Abiotic factors include WL, riverbed shape, WT, and hydrological conditions. Biological factors include fish development stage, habitat preference, and interspecific relationship (Jager and DeAngelis, 2018). The temporal dynamics of the silver carp in the early life history stage can directly reflect the varying characteristics of the adult fish spawning time. The WT for the silver carp spawning is generally required to be above 18°C; in this study, the fish eggs in the HK section were investigated from late May to mid-July, and the WT fluctuated in the range of 20.4–28.7°C. In the fish spawning season, the changes in river hydrology, such as the increase of water flow, the rise of water level, and the acceleration of river flow velocity, are important and essential factors causing the spawning peak of the fish (Zhang et al., 2021). In 2019, the runoff and WL began to rise in late May and remained high until the middle of July, which induced three fish egg peaks in the HK and AQ sections. Related studies have shown that WT, WF, and WTP

were essential environmental factors affecting the community structure of fish larvae (Machado et al., 2017). Furthermore, the GAM results showed that the hydrological factors have the different contribution rate to the abundance of fish larvae, which was in accordance with the reproductive biology of the silver carp (Kun et al., 2019).

When analyzing the spatial distribution of fish larvae abundance in the HK and AQ sections, it is found that the fertilized eggs were collected in the three sites except the Waterway of Poyang Lake in the HK section. It can be inferred that the supplement population of silver carp only came from the upstream section of the Yangtze River. Due to the different natural conditions such as riverbed shape, river flow velocity, and watershed dynamics between various sites in the section, the drift density of fish larvae varied greatly between different sites on the same river section. Interestingly, the egg density in the river center is significantly higher than that on both banks, which is consistent with the biological characteristics of silver carp egg development and drifting (Wang et al., 2019).

Possible Complementary Mechanism

Understanding the complementary mechanisms is critical to the effective conservation of wild fish populations (Goldenberg et al., 2019). There were numerous evidences that qualified relationships existed between hydrology and density of fish larvae (Doyle et al., 2002; Jenkins et al., 2015). When a natural flood with water velocity ≥0.7 m/s occurred in the Mississippi River, it can stimulate the sliver carp spawning behavior (Shuai et al., 2018). The project of biological regulation from TGD also can lead hydrological changes and stimulate the silver carp to spawn in the spawning season (Zhang et al., 2021). Unfortunately, it has been proven by field surveys that the construction of TGD had a dramatic influence on the abundance of silver carp larvae (Zhang et al., 2020). Dams in the Yangtze River have modified water hydrology and flow and then affected the silver carp migration and reproduction (Fu et al., 2003). Because the lower reaches of the Yangtze River are far away from the TGD, the hydrological characteristics are less affected (Doyle et al., 2002). Furthermore, the connectivity between Poyang Lake and the Yangtze River is conducive to the fish reproduction. The RL ecosystem forms the reason for the adult amount of resources of silver carp in the surveyed sections. Furthermore, the most suitable discharge of spawning habitats of silver carp in the Yangtze River were 15,000–21,300 m^3/s (Yu et al., 2018). Due to the inflow of tributaries along the river, this is a kind of essential topographic habitat for forming the bubble water (Shuai et al., 2018). In this water area, the adult sliver carp spawned and the fish in early life history stages developed. However, the complementary quantity and quality derived from the adult population absolutely depends on the parent fish. How many parent fish lived in the Yangtze River and whether they can spawn successfully should be considered systematically. Therefore, continuous field surveys on larvae and adult fish resources in the whole Yangtze River Basin and exploring the complementary relationship will be considered persistently.

Although only 4 years of systematic data were included in this study, we proposed that the adult silver carp has the distinctive preference in the habitat selection. Furthermore, being

the overfishing in the Yangtze River, the adult fish that can spawn in the spawning period all come from the up reach of the river, and downstream fish have less complement contribution to the larval fish population. In contrast, it is also found that the river flows, such as discharge, artificial flood, or flood pulses, are factors that effectively determined larval fish abundance in the Yangtze River. Based on the above results, we can propose an exchange regulating method that the parent fish can intercourse each other between the upstream and downstream reaches in the Yangtze River during their breeding season. By doing these, their population, perhaps, expands quickly and their breeding population can recover in the future, and it would be a preferable method to control the propagation of silver carps (Ban et al., 2019; Wang et al., 2019). Our study provides preliminary clues to understand how the adult silver carps recruit and migrate between sections along the Yangtze River. Besides, understanding the breeding characteristics of the silver carps in their native range and their protecting biography are also of great significance. Future research will focus on the detail complementary mechanism silver carp both in the natural habitat and invasion waters.

Occurrence Trend and Protection Suggestions

This study has carried out research on the temporal and spatial dynamics of adult and early resources of silver carps and analyzed the supplementary contribution of early resources in different sections of the lower reaches of the Yangtze River to adult populations. The research results provided theoretical support for the formulation of fishery resources conservation and management measures in the Yangtze River. The accumulation of these basic data can also provide a scientific basis for resource evaluation and species protection strategies of silver carps in the Yangtze River. Poyang Lake has typical habitat characteristics of connecting rivers and lakes; it is the key ecosystem to maintain the successful supplement of silver carp early resources to adult fish resources. However, how to ensure the connectivity of the RL effectively, so as to enhance the silver carp resources in the Yangtze River, should be focused on especially. Therefore, wading projects such as sand mining, shipping, and aquatic operations in

silver carp migration channels, spawning grounds, and feeding grounds must be prohibited during the spawning period. At the same time, the correlation analysis between adult and fish larvae resources of silver carp is conducive to clarify the complementary mechanism. In short, establishing a reliable biological data and explaining the supplementary contribution of early resources to adult resources will be the key content of later research.

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/s.

ETHICS STATEMENT

All sampling procedures involving animals were reviewed and approved by the Regulations for the Administration of Affairs Concerning Experimental Animals and approved and authorized by the State Council of People's Republic of China.

AUTHOR CONTRIBUTIONS

D-AF was responsible for data scoring and analysis, and writing the manuscript. D-PX conceived and designed the experiments. Y-FZ, PR, X-PX, Y-XP, and LR helped selecting the icythyoplankton sample, survey work, and data analysis during manuscript preparation. All authors have read and approved the final manuscript.

FUNDING

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