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Otolith microchemistry reveals the migration patterns of the flathead grey mullet *Mugil cephalus* (Pisces: Mugilidae) in Korean waters

Seung Eun Bae and Jin-Koo Kim*

Abstract

Background: The flathead grey mullet *Mugil cephalus* has the widest distribution among mugilid species. Recent studies based on mitochondrial DNA sequences showed that the species comprises at least 14 different groups, three of which occur in the northwest Pacific. We analyzed the otolith microchemistry of *M. cephalus* at several locations in Korea to improve understanding of migration pattern and population origin.

Results: We collected 123 sagittal otoliths from seven locations and determined their concentrations of eight elements (^7Li , ^{24}Mg , ^{55}Mn , ^{57}Fe , ^{60}Ni , ^{63}Cu , ^{88}Sr , and ^{138}Ba) using laser ablation inductively coupled plasma mass spectrometry. Mean otolith elemental ratios differed significantly among the locations. The Sr:Ca, Fe:Ca, and Ba:Ca ratios were significantly higher than others, and useful chemical signatures for investigating the habitat use of *M. cephalus* populations. We identified five diverse and complicated migration patterns using the otolith data that we collected: estuarine resident (type I), freshwater migrant (type II), estuarine migrant (type III), seawater resident (type IV), and seawater migrant (type V). A canonical discriminant analysis plot revealed separation of two groups (type II in the Yellow Sea vs. other types in remaining locations). Two locations on Jeju Island, despite their close proximity, had fish with quite different migration patterns, corroborating previous molecular studies that distinguished two groups of fishes.

Conclusion: We successfully showed that the migration patterns of the Korean mullet varied by location. Only fish from the western sector of Jeju had a unique migration pattern, which is likely confined population in this area. Among the eight otolith elements measured, the Sr:Ca ratio was found to be the best indicator of migration pattern and population origin.

Keywords: *Mugil cephalus*, Otolith microchemistry, Migration pattern, Korea, Population origin

Background

Improved understanding of marine fish population dynamics requires (i) the identification of ecologically different populations and (ii) a better knowledge of the life histories of individual fish in coastal and oceanic habitats (Yamane et al. 2012). It is difficult to predict the migration patterns of anadromous and estuarine fishes because of

the variability in seasonal, ontogenetic, and sex-related movements among individuals within populations (Secor et al. 1995). Many techniques have been developed for tracking fish movements and discerning connectivity, including natural biological tags (chemical, genetic, and parasitic) and artificial tags (acoustic, artificial chemistry, and archival tags) (Elsdon et al. 2008). Despite advances in external tagging, including acoustic tagging, radio tagging, and satellite telemetry, its application is often limited by budget, battery life, low rates of return, and size

* Correspondence: taengko@hanmail.net

Department of Marine Biology, Pukyong National University, 45 Yongso-ro, Nam-Gu, Busan 48513, Korea



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constraints; observations have been largely restricted to the adult phases of top predators (Elsdon et al. 2008; Sturrock et al. 2012).

Otolith microchemistry has recently provided increasingly important signals for reconstructing and tracking the environmental histories of fish. Otolith composition remains unchanged after deposition, and the chemical signals in these structures act as a historical record of environmental conditions (Campana 1999; Campana and Thorrold 2001; Miller et al. 2005; Sturrock et al. 2012). Otoliths are usually composed of calcium carbonate mineralized within a protein matrix. They grow daily and store minor and trace elements during biomineralization processes (Campana 1999). The deposition of otolith carbonate may be regulated by a range of factors, such as age, physiology, environmental stress, food availability, ambient temperature, diurnal and seasonal cycles, and the movement of individual fishes (Radtke and Shafer 1992). Because of these effects, otolith microchemistry can provide important data on migratory behavior and environmental factors. The level of gene flow can also be discerned when these data are combined with information on neutral genetic makers.

Mugil cephalus is a cosmopolitan euryhaline fish that is distributed in coastal, lagoonal, and estuarine waters between latitudes 42° N and 42° S. Recent studies have shown that the species comprises at least 14 different sub-groups, three of which exist in Taiwan. Shen et al. (2011) showed that the three groups are reproductively isolated, and that gene flow is therefore restricted. Appropriate conservation and management of species require information on the origins of each population and the connectivity among nursery areas. Previous investigations have revealed the life history cycle of *M. cephalus* and the diverse aquatic environments that the fish occupy at different life cycle stages. Some individuals remain in an environment of uniform salinity for extended periods of time (residents), while others regularly move among environments of differing salinities (migrants) (Chang et al. 2004; Wang et al. 2010; Fowler et al. 2016). It was recently shown that *M. cephalus* has more diverse migratory patterns than previously realized; estuarine resident, freshwater migrant, estuarine migrant, and seawater resident patterns have been identified (Fortunato et al. 2017). The estuarine-dependent populations have patterns of dispersal, retention, or physiological preference within specific salinity ranges; salinity may act directly or indirectly on controlling migration (Secor and Rooker 2000).

Although three genetic groups of *M. cephalus* in Taiwan have overlapping distribution ranges, they may have different patterns of migration and habitat usage among different coastal environments, reflecting adaptation across a wide range of environmental conditions

(Chang et al. 2004; Ke et al. 2009; Wang et al. 2010). Korean ocean waters have a complexity of structures and currents flows across time and space. Seasonal changes in environmental parameters in particular locations may influence gene flow patterns and the population structure of marine organisms (Kim et al. 2017; Bae et al. 2020a). Two genetic groups of *M. cephalus* have recently been identified in Korean waters. Gene flow between the groups is restricted, suggesting that they may be reproductively isolated (Bae et al. 2020b).

In the current study, we aimed to answer the following questions: (i) does otolith elemental composition vary significantly by geographic location? and (ii) is the genetic grouping of *M. cephalus* related to previously described migration patterns?

Materials and methods

Sample and otolith preparation

A total of 123 individuals were collected from seven locations in Korean waters (Fig. 1). The samples were collected by fishing, fishing nets, and local fish markets between 2017 and 2019: Yangyang (YY, $n = 16$, 290–340 mm in TL) in the East Sea, Busan (BS, $n = 19$, 187–317 mm in TL), Yeosu (YS, $n = 21$, 210–242 mm in TL), Wando (WD, $n = 20$, 375–535 mm in TL) in the Korean Strait, Jungmoon (JM, $n = 13$, 172–393 mm in TL), and Hangyeong (HG, $n = 20$, 53–75 mm in TL) off Jeju Island, and Mokpo + Gunsan (MP + GS, $n = 14$, 387–452 mm in TL) in the Yellow Sea. Prior to specimen preservation, sagittal otoliths were extracted and stored in deionized water or 95% ethanol; the elemental composition and structure of otoliths are not strongly affected by ethanol (Proctor and Thresher 1998). The right side of the otolith from all fish was embedded separately in epoxy resin and sectioned in the transverse plane using a saw fitted with a diamond-coated blade. Individual otolith sections were then polished with 1200 and 3400 silicate abrasive papers to expose the cores. The otoliths were photographed using a digital camera.

Otolith elemental analysis

Otoliths were analyzed for the concentrations of nine elements (^7Li , ^{24}Mg , ^{43}Ca , ^{55}Mn , ^{57}Fe , ^{60}Ni , ^{63}Cu , ^{88}Sr , and ^{138}Ba) by laser ablation inductively coupled plasma mass spectrometry. Nine elements were known as the most likely abundant and informative elements to serve as environmental tags indicators (Campana 2005; Moreira et al. 2018). These elements were routinely used to infer past location in fish (Li, Mg, Mn, Cu, Sr, and Ba) and to serve as environmentally influenced stock markers (Ni and Fe) (Campana 2005; Sturrock 2012). Among them, hard acid ions such as Li, Mg, Ca, Sr, and Ba typically have a residence time longer than the mixing time of the ocean and

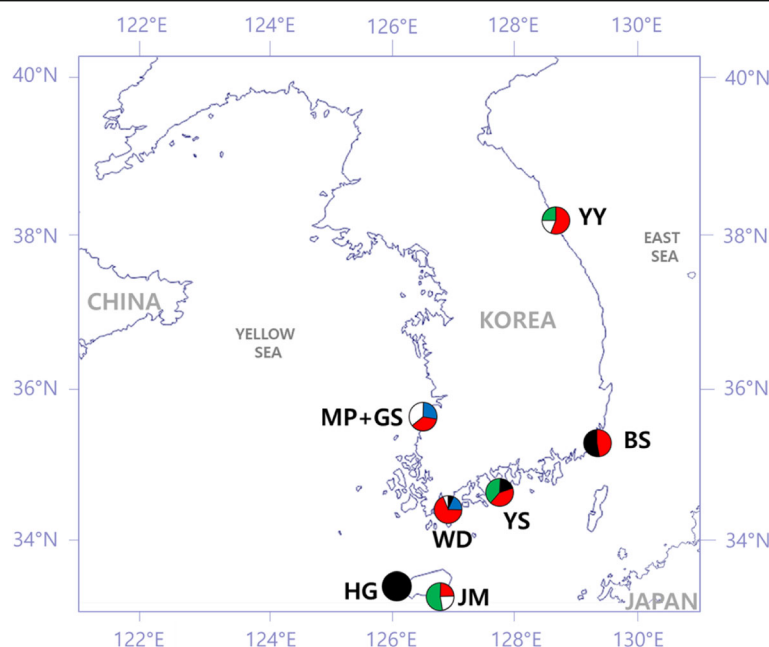


Fig. 1 Locations of the seven sampling sites in Korean waters. YY, Yangyang; BS, Busan; YS, Yeosu; WD, Wando; MP + GS, Mokpo+Gunsan; JM, Jungmoon off Jeju Island; HG, Hangyeong off Jeju Island. Pie charts represent the proportional frequencies of migration patterns. Type I (estuarine resident) is identified by black coloring and type II (freshwater migrant) by blue. Type III (estuarine migrant) and type IV (seawater resident) are identified by red and white, respectively. Type V (seawater migrant) is identified by green coloring

consequently, their concentrations tend to vary with salinity. On the other hand, soft and intermediate acid ions such as Cu and Mn are relatively weak, and they have characteristics making soft elements reactive and readily removed from seawater (Sturrock 2012). The laser spot energy density was set by the pulse frequency rate (10 Hz), beam diameter, and ablation rate. All elemental concentrations were standardized against the National Institute of Standards and Technology 612 glass standards (Pearce et al. 1997). The concentrations of all elements in the otoliths were transformed to element:Ca ratios. Microchemical concentrations were expressed as molar or micro ratios.

Statistical analyses

We used IBM SPSS Statistics version 22 (IBM Corp, Armonk, NY, USA), and the JMP software (Jones and Sall 2011) to identify statistically significant differences, and all element:Ca ratios were log-transformed for the statistical analyses. The measuring area of each otolith spanned the zone from the otolith central core to 1000 μm toward the perimeter. This area may include the early life history period of *M. cephalus*. Data were collected from the corresponding distances of the elemental profiles. Each element:Ca ratio was compared among sampling sites using the non-parametric Kruskal–Wallis test, because the elemental compositions of

the otolith core region were not normally distributed, and the variance was not homogeneous among locations. We used Bonferroni correction with Kruskal–Wallis test to obtain a 0.05 level of significance. Pearson's correlation analysis was used to examine the relationships between the elemental ratios in the otoliths. CDA (canonical discriminant analyses) were used to assess the ability of otolith elemental ratios to identify the origin of each population.

As previously suggested by Fortunato et al. (2017), we classified the migration pattern for each specimen based on the Sr:Ca ratio. An Sr:Ca ratio $< 3 \times 10^{-3}$ mmol/mol indicated a freshwater origin, that between 3×10^{-3} and 7×10^{-3} mmol/mol indicated an estuarine origin, and that $> 7 \times 10^{-3}$ mmol/mol indicated a marine origin. Canonical discriminant analyses were also performed to verify the correct assignment of individuals to migration patterns.

Results

Elemental otolith microchemistry

The average values and deviations of otolith element:Ca ratios in the zone from the otolith central core to 1000 μm toward the perimeter are listed in Table 1. All of the ratios varied significantly among locations (Kruskal–Wallis test, $P < 0.05$; Table S1). Some of the correlations between elemental ratios were significant (Pearson correlation analysis, $P < 0.05$, Table 2). The correlation between

Table 1 Means and standard deviations for *Mugil cephalus* otolith element:Ca ratios in the zone from the otolith central core to 1000 μm toward the perimeter according to location in Korea

Location	N	Li:Ca	Mg:Ca	Mn:Ca	Fe:Ca	Ni:Ca	Cu:Ca	Sr:Ca	Ba:Ca
YY	16	1.082 \pm 0.156	0.068 \pm 0.011	0.018 \pm 0.017	0.220 \pm 0.013	3.081 \pm 0.510	4.039 \pm 2.491	6.400 \pm 0.848	0.036 \pm 0.026
BS	19	2.458 \pm 0.576	0.099 \pm 0.024	0.015 \pm 0.011	0.414 \pm 0.077	4.949 \pm 0.491	10.621 \pm 5.697	5.494 \pm 0.715	0.060 \pm 0.037
YS	21	1.040 \pm 0.216	0.095 \pm 0.019	0.008 \pm 0.003	0.284 \pm 0.021	3.387 \pm 0.199	4.043 \pm 2.943	5.564 \pm 0.995	0.043 \pm 0.034
WD	20	2.782 \pm 1.570	0.138 \pm 0.042	0.051 \pm 0.050	0.319 \pm 0.030	4.706 \pm 0.484	6.073 \pm 2.254	4.804 \pm 1.358	0.051 \pm 0.042
JM	13	0.948 \pm 0.307	0.093 \pm 0.021	0.008 \pm 0.004	0.248 \pm 0.055	3.857 \pm 0.697	3.801 \pm 1.563	7.043 \pm 0.782	0.063 \pm 0.049
HG	20	3.763 \pm 4.434	0.136 \pm 0.116	0.005 \pm 0.002	0.300 \pm 0.051	5.151 \pm 2.719	4.899 \pm 1.725	4.435 \pm 0.424	0.013 \pm 0.003
MP + GS	14	1.253 \pm 0.525	0.098 \pm 0.029	0.050 \pm 0.089	0.231 \pm 0.029	3.736 \pm 1.106	6.051 \pm 6.892	5.672 \pm 1.886	0.035 \pm 0.039

YY Yangyang, BS Busan, YS Yeosu, WD Wando, JM Jungmoon in Jeju Island, HG Hangyeong in Jeju Island, MP + GS Mokpo+Gunsan

the ratios Fe:Ca and Cu:Ca showed a significantly positive relationship ($r = 0.453$, $P < 0.01$), whereas the Sr:Ca ratio was significantly negatively correlated with the Mn:Ca and Ba:Ca ratios ($r = -0.282$ and -0.280 , respectively, $P < 0.01$, Table 2).

The first axis of the CDA explained 61.1% of the total variation. The major discriminant factor in the first axis (CAN1) was the Fe:Ca ratio (eigenvalue = 3.301) (Table S2). The first axis contributed especially toward discriminating between locations BS, WD, or HG and the remaining four (Fig. 2). The second canonical function explained the remainder of the dispersion in the data; 28.4% of the variation in the second axis (CAN2) was attributed to differences between BS and HG (Table S2, Fig. 2). The main discriminant factor in the second axis was the Ba:Ca ratio. The rate of location reclassification ranged from 42.9% (MP + GS) to 95.0% (HG). Therefore, HG and BS were distinct from the other locations in terms of the Fe:Ca and Ba:Ca ratios based on the first and second discriminant axis.

Migration patterns

Otolith concentrations of Sr and Ba can provide information on habitat and migration patterns over the lifetime of individual fish. The Sr:Ca ratio ranged from 4.43 (HG) to 7.04 mmol/mol (JM) (Table 1). We detected five

migration patterns based on these ratios (Fig. 3). Type I refers to residing in an estuarine environment exclusively (estuarine resident); type II refers to migration from a freshwater habitat during early life to an estuarine or seawater habitat during adulthood (freshwater migrant); type III refers to migration from an estuarine environment during early life to seawater later (estuarine migrant); type IV refers to residing in a marine habitat exclusively (seawater resident); and type V refers to migration from a seawater habitat during early life to estuarine waters later (seawater migrant).

The otolith microchemistries of most locations were indicative of the type III migration pattern (estuarine migratory). The type II pattern was least common, occurring only at WD in the western Korea Strait and at MP + GS in the Yellow Sea (Table 3). Most locations exhibited more than two migratory patterns, whereas HG exhibited only the type I pattern (estuarine resident) (Table 3, Fig. 1). CDA showed that individuals of each type were accurately assigned to the original type, with > 50% accuracy. Type IV had the highest proportion of correct assignments (> 90%), and type III had the lowest proportion (57.9%) (Table 4). The CDA plot showed a clear separation of two groups (type II vs. other types) based on the first discriminant axis (Fig. 4). The variable

Table 2 Pearson correlation coefficients for the relationships among eight elemental ratios in the otoliths of *Mugil cephalus* collected from seven locations in Korean waters

	Li:Ca	Mg:Ca	Mn:Ca	Fe:Ca	Ni:Ca	Cu:Ca	Sr:Ca	Ba:Ca
Li:Ca								
Mg:Ca	0.154							
Mn:Ca	0.020	0.179*						
Fe:Ca	0.124	0.164	0.019					
Ni:Ca	0.312**	0.122	0.001	0.378**				
Cu:Ca	0.044	0.119	0.107	0.453**	0.278**			
Sr:Ca	-0.245**	-0.175*	-0.282**	-0.244**	-0.114	-0.015		
Ba:Ca	-0.193*	0.020	0.370**	0.101	-0.079	0.038	-0.280**	

* $P < 0.05$

** $P < 0.01$

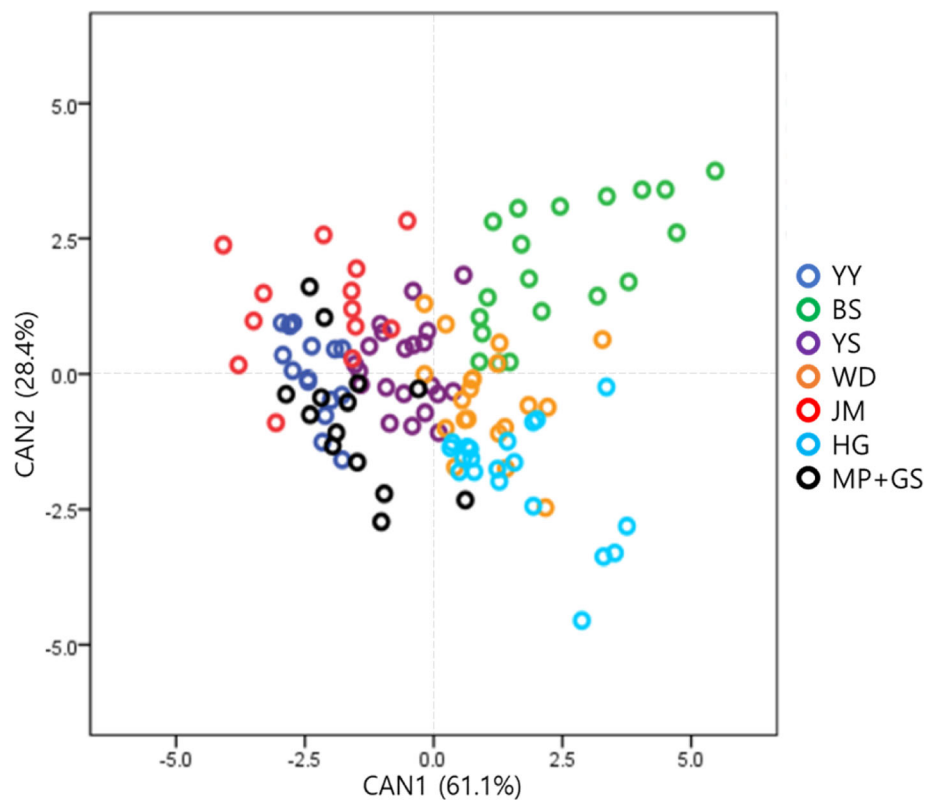


Fig. 2 Two-dimensional canonical discriminant analysis plot of seven Korean locations based on the otolith microchemistry of *Mugil cephalus*. CAN1 and CAN2 are the first and second axes of the analysis. The percentages in parentheses are the proportions of total variation explained by each of the two axis. YY, Yangyang; BS, Busan; YS, Yeosu; WD, Wando; MP + GS, Mokpo+Gunsan; JM, Jungmoon in Jeju Island; HG, Hangyeong in Jeju Island

that best explained the first axis variation was the Sr:Ca ratio (eigenvalue = 2.765, Table S3).

Discussion

Spatial variation in otolith microchemistry

The elemental concentrations in otoliths differed significantly among locations. These concentrations are strongly related to the chemical compositions of the environment in which individuals reside during a particular period of time (Campana 1999; Campana and Thorrold 2001). The ratios of Ba, Fe, Cu, Ni, Mn, and Sr are correlated with environmental indicators such as salinity (Campana 1999; Chang et al. 2012; Daros et al. 2016). In particular, Sr and Ba concentrations are negatively correlated with salinity (Campana 1999; Elsdon and Gillanders 2005; Wang et al. 2010). We found that Sr and Ba were negatively correlated ($r = -0.280$, $P < 0.01$), in line with previous studies. In our CDA analysis, HG and BS were distinct from the other locations in terms of the Fe:Ca and Ba:Ca ratios measured in otoliths, suggesting that HG and BS are relatively heterogeneous in their chemical compositions. Three elemental ratios, including Fe:Ca, previously measured in the otoliths of juvenile pelagic shortbelly

rockfish (*Sebastes jordani*) were used to discriminate among the populations residing in different water masses; these otolith signatures were good predictors of water mass residency (Nishimoto et al. 2010). *Dicentrarchus labrax* specimens living at two different locations had distinct otolith concentrations of some elements; elevated concentrations Fe and Mn in these otoliths may reflect the natural release of trace metals from sediments into seawater (Traina et al. 2015). High concentrations of Fe may be attributed to the presence of large quantities of organic particulate matter introduced by rivers or terrestrial runoff. We found that otolith Sr:Ca, Ba:Ca, and Fe:Ca ratios are useful natural markers for distinguishing among *M. cephalus* specimens from diverse environments.

In our study, the Sr:Ca and Ba:Ca ratios were highest at JM (southern Jeju Island) and lowest at HG (western Jeju Island). Jeju Island is directly influenced by range of ocean currents and water mass movements, such as the Kuroshio Current, Taiwan Current, Changjiang diluted water (CDW) of the East China Sea, yellow bottom water, and river inflows to the South Sea. All of these flows are subject to large seasonal variations (Ko et al. 2007; Lie and Cho 2016; Lim et al. 2017). The Tsushima

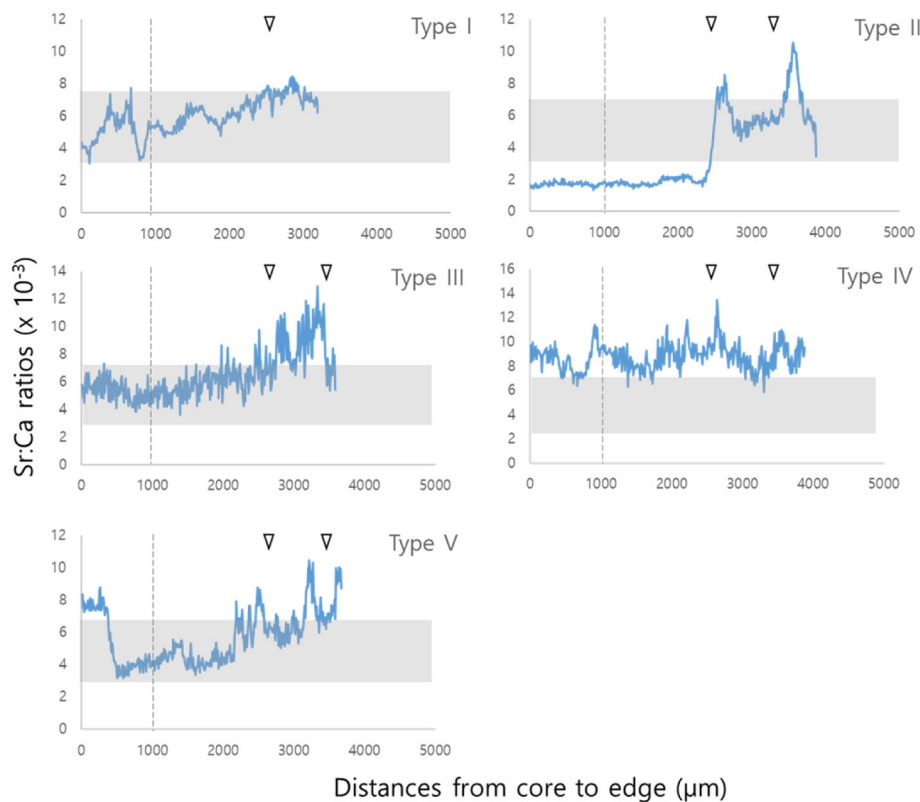


Fig. 3 Five migration patterns of *Mugil cephalus* inferred by the Sr:Ca ratios in the zone spanning from the otolith core to 1000 μm toward the perimeter. Data were collected from seven locations in Korean waters. The gray horizontal bar shows the critical levels for the environmental limits based on water salinity (following Chang et al. 2004). Type I, estuarine resident; type II, freshwater migrant; type III, estuarine migrant; type IV, seawater resident; type V, seawater migrant. White down-pointing triangle indicates the otolith annual ring. Distances refer to the span (in micrometer) from the otolith core the perimeter

Current and Cheju Warm Current, which are branches of the Kuroshio Current, contain warm waters with salinities; they are the major flows affecting the formation of water masses around Jeju Island. In winter, a tongue-shaped thermohaline front forms between the Cheju Warm Current and coastal waters (Lie et al. 2009;

Hwang et al. 2014). However, the northeastward spreading of the Changjiang flow brings diluted low salinity water to the western side of Jeju Island in summer (Lie and Cho 2016; Lim et al. 2017). Thus, there are large differences in water salinity between summer and winter off Jeju Island, and the annual salinity values are higher off the eastern coast of Jeju Island and in the East Sea than off the western coasts of this island (Park et al. 2015). Furthermore,

Table 3 The occurrence of five *Mugil cephalus* migration patterns at seven sites, inferred from Sr:Ca ratios in the zone spanning the otolith core to 1000 μm toward the perimeter

	YY	BS	YS	WD	JM	HG	MP + GS	Total
Type I	0	9	4	1	0	20	0	34
Type II	0	0	0	4	0	0	4	8
Type III	9	10	9	14	3	0	5	50
Type IV	3	0	0	1	3	0	5	12
Type V	4	0	8	0	7	0	0	19

YY Yangyang, BS Busan, YS Yeosu, WD Wando, JM Jungmoon in Jeju Island, HG Hangeyeong in Jeju Island, MP + GS Mokpo+Gunsan

Type I estuarine resident, Type II freshwater migrant, Type III estuarine migrant, Type IV seawater resident, Type V seawater migrant

The proportions of the correct classification determined by canonical discriminant function analysis are presented in Fig. 1

Table 4 The correct classification rate of the canonical discriminant analysis of otolith for each migratory pattern. Number of individuals which included in original patterns are shown in brackets

	Type I	Type II	Type III	Type IV	Type V	Total
Type I	76.5	2.9	20.6			34 (26)
Type II	25.0	75.0				8 (6)
Type III	18.0	2.0	60.0	6.0	14.0	50 (30)
Type IV				91.7	8.3	12 (11)
Type V			15.8	26.3	57.9	19 (11)

Type I estuarine resident, Type II freshwater migrant, Type III estuarine migrant, Type IV seawater resident, Type V seawater migrant

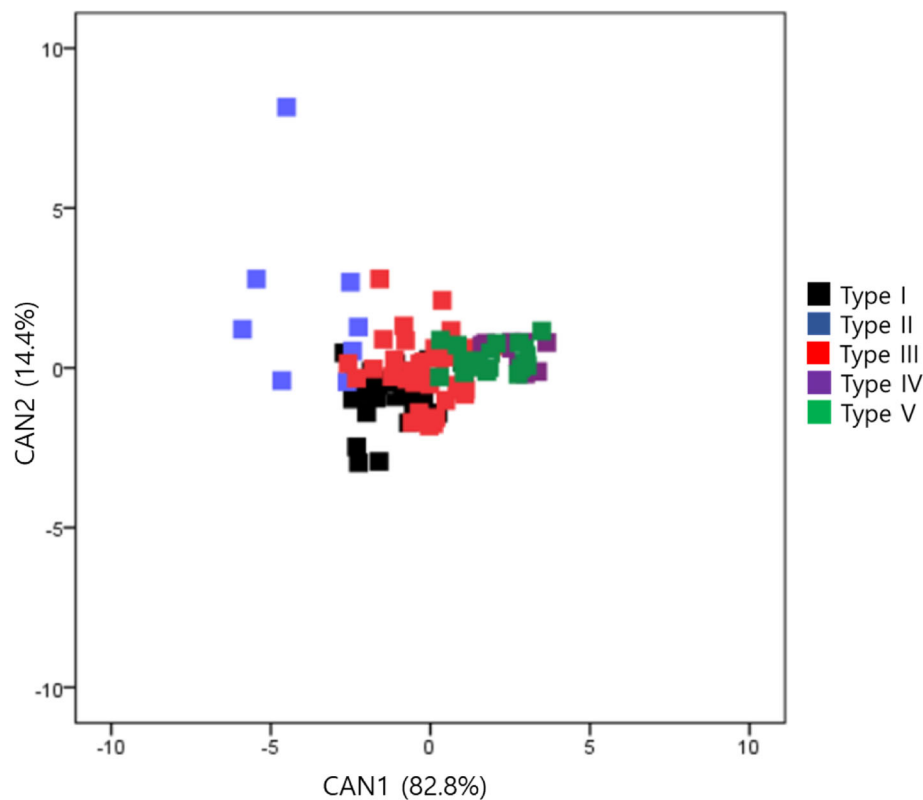


Fig. 4 Two-dimensional canonical discriminant analysis (CDA) plot (first and second canonical axes included) of five *Mugil cephalus* migration patterns based on otolith microchemistry. Type I, estuarine resident; type II, freshwater migrant; type III, estuarine migrant; type IV, seawater resident; type V, seawater migrant. The percentages in parentheses are the proportions of total variation explained by each of the two axis

temperature, salinity, and the dissolved oxygen concentration vary among locations and seasons. Temperature also significantly affects the incorporation of Sr and Ba into the otoliths of larval Pacific cod (DiMaria et al. 2010). Overall, environmental parameters and their seasonal variability at each location appear to affect the incorporation of elements into the otoliths of individual fishes.

The influence of environmental factors on migratory patterns

Our study provided the first evidence for the five migratory patterns in Korean *M. cephalus*. The variation in migratory patterns among individuals was reflected in the measured Sr:Ca ratios, which revealed diversity in habitat use and migration over the lifetime of different individuals.

Our CDA analysis showed that the type II migration pattern was distinguished from others based on the Sr:Ca ratio, suggesting that *M. cephalus* in the Yellow Sea (MP + GS) and the western Korea Strait (WD) (fish migration patterns at both sites were classified as type II) may have a migration pattern distinct from those in other locations. Type II fish are freshwater migrants that prefer low-salinity and freshwater habitats during early

life. According to Chang and Iizuka (2012), adults of mugilids can migrate to freshwater environments to avoid competition, which suggests the existence of specific ecological niches. In Taean, adults of *M. cephalus* tend to be collected, indicating that the larvae stayed in estuarine or freshwater and then migrate to the coastal water after they reach sexual maturity (Hong et al. 2014). Therefore, WD and MP + GS may have a similar migration pattern. This strong freshwater effect was not evident in other migration types. There are major freshwater inputs into the Yellow Sea (Han, Geum, and Yeongsan Rivers). Furthermore, the flow of the low-salinity Korean Coastal Currents changes seasonally along Korean coastlines (Yang and Youn 2007; Hwang et al. 2014). According to Park et al. (2017), when compared to spatiotemporal distribution characteristics of salinity in the coastal waters of Korea, the salinity was relatively lower off the western coasts, which have a greater discharge of freshwater and high tide than the eastern coasts throughout the year (Fig. S1). In addition, the salinity variability between 2017 and 2019 showed similar tendency (Fig. S2), indicating that these variabilities of salinity in coastal waters may have the correlation with Sr:Ca ratios. These particular environmental

characteristics may be related to fish migration patterns and population structures. Many previous studies have shown that the diverse ocean currents and water masses around Korea may affect the population structures of marine fish (Kim et al. 2017; Bae et al. 2020a). For example, *Takifugu niphobles* comprises two genetic groups that are geographically separated (Yellow Sea vs. East Sea + Korea Strait). This may be evidence of gene flow restriction between two groups mediated by oceanographic processes that have promoted local environmental adaptation, which is expressed through different habitat uses (Bae et al. 2020a).

Our study identified for the first time a seawater migrant pattern in which fish moved from marine waters to estuaries during the early life stages, followed by irregular movements between estuarine and offshore waters during later life. The seawater migrant pattern was very frequent at JM off the southern coast of Jeju Island. The estuarine resident pattern was most frequent at HG on the western shore of Jeju Island. The complex spawning behavior of *M. cephalus* is related to water column height and salinity changes with temperature (Ibáñez and Gutierrez-Benitez 2004). As mentioned, these different migration patterns may be influenced by the oceanic currents around Jeju Island. In particular, the southern coastal waters may be affected by complex hydrographic factors, such as submarine groundwater discharge, streams near the Chenjiyeon and Jeongbang waterfalls (Lee and Kim 2007, Yoon 2016; Kwon et al. 2018), and/or the high-temperature/high-salinity Tsushima Warm Current (Choi et al. 2008). Furthermore, the western and southern coasts of Jeju Island are dominated by different combinations of salinity and temperature (low salinity and low temperature vs. high salinity and high temperature), a difference that is expressed in the community structures of phytoplankton (Lee et al. 2009; Kwon et al. 2018) and fish (Choi et al. 2008). Thus, these seasonal and spatial variations in environmental parameters could be important factors in population structuring and the habitat selection of individuals.

Inferring population structure and origin

We found that *M. cephalus* individuals in most locations showed a variety of migratory patterns, which may indicate a mixture of multiple spawning populations. Previous studies also identified mixtures of migratory and resident *M. cephalus* near Taiwan, thereby demonstrating the existence of multiple cohorts and/or specific ecological features in *M. cephalus* (Chang et al. 2000, 2004; Ke et al. 2009; Wang et al. 2010; Chang and Iizuka, 2012). Wang et al. (2011) showed that *M. cephalus* can be divided into three types: marine, brackish water, and freshwater types, as revealed by temporal changes in otolith microchemistry. We found that the brackish type

was predominant and the freshwater type rare (0.07%), suggesting the existence of potential population structures originating from different nursery grounds. In most of the locations we evaluated, *M. cephalus* had estuarine-origin and migratory patterns, indicating that the species tends to move into estuaries during early life. After the larvae passively drift into estuaries, the juveniles undergo physiological and morphological shifts and experience changes in a gradient of environmental factors as they transition toward the nursery habitat (Hsu et al. 2009; Zydlewski and Wilkie 2012). The juveniles of *M. cephalus* are generally very dependent on freshwater and oligohaline habitats, because living in a fully marine habitat would require a large energy expenditure for osmoregulation. Adults migrate to optimal-salinity habitats to benefit from the lowest energy expenditure and highest growth rate (Cardona 2000; Fazio et al. 2013; Wang 2014; Gorski et al. 2015). Based on otolith annual rings described by Zhang et al. (2011), most of the types in our study became apparent over 2 years, revealing a high rate of residing in the estuaries and in seawater during aging. Our findings were concordant with those of Chang et al. (2004), showing that adult *M. cephalus* tend to migrate to higher-salinity offshore waters as they grow.

Chemical environments vary among different natal areas, and juvenile *M. cephalus* can be expected to show distinct chemical signatures representative of their natal habitats (Morrison et al. 2016). We showed that type III was the dominant migration pattern in Korean *M. cephalus*, and this finding suggests that populations may share nursery grounds. However, *M. cephalus* specimens from HG (western sector of Jeju Island) were characterized only as type I (estuarine resident) and had lower elemental ratios (Sr:Ca and Ba:Ca) compared with those found in other locations. This indicates that the population may be confined to HG. Similarly, the different microchemical ratios (Li, Mg, and Mn) in *Thunnus orientalis* otoliths indicate that the populations are divided into two potential nursery areas (East Sea + East China Sea vs. Pacific Ocean) (Rooker et al. 2001). We found two migration patterns off Jeju Island (migratory in JM and resident in HG). The spatial and temporal differences in spawning migration patterns can also affect the genetic structure of *M. cephalus* (Ke et al. 2009; Shen et al. 2011, 2015). Mitochondrial DNA sequences showed that *M. cephalus* in Korean waters comprises two groups (*Mugil* sp. C, NWP1 and *Mugil* sp. I, NWP2), and these two groups coexist only off Jeju Islands (Bae et al. 2020b). These genetic findings are concordant with our results showing the presence of two potential populations. Both otolith microchemistry and molecular markers have been used recently to identify unique population structural characteristics

(Miller et al. 2005; Liu et al. 2010; Collins et al. 2013; Taillebois et al. 2017). Therefore, the migration patterns we detected may indicate multiple origins of *M. cephalus* in Korean waters.

Conclusion

The otolith Sr:Ca ratios that we measured revealed five migration patterns among *M. cephalus* populations in Korean waters. Most individuals had estuaries origins, indicating that they used estuaries as nursery grounds. Most locations had fish with diverse migration patterns. Some individuals in the Yellow Sea and in the western Korea Strait remained in environments with very low salinities, and tend to migrate to the offshore after they reach sexual maturity. This showed that they have the adaptability to tolerate a wide range of environmental conditions. Therefore, the habitat use of flathead grey mullet can change with age according to the optimal conditions for survival and growth. Completely different migration patterns were found between *M. cephalus* specimens collected from two locations off Jeju Island (type I only in HG vs. types III, IV, and V in JM). This difference may be due to the dominating influence of the Tsushima Warm Current and/or coastal waters, including the discharge of submarine freshwater and waterfalls at JM, resulting in the occurrence of two different groups (a migratory group at JM and a resident group at HG). The diversity of the *M. cephalus* may reflect flexible adaptation to local environments.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s41610-020-00164-9>.

Additional file 1: Table S1. Kruskal–Wallis H-tests for significant differences among locations in *Mugil cephalus* otolith element:Ca ratios in the zone spanning from the otolith core to 1000 µm toward the perimeter. **Table S2.** Standardized canonical (CAN) coefficients for eight elements ratios. The eight elements were ⁷Li, ²⁴Mg, ⁵⁵Mn, ⁵⁷Fe, ⁶⁰Ni, ⁶³Cu, ⁸⁸Sr, and ¹³⁸Ba. They were measured at seven Korean locations in *Mugil cephalus* otoliths in the zone spanning from the otolith core to 1000 µm toward the perimeter. CAN1–CAN6 are the axes of the canonical discriminant analysis. **Table S3.** Standardized canonical (CAN) coefficients based on eight elemental ratios (⁷Li, ²⁴Mg, ⁵⁵Mn, ⁵⁷Fe, ⁶⁰Ni, ⁶³Cu, ⁸⁸Sr, and ¹³⁸Ba) in the five migration patterns of *M. cephalus*. CAN1–CAN4 are the axes of the canonical discriminant analysis. **Fig. S1.** The distributions of salinity in (a) February, (b) May, (c) August, and (d) November in the coastal area of Korea in 2015. Data were obtained from the Park et al. (2017). **Fig. S2.** The variability of salinity in the coastal area of Korea between 2017 and 2019. Data were obtained from the MEIS (Marine Environment Information System) (<https://www.meis.go.kr>)

Abbreviations

CDA: Canonical discriminant analysis; CDW: Changjiang diluted water; NWP: Northwest Pacific

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Authors' contributions

SEB designed the study, performed the experiments and data analysis, and wrote the manuscript. JKK participated in the design of the study and reviewed/edited the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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