



## Diverse migration strategies of arid catfishes along a salinity gradient in the Mekong River

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### ABSTRACT

Arid catfishes (Ariidae family) are important migratory fish species in the Mekong River, with some species representing a major harvest component from the river. Limited biological information exists, and in particular their migration patterns are not well understood. This study examined life history strategies of three abundant arid catfishes (*Cephalocassis borneensis*, *Arius maculatus*, and *Osteogeneiosus militaris*) in the Mekong River using otolith chemistry. Multiple trace elements in otolith sections were quantified using two analytical techniques: Laser Ablation – Inductively Coupled Plasma – Mass Spectrometry and X-ray fluorescence microscopy. We found that 83 % of *C. borneensis* samples completed their life cycle exclusively in fresh water in the Mekong River, while 17 % samples of this species were occasionally found in higher salinity (brackish) waters. The two other species (*A. maculatus* and *O. militaris*) generally occupied higher salinity (estuary and coastal) areas, but demonstrated complex migratory patterns with up to three migration strategies observed (including both residents and migrants). With such complex migration strategies, management and conservation interventions are a challenge for these fish species.

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## 1. Introduction

Understanding animal movements across habitats is essential to support management and conservation efforts (Allen and Singh, 2016). Species that migrate long distances are likely to be at risk due to disconnection of critical habitats through human activities (Brink et al., 2018). This is particularly pertinent to animals that migrate across complex landscapes that are undergoing modification because of human pressures, such as fish migration in large river systems (Lucas and Baras, 2001). The Mekong River represents one such landscape, with large numbers of fish species undertaking long distance migrations and adopting multiple migration strategies to utilise the diversity of habitat available, including from the sea to upland areas and exploitation of productive floodplain wetlands (Cowx et al., accepted; Vu et al., 2022a; Vu et al., 2022b). These fish species are, however, threatened by human activities such as hydropower development and agricultural intensification that disrupt river longitudinal connectivity and disconnect floodplain habitats from the river network (Dudgeon, 2011; Kang et al., 2009).

Ariidae catfishes are a diverse group of fishes, comprising 156 species globally (Froese and Pauly, 2023). They are particularly abundant in estuaries in tropical regions (Dantas et al., 2010). Although 28 ariid catfish species are listed as occurring in the Mekong River (MRC, 2017), only nine have been described in detail and their migration patterns are not fully understood (Praxaysombath et al., 2021; So et al., 2018; Tran et al., 2013): some are exclusively freshwater, estuarine or marine species, while others may move across salinity gradients (Froese and Pauly, 2023). Irrespective, catches of ariid catfishes contribute a major component to the Lower Mekong fisheries, particularly in the Mekong Delta. For example, spotted catfish (*Arius maculatus*) is among the top ten fish species caught in the Vietnamese Mekong Delta (MRC, 2017).

Otolith chemistry is a powerful tool to understand fish movements, habitat use, natal origin, stock discrimination, growth or physiology (Carlson et al., 2017; Reis-Santos et al., 2023; Walther, 2019). For example, movements of ariid catfishes across salinity gradients (*Neoarius graeffei*, *N. midgleyi*, and *N. leptaspis* in the Daly River, Australia, and *Plicofollis tenuispinis* in a coastal area of India) were revealed by otolith chemistry (Kubota et al., 2015; Oughton, 2014). *Neoarius leptaspis* spawns in brackish or marine waters, then moves into fresh water for feeding, while *N. graeffei* is almost exclusively restricted to freshwater habitats. Although otolith chemistry has been used to examine life histories of several Mekong fish species (Fukushima et al., 2014; Vu, 2022; Yokouchi et al., 2018), none of the ariid catfish species have been included in these studies.

Considerable development is presently taking place in the Mekong, especially hydropower and agricultural developments that are disrupting the ecological integrity and functioning of the river system (MRC, 2022). These developments are creating physical barriers to key migratory pathways and also have the potential to disrupt movement cues through altered flow regimes and changes in water quality. As such there is an urgent need to define migratory strategies across a range of different species. The objective of this study was to examine life history strategies of three important ariid catfish species (*Cephalocassis borneensis* (Bleeker), *Arius maculatus* (Thunberg) and *Osteogeneiosus militaris* (Linnaeus)) in the Lower Mekong Basin (LMB) based on otolith chemistry.

## 2. Methods

### 2.1. Water chemistry

Concentrations of elements in fish otoliths, such as barium and strontium, reflect ambient water chemistry (Campana, 1999; Reis-Santos et al., 2023; Zimmerman, 2005), therefore these elements can be used as proxies to track fish movements across different salinity gradients. Recent studies have shown that  $^{24}\text{Mg}$ ,  $^{25}\text{Mn}$ ,  $^{44}\text{Ca}$ ,  $^{88}\text{Sr}$ , and

$^{138}\text{Ba}$  were significantly different between fresh and marine waters in the LMB (Tran et al., 2019; Vu et al., 2021a). Therefore, these elements were selected for this study to investigate migration patterns of ariid species in the LMB. In addition, tidal range at the mouth of the Mekong River was 3.74 m over a daily cycle and saline water can penetrate 70 – 85 km inland from the river mouth (Nguyen, 2016; Vu et al., 2021a).

### 2.2. Otolith collection and preparation

Three common ariid species were selected for the study but information on migration and other biological behaviour is limited. *Cephalocassis borneensis* is considered a freshwater species, while *Arius maculatus* and *Osteogeneiosus militaris* are considered brackish and/or marine species. Field trips were conducted to collect samples of these three species, starting from Luang Prabang (Lao PDR) through Thailand, Cambodia, Vietnamese Mekong Delta, and coastal areas. These fish collection trips covered over 2000 km along the Mekong River. Ariid catfishes were, however, only found in Vietnam and Cambodia (Fig. 1). Collections relied on local fishers, but some samples were collected from local markets. Capture locations were obtained from fishers or fish vendors during sample collection. Field guides were used to ensure correct fish identification (Nagao Natural Environment Foundation, 2021; So et al., 2018; Tran et al., 2013).

Standard length (nearest mm) and body weight (nearest g) were recorded for each individual fish before removing the lapilli otoliths (Table 1). Otoliths of these ariid species are oval and relatively large: *C. borneensis* (weight: 232 mg  $\pm$  108; length: 8 mm  $\pm$  1; width: 6 mm  $\pm$  1; thickness: 4 mm  $\pm$  0.6); *A. maculatus* (weight: 209 mg  $\pm$  81; length: 8 mm  $\pm$  1; width: 6 mm  $\pm$  1; thickness: 3 mm  $\pm$  0.5); *O. militaris* (weight: 228 mg  $\pm$  109; length: 9 mm  $\pm$  1; width: 7 mm  $\pm$  1; thickness: 3 mm  $\pm$  0.5). No deformities were observed for otoliths from these species. Otoliths were then cleaned with distilled water, air-dried, the otolith core marked with a pencil, and the otolith embedded in araldite (GY502) and hardener (HY956). The epoxy resin encompassing the otoliths was allowed to harden for three days at room temperature. A transverse line through the core of otoliths was drawn on the resin to guide sectioning. A low-speed saw with two diamond blades (TechCut 4, Allied High Tech) separated by a spacer was used to section along the transverse line to obtain an otolith section of around 700  $\mu\text{m}$  thickness. Otolith sections were polished using a series of lapping films (30  $\mu\text{m}$  and 3  $\mu\text{m}$ ) until the core was exposed. Finally, multiple otolith sections were glued to microscope slides using CrystalBond 509. The slides were washed with ultrapure water, air-dried overnight in a laminar flow hood, and stored in acid-washed containers to prevent contamination, prior to chemical analysis. Indium (30 ppm) was mixed in both araldite and CrystalBond, and used as a marker to detect the border between the outer otolith and epoxy resin during data processing. In addition, both right and left otoliths were prepared; otolith sections with the clearest cores were used for chemical analysis.

### 2.3. Elemental analysis of otoliths

Two analytical techniques were used to quantify trace elements in otoliths: Laser Ablation – Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS) at Adelaide Microscopy, University of Adelaide, and Scanning X-ray Fluorescence Microscopy (SXFEM) at the Australian Nuclear Science and Technology Organisation in Melbourne. For LA-ICPMS, concentrations of  $^{24}\text{Mg}$ ,  $^{25}\text{Mn}$ ,  $^{44}\text{Ca}$ ,  $^{88}\text{Sr}$ ,  $^{138}\text{Ba}$  were quantified along line transects from the core to the edge of each otolith at a speed of 3  $\mu\text{m}/\text{s}$  and spot diameter of 30  $\mu\text{m}$ . Prior to laser ablation, cleaning was conducted along each laser ablation path to remove dust and contaminants using a pre-ablation process at 30  $\mu\text{m}/\text{s}$  (spot diameter of 30  $\mu\text{m}$ ). NIST 612 and MACS 3 standards were analysed at the beginning, during (every 10 runs), and end of each run, and used to correct for instrumental drift. Iolite software (version 2.5) was used to process LA-ICPMS data.

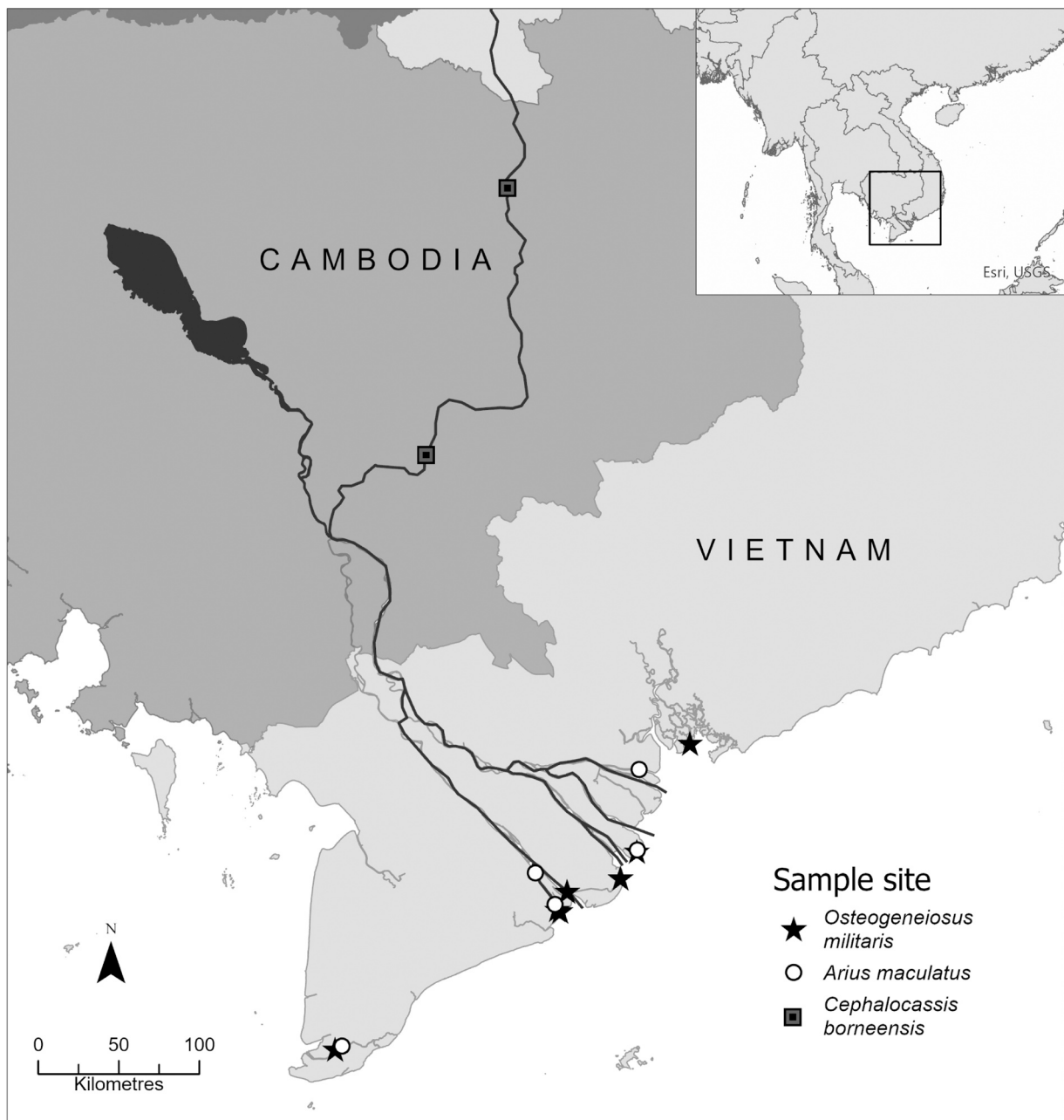


Fig. 1. Fish collection locations in the Lower Mekong Basin.

Table 1

Fish species collected for otolith microchemistry analysis by two analytical instruments (LA-ICPMS and SXFM). Fr: Freshwater; Br: Brackish; Ma: Marine. See [Supplementary material 1](#) for more details.

Species name	Distribution	Mean standard length (mm) $\pm$ SD	Number of otoliths for		Speed in elemental analysis of otoliths ( $\mu\text{m/s}$ )	
			LA-ICPMS	SXFM	LA-ICPMS	SXFM
<i>Cephalocassis borneensis</i>	Fr/Br	139 $\pm$ 29	24	2	3	200–10000
<i>Arius maculatus</i> (spotted catfish)	Fr/Br/Ma	155 $\pm$ 34	32	2	3	200
<i>Osteogeneiosus militaris</i> (soldier catfish)	Fr/Br/Ma	214 $\pm$ 55	25	2	3	90–200

For SXFM, concentrations of 13 elements ( $^{75}\text{As}$ ,  $^{138}\text{Ba}$ ,  $^{80}\text{Br}$ ,  $^{44}\text{Ca}$ ,  $^{52}\text{Cr}$ ,  $^{64}\text{Cu}$ ,  $^{56}\text{Fe}$ ,  $^{25}\text{Mn}$ ,  $^{59}\text{Ni}$ ,  $^{207}\text{Pb}$ ,  $^{207}\text{PbM}$ ,  $^{79}\text{Se}$ ,  $^{88}\text{Sr}$ , and  $^{65}\text{Zn}$ ) was mapped across the surface of the otolith sections by SXFM (“L” and “M” refer to the L and M emission lines, respectively). But for the purposes of life history reconstruction, Ba and Sr provided the most useful information. A Maia detector was used to produce high-definition and

quantitative element images at 18.5 keV (Howard et al., 2020). An aluminum foil with a hole for the direct beam was attached to the detector window, to attenuate the dominant Ca fluorescence signal that would otherwise saturate the counting electronics. SXFM data were processed with GeoPIXE software (version 7.5). Ratios of Sr:Ca were calculated in Excel and then imported to ArcMap (version 10.6) to

produce Sr:Ca maps while concentrations (ppm) in otoliths were mapped for other elements. The majority of otolith sections were analysed by LA-ICPMS instrument while a few otoliths were mapped by SXFM (Table 1) due to time constraints. For example, it took 16 min to run a transect from the core to the otolith edge by LA-ICPMS at 3  $\mu\text{m/s}$  for an otolith of *A. maculatus* (7.21 mm in length and 5.64 mm in width; 150-TD7), while it took 77 min to map the distribution of elements in an entire otolith section by SXFM at 200  $\mu\text{m/s}$ .

#### 2.4. Data analysis

Element:Ca ratios were calculated and smoothed using a 7-point moving average for LA-ICPMS. These ratios were plotted from the core (at birth) to the edge of the otoliths (at capture) to examine life history strategies for each individual fish. Currently, relationships between ambient salinity and elemental concentration in otoliths have not been validated for ariid species, but thresholds for freshwater, brackish, and marine waters were determined for pangasiid catfishes (Vu et al., 2022a). Pangasiids belong to the same order (Siluriformes) and occur across the same study region as ariid fishes. Hence, those thresholds were used to help understand fish movements of ariid catfishes between fresh and marine waters in this study: otolith Sr:Ca ratios ( $\times 1000$ )  $\leq 3.25$ ; 3.25–10.17; and  $>10.17$  correspond to freshwater, brackish, and marine residence, respectively. Profiles of Sr:Ca ratios for each ariid catfish individual were classified into groups that have similar patterns by visual classification (e.g. freshwater, brackish, marine or movement between fresh and marine waters). Unfortunately, formation of annual growth increments in otoliths for ariid catfish has not been validated, so ageing and relating elemental concentrations to age was not feasible.

### 3. Results

#### 3.1. Otolith microstructure

Translucent and opaque bands were difficult to determine for most otoliths. Hence, ageing of ariid catfishes remains a challenge in the LMB, and only a few otoliths were able to be aged. For example, a spotted catfish (*A. maculatus*) was estimated as over two years old (see Fig. 2). Additionally, around 24–30 narrow increments were found within a translucent band for some individuals of ariid catfishes (*C. borneensis*; *A. maculatus*; and *O. militaris*), however, these narrow increments were not found near the core (Fig. 2).

#### 3.2. Otolith chemistry

Concentrations of 14 elements were examined in otoliths of ariid catfish species. Ratios of Sr:Ca were found to be the most useful

indicators to detect fish movements across a wide range of salinities from freshwater to marine environments. For example, Sr:Ca ratios indicate that *C. borneensis* is a freshwater species while spotted catfish (*A. maculatus*) and soldier catfish (*O. militaris*) inhabit higher salinity gradients (brackish/marine) (Fig. 3).

##### 3.2.1. *Cephalocassis borneensis*

Variation in Sr:Ca (mean:  $3.21 \pm 0.79$ , range: 0.97–10.94), Ba:Ca (mean:  $0.47 \pm 0.25$ , range: 0.06–2.52), Mg:Ca (mean:  $0.08 \pm 0.12$ , range: 0.01–4.97), and Mn:Ca (mean:  $0.02 \pm 0.03$ , range: 0.0002–1.51) ratios indicate *C. borneensis* is a freshwater species, although a few individuals occasionally moved to higher salinity water for a short period of time during their life cycle. Two migration patterns were identified (Fig. 4):

- Pattern 1 (freshwater residence: 83 % of samples,  $n=20$ , Figs. 4a and 4c): most *C. borneensis* exhibited residency in fresh water throughout their life history with no or little connection to higher salinity waters. Ratios of Sr:Ca along the life-history transects varied exclusively around the threshold for fresh water.
- Pattern 2 (freshwater residence with occasional movements to brackish water: 17 % of samples,  $n=4$ , Figs. 4b and 4d): small proportion of samples occasionally entered higher salinity waters (suggesting inhabiting estuarine or coastal areas) for short period of time, then returned to freshwater. Ratios of Sr:Ca peaked up to 10.94.

##### 3.2.2. Spotted catfish (*Arius maculatus*)

Variation of Sr:Ca (mean:  $8.66 \pm 4.30$ , range: 1.57–24.31), Ba:Ca (mean:  $0.19 \pm 0.16$ , range: 0.002–1.19), Mg:Ca (mean:  $0.06 \pm 0.08$ , range: 0.01–0.83), and Mn:Ca (mean:  $0.02 \pm 0.04$ , range: 0–0.66) ratios suggested that *A. maculatus* is an estuarine species, moving across a wide range of salinities from freshwater to marine environments. Larvae of this species likely use mangrove forests along the coast or river mouths as juvenile habitats. At least three different migration strategies were found for this species (Fig. 5).

- Pattern 1 (moving between freshwater and marine environments: 63 % of samples,  $n = 20$ , Figs. 5a and 5d): the majority of *A. maculatus* showed dynamic migration patterns, moving across freshwater and marine environments. They spawned in habitats with high salinity (Sr:Ca:  $9.49 \pm 3.99$  at the core, suggesting in brackish or marine waters), larvae/juveniles then moved to lower salinity water (suggesting riverine residence) for a period of time before returning to brackish and marine waters. Some moved repeatedly between freshwater and marine environments.
- Pattern 2 (brackish and marine residence: 28 % of samples,  $n = 9$ , Fig. 5b): around one third of *A. maculatus* spawned in high salinity

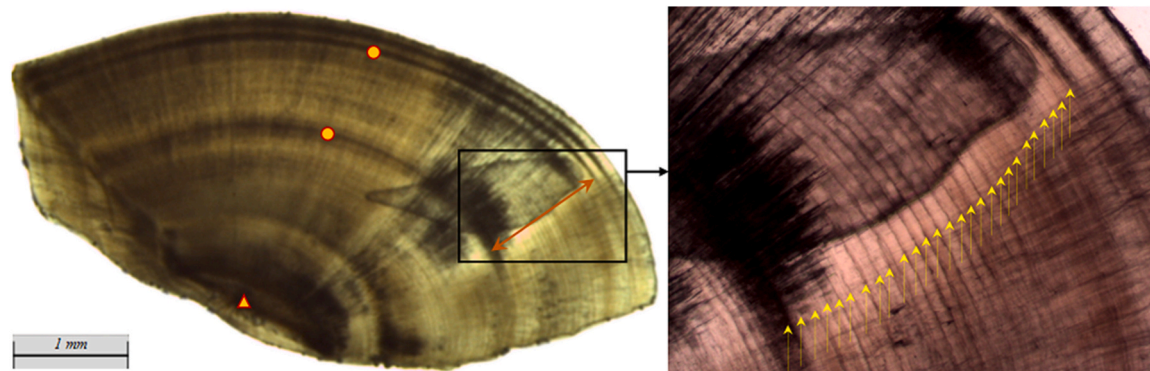
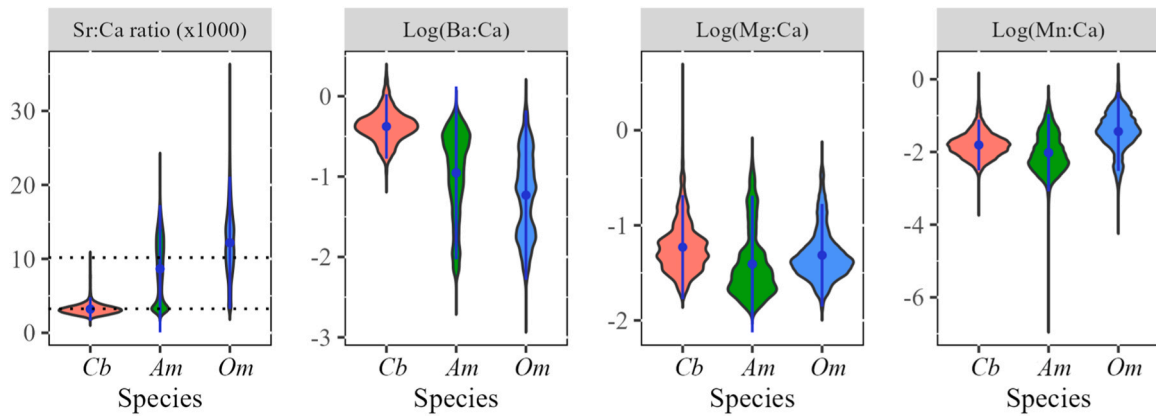
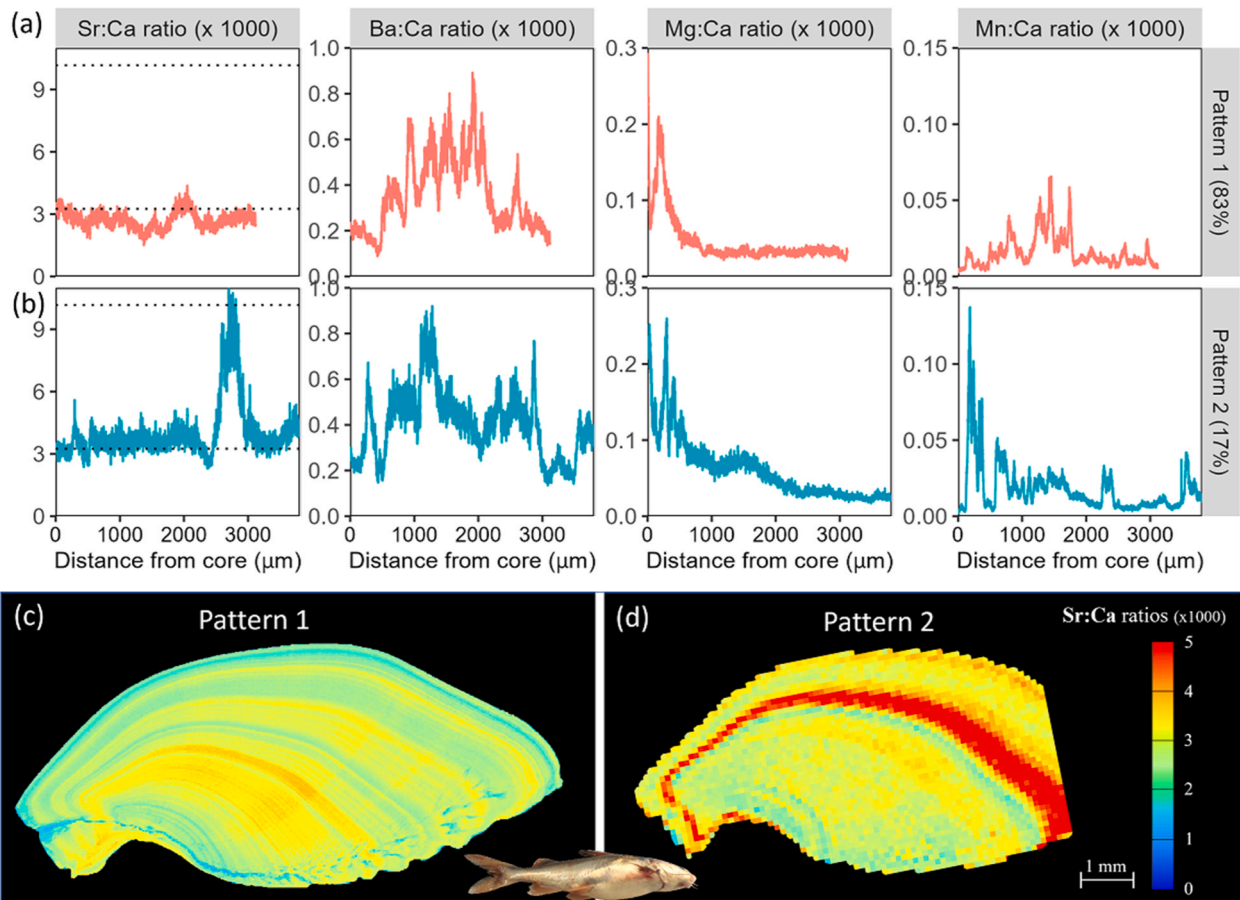


Fig. 2. Microstructures of an otolith section of *A. maculatus* (body standard length: 132 mm) under transmitted light. It was estimated to be two years old (yellow triangle: the core; yellow dots: annual increments). There were 26 narrow increments in the second year. Images of individual otolith sections are available on request.





**Fig. 3.** Violin plots showing variation in key element:Ca ratios of three ariid catfish species (*Cb*: *Cephalocassis borneensis*; *Am*: *Arius maculatus* – spotted catfish; *Om*: *Osteogeneiosus militaris* – soldier catfish) across the entire otolith transect. Dashed horizontal lines for Sr:Ca indicate freshwater (< 3.25), brackish water (3.25–10.17) and marine (>10.17) residence.



**Fig. 4.** Representative examples of variation in element:Ca ratios from the core to the otolith edge: (a): migration pattern 1; (b): migration pattern 2; and two-dimensional Sr:Ca maps for the two life history patterns: (c): migration pattern 1; and (d): migration pattern 2 of *C. borneensis*. Sr:Ca ratio (x1000) as environmental thresholds (dashed horizontal lines): freshwater residence if  $y < 3.25$  and brackish water residence if  $3.25 \leq y < 10.17$ . See [Supplementary material 2](#) for element:Ca profiles of individual otoliths; and [Supplementary material 3](#) for two-dimensional maps of other elements.

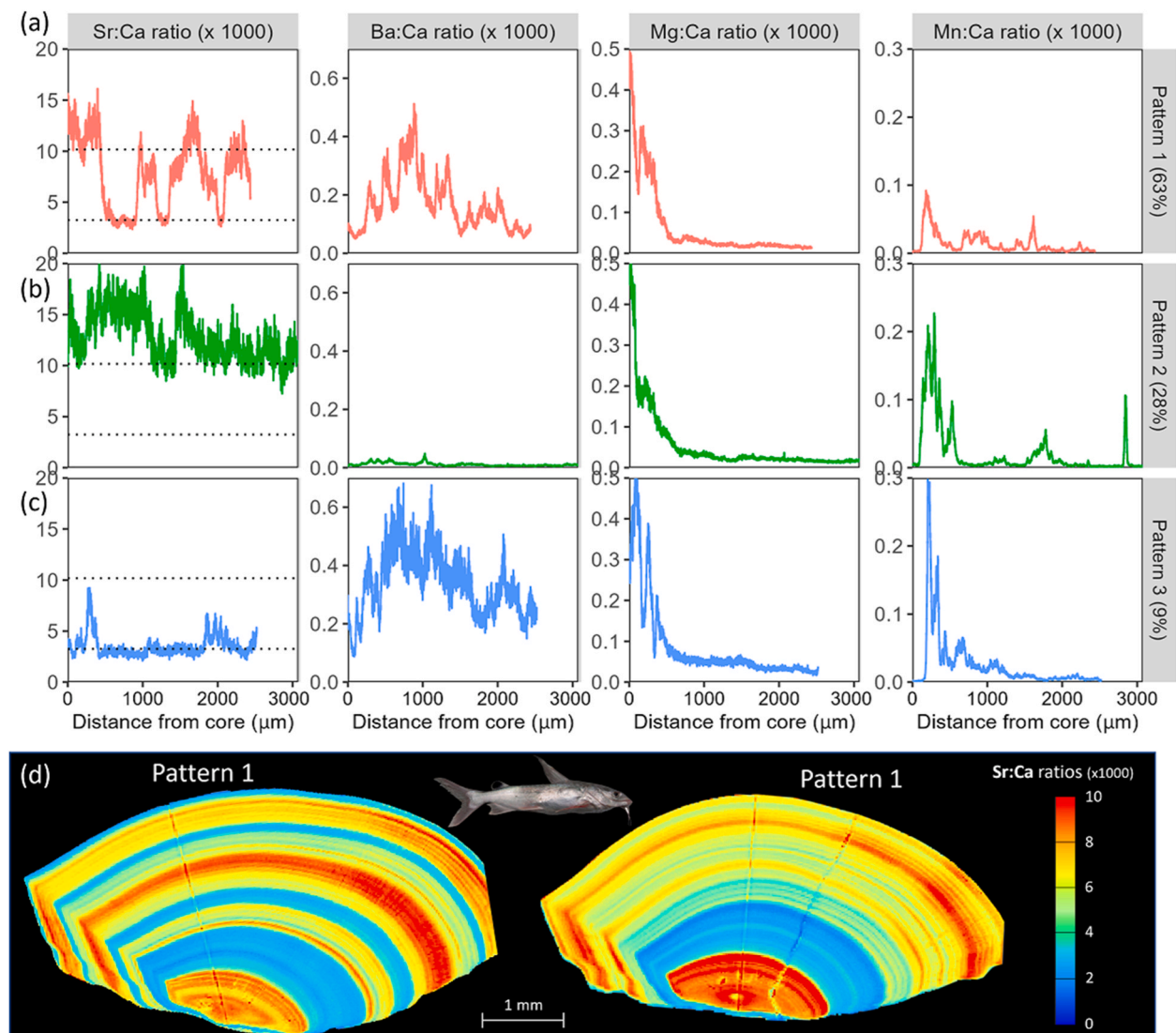
waters (Sr:Ca:  $10.48 \pm 3.69$  at the core, suggestive of marine waters), and did not enter freshwater. Hence, Ba:Ca ratios were very low for this pattern.

- Pattern 3 (freshwater residence with limited connection to brackish water: 9 % of samples,  $n=3$ , [Fig. 5c](#)): a small percentage of *A. maculatus* spawned (Sr:Ca:  $3.81 \pm 1.29$  at the core) and mainly

remained in lower salinity environment (river) with limited connection to brackish water.

### 3.2.3. Soldier catfish (*Osteogeneiosus militaris*)

Variation of Sr:Ca (mean: 12.11; range: 1.78–36.34), Ba:Ca (mean: 0.11; range: 0.001–1.62), Mg:Ca (mean: 0.06; range: 0.01–0.76), and Mn:Ca (mean: 0.07; range: 0–2.63) ratios indicate *O. militaris* is likely a



**Fig. 5.** Representative examples of variation in element:Ca ratios from the core to the otolith edge: (a): migration pattern 1; (b): migration pattern 2; (c): migration pattern 3; and two-dimensional Sr:Ca maps: (d): migration pattern 1 of *A. maculatus*. Sr:Ca ratio (x1000) as environmental thresholds (dashed horizontal lines): freshwater residence if  $y < 3.25$  and brackish water residence if  $3.25 \leq y < 10.17$ . See [Supplementary material 2](#) for element:Ca profiles of individual otoliths; and [Supplementary material 3](#) for two-dimensional maps of other elements.

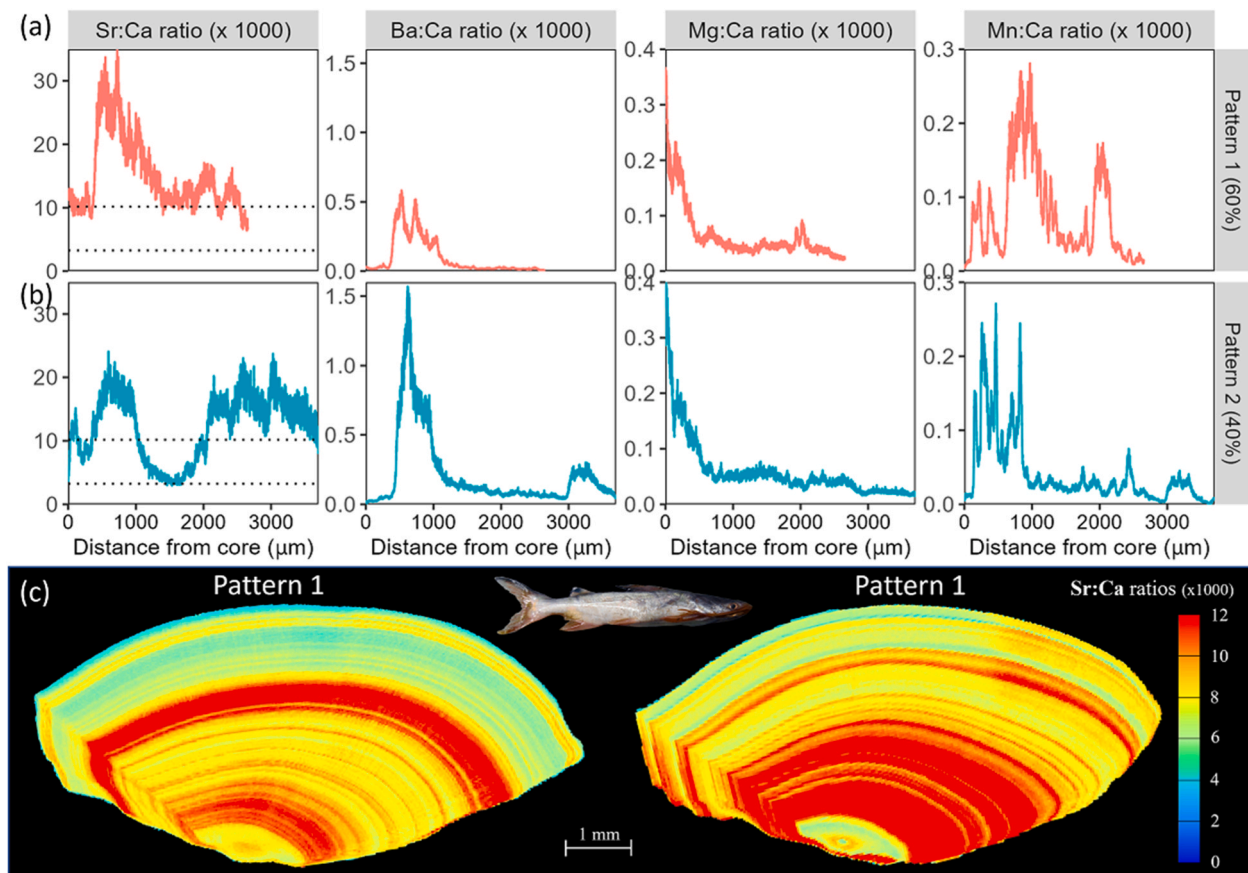
brackish/ marine species, moving across a wide range of salinities. Otolith Sr:Ca ratios of this species were relatively high at the core (Sr:Ca:  $9.35 \pm 2.93$ ), suggesting that they spawned in brackish or marine waters. Otolith Sr:Ca ratios often increased substantially beyond the core for a short period of time, suggesting that larvae of *O. militaris* drift to the sea for a short period of time before returning to coastal areas for feeding. At least two different migration strategies were found for this species (Fig. 6).

- Pattern 1 (brackish and marine residence: 60 % of samples,  $n = 15$ , Figs. 6a and 6c): the majority of *O. militaris* were found in high salinity waters (average of Sr:Ca ratios:  $13.08 \pm 3.80$ ; range: 4.94–36.34). They spawned in habitats with high salinity (Sr:Ca:  $9.36 \pm 3.10$  at the core, suggesting in brackish or marine waters), larvae/juveniles then moved to higher salinity water bodies (suggesting seawater). Regular movements between brackish and marine waters were found.
- Pattern 2 (brackish and marine residence with occasional connection to freshwater environments: 40 % of samples,  $n=10$ , Fig. 6b): these fish also spawned in habitats with high salinity (Sr:Ca =  $9.34 \pm 2.26$ )

at the core, suggesting they were found in brackish or marine waters, they occasionally moved to the river (average of Sr:Ca ratios:  $10.58 \pm 4.75$ ; range: 1.78–31.82).

#### 4. Discussion

The techniques used in this study enabled identification of diversity in migration patterns between and within species of ariid catfishes in the LMB. This suggests greater complexity in migration patterns of this family of species than previously thought (Poulsen et al., 2002). Fishes are typically classified into four broad migratory categories: potamodromy (moving about exclusively in freshwater), oceanodromy (living and migrating exclusively in marine water), estuarine (living exclusively in brackish water or estuarine), or diadromy (migrating regularly between fresh and marine waters) (Lucas and Baras, 2001). Each of these categories contains multiple sub-categories (Elliott et al., 2007; Potter et al., 2015; Welcomme et al., 2006). It was previously thought that each fish species followed only a single or few migration patterns. However, recent studies (Tran et al., 2021; Vu et al., 2022a, 2022b) found that individuals within a given species may exhibit



**Fig. 6.** Representative examples of variations in element:Ca ratios from the core to the otolith edge: (a): migration pattern 1; (b): migration pattern 2; and two-dimensional Sr:Ca maps (c): migration pattern 1 of *O. militaris*. Sr:Ca ratio (x1000) as environmental thresholds (dashed horizontal lines): freshwater residence if  $y < 3.25$  and brackish water residence if  $3.25 \leq y < 10.17$ . See [Supplementary material 2](#) for element:Ca profiles of individual otoliths; and [Supplementary material 3](#) for two-dimensional maps of other elements.

multiple migration patterns in a single river system, in this case the Mekong, and found different migration strategies of the same species (e.g. *Neoarius graeffei*) in different river systems (Limburg et al., 2001; Oughton, 2014; Stoot et al., 2023).

The results of this study suggest *C. borneensis* is a “freshwater straggler” based on the definition of Elliott et al. (2007) and Potter et al. (2015). All fish hatched in fresh water, and the majority remained exclusively in the river with only a few moving to higher salinity environments for a short period of time. Those moving to higher salinity environments then returned to the freshwater part of the river. They likely follow water currents to the estuaries for feeding, but are unlikely to tolerate higher salinity for a long period of time and so return to the river (probably because the salinity is above their salinity threshold). This migration pattern was also found in *Pangasius elongatus* in the Mekong River (Vu et al., 2022a) and some freshwater fish species, such as mud carps (*Henicorhynchus* spp.) and catfish (*P. elongatus*), were observed in the saline areas of the Mekong delta when sampling. Estuaries are dynamic ecosystems that are strongly influenced by sea tides and water discharge from the river (Vu et al., 2021a), hence freshwater and marine fish species are often found together. It is possible *C. borneensis* move to the lower delta during the annual flood season, which produces a spike of Sr:Ca on the otolith.

Spotted catfish (*A. maculatus*), one of the prevalent fishery species in the Vietnamese Mekong Delta, is abundant in the Mekong estuary (MRC, 2017). This species is an estuarine species with at least three migration patterns. This fish species spawns all year round, with two main spawning periods (March and August) (To and Tran, 2019). The adults of this species carry eggs and larvae in their mouth in the Mekong estuary and coastal areas (Fig. 7). Most *A. maculatus* (pattern 1 and 2)

spawn in higher salinity areas (e.g. Mekong estuary or coastal areas) and undertake repeated migrations between fresh and marine waters (pattern 1; 63 % of samples; Figs. 5a and 5d), while others remain in spawning areas (28 % of samples; pattern 2; Fig. 5b). This migration strategy (pattern 1) can be classified as amphidromous (Myers, 1949) or “estuarine migrant” (Elliott et al., 2007). Meanwhile 28 % of *A. maculatus* samples in early life stages remain in high salinity (estuary and seawater) as “estuarine resident” (Fig. 5b). Interestingly, a few *A. maculatus* (9 % of samples) spawn and remain in fresh water with limited connection to the Mekong estuary. This species is sometimes recorded in Cambodia (So et al., 2018).

Both *O. militaris* and *A. maculatus* occur mainly in estuaries and sea water. However, *O. militaris* can be found in fresh water up to 100 km from the sea, while *A. maculatus* are found even further upstream (up to 300 km from the sea) albeit in low numbers (Nagao Natural Environment Foundation, 2021; So et al., 2018). Although both species carry their eggs and larvae in their mouths, most *A. maculatus* larvae drift in the river currents to freshwater nursery habitats while larvae of *O. militaris* are flushed to the sea or mangrove forests in the coastal areas. Similarly, Pantulu (1963) suggested that *O. militaris* may migrate to the sea after spawning. Migration strategies of the ariid catfishes are facultative and demonstrate partial migration in the Mekong River, with both residents and migrant forms, co-existing in the same populations. Such migration strategies are also common for other fish species (Chapman et al., 2012; Vu, 2022). Some fishes tend to migrate to outside their natal range to maximise their growth and survival rates. Hence, growth rates and body conditions of migrants are often better than residents (Barrow et al., 2021; Gillanders et al., 2015; Vu et al., 2022b).

In this context, Mekong ariid catfishes are considered partial





**Fig. 7.** Adults of spotted catfish (a: *Arius maculatus*) and soldier catfish (b: *Osteogeneiosus militaris*) carrying eggs and larvae in buccal cavity.

migrants moving mostly within the estuary. Consequently, they are likely less vulnerable to river infrastructural development such as hydropower dams and irrigated agriculture for rice (Barrow et al., 2021; Cowx et al., accepted; Vu et al., 2021b), although coastal weirs and thousands of sluice gates for agricultural activities (to prevent salt intrusion) in the delta may be barriers for migrations of estuarine and diadromous species to access their key habitats in different regions (Bice et al., 2023).

Multiple factors are presently impacting the Mekong fisheries and results from this study suggest these may influence fisheries sustainability. For instance, ariid fish communities in the lower reaches of the LMB may be vulnerable to changes in flow regime. Flooding regimes (flood extent, timing and duration) are considered the most important factors driving Mekong populations (Halls and Hortle, 2021). Flooding for longer periods of time and larger flooded areas tend to produce higher fish production (Baran et al., 2003). Flow regulation caused by the large number of dams constructed or in development in the LMB have altered the flow regime dramatically leading to reduced amplitude of floods and shorter durations and reduced catches (Halls et al., 2013; Stewart et al., 2020). This is further compounded by the effects of climate change on the flooding regime and is likely to compromise the migratory fish stocks in the LMB, including the ariid catfishes that occupy the lower reaches in Vietnam and Cambodia.

One aspect that requires consideration is linking the migratory patterns to the life history cycle and growth of the target species. Ideally, it would be valuable to relate the migration patterns of ariid catfishes to the age or life history stage at which such events occur. However, this was not possible because no studies have been carried out on the age and growth of ariid catfishes in the Mekong. Nevertheless, annual growth increments have been found in some ariid catfishes (*G. genidens*, *N. graeffei*, *N. midgleyi*, *N. leptaspis*, *Netuma barba*, *N. bilineata*, *N. thalassina*, *P. dussumieri*, *P. tenuispinis*), and these included alternate translucent and opaque bands representing annual growth, but they have not been formally validated (Chen et al., 2011; Daros et al., 2022; Maciel et al., 2018; Oughton, 2014; Reis, 1986). Similarly, growth marks have been found in otoliths of other catfishes (*Brachyplatystoma rousseauxii* and *B. filamentosum*) but they are biannual (Alonso and Fabr e, 2003). There is little doubt that growth bands are found in the ariid catfish targeted in this study (see Fig. 2), and we speculate that the narrow increments within translucent bands on the otoliths may be related to the lunar-tidal cycle. The Mekong estuary is strongly influenced by tides with two high/low tides each month (Vu et al., 2021a), and these may be linked to the growth increments. Lunar cycles (14 days) have been found to

influence otolith growth in hilsa shad (*Tenualosa ilisha*, Clupidae) in a tropical river (Rahman and Cowx, 2006) and the same may be true in ariid catfishes. Similarly, otolith growth marks have been induced by lunar cycles for other fish species, such as *Ptychobarbus dipogon* (Cyprinidae) (Li et al., 2009); starry flounder (*Platichthys stellatus*, Pleuronectidae) (Campana, 1984); and myctophid fish (*Myctophum asperum*, Myctophidae) (Hayashi et al., 2001). Efforts to understand the growth characteristics of ariid catfishes in the LMB and relate these to life history tactics and migration patterns represents a potentially valuable area for future research.

This study showed flexible modes of migration of arid catfishes in the Mekong River. Both migrants and residents co-exist in the same river system. They appear able to adapt to a wide range of environments (river – ocean). Factors such as benefits (e.g. food availability), risks (e.g. predation and fishing), and costs (e.g. energy and long migration distance) may contribute to the complexity of migration strategies (Vu et al., 2022b). Consequently, management and conservation are challenging for fish species with such complex migrations, and will become more so under warming climates, increased drought conditions and saltwater intrusion in the delta.

#### CRediT authorship contribution statement

**An Vi Vu:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Cameron M. Kewish:** Writing – review & editing, Data curation. **Ian G. Cowx:** Writing – review & editing, Supervision, Methodology, Investigation. **Jason D. Thiem:** Writing – review & editing, Methodology, Conceptualization. **Gregory S. Doran:** Writing – review & editing, Supervision, Methodology, Investigation. **Martin Mallen-Cooper:** Writing – review & editing, Supervision, Methodology, Investigation. **Julia A. Howitt:** Supervision, Methodology, Investigation. **Bronwyn M. Gillanders:** Writing – review & editing, Methodology, Investigation. **Lee J. Baumgartner:** Writing – review & editing, Supervision, Methodology, Investigation. **Karin E. Limburg:** Writing – review & editing, Methodology, Investigation, Conceptualization.

#### Declaration of Competing Interest

We have no conflicts of interest to disclose for our manuscript titled “Diverse migration strategies of ariid catfishes along a salinity gradient in the Mekong River”.



## Data availability

Data will be made available on request.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107133.

## References

- Allen, A., Singh, N., 2016. Linking movement ecology with wildlife management and conservation. *Front. Ecol. Evol.* 3.
- Alonso, J.C., Fabré, N.N., 2003. Proceedings of the second international symposium on the management of large rivers for fisheries. In: Welcomme, R.L., Petr, T. (Eds.), *Sustaining Livelihoods and Biodiversity in the New Millennium*. Food And Agriculture Organization Of The United Nations & The Mekong River Commission, Phnom Penh, Cambodia.
- Baran, E., Makin, I. and Baird, I.G. 2003 Bayfish: A model of environmental factors driving fish production in the Lower Mekong Basin, pp. 1-20.
- Barrow, J.S., Yen, J.D.L., Koehn, J.D., Zampatti, B.P., Thiem, J.D., Tonkin, Z., Strawbridge, A., Morrongiello, J.R., 2021. Lifetime movement history is associated with variable growth of a potamodromous freshwater fish. *J. Anim. Ecol.* 90 (11), 2560–2572.
- Bice, C.M., Huisman, J., Kimball, M.E., Mallen-Cooper, M., Zampatti, B.P., Gillanders, B. M., 2023. Tidal barriers and fish – Impacts and remediation in the face of increasing demand for freshwater and climate change. *Estuar., Coast. Shelf Sci.* 289, 108376.
- Brink, K., Gough, P., Royte, J., Schollemma, P.P. and Wannings, H. (2018) From sea to source 2.0. Protection and restoration of fish migration in rivers worldwide, World Fish Migration Foundation, Groningen, Netherlands.
- Campana, S.E., 1984. Lunar cycles of otolith growth in the juvenile starry flounder *Platichthys stellatus*. *Mar. Biol.* 80 (3), 239–246.
- Campana, S.E., 1999. Chemistry and composition of fish otoliths: Pathways, mechanisms and applications. *Mar. Ecol. Prog. Ser.* 188, 263–297.
- Carlson, A.K., Phelps, Q.E., Graeb, B.D.S., 2017. Chemistry to conservation: Using otoliths to advance recreational and commercial fisheries management. *J. Fish. Biol.* 90 (2), 505–527.
- Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A., Brönmark, C., 2012. Partial migration in fishes: causes and consequences. *J. Fish. Biol.* 81 (2), 456–478.
- Chen, W., Al-Husaini, M., Beech, M., Al-Enezi, K., Rajab, S., Husain, H., 2011. Discriminant analysis as a tool to identify catfish (Ariidae) species of the excavated archaeological otoliths. *Environ. Biol. Fishes* 90 (3), 287–299.
- Cowx, I.G., Vu, A.V., Mallen Cooper, M., Baumgartner, L.J., T.Q., L, Z., H, Grill, G. and Sayer, C.A. accepted. Global swimways in the Lower Mekong: understanding the threats to fish migration in a species rich tropical river system. *Fisheries Science and Aquaculture*.
- Dantas, D.V., Barletta, M., Costa, M.F., Barbosa-Cintra, S.C.T., Possatto, F.E., Ramos, J.A. A., Lima, A.R.A., Saint-Paul, U., 2010. Movement patterns of catfishes (Ariidae) in a tropical semi-arid estuary. *J. Fish. Biol.* 76 (10), 2540–2557.
- Daros, F.A., Condini, M.V., Altafin, J.P., de Oliveira Ferreira, F., Hostim-Silva, M., 2022. Fish otolith microchemistry as a biomarker of the world's largest mining disaster. *Sci. Total Environ.* 807 (Pt 3), 151780-151780.
- Dudgeon, D., 2011. Asian river fishes in the Anthropocene: Threats and conservation challenges in an era of rapid environmental change. *J. Fish. Biol.* 79 (6), 1487–1524.
- Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G., Harrison, T.D., 2007. The guild approach to categorizing estuarine fish assemblages: A global review. *Fish Fish* 8, 241–268.
- Froese, R. and Pauly, D. 2023 FishBase. World Wide Web Electronic Publication. www.fishbase.org, version (06/2023).
- Fukushima, M., Jutagate, T., Grudpan, C., Phomikong, P., Nohara, S., 2014. Potential effects of hydroelectric dam development in the Mekong River Basin on the migration of siamese mud carp (*Henicorhynchus siamensis* and *H. lobatus*) elucidated by otolith microchemistry. *PLoS One* 9 (8), e103722.
- Gillanders, B., Izzo, C., Doubleday, Z., Ye, Q., 2015. Partial migration: growth varies between resident and migratory fish. *Biol. Lett.* 11, 20140850.
- Halls, A.S., Hortle, K.G., 2021. Flooding is a key driver of the Tonle Sap dai fishery in Cambodia. *Sci. Rep.* 11 (1), 3806-3806.
- Halls, A.S., Paxton, B.R., Hall, N., Hortle, K.G., So, N., Chea, T., Chheng, P., Putrea, S., Lieng, S., Ngor, P.B., Ngor, P., Chan, S., Vu, A.V., Nguyen, D.N., Doan, T.V., Sinthavong, V., Douangkham, S., Vannaxay, S., Renu, S., Suntornratana, U., Tiwarat, T., Boonsong, S., 2013. Integrated analysis of data from MRC fisheries monitoring Programmes in the Lower Mekong Basin. MRC technical paper No.33. Mekong River Commission, Phnom Penh, Cambodia, p. 130.
- Hayashi, A., Kawaguchi, K., Watanabe, H., Ishida, M., 2001. Daily growth increment formation and its lunar periodicity in otoliths of the myctophid fish *Myctophum asperum* (Pisces: Myctophidae). *Fish. Sci.* 67, 811–817.
- Howard, D.L., de Jonge, M.D., Afshar, N., Ryan, C.G., Kirkham, R., Reinhardt, J., Kewish, C.M., McKinlay, J., Walsh, A., Divitcos, J., Basten, N., Adamson, L., Fiala, T., Sammut, L., Paterson, D.J., 2020. The XFM beamline at the Australian Synchrotron. *J. Synchrotron Radiat.* 27 (5), 1447–1458.
- Kang, B., He, D., Perrett, L., Wang, H., Hu, W., Deng, W., Wu, Y., 2009. Fish and fisheries in the Upper Mekong: Current assessment of the fish community, threats and conservation. *Rev. Fish. Biol. Fish.* 19 (4), 465–480.
- Kubota, K., Yokoyama, Y., Kawakubo, Y., Seki, A., Sakai, S., Ajithprasad, P., Maemoku, H., Osada, T., Bhattacharya, S.K., 2015. Migration history of an arid Indian catfish reconstructed by otolith Sr/Ca and  $\delta^{18}\text{O}$  micro-analysis. *Geochem. J.* 49 (5), 469–480.
- Li, X., Chen, Y., He, D., Chen, F., 2009. Otolith characteristics and age determination of an endemic *Ptychobarbus dipogon* (Regan, 1905) (Cyprinidae: Schizothoracinae) in the Yarlung Tsangpo River, Tibet. *Environ. Biol. Fishes* 86 (1), 53–61.
- Limburg, K.E., Landergrén, P., Westin, L., Elfman, M., Kristiansson, P., 2001. Flexible modes of anadromy in Baltic sea trout: making the most of marginal spawning streams. *J. Fish. Biol.* 59 (3), 682–695.
- Lucas, M.C., Baras, E., 2001. Migration of freshwater fishes. Blackwell Science Ltd, London, UK.
- Maciel, T.R., Vaz-dos-Santos, A.M., Vianna, M., 2018. Can otoliths of *Genidens genidens* (Cuvier 1829) (Siluriformes: Ariidae) reveal differences in life strategies of males and females? *Environ. Biol. Fishes* 101 (11), 1589–1598.
- MRC, 2017. The Council study: Study on the sustainable management and development of the Mekong River, including impacts of mainstream hydropower projects. *BioRA Final Tech. Rep. Ser. Volume 1*, 695 (Specialists' report).
- MRC 2022 Sustainable hydropower development strategy: a Basin-wide strategy for a changing Mekong River Basin Mekong River Commission Secretariat, Vientiane.
- Myers, G.S., 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia* 1949, 89–97.
- Nagao Natural Environment Foundation (2021) Fishes of the Indochinese Mekong, Nagao Natural Environment Foundation, Tokyo.
- Nguyen, T.C., 2016. Saltwater intrusion - An evident impact of climate change in the md and propose adaptable solutions. *Am. J. Environ. Resour. Econ.* 1 (1), 1–8.
- Oughton, S.C. (2014) Movement of forklait catfish in Daly River, Northern Territory, as determined by otolith chemistry analysis, Charles Darwin University.
- Pantulu, V.R., 1963. Studies on the age and growth, fecundity and spawning of *Osteogeneios militaris* (Linn.). *ICES J. Mar. Sci.* 28 (2), 295–315.
- Potter, I.C., Warwick, R.M., Hall, N.G. and Tweedley, J.R. (2015), pp. 48-79, John Wiley & Sons, Ltd, Chichester, UK.
- Poulsen, A.F., Poeu, O., Viravong, S., Suntornratana, U. and Nguyen, T.T. 2002. Fish migrations of the Lower Mekong River Basin: Implications for development, planning and environmental management. MRC Technical Paper No.8, 62.
- Praxayombath, B., Utsugi, K., Phongsa, K., Nammavong, M., Vannachak, V., Phommachan, K., Phommavong, T., Phothana, V., Duangthasy, V. and Latsamy., S. (2021) Field guide to fishes of the Mekong Basin of Laos, Biology Department, Faculty of Natural Sciences, National University of Laos, Vientiane Capital, Lao PDR.
- Rahman, M.J., Cowx, I.G., 2006. Lunar periodicity in growth increment formation in otoliths of hilsa shad (*Tenulosa ilisha*, Clupeidae) in Bangladesh waters. *Fish. Res.* 81 (2), 342–344.
- Reis, E.G., 1986. Age and growth of the marine catfish, *Netuma barba* (Siluriformes, Ariidae), in the estuary of the Patos Lagoon (Brasil). *Fish. Bull.* 84 (3), 679–686.
- Reis-Santos, P., Gillanders, B.M., Sturrock, A.M., Izzo, C., Oxman, D.S., Lueders-Dumont, J.A., Hüsey, K., Tanner, S.E., Rogers, T., Doubleday, Z.A., Andrews, A.H., Trueman, C., Brophy, D., Thiem, J.D., Baumgartner, L.J., Willmes, M., Chung, M.-T., Charapata, P., Johnson, R.C., Trumble, S., Heimbrand, Y., Limburg, K.E., Walther, B. D., 2023. Reading the biomineralized book of life: expanding otolith biogeochemical research and applications for fisheries and ecosystem-based management. *Rev. Fish. Biol. Fish.* 33 (2), 411–449.
- So, N., Utsugi, K., Shibukawa, K., Thach, P., Chhuoy, S., Kim, S., Chin, D., Nen, P. and Chheng, P. (2018) Field guide to fishes of Cambodian freshwater bodies, Inland Fisheries Research and Development Institute, Fisheries Administration, Phnom Penh, Cambodia.
- Stewart, J., Hughes, J.M., Stanley, C., Fowler, A.M., 2020. The influence of rainfall on recruitment success and commercial catch for the large sciaenid, *Argyrosomus japonicus*, in eastern Australia. *Mar. Environ. Res.* 157, 104924-104924.
- Stoot, L.J., Butler, G.L., Niella, Y., Doran, G.S., Thiem, J.D., Taylor, M.D. and Baumgartner, L.J. 2023. Environmental effects on the seasonal distribution of an estuarine species *Neoarius graeffei* in Northern New South Wales, Australia. *Estuaries and Coasts*.
- To, H.M.T., Tran, D.D., 2019. Some of the reproductive biological characteristics of spotted catfish *Arius maculatus* (Thunberg, 1792) in Tran De estuary, Soc Trang province. *J. Fish. Sci. Technol.* (3/2019) 55–61.

- Tran, D.D., Shibukawa, K., Nguyen, P.T., Ha, H.P., Tran, L.X., Mai, H.V. and Utsugi, K. (2013) *Fishes of the Mekong Delta, Vietnam*, Can Tho University Publishing House, Can Tho.
- Tran, N.T., Labonne, M., Hoang, H.D., Panfili, J., 2019. Changes in environmental salinity during the life of *Pangasius krempfi* in the Mekong Delta (Vietnam) estimated from otolith Sr:Ca ratios. *Mar. Freshw. Res.* 70, 1734–1746.
- Tran, N.T., Labonne, M., Chung, M.-T., Wang, C.-H., Huang, K.-F., Durand, J.-D., Grudpan, C., Chan, B., Hoang, H.D., Panfili, J., 2021. Natal origin and migration pathways of Mekong catfish (*Pangasius krempfi*) using strontium isotopes and trace element concentrations in environmental water and otoliths. *PLoS One* 16 (6), e0252769.
- Vu, A.V. (2022) *Diversity in migration patterns of selected Mekong River fishes*, Charles Sturt University. Doctor of Philosophy. ([https://researchoutput.csu.edu.au/ws/portalfiles/portal/227418935/Diversity\\_in\\_migration\\_patterns\\_of\\_selected\\_Mekong\\_River\\_fishes\\_Full\\_PhD\\_Thesis.pdf](https://researchoutput.csu.edu.au/ws/portalfiles/portal/227418935/Diversity_in_migration_patterns_of_selected_Mekong_River_fishes_Full_PhD_Thesis.pdf)), Albury.
- Vu, A.V., Baumgartner, L.J., Doran, G.S., Mallen-Cooper, M., Thiem, J.D., Howitt, J.A., Limburg, K.E., Gillanders, B.M., Cowx, I.G., 2021a. Variability in water chemistry in the Lower Mekong Basin: Considerations for fish life history reconstruction. *Estuar., Coast. Shelf Sci.* 255, 107355.
- Vu, A.V., Hurtle, K.G., Nguyen, D.N., 2021b. Factors driving long term declines in inland fishery yields in the Mekong Delta. *Water* 13 (8), 1005.
- Vu, A.V., Baumgartner, L.J., Limburg, K.E., Doran, G.S., Mallen-Cooper, M., Gillanders, B.M., Thiem, J.D., Howitt, J.A., Kewish, C.M., Reinhardt, J., Cowx, I.G., 2022a. Life history strategies of Mekong pangasid catfishes revealed by otolith microchemistry. *Fish. Res.* 249, 106239.
- Vu, A.V., Baumgartner, L.J., Mallen-Cooper, M., Doran, G.S., Limburg, K.E., Gillanders, B.M., Thiem, J.D., Howitt, J.A., Kewish, C.M., Reinhardt, J., Cowx, I.G., 2022b. Diverse migration tactics of fishes within the large tropical Mekong River system. *Fish. Manag. Ecol.* 1–16.
- Walther, B.D., 2019. The art of otolith chemistry: Interpreting patterns by integrating perspectives. *Mar. Freshw. Res.* 70, 1643–1658.
- Welcomme, R.L., Winemiller, K.O., Cowx, I.G., 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. *River Res. Appl.* 22, 377–396.
- Yokouchi, K., Mai, H.V., Vo, T.T., Wakiya, R., Kawakami, T., Tanaka, C., Yoshinaga, T., Wada, M., Tran, D.D., Ha, H.P., Takita, T., Ishimatsu, A., 2018. Early life history of oxudercine goby *Pseudapocryptes elongatus* in the Mekong Delta, Vietnam. *Mar. Biol. Assoc. U. Kingd.* 98 (3), 597–604.
- Zimmerman, C.E., 2005. Relationship of otolith strontium-to-calcium ratios and salinity: Experimental validation for juvenile salmonids. *Can. J. Fish. Aquat. Sci.* 62, 88–97.