



# Life history of spinyhead croaker *Collichthys lucidus* (Sciaenidae) differentiated among populations from Chinese coastal waters

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**ABSTRACT:** Otolith microchemistry provides valuable information about the environmental history of individual fish, but few studies have considered the influence of population or stock on life history traits. This study used the Sr/Ca ratio as an index of habitat use of spinyhead croaker *Collichthys lucidus* from 2 different populations (northern and southern China populations), including lifetime otolith microchemistry profiles (n = 63 fish) and determinations of natal habitat selection (n = 352 fish). The otolith data revealed 3 life history patterns in *C. lucidus*: Pattern 1 individuals spent most of their lifetime (>95%) in mesohaline waters (Sr/Ca range: 3–7 mmol mol<sup>-1</sup>), particularly during early growth; Pattern 2 individuals migrated from hyperhaline waters (Sr/Ca ≥ 7 mmol mol<sup>-1</sup>) to mesohaline waters; and Pattern 3 individuals migrated from oligohaline waters (Sr/Ca < 3 mmol mol<sup>-1</sup>) to mesohaline waters. Pattern 2 and Pattern 3 were specific to the northern and southern China populations, respectively, and Pattern 1 was shared by the 2 populations. The otolith core Sr/Ca ratios showed that most *C. lucidus* selected mesohaline waters as their natal habitat (i.e. 90.6% of 352 total individuals); 12.5% (19 of 152) selected hyperhaline waters and fell within the northern China population, and 7% (14 of 200) selected oligohaline waters and fell within the southern China population. These results indicate that life history diversity exists in this species, as the pattern of habitat use largely differed between the northern and southern China populations. The overall findings highlight that the behavior of different populations should be considered when determining fish migration histories.

**KEY WORDS:** Natal habitat · Migration pattern · *Collichthys lucidus* · Sr/Ca · China · Partial migration

## 1. INTRODUCTION

Life history diversity among populations of a species in terms of habitat residency and movement patterns has both ecological and evolutionary implications, such as shaping distribution and abundance,

speciation, and resilience to changing environmental conditions (Kerr et al. 2010, Schindler et al. 2010, Chapman et al. 2011a). Many studies have shown that populations of fish can contain both migrant and resident individuals, a phenomenon defined as partial migration (Kerr & Secor 2009, Chapman et al.

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2011b, 2012). Partial migration is known to occur in a variety of habitats and across all spatial scales, and it is often reflected in a diversity of behaviors at the juvenile stages (Kerr & Secor 2012, Hegg et al. 2015, Arai et al. 2020).

Estuaries are an important environment for many fish species, especially during their early life stages, providing food resources and refuge from predation (Able 2005, Elliott et al. 2007). Numerous concepts have been proposed to categorize fish according to their pattern of estuarine use, with estuarine-dependent species defined as requiring brackish water at any given life stage (Able 2005). Estuarine species can be further divided into estuarine residents and estuarine migrants—with the former capable of completing their entire life cycle within the estuarine environment and the latter having the larval stage of their life cycle completed outside the estuary (Elliott et al. 2007). The movement of young fish within and between nursery habitats is influenced by the external forces they experience (e.g. food availability and predation risk), as well as by their own inherent characteristics (e.g. metabolic rate) (Kerr & Secor 2009, Conroy et al. 2015).

Otolith microchemical analysis has been widely applied to reconstruct fish movements and migrations (Secor & Rooker 2000, Elsdon et al. 2008, Avigliano & Volpedo 2016). Otoliths are metabolically inert, grow continuously over the lifetime of a fish, and incorporate trace elements as they grow (Campana 1999). Elemental deposition in otoliths is influenced by genetic, physiological, and environmental factors, but particularly reflects the concentration of elements in the surrounding water (Clarke et al. 2011, Sturrock et al. 2015, Izzo et al. 2018, Thomas & Swearer 2019, Thomas et al. 2020). Therefore, the chemicals deposited in otoliths can provide a chronological record of the environmental conditions that a fish is exposed to, and this record can be used to reconstruct a detailed migration history (Hermann et al. 2016, Hauser et al. 2019, Avigliano et al. 2021b). Different elemental ratios have been used to study displacements between environments with different salinities, with the ratio of strontium to calcium (Sr/Ca) being the most commonly used because it has been shown to be positively related to habitat salinity for many estuarine species (Chang et al. 2004b, Webb et al. 2012, Arai & Chino 2017). Seawater typically has a much higher concentration of Sr compared with freshwater (Mohan & Walther 2015, Walther & Nims 2015); thus, otolith Sr/Ca is a useful indicator of habitat in a species that occupies an environment with a salinity gradient (Chang et al. 2004b, Arai et al. 2005, Yang et al. 2006, Avigliano et al. 2018).

The spinyhead croaker *Collichthys lucidus* (Richardson) is an important commercial fish widely inhabiting the inshore waters of East Asia (Nguyen Van et al. 2020). This species is small-sized, matures at age 1 yr, and has high fecundity and strong adaptability to salinity (2–42 psu) (Wu & Wang 1996, Shan et al. 2007). It usually spawns during spring and early summer on sandy bottoms at 10–20 m depth, with planktonic eggs and larvae and benthic adults (Zhang et al. 1985). With the over-exploitation of predator fishes such as the small yellow croaker *Larimichthys polyactis* and large yellow croaker *L. crocea*, the biomass of *C. lucidus* has rapidly increased, and its production has risen accordingly (He & Li 1988, Huang et al. 2010, Hu et al. 2015). Despite the output of *C. lucidus* from the coast of China exceeding 200 000 t in 2018 (Fishery Knowledge Service System; <http://fishery.ckcest.cn/featureYearbook.html>), the species is considered overfished in some traditional fishing grounds, including the Yangtze River Estuary (Hu et al. 2015) and Minjiang River Estuary (Huang et al. 2010). Several studies have reported population differentiation of *C. lucidus* between distinct estuaries based on genetics (e.g. Zhao et al. 2015, Song et al. 2019) and morphology (e.g. X. H. Liu et al. 2015). Our previous work indicated the presence of 2 populations in China—namely the northern and southern populations—based on various methods (i.e. mitochondrial DNA, microsatellites, parasite tags, and otolith chemistry) (Zhang et al. 2021a,b). However, ecological knowledge of this fish is based mainly on the northern China population (Shi et al. 2011, H. B. Liu et al. 2015). It has been reported that *C. lucidus* completes different life history stages in the Yangtze River Estuary (Shi et al. 2011); however, this species requires high salinity for spawning (H. B. Liu et al. 2015). Therefore, more information is warranted to completely understand its life history and habitat use.

Analytical techniques used to decipher ontogenetic changes via otolith chemical time-series typically entail spot, line, or plane analyses of scans made with an electron probe micro-analyzer (EPMA) (H. B. Liu et al. 2015, Arai et al. 2020, Gonzalvo et al. 2021) or laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) (Hermann et al. 2016, Avigliano et al. 2018, Pan et al. 2020). Here, we used LA-ICP-MS spot and line scans on otoliths of *C. lucidus* collected from estuaries and bays along the coast of China. Our objectives were to (1) determine the migration patterns of *C. lucidus* from different estuaries in China, (2) ascertain whether the species' life history varied between different genetic populations, and (3) establish whether high-salinity water is essential during the early life history of this species.

Table 1. Sampling information on spinyhead croaker *Collichthys lucidus* from Chinese coastal waters. –: not studied

Estuary	Sampling date	Transect line analysis			Nucleus spot analysis		
		No. of specimens	Body length (mm)	Estimated age (years)	No. of specimens	Body length (mm)	Estimated age (years)
<b>Northern China population</b>		29			152		
Yellow River Estuary	Nov 2019	5	148.2–167.6	1+ to 2+	32	145.9–172.3	1+ to 3+
Yalu River Estuary	Nov 2019	7	99.5–131.1	0+ to 1+	40	99.5–131.1	0+ to 1+
Haizhou Bay	Sep 2019	6	92.8–112.1	0+ to 1+	40	92.6–132.9	0+ to 1+
Yangtze River Estuary	Oct 2019	11	103.7–111.4	0+ to 1+	40	85.2–122.7	0+ to 1+
<b>Southern China population</b>		34			200		
Oujiang River Estuary	Nov 2019	5	114.0–124.7	1+	40	112.1–130.6	1+ to 2+
Minjiang River Estuary	Oct 2019	6	96.8–102.3	0+	40	91.1–105.5	0+ to 1+
Jinjiang River Estuary	Nov 2019	3	172.0–182.0	3+	–	–	–
Hanjiang River Estuary	Oct 2019	4	71.4–79.6	0+	40	66.9–80.8	0+
Pearl River Estuary	Sep 2019	10	97.1–107.8	0+	40	94.9–107.9	0+
Jianjiang River Estuary	Oct 2019	6	111.6–121.8	0+ to 1+	40	101.6–123.6	0+ to 1+

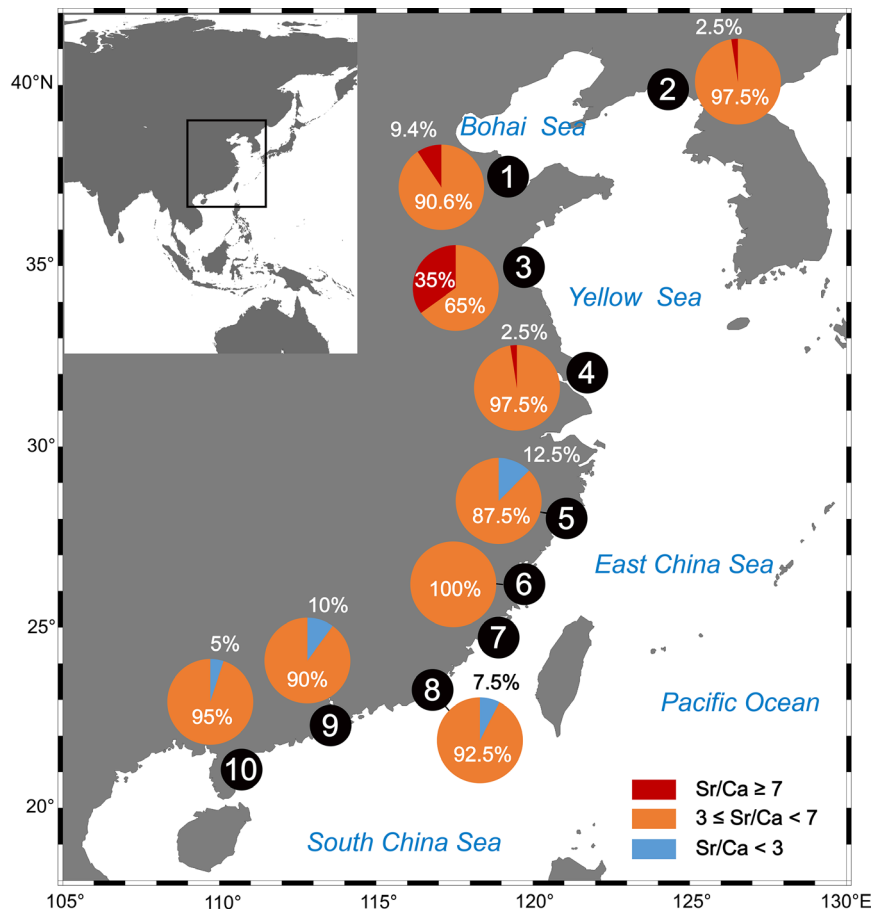


Fig. 1. Sampling estuaries of spinyhead croaker *Collichthys lucidus*. 1: Yellow River Estuary; 2: Yalu River Estuary; 3: Haizhou Bay; 4: Yangtze River Estuary; 5: Oujiang River Estuary; 6: Minjiang River Estuary; 7: Jinjiang River Estuary; 8: Hanjiang River Estuary; 9: Pearl River Estuary; 10: Jianjiang River Estuary. Charts show the otolith core Sr/Ca ratio classification of the fish except for samples from Jinjiang River Estuary

## 2. MATERIALS AND METHODS

### 2.1. Fish collection

*Collichthys lucidus* were collected at 10 locations, including most of the traditional fishing grounds for this species along China's coastline (Table 1, Fig. 1), such as the Pearl River Estuary and Yangtze River Estuary. Specimens from the Bohai Sea and Yellow Sea belonged to the northern China population and the rest (East China Sea and South China Sea) belonged to the southern China population (Fig. 1). Fish were collected from the catches of local fishermen in autumn (September–November) 2019, deep-frozen, and then transported to the laboratory. After thawing, the fish were measured for body length to the nearest 0.1 mm, sexed, and dissected to remove the sagittal otoliths. The extracted otoliths were cleaned of organic tissues with ultrasonic waves (5 min) in ultrapure water, air-dried, and then stored in Eppendorf vials until further analysis.

### 2.2. Otolith preparation

The otoliths were embedded separately in plastic tubes using epoxy resin and sectioned in the transverse

plane using a saw fitted with 2 diamond-edged blades, creating a cross-section of the center of the otolith with a thickness of  $\sim 450\ \mu\text{m}$ . This thin cross-section was polished using a rotary polishing wheel with 600- and 1200-grit paper to expose the core. The sections were attached to petrographic slides (3 sections slide<sup>-1</sup>) using mounting adhesive and then sonicated for 8 min in ultrapure water, dried at room temperature, and stored for later analysis. As there is typically no significant difference in elemental signatures between the right and left otoliths from the same fish (Campana et al. 2000), the left sagittal otoliths were used for 'life history transects' from the core to the dorsal edge (transect analysis,  $n = 63$ ) and the right sagittal otoliths were used for spot analysis of the core area (spot analysis,  $n = 352$ ) (Table 1). The left otoliths were randomly selected from the different sexes.

### 2.3. Microchemical analysis

Determination of the trace elements in the otoliths was conducted by the Guangzhou Tuoyan Testing Technology Co. Otolith element concentrations were measured with a Thermo Fisher Scientific™ iCAP RQ ICP-MS combined with a New Wave Research UP193 laser ablation system. Helium was used as the

carrier gas in the ablation cell, and argon was also added before being introduced into the ICP. Two of the National Institute of Standards and Technology Standard Reference Materials (NIST610 and NIST 612) were analyzed at the beginning and end of each analytical run consisting of 9 samples for drift monitoring. The laser ablation transects of the left otoliths were selected from the core to edge, ablated at a beam width of  $20\ \mu\text{m}$ , with a pulse frequency of 10 Hz and a transect speed of  $5\ \mu\text{m s}^{-1}$  (Fig. 2). The ablation procedure for the natal elemental signatures of the nucleus of right otoliths involved a 30 s sample signal and 35 s control signal, with a beam width of  $50\ \mu\text{m}$ , a pulse frequency of 8 Hz, and energy density of  $5\ \text{J cm}^{-2}$  (Fig. 2).

Following data processing of the trace elements in otoliths, the concentrations of  $^{88}\text{Sr}$  and  $^{43}\text{Ca}$  isotopes were calculated for each otolith sample using the software ICPMSDataCal 10.8 (Liu et al. 2008) and Iolite 4 (Paton et al. 2011). To convert elemental signals (intensity) to concentrations, NIST612 and NIST610 were used for calibration of the nucleus elemental signals, and NIST612 and Ca (38.3% weight; Sturgeon et al. 2005) were used for calibration and as internal standards for the transect signals. Limits of detection ( $0.003\ \text{mmol mol}^{-1}$ ) and uncertainty (2.8%) of the nucleus spot analysis showed acceptable values for  $^{88}\text{Sr}$ . To smooth the transect-line data, data

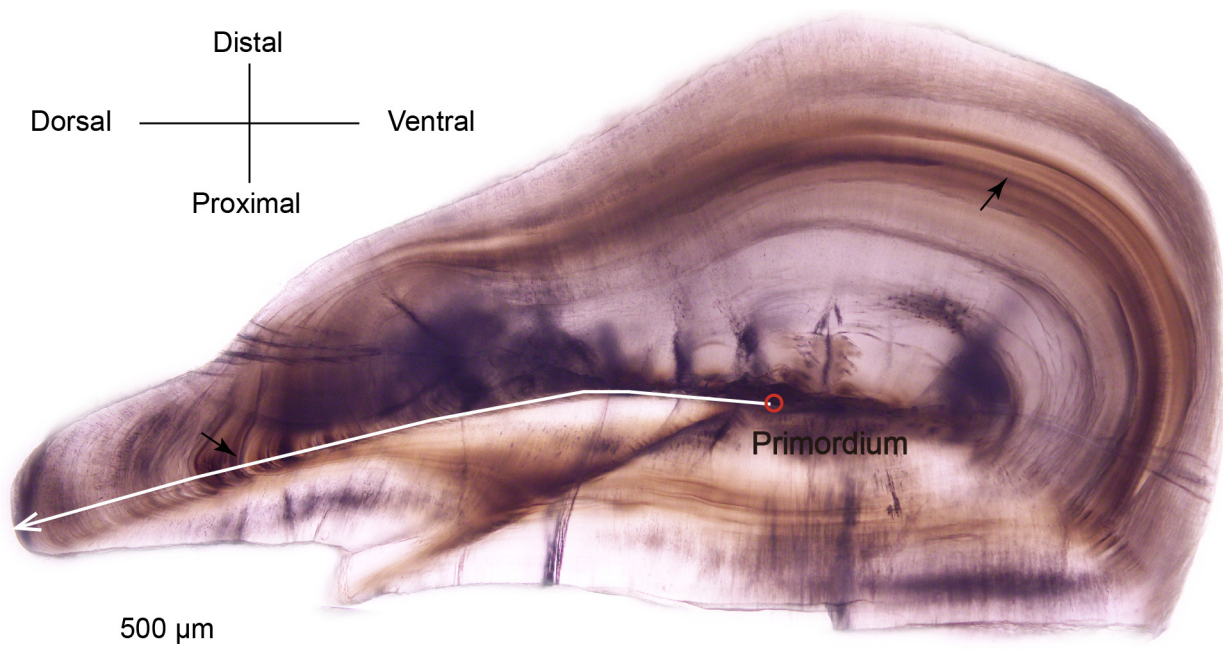


Fig. 2. Left otolith sections of spinyhead croaker *Collichthys lucidus*. White line: core-to-edge laser ablation transects of left otolith; red circle: core region of right otolith used for core microchemistry analyses; black arrow: positions of annuli (estimated age = 1 yr, body length = 148.2 mm, female)



points in excess of 2 standard deviations from the mean of the 12 following data points were removed, and spikes were excluded by eye. Finally, the average of the 12 data points (line length  $\sim 7 \mu\text{m}$ ) was calculated as the element concentration at this point (Heimbrand et al. 2020). This was a conservative approach to remove outliers, and the calculation clearly filtered out erroneous data that were likely a result of instrument noise rather than ecologically relevant values (McMillan et al. 2017, Nelson et al. 2021). The product between the analysis time and the scanning speed was used to calculate the distance from the otolith core to the edge. Sr concentrations were expressed in relation to Ca ( $\text{mmol mol}^{-1}$ ).

#### 2.4. Age estimation

Following the otolith chemical analysis, the age of each fish was determined using the same otolith. Age was estimated by counting the annual growth rings, which were made visible by immersing the otolith sections in distilled water. Age readings were carried out by one of the authors (S.Z.) using an Olympus BX53 microscope at  $40\times$  magnification. Because the majority of specimens studied were young fish (age 0+ or 1+), the interpretation error by one reader should be limited. A whole year was counted when the outer edge of an opaque zone was visible (Katayama 2018).

#### 2.5. Statistical analysis

To assess whether the ontogenetic changes in the Sr/Ca profiles were significant, a change-point analysis (CPA) was performed on the data for individual fish using a pruned exact linear time (PELT) algorithm (Killick et al. 2012) with the package 'changepoint' in R v.4.1.2 (R Core Team 2022). CPA defines the point in a time-series analysis where a statistically significant change occurs, making it suitable to identify changes in otolith Sr/Ca ratios along transect lines (Killick et al. 2012). The PELT algorithm automatically divides a lifetime profile with multiple change points to identify where a stable segment started and then generates mean values for each segment (Killick & Eckley 2014, Killick et al. 2016). This analysis was performed using the modified Bayes information criterion penalty. As the length of time series data varied, a quantitative approach to determine the life history pattern of this species was not applicable.

Upon visual inspection of Sr/Ca ratio chronologies, 3 distinct life history patterns were assigned which mainly differed from early life history. Pattern 1 was characterized by Sr/Ca ratios typically around  $5 \text{ mmol mol}^{-1}$  during their whole life history (see e.g. Fig. 3A,B). Pattern 2 was characterized by high Sr/Ca ratios ( $\sim 7 \text{ mmol mol}^{-1}$ ) during early life history, descending to  $\sim 5 \text{ mmol mol}^{-1}$  for the rest of the lifetime (see e.g. Fig. 3C,D). Pattern 3 was characterized by a low Sr/Ca ratio ( $\sim 3 \text{ mmol mol}^{-1}$ ) during early life history, rising to  $\sim 5 \text{ mmol mol}^{-1}$  for the rest of the lifetime (see e.g. Fig. 3E,F).

Kruskal-Wallis followed by Dunn's multiple-comparisons tests were conducted to determine differences between the average nucleus Sr/Ca ratios among the sample locations and the 2 populations, as data could not be transformed to satisfy both normality and homoscedasticity assumptions. A Pearson test was conducted to determine the relationship between sex and nucleus Sr/Ca ratios. The significance level was set as  $\alpha = 0.05$ .

### 3. RESULTS

#### 3.1. Migration patterns

A total of 63 samples were analyzed and visualized in Figs. 3 & S1–S4 in the Supplement at [www.int-res.com/articles/suppl/b031p065\\_supp.pdf](http://www.int-res.com/articles/suppl/b031p065_supp.pdf). Core-to-edge Sr/Ca ratios ranged from 1.94 to  $9.18 \text{ mmol mol}^{-1}$ , with the lowest data point recorded for the Oujiang River Estuary (Fig. S4I) and the highest for the Haizhou Bay (Fig. S3E).

Three life history patterns in *Collichthys lucidus* were identified based on the mean value of CPA results from the core-to-edge Sr/Ca ratios of individual fish (Figs. 3 & S1–S4). In Pattern 1 fish, most of the lifetime (95.8–100%) was denoted by moderate Sr/Ca ratios ( $3\text{--}7 \text{ mmol mol}^{-1}$ ; Figs. 3A,B & S1–S2). One specimen (DYC-14) from the Yellow River Estuary showed a low Sr/Ca ratio at a length of  $\sim 2400 \mu\text{m}$  from the core (the lowest Sr/Ca ratio was 2.51; Fig. S1H); 2 specimens from the Jinjiang River Estuary showed the highest Sr/Ca ratios during the adult stage at  $7.62 \text{ mmol mol}^{-1}$  (specimen QZC-1; Fig. S2F) and  $7.10 \text{ mmol mol}^{-1}$  (specimen QZC-5; Fig. 3A). The first-stage life history of Pattern 1 specimens showed a moderate Sr/Ca ratio (mean value of Sr/Ca ratios ranged from 3.75 to  $6.03 \text{ mmol mol}^{-1}$ ). Pattern 2 fish migrated from high Sr/Ca ratios ( $\geq 7 \text{ mmol mol}^{-1}$ ) to moderate Sr/Ca ratios (Figs. 3C,D & S3). This pattern showed a relatively high Sr/Ca ratio phase from the

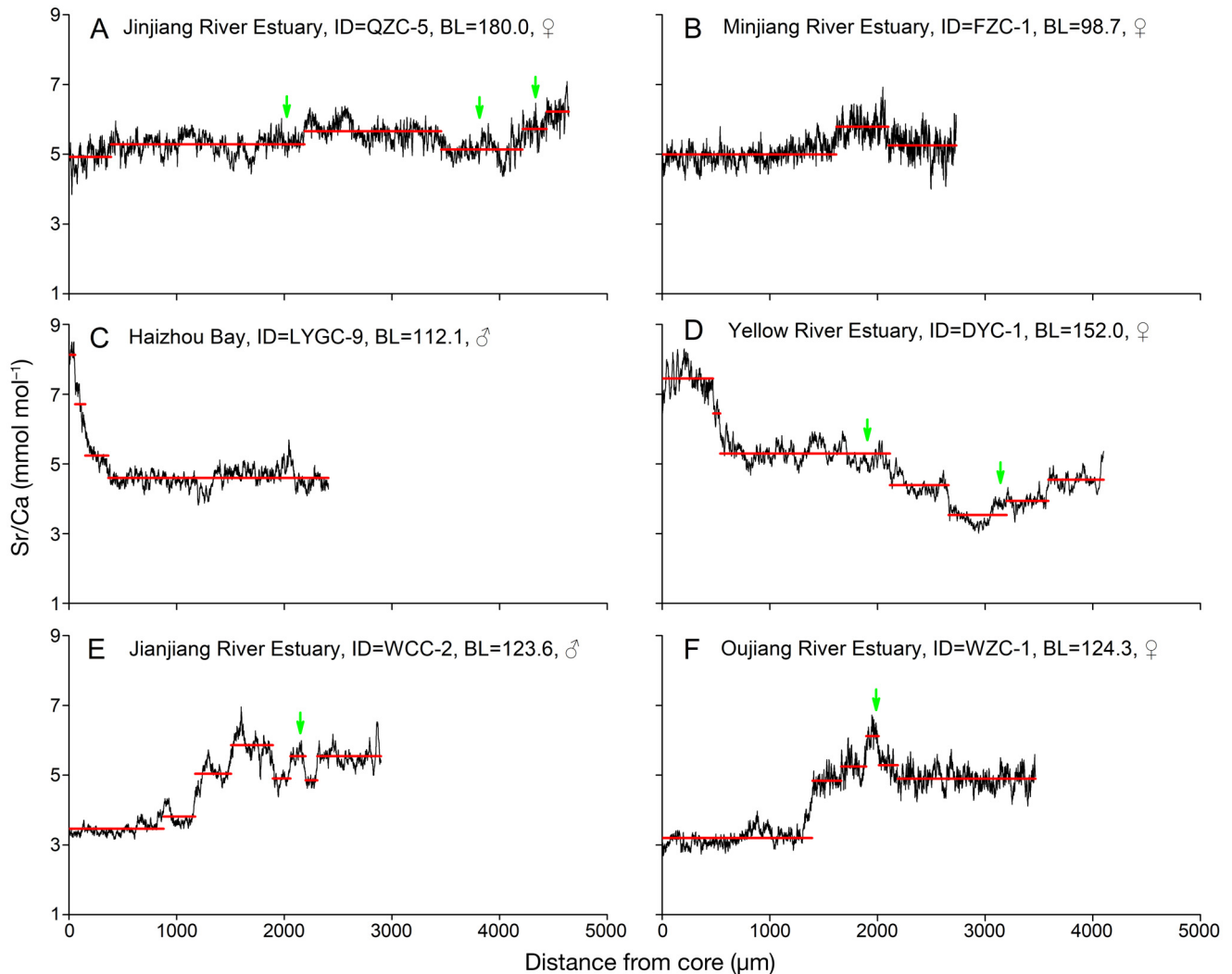


Fig. 3. Representative samples of spinyhead croaker *Collichthys lucidus* otolith core-to-edge Sr/Ca profile (black line) for (A,B) Pattern 1, (C,D) Pattern 2, and (E,F) Pattern 3 individuals. Arrow: position of the annuli; horizontal red line: changes in Sr/Ca profile obtained from the change-point analysis. Other samples are shown in Figs. S1–S4. BL: body length

otolith core to a point at approximately 75–500  $\mu\text{m}$  based on the mean Sr/Ca ratios of the first stage (6.34–8.13  $\text{mmol mol}^{-1}$ ). Thereafter, the ratios decreased sharply, and moderate Sr/Ca ratios were maintained to the otolith edge (Fig. 4A–C). For Pattern 2, the highest Sr/Ca ratio was 9.18  $\text{mmol mol}^{-1}$  in specimen LYGC-7 (Fig. S3E) and the lowest was 3.01  $\text{mmol mol}^{-1}$  in specimen DYC-1 (Fig. 3D). Pattern 3 fish migrated from low Sr/Ca ratios ( $\sim 3 \text{ mmol mol}^{-1}$ ) to moderate Sr/Ca ratios (Figs. 3E,F & S4). This pattern showed a relatively low Sr/Ca ratio phase from the core to a point at approximately 140–1400  $\mu\text{m}$ , based on the lowest mean Sr/Ca ratios of the first- and second-stage life history (2.50–3.78  $\text{mmol mol}^{-1}$ ). Thereafter, Sr/Ca ratios increased sharply, and mod-

erate Sr/Ca ratios were maintained to the otolith edge (Figs. 3E,F & S4).

Pattern 1 was the dominant life history pattern, seen in 55.5% (35 of 63) of the *C. lucidus* otolith lifetime microchemistry profiles, whereas 15.9% (10 of 63) and 28.6% (18 of 63) of the samples showed Pattern 2 and Pattern 3 traits, respectively. Furthermore, 34.5% (10 of 29) of *C. lucidus* from the northern China population exhibited Pattern 2 traits and 65.5% (19 of 29) had Pattern 1 traits. There were 52.9% (18 of 34) of *C. lucidus* from the southern China population with Pattern 3 traits and 47.1% (16 of 34) with Pattern 1 traits. These results suggest that the migration pattern of *C. lucidus* is differentiated between the northern China and southern China populations.

### 3.2. Natal habitat use of *C. lucidus*

The nucleus Sr/Ca ratios of *C. lucidus* ( $n = 352$ ) ranged from  $2.42 \text{ mmol mol}^{-1}$  (Oujiang River Estuary) to  $8.78 \text{ mmol mol}^{-1}$  (Yellow River Estuary), averaging ( $\pm$ SD)  $4.62 \pm 1.25 \text{ mmol mol}^{-1}$ . Sex was not significantly relevant to the nucleus Sr/Ca ratios (Pearson correlation,  $r = -0.023$ ,  $p > 0.05$ ). Significant regional differences in otolith core Sr/Ca ratios were detected among locations (Kruskal-Wallis test,  $H_8 = 215.58$ ,  $p < 0.001$ ). The otolith core Sr/Ca ratios of the northern China population averaged  $5.36 \pm 1.17$  (range:  $3.13\text{--}8.78 \text{ mmol mol}^{-1}$ ), which was significantly higher than that of the southern China population (Kruskal-Wallis test,  $H_1 = 97.15$ ,  $p < 0.001$ ), which averaged  $4.05 \pm 0.98$  (range:  $2.43\text{--}6.89 \text{ mmol mol}^{-1}$ ) (Fig. 4). The Dunn's and Kruskal-Wallis multiple-comparisons tests indicated that the Sr/Ca ratios of *C. lucidus* from Haizhou Bay, averaging  $6.39 \pm 1.16$  (range:  $4.13\text{--}8.64 \text{ mmol mol}^{-1}$ ), were significantly higher than those of other sampling sites (Fig. 4). The Sr/Ca ratios of *C. lucidus* from the Minjiang River Estuary, averaging  $5.46 \pm 0.57$  (range:  $4.35\text{--}6.89 \text{ mmol mol}^{-1}$ ), were significantly higher than those of other samples in the southern China population (Fig. 4).

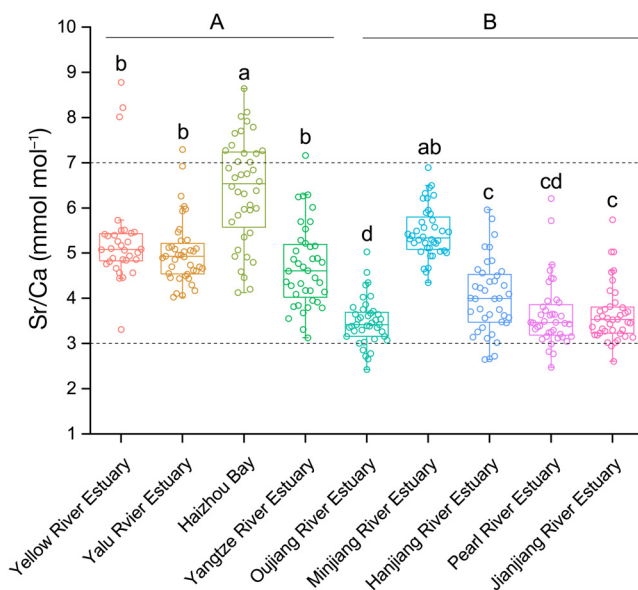


Fig. 4. Otolith nucleus elemental concentrations for spinyhead croaker *Collichthys lucidus* collected from Chinese coastal waters. The box plot represents 25th, 50th, and 75th percentiles. Significant differences ( $p < 0.05$ ) between sampling sites are indicated by different lowercase letters; significant differences ( $p < 0.05$ ) between north China population and south China population are indicated by different capital letters. Horizontal dash line: assumed threshold for high ( $\geq 7 \text{ mmol mol}^{-1}$ ), moderate ( $3\text{--}7 \text{ mmol mol}^{-1}$ ), and low ( $< 3 \text{ mmol mol}^{-1}$ ) Sr/Ca ratios

Of the total *C. lucidus* individuals sampled, 5.4% (19 of 352) showed high and 4% (14 of 352) showed low Sr/Ca ratios for the natal habitat; the rest (90.6%, 319 of 352 individuals) possessed moderate Sr/Ca ratios. In the northern China population, 12.5% (19 of 152 individuals) showed high Sr/Ca ratios for the natal habitat while the rest had moderate Sr/Ca ratios. The proportion of high Sr/Ca ratios ranged from 2.5 to 35% among the northern China locations, and the sample from Haizhou Bay had the highest proportion of high Sr/Ca ratios (35%, 14 of 40 ind.) (Fig. 1). In the southern China population, 7% (14 of 200 ind.) showed a low Sr/Ca ratio for the natal habitat; the rest had a moderate Sr/Ca ratio. The proportion of low Sr/Ca ratios ranged from 0 to 12.5% among the southern China locations, with 100% of the sample from the Minjiang River Estuary having a moderate Sr/Ca ratio (Fig. 1). The overall otolith-core results revealed a moderate Sr/Ca ratio for most *C. lucidus*; the small portions of fish having high and low Sr/Ca ratios were specific to the northern China and southern China populations, respectively.

## 4. DISCUSSION

Previous brackish-water catch surveys showed *Collichthys lucidus* to be an estuarine-dependent species (He & Li 1988, Zhang 1998, Zhang et al. 2010). In the present study, the sampled *C. lucidus* spent most of their lifetime with moderate otolith Sr/Ca ratios ( $3\text{--}7 \text{ mmol mol}^{-1}$ , typically  $\sim 5 \text{ mmol mol}^{-1}$ ). It can be deduced that moderate Sr/Ca ratios indicate a brackish-water life history, whereas high and low Sr/Ca ratios indicate hyperhaline waters and oligohaline waters, respectively, with the assumption that habitat salinity positively corresponds to the amount of Sr/Ca incorporated into the otoliths. Chang et al. (2004a) suggested reference values to denote marine, freshwater, and estuarine use by flathead grey mullet *Mugil cephalus* based on otolith Sr/Ca ranges (e.g.  $3\text{--}7 \text{ mmol mol}^{-1}$  for estuarine waters), which are also widely used for species of *Coilia* grenadier anchovies (Yang et al. 2006, Jiang et al. 2019). We are aware that our brackish water threshold of  $3\text{--}7 \text{ mmol mol}^{-1}$  is subjective and that its modification could influence interpretation of the natal habitat selection in *C. lucidus*. However, the 3 migration behaviors detected based on the results of the otolith transect line analysis were relatively different from each other, and modification of thresholds should not change the defined life history patterns.

In the 3 life history patterns of *C. lucidus* defined in the present study, we observed considerable within-pattern variation for some individuals. This variation was mainly characterized by the intense fluctuations at some life stages, likely due to the dynamic and transitory environmental processes in estuarine waters. In addition, the life history pattern for some Pattern 1 specimens (e.g. Figs. S2H,I,M) were not obviously distinguishable from Pattern 3 based on the present classification principle. The assignment of life history patterns through a quantitative approach, such as agglomerative hierarchical clustering performed by the 'TSclust' package (Montero & Vilar 2014) in R, might provide more quantifiable and objective results.

Among elements incorporated into the otolith, Sr/Ca and Barium (Ba)/Ca ratios are the most common markers used to reconstruct the environmental history of fish (Izzo et al. 2018). The incorporation of Ba into otoliths has been found to be inversely correlated with Sr in most studies (Tabouret et al. 2010, Magath et al. 2013, Izzo et al. 2018), but that was not observed in the present study (data not shown). The mechanism of Ba incorporation into the otolith of *C. lucidus* may be species-specific, and further study is necessary before it can be used as an environmental tracer. Laboratory rearing experiments with juvenile *C. lucidus* showed an optimum salinity range of 5–29 psu and an extreme salinity range of 2–42 psu (Shan et al. 2007). Secor & Rooker (2000) summarized that the regimes for fresh, estuarine, and marine water are 0–5, 5–25, and 25 psu, respectively. Therefore, the phases of high or low Sr/Ca concentrations in some otoliths in this study might be an indication that *C. lucidus* can hatch and develop for a short time in either a marine or freshwater environment before living in brackish water (Figs. 3C–F & S3–S4). In this case, the life history patterns of *C. lucidus* might be correctly classified as estuarine resident (Pattern 1), marine–estuarine migrant (Pattern 2), and freshwater–estuarine migrant (Pattern 3).

Most *C. lucidus* individuals in both the northern China and southern China populations showed a preference for brackish water (Pattern 1), and this finding is consistent with previous studies (He & Li 1988, Zhang 1998, Zhang et al. 2010, H. B. Liu et al. 2015). Interestingly, Pattern 2 and Pattern 3 were specific to the northern and southern populations, respectively, which were differentiated mainly in terms of their early life history. Individual fish can choose to disperse or remain resident early in life, and this decision is influenced by an array of factors including environmental conditions (e.g. tempera-

ture, food availability) (Peiman et al. 2017, Nevoux et al. 2019), water-flow conditions (Conroy et al. 2015), predation risk (Skov et al. 2011), and behavioral traits (Chapman et al. 2011c). However, the cause of divergent migration behavior among *C. lucidus* populations, as determined in this study, is still unknown. Diversity in migration behavior has been documented in many fish species, such as *Mugil* spp. (Chang et al. 2004b, Avigliano et al. 2021a), *Coilia* spp. (Yang et al. 2006, Jiang et al. 2019), and sticklebacks *Gasterosteus* spp. (Arai et al. 2020). This is the first report to demonstrate that the life history of *C. lucidus* is differentiated among populations in coastal China.

It is increasingly recognized that individuals within a population may differ simply because they encounter different environments or food webs during their earlier life stages, a phenomenon referred to as carryover effects (Conroy et al. 2015, Van Allen & Rudolf 2016, Saboret & Ingram 2019). Carryover effects occur in any situation in which an individual's previous history and experience explain their current performance in a given situation (O'Connor et al. 2014). For example, early life history characteristics could alter individual physiology or behavior, which subsequently influence the phenotype or performance of the individual with respect to bioenergetics and growth characteristics (Morinville & Rasmussen 2003, Gillanders et al. 2015, Gallagher et al. 2018). Moreover, divergent life history characteristics may enable each population contingent to uniquely contribute to the aggregate population dynamics, and this ultimately carries over to productivity, stability, and resilience at the population level (Kerr et al. 2010, Schindler et al. 2010).

The *C. lucidus* displaying Pattern 2 or Pattern 3 traits showed high or low Sr/Ca ratios, respectively, only during their early life history and did not return to similar waters during the rest of their lifetime, even during the reproduction period (wherein sexual maturity can be attained by age 1 yr). However, some Pattern 1 fish exhibited high or low Sr/Ca ratios during points in their history (Fig. 4A,H), though most of their lifetime was marked by moderate Sr/Ca ratios. This suggests that the migration pattern of *C. lucidus* is not determined by the pattern possessed by the parents. The planktonic eggs and early-stage larvae of *C. lucidus* are passively dispersed in a phase that lasts for ~25 d (Liu et al. 2018). Daily growth increments in the otoliths of larvae ranged from 7.4 to 16.2  $\mu\text{m}$  (Ou et al. 2012), which would not entirely cover the early life stage of the high or low Sr/Ca ratios. Thus, the entire passive dispersal phase would



be indicated in an otolith width of 185–405  $\mu\text{m}$ ; however, our results show the life history with a high or low Sr/Ca ratio was indicated in wider otolith widths of 340–500  $\mu\text{m}$  (Pattern 2 fish) or 600–1400  $\mu\text{m}$  (Pattern 3 fish), respectively. This result indicates that *C. lucidus* is able to live in hyperhaline or oligohaline environments during not only the larval and post-larval stages, but also sometimes into the juvenile stage.

H. B. Liu et al. (2015) found that *C. lucidus* in the Yangtze River Estuary showed high Sr concentrations in the otolith cores ( $\geq 7 \text{ mmol mol}^{-1}$  in 93.3% of 15 specimens), indicating that they might prefer to spawn in seawater habitats; interestingly, the proportion of specimens with a high Sr/Ca ratio was obviously lower (2.5%) in the present study, even though both studies sampled from the same estuary. However, compared to the present study, H. B. Liu et al. (2015) examined a longer radius from the core (90 vs. 25  $\mu\text{m}$ ), used a different method of analysis (EMPA with transect line analysis vs. LA-ICP-MS with spot analysis), and involved different sampling generations/years, which may have contributed to this phenomenon; therefore, further investigations are needed for confirmation. Furthermore, *C. lucidus* was found to spawn principally in estuarine waters at the time of large flood tides (salinity  $\sim 25$  psu) in the Feiyunjiang River Estuary (Shan et al. 2006), which encompasses the southern China population. Thus, the minor fraction of *C. lucidus* with a hyperhaline or oligohaline spawning pattern might be neglected by empirical observations.

Analyses of otoliths to determine the natal habitat of *C. lucidus* showed generally moderate Sr/Ca ratios across sampling sites and populations. However, the proportion of Sr/Ca ratios categorized as moderate is changeable with artificial threshold values. As mentioned, otolith elemental concentrations are influenced by environmental (e.g. salinity and temperature) (Chang et al. 2004a, Izzo et al. 2018), physiological (e.g. ontogeny, growth, and reproduction) (Sturrock et al. 2015), and genetic factors (Clarke et al. 2011, Barnes & Gillanders 2013). The northern China population showed significantly higher Sr/Ca ratios than the southern China population of *C. lucidus*, which may indicate that the Sr concentrations in the otoliths are relatively influenced by intrinsic factors (i.e. genetics) in this species. Two previous studies had reported genetic differences (stock or population differences) in otolith chemistry for Atlantic silver-side *Menidia menidia* (Clarke et al. 2011) and mullet *Argyrosomus japonicus* (Barnes & Gillanders 2013), but the mechanism was not clear. The average natal Sr/Ca ratio was significantly higher in fish from

Haizhou Bay compared to fish from the estuary locations, possibly implicating the generally higher salinity caused by insufficient freshwater flow in that area.

## 5. CONCLUSIONS

Chronological analysis of otolith microchemistry in *Collichthys lucidus* from the coast of China revealed 3 life history patterns, with the species variously using estuarine, hypersaline, or oligosaline waters during their early life history. Estuarine waters were the most common natal habitat selected by *C. lucidus*; the otolith Sr/Ca ratios showed that individuals spent most of their lifetime in brackish water. The migration behaviors of a small proportion of individuals were differentiated between the northern China and southern China populations. Owing to a lack of elemental analysis of water samples from the sampling environments to validate the otolith Sr concentrations, the results obtained in this study could not clearly detect movement between environments. Therefore, laboratory validation of these environmental effects (especially for salinity) on the incorporation of trace elements in otoliths would improve the application of otolith microchemistry to ecological studies in the wild. Further studies with more extensive sampling will be necessary to better explain these life history details and determine how common the different migratory behaviors might be within this widespread species. Expression of diverse life history tactics may be advantageous to an estuarine-dependent fish, such as *C. lucidus*, as a means of offsetting environmental variability and ensuring the persistence of populations. However, the diverse life history (partial migration) of *C. lucidus* among populations presents a complication for the management of this exploited species because overexploitation itself might decrease the diversity of the species.

*Acknowledgements.* We are grateful to Yvette Heimbrand for her assistance with the analysis of the otolith-transect-line data and to Yang Xiao for his assistance with the LA-ICP-MS experiment and data pre-processing. We thank Cynthia Kulongowski from Liwen Bianji (Edanz) ([www.liwenbianji.cn/](http://www.liwenbianji.cn/)) for editing the English text of a draft of the manuscript. This work was supported by the National Key Research and Development Program of China (2018YFD0900902), the Key Special Project for Introduced Talents Team of Southern Marine Science and Engineering Guangdong Laboratory (GML2019ZD0605), and the Central Public-interest Scientific Institution Basal Research Fund, South China Sea Fisheries Research Institute, CAFS (2019TS26 and 2020TD05).

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Editorial responsibility: Helmut Segner,  
Bern, Switzerland  
Reviewed by: 3 anonymous referees

Submitted: February 1, 2022  
Accepted: May 18, 2022  
Proofs received from author(s): July 9, 2022