

Letter to the editor

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Declined fitness in larvae born from long-distance migrants of anadromous *Coilia nasus* in the lower reaches of the Yangtze River, China

DEAR EDITOR,

Anadromous *Coilia nasus* is a socioeconomically important species from the middle and lower reaches of the Yangtze River, China. Here, we compared growth and feeding of *C. nasus* larvae in four reaches along the full migration corridor of the river (640 km) to determine how fitness varies between progenies of short- and long-distance migrants. Results demonstrated that larvae collected in downstream sections grew faster, exhibited higher feeding intensities, and consumed larger zooplankton (a favored food resource). Our results did not support the parent-offspring trade-off theory, which predicts that the costs and benefits of migration increase with migration distance, and higher parental costs with long migration should be offset by increased offspring fitness. We suggest pervasive human impacts along the river are likely driving the observed ecological patterns. Overfishing has resulted in a truncated body size in migrants, which shortens their migration distance; isolation of floodplain lakes from the river restricts fish spawning and nursing to suboptimal lotic river habitats; and higher discharge experienced by larvae born from long-distance migrants in the upstream river reaches during the later flooding season results in declined feeding intensity and slower growth compared to those produced from short-distance migrants in the earlier season. We predict that a fishing ban in the Yangtze River will allow fish to grow larger and older so they can access floodplain lakes further upstream, which will further enhance recruitment of the *C. nasus* population.

Anadromous fish species migrate as adults from the sea to freshwater areas for reproduction, after which larvae and juveniles descend to the sea to grow and mature. The migration of many fish species (such as American shad *Alosa*

sapidissima and brown trout *Salmo trutta*) is flexible, with migration distances and migration and breeding times varying among individuals. Migration distance is usually a condition-dependent decision, i.e., larger and older fish in good condition migrate further, whilst smaller and younger fish in poor condition migrate shorter distances or even reside *in situ* (Brodersen et al., 2008). The parent-offspring trade-off theory predicts that the costs and benefits of migration increase with migration distance, and the greater parental costs of long migration should be offset by increased offspring fitness, e.g., higher feeding intensity, growth rate, and survival rate in the early life stages. This migration distance-related parent-offspring trade-off has been verified in Atlantic cod *Gadus morhua* (Färber et al., 2018).

Populations of anadromous *C. nasus* in the Yangtze River have declined dramatically since the 1970s. Additionally, while fish harvests were dominated by individuals 3 years and older before the 1990s, such fish have become increasingly rare in the past several decades. Migratory *C. nasus* fish historically reached Dongting Lake, the second largest floodplain lake in the basin, located some 1 400 km upriver of the estuary. Currently, however, migration only occurs up to Poyang Lake, located 844 km upriver of the estuary (Li et al., 2007).

According to our previous research, spawning of *C. nasus* occurs earlier in the estuary (May and June) than in the upstream reaches (e.g., August at Anqing, located 640 km from the estuary). Furthermore, mature adults in the estuary are smaller than adults in upstream sections (Li et al., 2007). In the current study, we compared the growth and feeding behavior of *C. nasus* larvae in four reaches along the full migration corridor of the river, i.e., Chongming (N31°30'58",

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E121°39'36"; estuary), Jingjiang (N31°57'30", E120°07'51"; 180 km from the estuary), Nanjing (N31°48'04", E118°31'31"; 460 km from the estuary), and Anqing (N30°29'13", E116°59'34"; 640 km from the estuary) (Figure 1A), to determine how fitness varies between progenies of short- and long-distance migrants.

In 2009 and 2010, *C. nasus* larvae were sampled every 20–30 d during the spawning periods in each river section, i.e., May–August at Chongming and Jingjiang, June–September at Nanjing, and July–September at Anqing. In 2009, no larvae were collected at Nanjing in June or at Anqing in July. Additionally, due to flooding concerns, no sampling was conducted at Nanjing in July 2010. Hence, in 2010, sampling at both Nanjing and Anqing was conducted in August and September. Larvae were collected at Chongming, Nanjing, and Anqing using a conical trawl net (Huang et al., 2014) and at Jingjiang using an ichthyoplankton trap net (Song et al., 2018). A flow meter was used to measure volume of the filtered water over the course of sampling. The collected larvae were immediately fixed and identified to species (*C. nasus*), with larval density calculated as the number of individuals per 100 m³ of filtered water. Growth and diet analyses of larvae are described in the Supplementary Materials and Methods.

In total, 18 660 and 11 170 *C. nasus* larvae were collected in 2009 and in 2010, respectively. Peak abundance occurred in June and July in Chongming and Jingjiang, and in August in Nanjing and Anqing (Figure 1B, C). The highest abundance was recorded in Chongming, which decreased in an upstream direction in both years. Peak abundance was higher in 2009 than in 2010 in all four sampling reaches (Figure 1B, C).

Body length (BL, 0.1 mm) was measured in a total of 2 582 and 2 551 individuals and otolith microstructure was measured in a subsample of 906 and 487 individuals in 2009 and 2010, respectively (Supplementary Table S1). The BL measurements varied from 5.4 to 26.9 mm and estimated age ranged from 5 to 43 d. Furthermore, the estimated hatch dates ranged from 15 May to 6 September. In general, hatch dates spanned a long period, with the highest peak occurring earlier in Chongming and Jingjiang than in Nanjing and Anqing in both years (Supplementary Table S1 and Figure S1).

We analyzed early life traits in 662 individuals from the peak hatching periods. Significant linear regression of BL-at-age was fitted for each sampling site in each year ($P=0<0.05$; Figure 1D, E). Growth rates (i.e., regression slope coefficients) varied from 0.57 to 0.70 mm per day. Analysis of covariance (ANCOVA) indicated that sampling site, year, and their interaction significantly affected growth rate ($P=0<0.05$, Supplementary Table S2). Furthermore, pairwise comparisons revealed that the growth rates at Chongming and Jingjiang were significantly higher than those at Nanjing and Anqing in both years (Bonferroni correction, $P=0$ and $0.003<0.05/16$). The growth rates at Chongming and Jingjiang in 2009 were significantly higher than the rates in 2010 ($P=0<0.05/16$). The incremental widths of the larval otoliths were significantly greater at Chongming and Jingjiang than at Nanjing and Anqing from day 9 onwards in both years ($P<0.05$, Supplementary Figure S2). Furthermore, the incremental widths were significantly larger in 2009 than in 2010 in some

larvae at each reach ($P<0.05$).

Chongming (and at Jingjiang in 2010) showed significantly lower water temperature and water discharge than Nanjing and Anqing ($P<0.05$, Supplementary Table S2). Multiple regression analysis revealed that the effect of water temperature on larvae was not significant ($P=0.06$), while the effect of water discharge was negatively significant ($P=0.03$). The water discharge (WD) to growth rate (G) relationship was fitted to a linear function, $G=0.76+2.88\times 10^{-6}$ WD ($n=8$, $r^2=0.40$, $P=0.09$).

Gut contents were analyzed in 380 and 250 larvae from 2009 and 2010, respectively (Supplementary Table S3). Feeding intensity was higher in Chongming than in the other sampling sites in both years and higher in each reach in 2009 than in 2010; however, the percentage of empty guts showed the reverse pattern (Figure 1F, G). The larval diets were primarily composed of *Schmacheria*, *Sinocalanus*, Diptomidae, Cyclopinae, Cladocera, and fish larvae (Supplementary Table S3). Biplots of the first two principal component analysis (PCA) axes based on the relative importance index (IRI) of larval diets showed that diet composition varied spatially and temporally. Specifically, larvae from Chongming and Jingjiang tended to consume a higher portion of larger-sized zooplankton, i.e., *Schmacheria* (especially in 2009), while larvae from Nanjing and Anqing tended to consume a higher portion of smaller-sized prey, i.e., Cyclopinae and Cladocera (Supplementary Table S3 and Figure S3).

Our results demonstrated that growth and feeding intensity of *C. nasus* larvae decreased in an upstream direction. Specifically, larvae at Chongming and Jingjiang grew faster than conspecifics at Nanjing and Anqing; feeding intensity was higher at Chongming than at the other three reaches; and larval diets at Chongming and Jingjiang contained a higher portion of larger zooplankton (*Schmacheria*) than those at Nanjing and Anqing. Larvae in Chongming and Jingjiang were born earlier under lower water temperature and water discharge conditions compared to larvae in the upper reaches (Supplementary Table S2). Our results showed that water discharge was a significant factor negatively related to larval growth, whereas water temperature was not. In general, high water discharge levels increase water turbidity, directly reducing primary productivity, autochthonous prey resource availability, and feeding success of larval fish (Haworth & Bestgen, 2016). Water discharge increased in the lower reaches of the Yangtze River in April, with high water levels maintained through to August in 2009 and 2010. In association with the increase in water discharge, zooplankton abundance is high in May and June, but decreases in July and August (Tan et al., 2022). Thus, increased water discharge experienced by late-born larvae in the upstream river reaches represents a potential explanation for the decreased feeding intensity and slower growth of larval fish in these habitats. Furthermore, compared to 2009, the higher water discharge in 2010 was also associated with lower feeding intensity and slower growth.

The spawning migration of fish often involves the parent-offspring trade-off theory, which predicts that the greater parental costs of long migration should be offset by increased

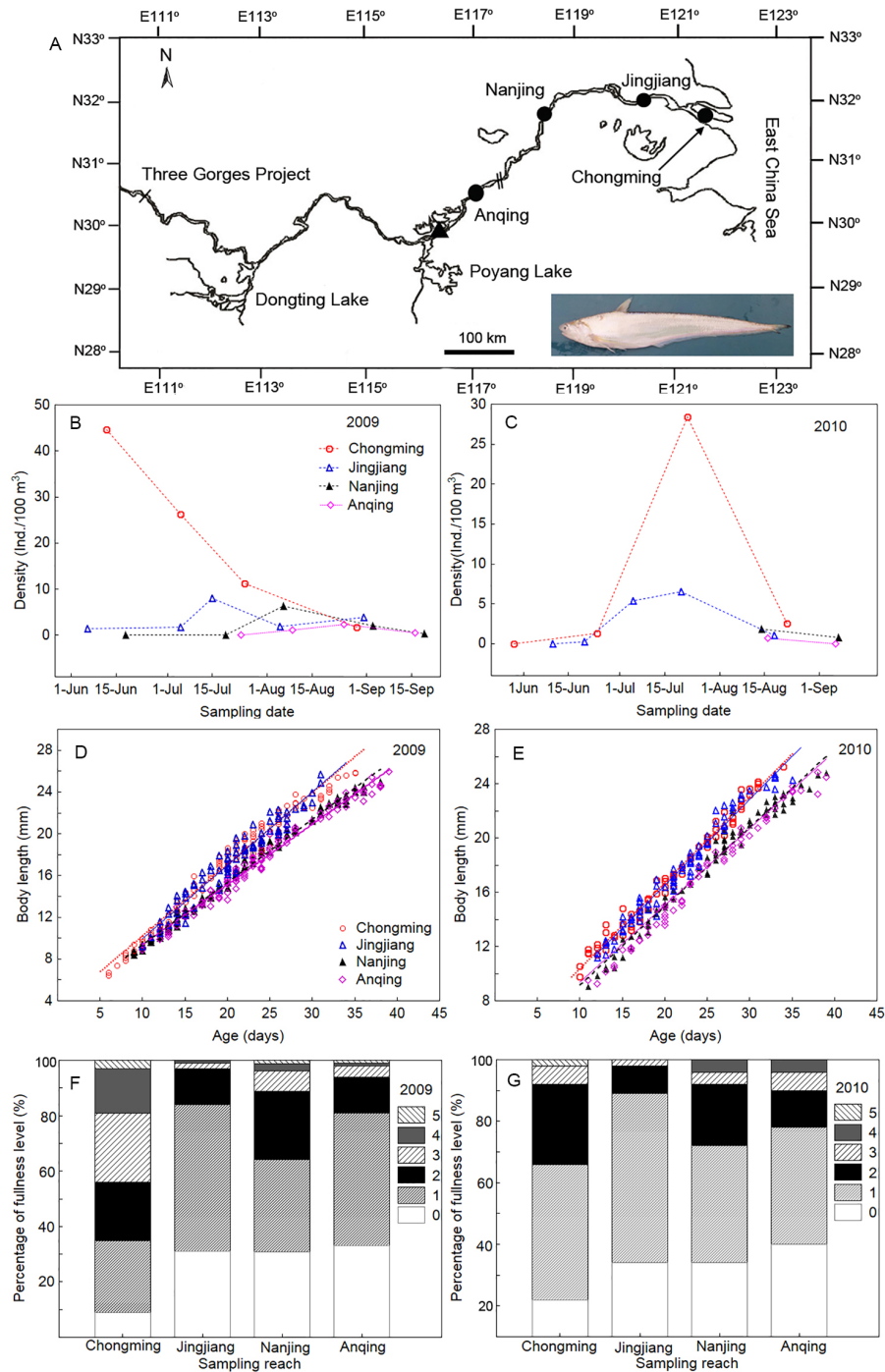


Figure 1 Abundance, body length-at-age relationships, and feeding intensity profiles of *Coilia nasus* larvae at Chongming, Jingjiang, Nanjing, and Anqing in the Yangtze River in 2009 and 2010

A: Map of middle and lower reaches of the Yangtze River, China, showing four sampling sites (●) for *C. nasus* larvae, including locations of Datong Hydrological Station (//) and Jiujiang Meteorological Station (▲) and a picture of *C. nasus*. B, C: Temporal fluctuations in abundance of *C. nasus* larvae at Chongming (red circles), Jingjiang (blue triangles), Nanjing (black triangles), and Anqing (purple rhombus) in 2009 (B) and 2010 (C). D, E: Body length-at-age relationships of *C. nasus* larvae at Chongming (red circles), Jingjiang (blue triangles), Nanjing (black triangles), and Anqing (purple rhombus) in 2009 (D) and 2010 (E). Regressions were $y=0.69x+3.36$ ($r^2=0.97$, 2009) and $y=0.63x+4.04$ ($r^2=0.98$, 2010) at Chongming, $y=0.70x+2.92$ ($r^2=0.95$, 2009) and $y=0.63x+3.85$ ($r^2=0.97$, 2010) at Jingjiang, $y=0.60x+3.35$ ($r^2=0.99$, 2009) and $y=0.58x+3.34$ ($r^2=0.98$, 2010) at Nanjing, and $y=0.58x+3.61$ ($r^2=0.98$, 2009) and $y=0.57x+3.69$ ($r^2=0.94$, 2010) at Anqing, respectively. F, G: Percentage compositions of gut at different fullness levels, i.e., 0 (empty), 1 ($\leq 25\%$ full), 2 ($\leq 50\%$ full), 3 ($\leq 75\%$ full), 4 (full), and 5 (distended with thin stomach wall) for *C. nasus* larvae at Chongming, Jingjiang, Nanjing, and Anqing in the Yangtze River in 2009 (F) and 2010 (G).

offspring fitness (Färber et al., 2018). Based on that theory, offspring of long-distance migrants should grow faster and feed better than offspring of short-distance migrants. However, our results showed declined fitness in *C. nasus* larva born from long-distance migrants, contradicting the parent-offspring trade-off prediction. We suggest that pervasive human impacts, such as overfishing and isolation of floodplain lakes from the river, are likely driving the reversal of the prediction. First, the lack of connectivity with floodplain lakes restricts fish spawning and nursing to suboptimal lotic river habitats. There are many floodplain lakes along the middle and lower reaches of the Yangtze River. Under natural situations, these lakes are permanently or seasonally connected to the river, thus forming lake-river complexes (Chang & Cao, 1999). *Coilia nasus* spawning migration has adapted to this system, with fish migrating upstream and entering the lentic floodplain lakes to spawn and nurse. Their fertilized eggs are surrounded by an oil droplet to ensure they float on the water surface, and thus lentic habitats are ideal for their development and hatching (Cao et al., 2007). Zooplankton densities are also much higher in lentic floodplain lake habitats than in high-flow rivers (Tan et al., 2022). Earlier-born larvae in downstream floodplain lakes should experience lower water temperature and potentially slower growth than later-born larvae in upstream floodplain lakes. Furthermore, migration distance is size and condition dependent (Brodersen et al., 2008). As smaller and younger adults are much more abundant than larger and older adults, offspring from downstream spawning grounds should be much more abundant than offspring from upstream reaches. Hence, the offspring of long-distance migrants may nurse in floodplain lakes at relatively low density and competition and may exhibit higher feeding intensity and faster growth. Thus, in natural situations, the fitness of larvae from long-distance migrants should be higher than that of larvae from short-distance migrants, thereby reflecting the parent-offspring trade-off prediction (Färber et al., 2018). Although there are no historical data on larval fitness in the population, this prediction may be verified in the future with population recovery.

This natural floodplain lake-river complex has changed dramatically since the 1950s. Many lakes are now isolated from the river, and only two major lakes remain naturally connected, i.e., Poyang Lake and Dongting Lake (Chang & Cao, 1999). Due to overfishing, the current *C. nasus* population is primarily composed of individuals younger than 3 years, and the migration range has shortened to the reaches below Poyang Lake (Li et al., 2007). The lack of connectivity to the floodplain lakes along the full migration corridor means that fish can only spawn and nurse in lotic river habitats. Compared to the lentic floodplain lakes, spawning and nursery grounds in the river are limited and suboptimal (Chen et al., 2020; Tan et al., 2022). In addition, the long-distance migrants invest more in migration but fail to obtain the benefits of the optimal spawning grounds and nurseries for their offspring. Worse still, long-distance migrants spawn later in the season to synchronize with flooding. The higher discharge experienced by late-born larvae of long-distance migrants in upstream regions during the flooding season results in a decrease in feeding intensity and growth compared to those

produced from short-distance migrants earlier in the season.

Fishing of *C. nasus* has been banned in the Yangtze River since 2019. Consequently, the proportion of older and larger adults should increase. These larger-sized adults should cover longer migration distances and be able to enter Poyang Lake or even Dongting Lake, thus providing the opportunity to test the parent-offspring trade-off theory of migration. We predict that recruitment success of the population in these lakes will be high, which will contribute to faster recovery of the population.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

The *C. nasus* catches obtained for this study were allowable during our Yangtze River field surveys in 2009 and 2010. All specimen collection protocols adhered to the common experimental procedures for fish collection in China.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Y.F.H. and S.G.X. conceived the study, analyzed the data, and developed the manuscript draft. A.L.R. and B.R.M. revised the manuscript. All authors read and approved the final version of the manuscript.

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Yan-Fei Huang^{1,2}, Andrew L. Rypel³, Brian R. Murphy⁴,
Song-Guang Xie^{1,*}

¹ State Key Laboratory of Marine Resources Utilization in South China Sea, Hainan University, Haikou, Hainan 570228, China

² College of Life and Environmental Science, Hunan University of Arts and Sciences, Changde, Hunan 415000, China

³ Department of Wildlife, Fish & Conservation Biology and Center for Watershed Sciences, University of California Davis, Davis CA 95616, USA

⁴ Department of Fish and Wildlife Conservation, Virginia Polytechnic and State University, Blacksburg VA 24061, USA

*Corresponding author, E-mail: xiesg@hainanu.edu.cn

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