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Migration patterns and habitat use of the tapertail anchovy *Coilia mystus* in the Oujiang River Estuary and the Zhujiang River Estuary, China

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Abstract

Habitat use of the tapertail anchovy (*Coilia mystus* Linnaeus, 1758) from the Oujiang River Estuary and the Zhujiang (Pearl) River Estuary was studied by examining the environmental signatures of Sr and Ca in otoliths using electron probe microanalysis. Individuals from the Oujiang River had higher and varied Sr:Ca ratios (expressed as (Sr:Ca)×1 000, 3.83–13.0 average) in the otolith core regions, suggesting that they were born in brackish or sea waters, and that a freshwater habitat might not be necessary for egg hatching and larval growth. While, individuals from the Zhujiang River had lower Sr:Ca ratios (0.39–2.51 average) in the core regions, suggesting a freshwater origin. After hatching, anchovies from the Zhujiang River migrate downstream to the river estuary close to brackish water. Our results demonstrated varied habitat use for spawning during stages of early life history between the two populations, and suggested that such variations are promoting diversity of life history strategies of this species.

Key words: *Coilia mystus*, Oujiang River Estuary, Zhujiang (Pearl) River Estuary, habitat use, otolith microchemistry

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1 Introduction

Coilia species are very important harvested fishes in China. Among them, the tapertail anchovy (*Coilia mystus* Linnaeus 1758) distributes most widely along the Chinese coasts (Yuan and Qin, 1984). As an anadromous fish, most adult *C. mystus* migrate from the sea to the rivers for spawning in March–August (He et al., 2011). Because anchovies migrate short distances from the river mouth and mainly spawn around estuarine areas, there are frequent disputes on the necessity of a freshwater environment for egg hatching or larval growth (Zeng and Dong, 1993; Yang et al., 2006a).

However, it is very difficult to precisely monitor the spatial and temporal patterns of the habitat use of *C. mystus* during its entire life history by traditional catch analysis methods. Noteworthy, otolith, which is located in the inner ear of teleost fish and used to be treated just as timekeeper, has been believed to be a useful recorder of environmental life history, because it grows continually throughout life (Campana, 1999) and is not subject to resorption (Campana and Thorrold, 2001). Alternatively, strontium (Sr) and calcium (Ca) in the otoliths have been believed to be effective natural indicators which can provide researchers with a powerful approach to precisely estimate habitat use and migration of fish between regimes with different salinities (Secor and Rooker, 2000; Tsukamoto et al., 2011; Kubota et al., 2015; Sousa et al., 2016). Specifically, the otolith ratios of Sr:Ca can possibly be used as habitat salinity markers for wild diadromous fishes (Yang et al., 2011), even being successful in the corresponding studies by limited (e.g., <10) otolith samples (Chatterjee et al., 2015; Jiang et al., 2016; Chino et al., 2017). Recently, by the markers, Liu et al. (2018) gave an evidence of estuarine-origin individuals of *Coilia nasus*; Chen et al. (2016) proved that not all long supermaxilla-type *C. nasus* in the Changjiang (Yangtze) River migrate anadromously; and Arai and Chino (2018) confirmed that some marine-resident *Anguilla marmorata* have never migrated into a freshwater habitat by analysing the otolith Sr and Ca.

In our previous studies, Yang et al. (2006a, b) indicated that a freshwater environment may be needed for hatching or early ontogenetic development of *C. mystus* in the Changjiang River Estuary. Unfortunately, no data has been available on the habitat usage of *C. mystus* in the other main river (e.g., the Oujiang River,

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the Zhujiang River) estuaries in China. Genetic divergence showed that there was differentiation among some populations from different river estuaries (i.e., Changjiang River, Minjiang River, Zhujiang River; Chen et al., 2008; Chen and Cheng, 2012). Interestingly, another *Coilia* species, *C. nasus* from some estuaries along the Chinese coasts were proved to have quite different life patterns (Jiang et al., 2014). Therefore, we hypothesized that *C. mystus* in these river estuaries might have their special habitat use patterns for adaptation of the geographic difference. To test the above hypothesis, in the present study, Sr:Ca ratios in the otoliths were examined using electron probe microanalysis (EPMA) to reconstruct the life history of *C. mystus* from the Oujiang River Estuary and Zhujiang River Estuary. The objectives of this study are (1) to identify the migration patterns and habitat conditions of these two populations to discuss the adaptability of *C. mystus* to different estuarine environments, (2) to investigate whether freshwater is important for *C. mystus* during their early development since the spawning grounds are usually close to the estuary, and (3) to confirm the population connectivity between these two populations based on their life patterns and characteristics of habitats conditions.

2 Materials and methods

2.1 *Study sites and fish sampling*

A total of ten *C. mystus* individuals (*C. mystus* from the Oujiang River Estuary, OJCM) were caught from the Oujiang River Estuary (28°00′N, 120°50′E; SI) in June 2010. An additional ten individuals (*C. mystus* from the Shiwuchong in the Zhujiang River Estuary, SWCM) were caught from the Zhujiang (Pearl) River Estuary (22°29′N, 113°42′E; SII) in December 2011 (Fig. 1). All fish from the Oujiang River Estuary were 1-year-old mature females with mean body length and weight of (21.1±0.8) cm and (37.0±5.3) g, respectively. The fish from the Zhujiang River Estuary were young-of-the year (YOY) fish with mean body length and weight of (17.6±0.8) cm and (14.6±1.4) g, respectively (Table 1).

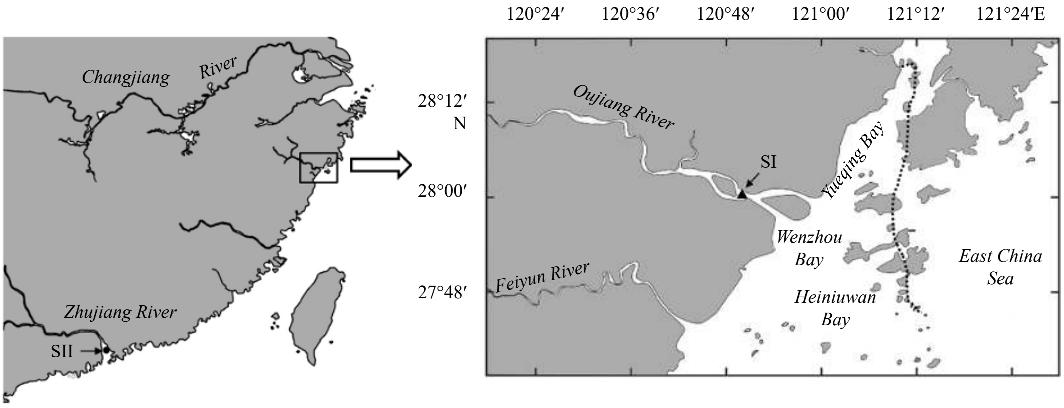

Fig. 1. Map showing *Coilia mystus* sampling sites. OJCM group located in the Oujiang River Estuary (▲, SI) and SWCM group located in the Zhujiang River Estuary (●, SII). The dot line showed the relatively tight island chain on the east and north of the Oujiang River Estuary.

Table 1. Sampling details of *Coilia mystus* used in the present study

Sampling location	Sample code	Total length/cm	Body weight/g
Oujiang River Estuary	OJCM01	20.00	29.49
	OJCM02	21.00	37.04
	OJCM03	20.30	33.76
	OJCM04	21.60	36.35
	OJCM05	21.00	35.81
	OJCM06	21.60	43.10
	OJCM07	22.40	40.22
	OJCM08	21.40	30.45
	OJCM09	21.70	46.54
	OJCM10	20.30	36.85
Zhujiang River Estuary	SWCM01	17.50	14.0
	SWCM02	19.20	16.8
	SWCM03	17.10	12.7
	SWCM04	16.90	13.0
	SWCM05	16.40	15.5
	SWCM06	18.00	15.5
	SWCM07	17.80	15.2
	SWCM08	16.80	12.8
	SWCM09	18.20	15.7
	SWCM10	17.70	14.6

2.2 *Otolith analysis*

Otoliths were extracted and embedded in epoxy resin (Epofix; Struers, Copenhagen, Denmark) in the frontal plane. All otoliths were ground to expose the core with an automated polishing wheel (LaboPol-35; Struers, Copenhagen, Denmark). All samples were then cleaned in an ultrasonic bath and rinsed with Milli-Q water. For EPMA measurements, all otoliths were carbon coated by a high-vacuum evaporator (JEE-420, JEOL Ltd, Tokyo Japan).

The otoliths were used for life history transect analysis of Sr and Ca concentrations, which were measured along a line down the longest axis of each otolith from the core to the edge by a wavelength dispersive X-ray electron microprobe (JXA-8100, JEOL Ltd, Tokyo Japan). Calcite ($CaCO_3$) and Tausonite ($SrTiO_3$) were used as standards. The accelerating voltage and beam current were 15 kV and 2×10^{-8} A, respectively. The electron beam was focused on a point 5 μm in diameter, with measurements spaced at 10 μm intervals. The X-ray intensity maps of Sr concentration were made of the representative otoliths using the same microprobe in accordance with the aforementioned life history transect. The beam current was 5×10^{-7} A, counting time was 30 ms, and pixel size was 6×6 μm in diameter.

According to our previous X-ray intensity map studies (Yang et al., 2006a, b; Jiang et al., 2014; Chen et al., 2016) on otoliths of *Coilia* species, bluish ($(Sr:Ca)\times1\,000<3$), greenish-yellowish ($7\geqslant(Sr:Ca)\times1\,000\geqslant3$), and reddish regions ($(Sr:Ca)\times1\,000>7$) were characteristic of freshwater (low salinity, <5), brackish water (medium salinity, 5–25), and sea water (high salinity, >25) (Secor and Rooker, 2000), respectively, by corresponding 16 colour map patterns of Sr content from blue (lowest) through green and yellow to red (highest).

2.3 *Data analysis*

Statistical analysis was performed SPSS 19.0 (IBM Corp., Armonk, NY, USA) and the Mann-Whitney *U*-test was used to test the differences between otolith Sr:Ca ratios (customarily using (Sr:Ca)×1 000 throughout in the present study). A sequential regime shift algorithm was applied to identify the chemical properties of different phases in the life history of *C. mystus* in this study. By reference to Rodionov's work (Rodionov, 2004), the significance level was 0.1, the cut-off length was 10, and Huber's weight parameter was 1.

3 Results

Sr:Ca ratios in otolith cores were highly variable among all anchovies. One dramatic difference between individuals from the Oujiang River Estuary and the Zhujiang River Estuary was that the mean Sr:Ca ratios of the former (4.69±1.62 to 9.17±1.56) were dramatically higher than those of the latter (1.07±0.77 to 3.56±1.87) (*P*<0.01, Mann-Whitney *U*-test). By comparison of otolith Sr and Ca results in the present study, all fish could be divided into three microchemical patterns (Fig. 2). In general, two Sr:Ca ratio patterns could be found among the otoliths of *C. mystus* from the Oujiang River. Pattern I presented high (>7, 7.03±1.09 to 8.07±1.22) Sr:Ca ratio phases in the inner (OJCM01, OJCM02, OJCM08, OJCM09, and OJCM10) or whole regions (OJCM04 9.01±1.44 and OJCM06 9.17±1.56) of the otoliths (*P*<0.01, Mann-Whitney *U*-test). Pattern II showed a continuously low Sr:Ca ratio (around 5) phase toward the edge of the otoliths of OJCM03 (5.21±1.12), OJCM05 (4.69±1.62), and OJCM07 (6.25±1.29). Unlike the above two patterns of *C. mystus* from the Oujiang River, pattern III in otoliths of *C. mystus* from the Zhujiang River showed a consistently lower Sr:Ca ratio core region (0.39–2.51).

In the X-ray intensity maps, usually the greenish-reddish cores were found in two distinct patterns in fish from the Oujiang River Estuary Outside of the core areas in otoliths, colour profiles presented significant differences. Among them, Pattern I showed a large reddish region just outside of the core area. By contrast, Pattern II seemed to be quite stable with large greenish regions in the central areas of the otoliths, except for some reddish and blue concentric rings. Unlike the above fish from the Oujiang River Estuary, the otoliths of fish from the Zhujiang River Estuary (Pattern III) had special blue core areas with some greenish and blue bands in neighbouring areas (Fig. 3).

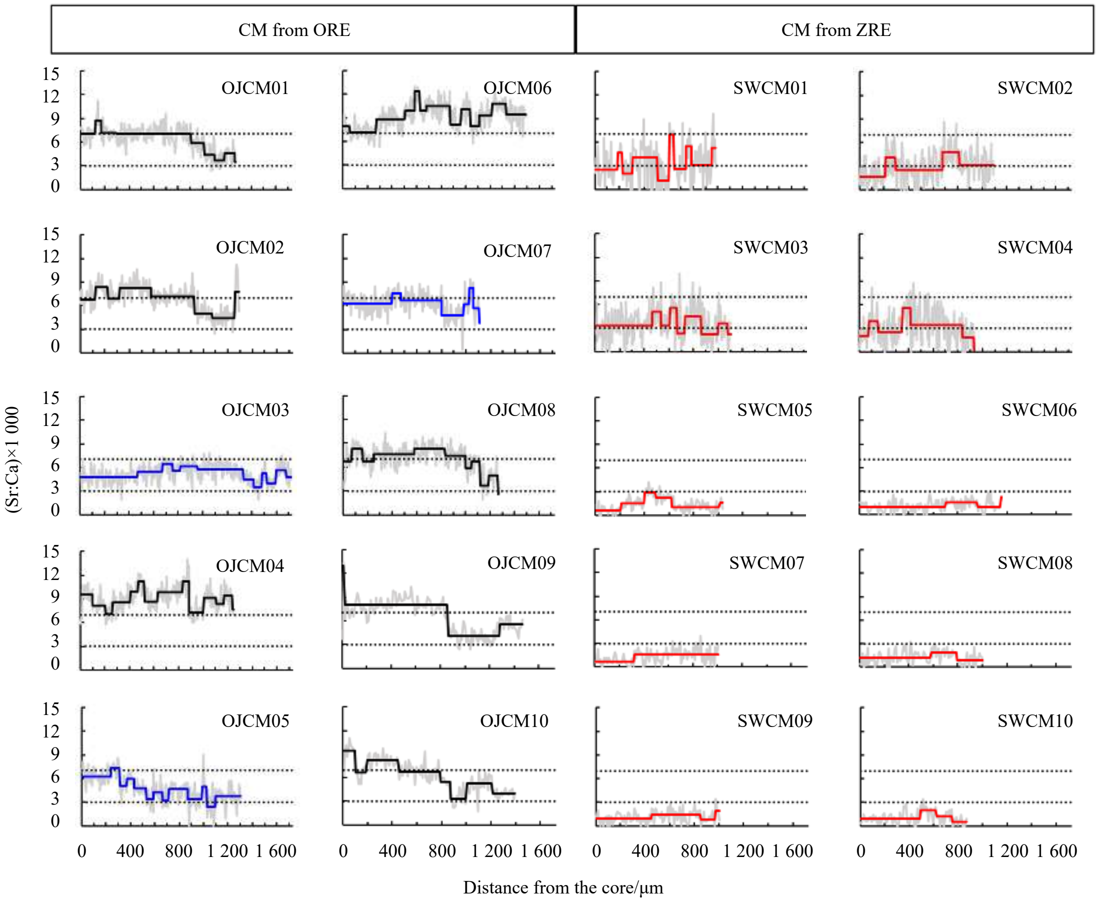

Fig. 2. Fluctuation of otolith Sr:Ca ratios of concentration along line transects from the core (0 μm) to the edge in the sagittal plane of the otolith of *Coilia mystus* (CM) from the Oujiang River Estuary (ORE) and the Zhujiang River Estuary (ZRE). The grey line presents the change of the Sr:Ca ratios the otolith from core to the edge, while the black line (Pattern I), blue line (Pattern II), and red line (Pattern III) represents the pattern of change in a given regime as defined using the Rodionov approach. Two dot lines reflected the Sr:Ca ratios of 3 (lower) and 7 (higher).

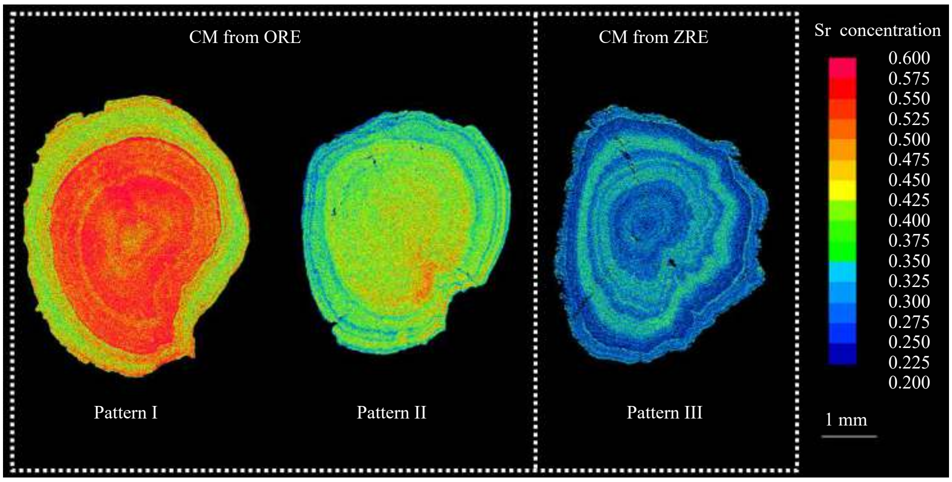

Fig. 3. Three types of two-dimensional mapping using X-ray electron microprobe analyses of the Sr concentrations in the sagittal otolith plane of *Coilia mystus* (CM) from the Oujiang River Estuary (ORE, Patterns I and II) and the Zhujiang River Estuary (ZRE, Pattern III), China. The values corresponding to Sr concentrations are represented by 16 colours from red (highest) through yellow and green, to blue (lowest).

4 Discussion

4.1 *Migratory history of Coilia mystus from the Oujiang River estuary*

Coilia mystus are believed to be an estuarine fish. Yang et al. (2006b) documented small core regions with low Sr:Ca ratios of 1.38–4.56, tracking with the bluish colour patterns of the X-ray intensity maps (i.e., freshwater habitat) in otoliths of *C. mystus* from the Changjiang River Estuary, implying that this fish hatched in a freshwater habitat. Contrastingly, otoliths from the Oujiang River Estuary had greenish-reddish cores with high Sr:Ca ratios (3.83 to 13.0, i.e., brackish or salt water habitats), indicating that the freshwater habitat might not be necessary for these fish.

The salinity in the Oujiang River Estuary is frequently affected by tidal influences. With a flood tide, salinities in our sampling site were usually around 5–10 (i.e., brackish water), but at the time of the ebb tide, salinities decreased to <5 (i.e., freshwater; Jiang et al., 2009). A previous study reported that *C. mystus* in the Oujiang River Estuary might prefer to spawn in a freshwater habitat (Zhong et al., 2009). However, the large reddish regions adjacent to the core in otolith Pattern I strongly suggested that a freshwater habitat would not be necessary for egg hatching and early larval development (Fig. 3). Because of the island chain around the Oujiang River Estuary, the tidal currents flow in the river from three directions (Jiang et al., 2009). Consequently, the corresponding water regions have been partitioned into three different salinity regimes (i.e., salinity of 0.5–5, 5–18, and >30) (Song et al., 2012). As mentioned, all otoliths from the Oujiang River Estuary could be divided into two microchemical patterns. Pattern I (OJCM01, OJCM02, OJCM04, OJCM06, OJCM08, OJCM09, and OJCM10) usually presented a higher otolith Sr:Ca ratio in central areas of the otolith (reddish colour in Fig. 3). In particular, OJCM04 and OJCM06 generally showed consistently higher (>7) Sr:Ca ratios over the whole otolith. Pattern II (OJCM03, OJCM05 and OJCM07) was characterized by lower otolith Sr:Ca ratio (bluish colour in Fig. 3). After spawning in the Oujiang River Estuary, the floating eggs are rushed quickly downstream in different directions to the estuarine and even the marine areas. Of these, some might be blocked by the east and north island chains (Pattern II), allowing them to develop in nearshore waters with otolith microchemical markers of relatively lower salinity habitats (i.e., the Wenzhou Bay and Yueqing Bay), while others may be rushed southward and dispersed into the sea (Pattern I).

4.2 *Migratory history of Coilia mystus from the Zhujiang River Estuary*

Similar to the otolith patterns of *C. mystus* from the Changjiang River Estuary (Yang et al., 2006b), those of the fish from the Zhujiang River Estuary showed blue core regions with Sr:Ca ratios of 0.39 to 2.51, which revealed that all of them were freshwater-origin individuals. But by comparison with those estuarine-origin individuals from the Oujiang River Estuary, this phenomenon showed that the freshwater habitat might not be necessary during the early life history of this species, especially during the hatching phase. On the other hand, it was still worth noting that although those from the Zhujiang River Estuary and the Changjiang River Estuary had a similar blue core, the fluctuations of otolith Sr:Ca ratios of the Zhujiang River *C. mystus*, with a larger blue core region and some greenish or blue bands in neighbouring areas, were quite different from the pattern of Changjiang River *C. mystus* with a small blue core and large regions of greenish or reddish colour outside (Yang et al., 2006b). Pattern III showed that the Zhujiang River *C. mystus* might be born in a freshwater habitat and then extend their habitats to the neighbouring brackish waters. Unlike the Changjiang River Estuary and the Oujiang River Estuary, there are some freshwater outlets in the Zhujiang River Estuary (Callahan et al., 2004). With the characteristics of otolith microchemistry of *C. mystus* from the Changjiang River and Oujiang River, it can be inferred that soon after spawning, the young generation leave freshwater regions and hardly returned until the next spawning season. It is noteworthy that all individuals of this study were caught in the freshwater region (Jiang et al., 2015) during non-spawning season, reflecting that *C. mystus* from the Zhujiang River Estuary might prefer the lower salinity regions as their over-wintering ground or habitat. By consideration of their Sr:Ca ratios with constantly lower values over the whole otolith, anchovies from the Zhujiang River Estuary possibly have a unique migratory history similar to that of blueback herring (*Alosa aestivalis*), some of which might stay in the estuarine and freshwater nurseries even after the young-of-year period (Limburg and Turner, 2016).

In conclusion, *C. mystus* from the Oujiang River Estuary were quite different from those of the Zhujiang River Estuary, which strongly suggests no population connectivity between each other, and the corresponding fish resources should belong to two geographically separate populations (Fig. 4). For the Zhujiang River population, *C. mystus* were born in freshwater and then migrated downstream into brackish waters. For the Oujiang population, mature *C. mystus* may chose freshwater habitat as their spawning ground, but larvae can also live in higher salinity waters during their early life history. These results show that *C. mystus* differs from some estuarine fish (e.g., *Collichthys lucidus*, *Larimichthys polyactis*) which need water of a specific salinity during egg hatching and early development (Liu et al., 2015; Xiong et al., 2017). Although larvae can survive in waters of different salinities (freshwater, brackish water and seawater), mature fish always choose to spawn in freshwater. All the results of the present study reflect that *C. mystus* shows a strong ability to adapt to different estuarine habitats and that the differences between geographic habitats might be an important driving force promoting the diversity of the life history strategies of *C. mystus*.

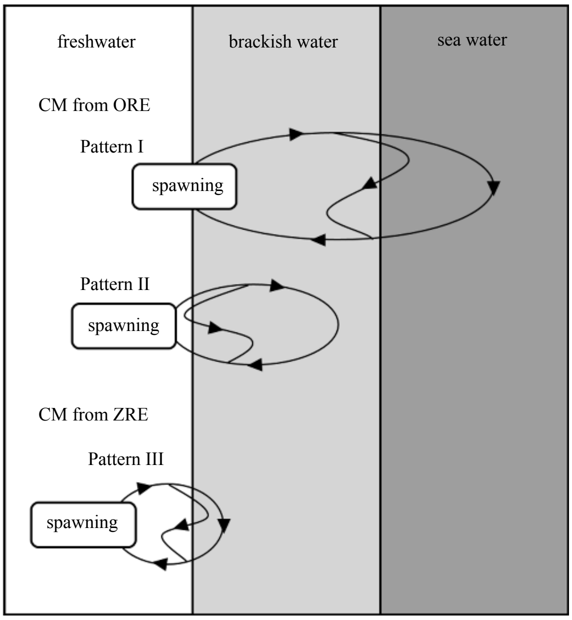

Fig. 4. Diagrammatic sketch of the life history patterns of *Coilia mystus* (CM) from the Oujiang River Estuary (ORE, Patterns I and II) and the Zhujiang River Estuary (ZRE, Pattern III). The arrows represent the possible dispersion patterns in and during the non-spawning migratory phases.

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