ARTICLE

Diverse migration tactics of fishes within the large tropical Mekong River system

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Abstract

Fish often migrate to feed, reproduce and seek refuge from predators and prevailing environmental conditions. As a result, migration tactics often vary among species based on a diversity of life history needs, although variation within species is increasingly being recognised as important to population resilience. In this study, within- and among-species diversity in life history migratory tactics of six Mekong fish genera was examined using otolith microchemistry to explore diadromous and potamodromous traits. Two species were catadromous and one species was an estuarine resident, while the remaining three species were facultative in their migration strategies, with up to four tactics within a single species. Migrant and resident contingents co-existed within the same species. Management, conservation and mitigation strategies that maintain connectivity in large tropical rivers, such as effective fishway design, should consider a diversity of migration tactics at the individual level for improved outcomes.

KEYWORDS
Diadromy, fish migration, Mekong River, otolith microchemistry, trace metals

1 | INTRODUCTION

Migration is a common and fundamental life history tactic for many fishes (Lucas & Baras, 2001). Fish move between critical habitats to optimise feeding, reproduction and seek refuge from predators and changing environmental conditions (Northcote, 1978). Among species, movement patterns range from daily to annual scales, short to long distances (metres to thousands of kilometres), longitudinal to lateral directions and diel vertical movements through the water column (Lucas & Baras, 2001). Fish migration can be classified into four broad categories: diadromy (migrating between freshwater and marine habitats), potamodromy (migrating within fresh water), oceanodromy (living within marine water) and estuarine (migrating within the estuary) (Lucas & Baras, 2001). Three subcategories of diadromy include anadromy (growing at sea, but migrating to fresh water for spawning), catadromy (growing in fresh water, but migrating to the sea for spawning) and amphidromy (juveniles migrating between fresh water and the sea, with adults remaining in one habitat or biome for growth and spawning) (McDowall, 1992).

In a review of fish migration, Riede (2004) identified at least 1873 migratory species. This seems remarkably low given that some 25% of freshwater fish species are considered migratory in the Mekong alone (MRC, 2017), and migratory species are prevalent in species-rich large tropical rivers (Winemiller et al., 2016). This highlights the need to improve understanding of migratory behaviours of fish species globally, particularly in large tropical rivers that support high endemicity, including many vulnerable and threatened fish species (Duponchelle et al., 2021; Hermann et al., 2021). Filling this critical knowledge gap would improve management and conservation of these important resources, which are essential food for many rural communities (Dugan et al., 2010; Ziv et al., 2012).

Although species differ in migratory patterns, migratory patterns also differ within species, particularly where migrants and residents co-exist within a single population (Chapman, Skov, et al., 2012). Migration strategies can differ among individuals in the same population. For example, anguillid eels (*Anguilla* spp.) demonstrate diverse migration patterns in both temperate and tropical regions (Arai & Chino, 2012; Daverat et al., 2006). Some giant mottled eels, *Anguilla marmorata* Quoy and Gaimard, never entered freshwater environments while others migrated between freshwater and marine habitats (Arai & Chino, 2018; Chino & Arai, 2010). Other fish species, such as the hilsa shad, *Tenualosa ilisha* Hamilton; blueback herring, *Alosa aestivalis* Mitchill; and barramundi, *Lates calcarifer* Bloch, also varied in migration patterns within rivers (Blaber et al., 2003; Brodersen et al., 2014; Crook et al., 2017; Limburg & Turner, 2016). This behaviour has been attributed to several factors, such as fish body condition, habitat conditions and interactions with other species. Among these factors, body condition is likely to be an important factor for regulating migration strategy because stronger, healthier individuals are better able to conduct long-distance migrations (Brodersen et al., 2014).

The Mekong River is the longest river in Asia (4909 km in length) (Liu et al., 2009) and supports a diverse fish community. The system is largely fresh water but terminates in a complex delta system in Vietnam. Local knowledge and anecdotal information suggest that long-distance migration is important for numerous Mekong fish species, although little published information supports this assertion, including lack of information on the diversity of migration tactics between and within species (Baran, 2006; Vu et al., 2020). In addition, the Mekong is experiencing significant development, including construction of dams, irrigation infrastructure and aquaculture (Baumgartner et al., 2021; MRC, 2019). Therefore, understanding the diversity of migration strategies is important to ensure species are not extirpated.

Otolith microchemistry can help understand fish migration pathways from birth to capture, because otoliths grow continuously and absorb trace elements from ambient water that reflects the surrounding environment (Campana, 1999; Jones, 1992). This method has been widely used to answer difficult questions about fish ecology (Walther, 2019). Concentrations of elements can be quantified along otolith transects from core (birth) to edge (capture), or elements in the whole otolith can also be mapped to interpret migration tactics. This approach is suitable for understanding diadromous and potamodromous fish migrations within a complex river such as the Mekong.

Migration tactics of most Mekong fishes are poorly understood. Limited information on fish migration is a critical knowledge gap for management and conservation (Baran, 2006; Vu et al., 2020). In this study, migration tactics of six Mekong fish species were investigated to supplement previous research on pangasiid catfishes (Vu et al., 2022). Our objectives were to determine whether (1) migration tactics varied within and among selected Mekong fish species, based on otolith microchemistry and (2) migration tactics were associated with body condition, body length and distance to the sea. We hoped that our findings would contribute to improved management and conservation of migratory fishes and fisheries in the Lower Mekong Basin (LMB), which are threatened by water resource development (Baumgartner et al., 2021; Winemiller et al., 2016).

2 | METHODS

2.1 | Study area

The Mekong River supports over 1000 fish species, the third highest globally (MRC, 2017; Welcomme, 1985). It flows through six countries (China, Lao PDR, Myanmar, Thailand, Cambodia and Vietnam) and is the 10th longest river in the world (Liu et al., 2009). Mekong fisheries play a key role in food consumption and livelihoods for millions of people, particularly in rural communities (Dugan et al., 2010; Ziv et al., 2012). Fisheries yield 2.3 million tonnes of fish worth $11 billion from the LMB each year (So et al., 2015). Around 80% of households in rural areas of Lao PDR, Thailand and Cambodia, and 60%–95% of households in the Mekong delta of Vietnam participate in fishing (Hortle, 2007). Consumption of fish and other aquatic animals averages 62.8 kg per capita per year (So et al., 2015).

The importance of Mekong fisheries is not always recognised by decision-makers because the Mekong capture fishery is underestimated in national statistics (Ainsworth et al., 2021). Additionally, fishers throughout the region have consistently reported declining catch rates, with a trend towards smaller fish sizes and decreasing total value of fish caught (Ngor et al., 2018; Vu, Hortle, & Nguyen, 2021). In particular, catches of many migratory fish species are declining in the Mekong River (MRC, 2017).

2.2 | Otolith collection and preparation

Between 2016 and 2020, 119 individual fish of six species (*Lates calcarifer* (Bloch), *Anguilla marmorata* Quoy & Gaimard, *Pisodonophis boro* (Hamilton), *Hilsa kelee* (Cuvier), and *Polynemus melanochir* Valenciennes and *Plotosus canius* (Hamilton)) were collected from local fishers in the LMB from Luang Prabang (Lao PDR, over 2000 km from sea) to the sea (Figure 1 and Table 1). Specimens were also collected from local markets. These six species were selected because they are all found in both freshwater and brackish or marine habitats associated with the Mekong River, with two likely to be diadromous and four of unknown migratory strategy. *Lates calcarifer* is facultatively catadromous (Crook et al., 2017; Milton & Chenery, 2005), *Anguilla marmorata* is diverse in migration patterns (Arai et al., 2013; Tsukamoto et al., 1998), and other species are of unknown migration patterns. Body length and weight of each individual were measured prior to otolith removal. Pairs of sagittal otoliths were removed for five species (*A. marmorata*, *P. boro*, *H. kelee*, *L. calcarifer* and *P. melanochir*) and lapilli for one species (*P. canius*).

Otoliths were washed and stored in labelled paper envelopes in the field. In the laboratory, otoliths were washed with ultrapure water and ethanol, air-dried and stored separately in labelled plastic bags until embedding in an epoxy resin (Araldite GY502) and hardener (HY956). Each embedded otolith was cut into sections (500–800 μm thickness, including the core) using a low-speed saw (TechCut 4; Allied High Tech) with diamond blades. Otolith sections were then polished by hand using a combination of sandpaper and diamond lapping films, of varying coarseness of grades, until the core appeared. Right and left otoliths were both prepared, and the section with the clearest core was used for trace element analysis. Using only one otolith is appropriate because elemental composition between left and right otoliths is similar (Campana et al., 2000). Polished sections were mounted on microscope slides using thermoplastic glue (CrystalBond 509), and slides were cleaned with
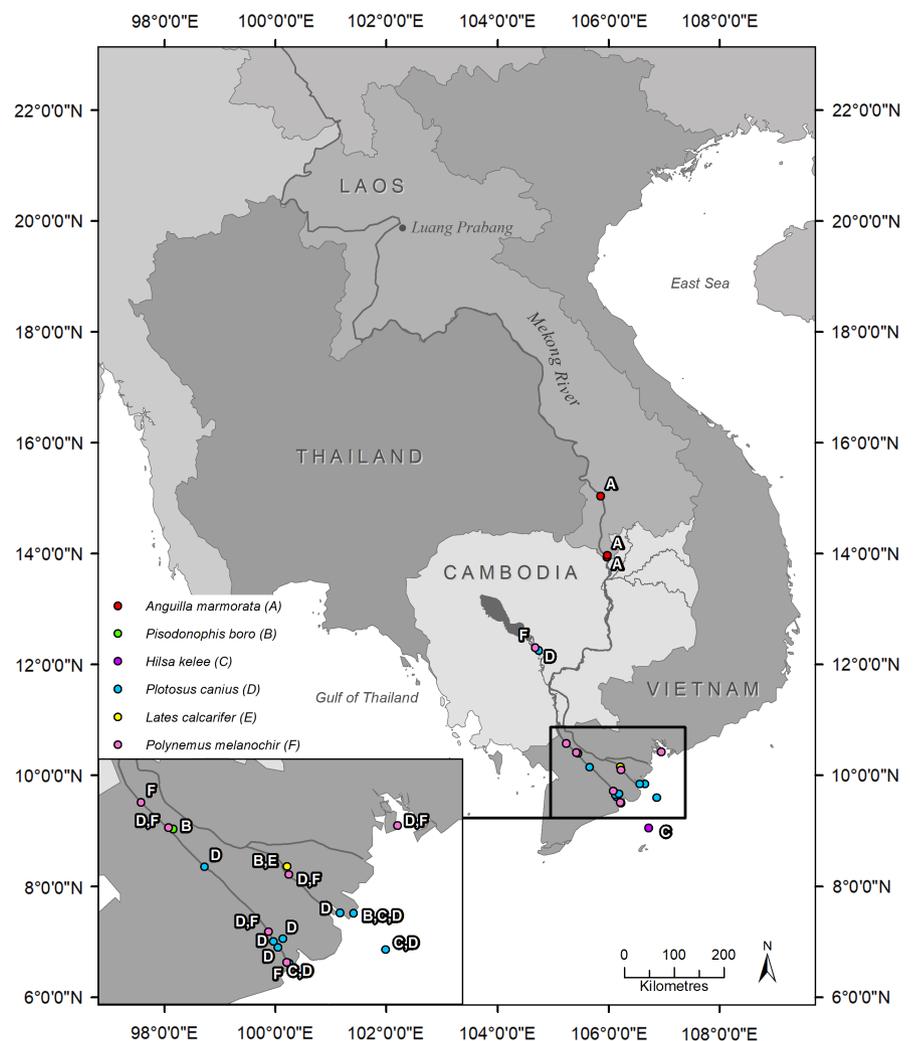

FIGURE 1 Sampling location for fish otoliths in the Lower Mekong Basin. See Appendix S1 for detailed information of each individual specimen

TABLE 1 Fish species collected for otolith microchemistry analysis. F, freshwater; B, brackish; M, marine. Some otoliths were run by both LA-ICPMS and SXFM or only one of these analytical instruments. See Appendix S1 for detailed information of each fish individual

Scientific name	Common name	Capture environment	Mean standard length (cm) ± SD	Number of otoliths for		Speed in elemental analysis of otoliths (µm/s)	
				LA-ICPMS	SXFM	LA-ICPMS	SXFM
Anguilla marmorata	Giant mottled eel	F	96.18 ± 23.42	4	4	3	100
Pisodonophis boro	Rice-paddy eel	FB	59.73 ± 10.25	16	4	3	50–100
Hilsa kelee	Kelee shad	BM	18.64 ± 2.30	24	6	3	100–250
Plotosus canius	Gray eel-catfish	FBM	46.10 ± 18.06	38	4	3	100
Lates calcarifer	Barramundi	F	44.50 ± 8.90	4	4	3	100–250
Polynemus melanochir	Blackhand paradise	FB	16.17 ± 2.18	29	4	3	100

ultrapure water in a sonicator for 5 min, dried in a laminar flow hood for ~12 h to eliminate sources of contamination and stored in sealed plastic tubes for trace element analysis. Indium was added to both the CrystalBond and resin at 30 ppm to allow the marginal edge of otolith sections and resin materials to be detected during data processing.

2.3 | Elemental analysis of otoliths

Four elements (^{88}Sr, ^{138}Ba, ^{44}Ca and ^{115}In) were quantified in otoliths using two analytical instruments, laser ablation—inductively coupled plasma mass spectrometry (LA-ICPMS) and scanning X-ray fluorescence microscopy (SXFM), because these elements (including Sr:Ca and Ba:Ca ratios) are highly correlated with ambient salinity in the LMB (Tran et al., 2019; Vu, Baumgartner, et al., 2021). For LA-ICPMS, elements were quantified along a life history transect from the core to the proximal edge of otolith sections using a LA-ICPMS system (New Wave NWR213 and Agilent 7900 ICPMS) at Adelaide Microscopy, University of Adelaide. Line transects were ablated at a pulse rate of 5 Hz, fluence of 10.5 J/cm^2, speed 3 µm/s and spot diameter of 30 µm. Otoliths were pre-ablated to remove dust and contaminants on the sample surface (30 µm/s speed, other parameters the same as analysis). Each analysis included a 30-sec gas background recorded at the start of the analysis with the laser switched off. A glass reference material NIST 612 (National Institute of Standards and Technology) was ablated at the beginning and end of each session, and after every 10 samples, a calcium carbonate pressed powder pellet MACS 3 (US Geological Survey) was analysed at the beginning and end of each session. The NIST 612 and MACS 3 standards were used to correct for drift and instrument mass bias. Data were processed with the Iolite software version 2.5 (Paton et al., 2011) and converted to concentrations using the Trace Elements IS Data Reduction Scheme in the Iolite software. ^{43}Ca was used as an internal standard element (39 wt% Ca) to correct for variation in materials ablated between samples.

While LA-ICPMS was used to analyse otolith transects, SXFM was used to map distributions of ^{88}Sr and ^{44}Ca in otoliths to create two-dimensional Sr:Ca maps for each species (Table 1). Although mapping techniques provide more information in terms of spatial variation of elements, the process is more time-consuming than creating line transects, so only a few otoliths were mapped. The Maia detector with an aluminium foil filter taped onto the front window of the detector array was used to increase sensitivity for trace elements relative to the high calcium fluorescence at the Australian Synchrotron X-ray fluorescence microscopy beamline (Howard et al., 2020). Speed in elemental analysis of otoliths varied between species due to different otolith sizes (see Table 1). GeoPIXE software (version 7.5) was used to process and calibrate SXFM data. Concentrations of Ca quantified from LA-ICPMS were used to calibrate for SXFM data. Two-dimensional Sr:Ca maps were produced using ArcMap (version 10.6).

2.4 | Data analysis and classification of fish migration

Otolith Sr:Ca and Ba:Ca ratios were smoothed using a 7-point moving average to reduce noise for LA-ICPMS data. Profiles of these ratios were plotted from the core to the edge of the otolith together with thresholds of environments (fresh, brackish and marine waters) to interpret migratory strategies. A fish was classified as resident in (1) fresh water if the Sr:Ca ratio (×1000) was ≤3.25, (2) marine water if the Sr:Ca ratio (×1000) was >10.17, and brackish water if the Sr:Ca ratio was between the above thresholds (Vu et al., 2022). Thresholds were established by quantifying elements in otoliths that were collected from aquaculture systems (known salinity). Additionally, the regime shift technique (Rodionov, 2004) was used to distinguish zones along a transect profile that were chemically different between adjacent zones. A new regime shift or otolith zone was created if mean values of two adjacent zones differed significantly using a two-tailed Student's *t*-test. $p < 0.01$ was set to distinguish zones along an otolith transect that differed chemically between adjacent zones or between environments or habitats. These zones can be referred to environments or habitats because elemental concentrations (e.g. Sr:Ca and Ba:Ca) between zones differed significantly.

Migration tactics of the six species (Table 1) were classified as diadromous (anadromous, catadromous and amphidromous), or fresh

water, estuarine or marine. Classification was based on thresholds of habitat use (Sr:Ca ratios; Figure 2). Individual fish was grouped into similar migration patterns by examining variation of Sr:Ca ratios at the core (spawning biome) and along the otolith chemistry profile (movement or not into other biomes). This classification was previously described (Arai & Chino, 2018; Arai et al., 2013).

In addition, three factors (body condition, standard length and distance of capture location to the sea) were compared between migrants and residents of *P. canius* and *P. melanochir* because sampling sites of these species covered a large area of the LMB with larger sample sizes. A Wilcoxon test was used to compare average body condition, standard length and capture location against two independent groups (migrants versus residents). Fulton's index ($K = 100 \times W/L^3$, where W is body weight in g and L is standard length in cm) was used to assess body condition for each individual. Fish body condition changes over time, but was only determined at the time of capture, so was assumed to correlate to body condition (Fulton, 1904). Individuals were assigned as residents if they stayed in the same environment or migrants if they stayed in different environments.

3 | RESULTS

Variation in Sr:Ca and Ba:Ca ratios at the core and edge of otoliths (Figure 3) and otolith chemistry profiles (Figures 4–9) identified two catadromous species (*A. marmorata* and *P. boro*), and one estuarine

resident (*L. calcarifer*). Three other species (*H. kelee*, *P. canius* and *P. melanochir*) did not fit into migratory categories (Figure 2) because they displayed up to four migration patterns within a species.

For *A. marmorata*, ratios of Sr:Ca (×1000) along the otolith profile (mean = 1.70; range = 0.63–19.01; n = 4) indicated typical catadromous migration, with high Sr:Ca ratios at the core that dropped sharply from the core to the edge of otolith. Two groups were identified (four samples) based on variation in Sr:Ca ratios (Figure 4): (1) Pattern 1 (three of four samples) had high Sr:Ca ratios at the core, but dropped quickly and remained low all the way to the edge of otoliths. This suggests that they spawned at sea, glass eels then moved immediately to the river for feeding with no signature indicating return to the sea. One individual likely showed a brackish or coastal origin because Sr:Ca ratios (×1000) were 7.81 at the core; and (2) Pattern 2 (1 of 4 samples) spawned in brackish or marine water, glass eels or elver then moved to water with lower salinity (possibly the estuary), then moved between fresh and brackish waters for about 1 year, before migrating to the fresh water in the river where they spent the remainder of their life.

For *L. calcarifer*, ratios of Sr:Ca (×1000) along the otolith profile (mean = 6.52; range = 3.34–16.19; n = 4) indicated they were estuarine residents that did not enter fresh water. Two groups were identified within this species (Figure 5): (1) Pattern 1 (2 out of 4 samples) always remained in brackish water, with no connection to either fresh or marine waters; and (2) Pattern 2 (2 out of 4 samples) moved between brackish and marine waters, with some individuals of marine origin and others of brackish origin.

FIGURE 2 Hypothetical diagram of life histories in relation to Sr:Ca ratios in fish otoliths. An otolith image (bottom) shows a core, annual growth rings, and a life-history transect/profile. Variation of Sr:Ca ratios from core (formed at birth) to edge of otolith (formed just before capture) reflects movements between environments during a fish's life. Fish species remain alive after spawning—multiple spawning times (iteroparous) while some species die after first spawning—spawning once only (semelparous)
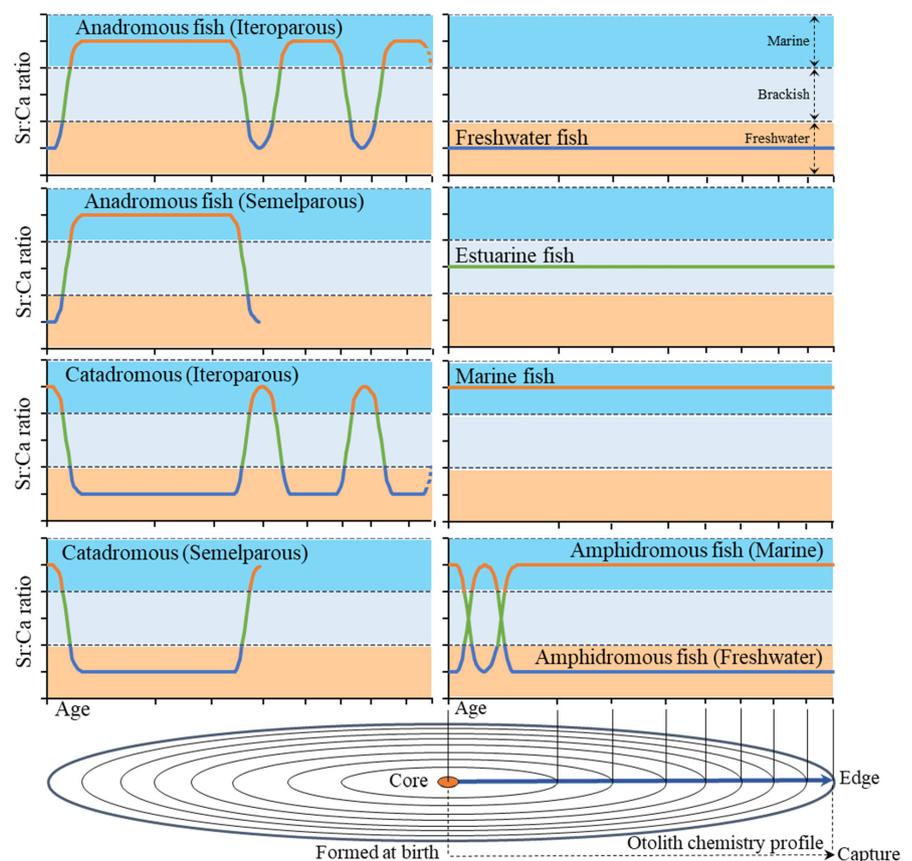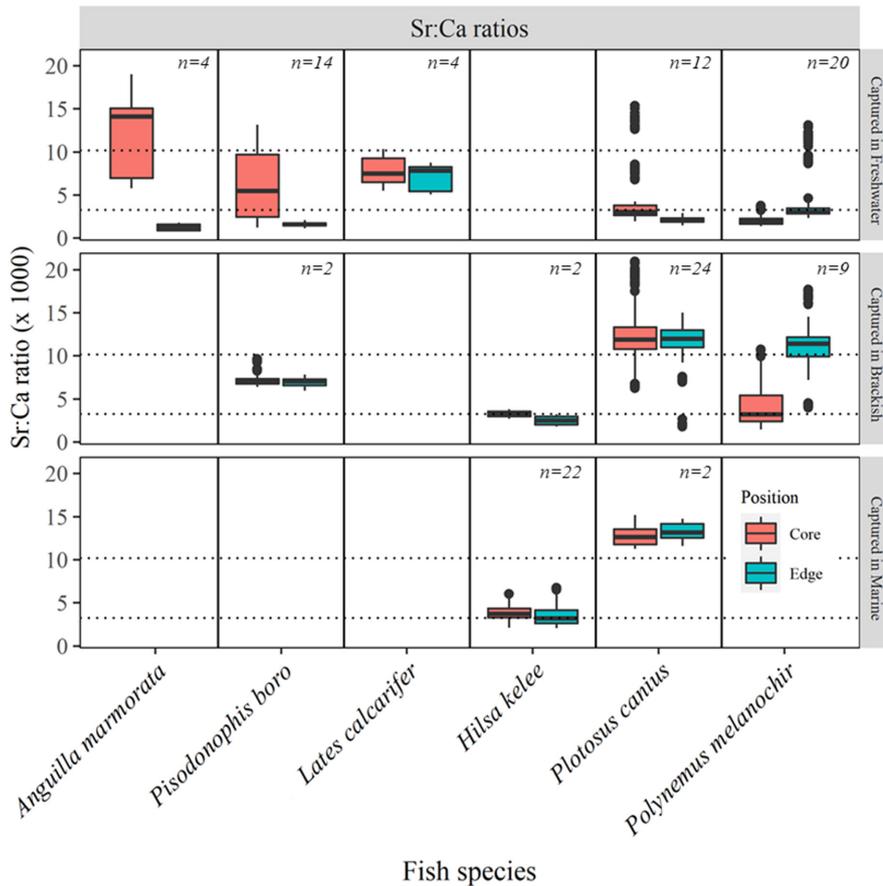
FIGURE 3 Box plots showing variations of Sr:Ca ratios at the core (birth: in orange) and edge (capture: in green) of otoliths of Mekong fishes at different capture environments. Box plots show minimum, maximum, and median values, outliers (data points lay outside the whiskers at 1.5 times the interquartile range above the upper quartile and below the lower quartile), and interquartile range in the data set. "*n*" indicates sample sizes. Dashed horizontal lines are environmental thresholds (freshwater residence if $y < 3.25$; brackish water residence if $3.25 \leq y < 10.17$; and marine water residence if $y > 10.17$). See Appendix S2 for Ba:Ca ratios

For *P. boro*, Sr:Ca ratios (×1000) along the otolith profile (mean = 2.18; range = 0.77–13.14; *n* = 16) indicated it was catadromous, with three different migration patterns (Figure 6): (1) Pattern 1 (50% of samples) was typically catadromous, with spawning in marine water, glass eels moving immediately to the river for feeding without returning to the sea; (2) Pattern 2 (12% of samples) was also typically catadromous, with spawning in brackish or marine water, glass eels moving to the river for a short period before returning to brackish water until capture; and (3) Pattern 3 (38% of samples) spawned and remained in the river for their entire lives with no evidence of life in brackish or marine waters.

For *H. kelee* (previously unknown migration strategies), ratios of Sr:Ca ×1000 (mean = 3.04; range = 0.22–7.35; *n* = 24) along the otolith profile indicated three patterns (Figure 7). Fish exhibiting pattern 3 (33% of samples) were potentially catadromous, while fish displaying patterns 1 (42% of samples) and 2 (25% of samples) were of flexible origin and movement, including lowland freshwater residency and movements into the estuary: (1) Pattern 1 (42% of samples) was estuarine, with juveniles remaining in the fresh water–estuarine transition zone, and some older fish (possibly subadults or adults) entering brackish waters; (2) Pattern 2 (25% samples) was estuarine, but frequently entered brackish, probably marine, waters as subadults or adults, and sometimes more than once; and Pattern 3 (33% of samples) was brackish in early life, but entered fresh water and returned to brackish water in later life, possibly as subadults or adults.

For *P. canius* (previously unknown migration strategy), Sr:Ca ratios (×1000) varied greatly along otolith profiles (mean = 8.52; range = 0.95–20.92 *n* = 38), with four distinct groups (Figure 8): (1) Pattern 1 (24% of samples) indicated the fish were freshwater residents (Sr:Ca ratios in otoliths were consistently low), with no connection to either brackish or marine waters; (2) Pattern 2 (21% of samples) was marine resident (Sr:Ca ratios in otoliths were consistently high), and sometimes moved to brackish water, but not into fresh water; (3) Pattern 3 (34% of samples) was potentially amphidromous (marine) and spawned in marine water, while fry, fingerlings and juveniles moved immediately to fresh water before returning to marine water; and (4) Pattern 4 (21% of samples) was of estuarine–marine transition origin, with fry and fingerlings drifting to the sea for a short time, before migrating to brackish water and returning to the sea until capture.

For *P. melanochir*, migration patterns were complex among four groups (Figure 9). Ratios of Sr:Ca (×1000) varied greatly along otolith profiles (mean = 4.73; range = 1.23–21.90; *n* = 29), with four groups: (1) Pattern 1 (48% of samples) was freshwater residents (Sr:Ca ratios in otoliths were consistently low), with no connection to either brackish or marine waters; (2) Pattern 2 (21% of samples) spawned in fresh water, with larvae and juveniles remaining in fresh water before moving to marine water; (3) Pattern 3 (17% samples) was similar to pattern 2, but they returned to fresh water after migrating to marine water; and (4) Pattern 4 (14% of samples) was of brackish origin, but regularly migrated between brackish and marine waters, with no connection to fresh water.
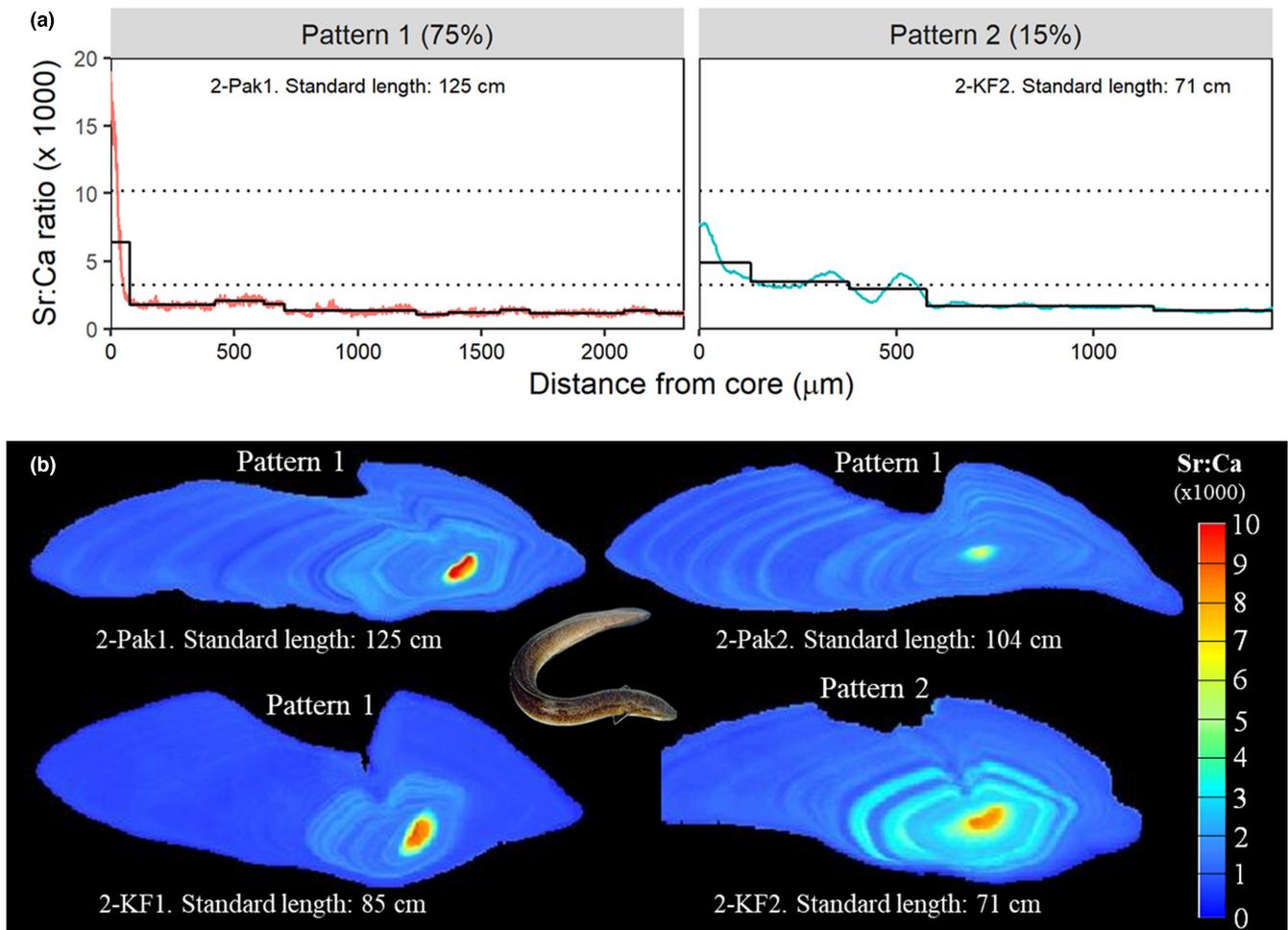
FIGURE 4 Variations of Sr:Ca ratios from core to edge of otoliths of *Anguilla marmorata*. (a) Dashed horizontal lines are environmental thresholds: freshwater residence if $y < 3.25$; brackish water residence if $3.25 \leq y < 10.17$; and marine water residence if $y > 10.17$. Black lines indicate Sr:Ca ratios that are chemically different between two adjacent zones (identified by regime shift analysis). (b) Two-dimensional Sr:Ca ratio maps. See Appendix S3 for individual plots of Sr:Ca ratios and Ba:Ca ratios. Specimen codes and total length are indicated

Migrants and residents differed significantly in capture location ($z = -2.37$; $p < 0.05$) and body length ($z = -2.03$; $p < 0.05$), but not in body condition ($z = -1.18$; $p > 0.05$) (Figure 10). For example, Mekong fish (e.g. *P. melanochir*) migrated between fresh and marine waters if they were near the Mekong estuary, but not if they were farther upstream (>150 km). Fish were more likely to migrate when they were young and small (e.g. *P. canius* ≤25 cm) than when they were older and large (>25 cm). Mekong fishes tended to migrate between fresh and brackish waters if they were in better condition, although migration was not significantly correlated to body condition.

4 | DISCUSSION

4.1 | Plasticity of fish migration

Migration in fishes has been defined as large numbers of fish within a population regularly moving between habitats (Northcote, 1978). However, Mekong fish species exhibited multiple strategies within

and between species to optimise their growth and survival (this study; Vu et al., 2022). Migrant (migrating between fresh and marine waters with multiple strategies) and resident (either in fresh or marine waters) components of populations were evident in Mekong fish species. Plasticity in fish migration strategies (facultative migration), such as in eels and salmonids, is also common in other river systems (Chapman, Skov, et al., 2012; Limburg et al., 2001; Secor & Kerr, 2009). This has considerable implications for understanding ecological implications of migration at both the species and individual level for improved management and conservation in tropical river systems. Management plans or mitigation measures should reflect such diversity of migration strategies between and within a species to sustain fisheries resources for conservation, food security, and livelihoods of millions of local people (Schindler et al., 2010; Waldman et al., 2016).Eels in the Mekong River (*A. marmorata* and *P. boro*) are catadromous. However, both species were diverse in migration strategies (obligatory and facultative). Similarly, several strategies have been found in *A. marmorata* in other river systems (Arai & Chino, 2012; Arai & Chino, 2018). None of the *A. marmorata*
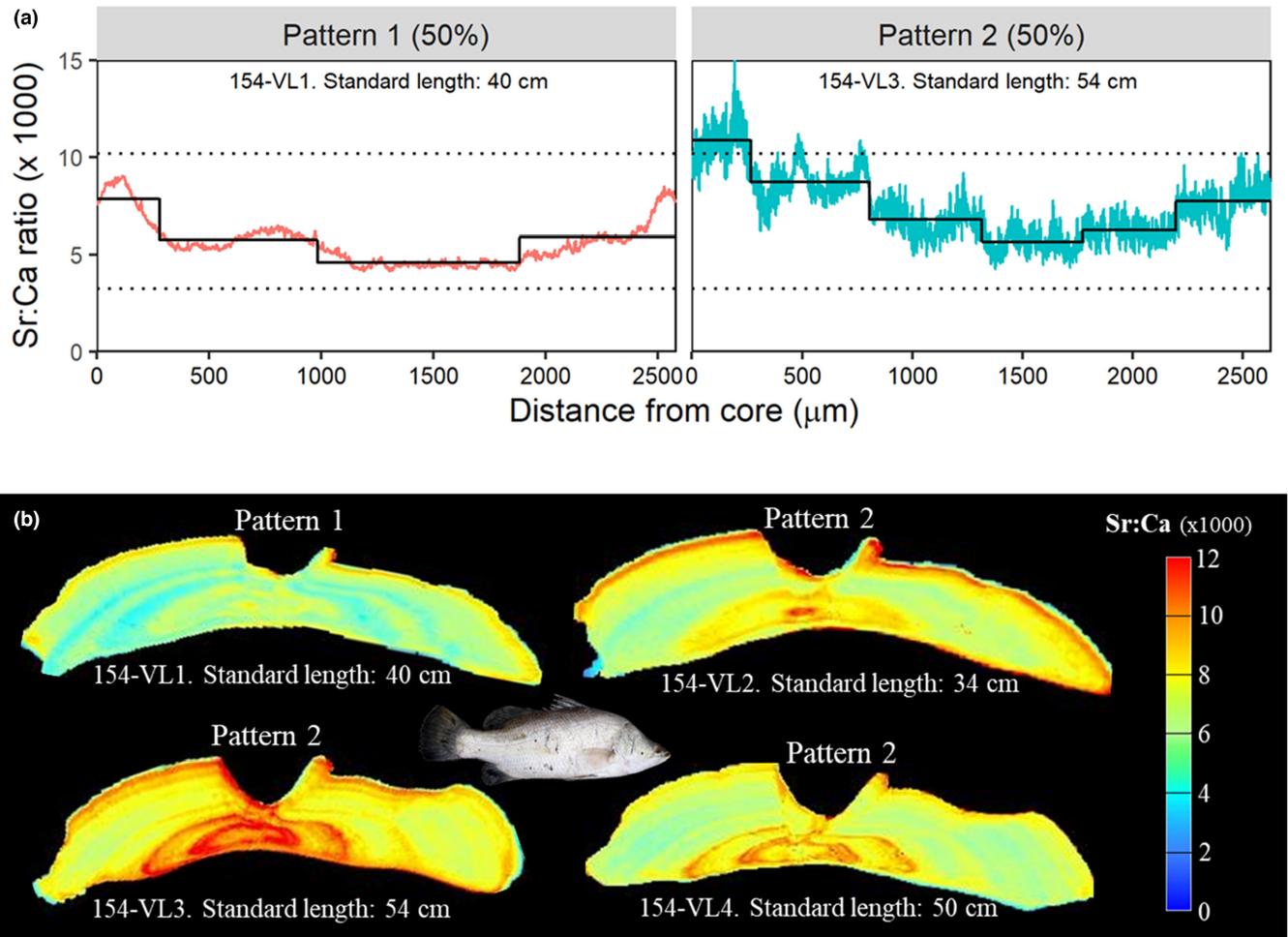
(a)

(b)

FIGURE 5 Variations of Sr:Ca ratios from core to edge of otoliths of *Lates calcarifer*. (a) Dashed horizontal lines are environmental thresholds: freshwater residence if $y < 3.25$; brackish water residence if $3.25 \leq y < 10.17$; and marine water residence if $y > 10.17$. Black lines indicate Sr:Ca ratios that are chemically different between two adjacent zones (identified by regime shift analysis). (b) Two-dimensional Sr:Ca ratio maps. See Appendix S3 for individual plots of Sr:Ca ratios and Ba:Ca ratios. Specimen codes and total length are indicated

collected in the Mekong River returned to the sea, because no marine signature was detected along otolith profiles (550 μm apart from the core to the edge of otolith, probably 1 year old), which may be due to a small sample size or because they were captured prior to emigration for spawning. Also, chemical analyses may not detect a marine signature if residence in brackish water was too brief, because at least 20 days of exposure is required for otoliths to fully reflect ambient water chemistry (Elsdon & Gillanders, 2005). However, this was unlikely in our study because specimens were collected in the Mekong River, about 700 km from the sea and *A. marmorata* is a slow swimmer (Hikaru & Ryoshiro, 2020). Migration of *P. boro* was similar to that of *A. marmorata*, but with more diverse migration strategies. For example, consistently low Sr:Ca ratios suggest that they spawned and remained in fresh water throughout life (Rainboth, 1996). Meanwhile, other individuals migrate between fresh and marine waters (catadromy; Riede, 2004).

Australian *L. calcarifer* have three migration strategies, estuarine, catadromy—sequential hermaphrodism and catadromy—delayed female spawning (Crook et al., 2017), while Mekong barramundi have two migration strategies ($n = 4$ individuals). Mekong barramundi were mainly distributed along the coast, and only rarely in the Mekong

River, up to 650 km from the coast. Interestingly, faster growth rates of *L. calcarifer* in fresh water than in brackish water (Milton et al., 2008) suggest that a connection between fresh and brackish waters may be critical for fast growth. Migration strategies of other Mekong species (*P. melanochir*, *P. canius* and *H. kelee*) were also more diverse than previously understood. Migratory (with multiple migration strategies between fresh and marine waters) and resident (in both fresh and marine waters) individuals existed within these species. This diversity of migration patterns within species complements that found for pangasiid catfishes in the Mekong, where at least three migratory tactics were found among individuals within each species (Vu et al., 2022). Further, although only a few individuals of some species, such as *A. marmorata* and *L. calcarifer*, were sampled in this study, increased sample size of these species from a greater array of habitats could result in identification of a higher number of migratory tactics than we observed. Similarly, if otolith microchemistry studies are carried out on more species, a diverse array of migratory tactics will likely be found among and within more species in the Mekong region, and other large species-rich rivers in tropical and subtropical regions.

Understanding mechanisms and implications of facultative migration is essential for management and conservation (Lennox
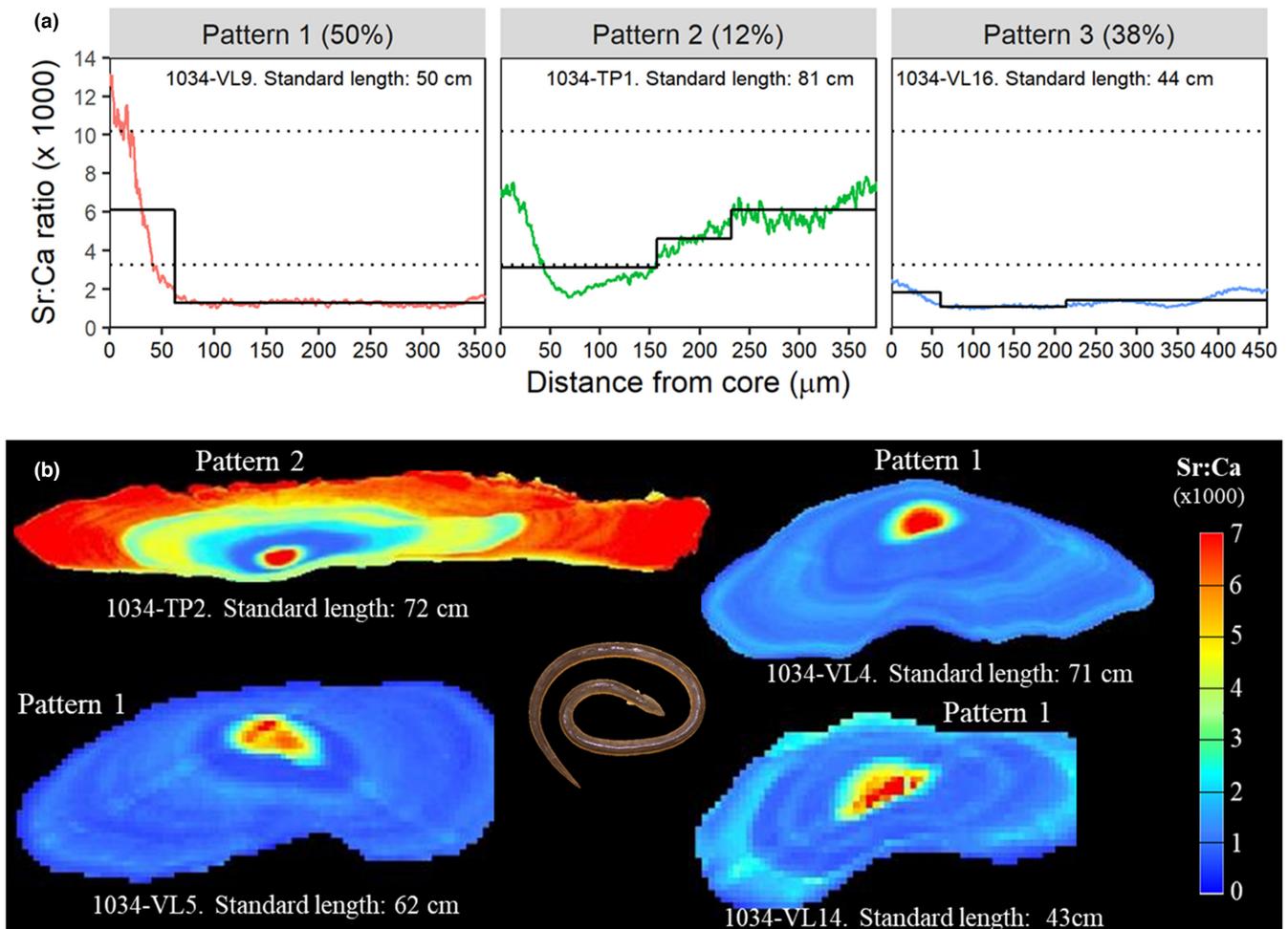
FIGURE 6 Variations of Sr:Ca ratios from core to edge of otoliths of *Pisodonophis boro*. (a) Black solid lines indicate Sr:Ca ratios that are chemically different between two adjacent zones; dashed horizontal lines are environmental thresholds: freshwater residence if $y < 3.25$; brackish water residence if $3.25 \leq y < 10.17$; and marine water residence if $y > 10.17$. Black lines indicate Sr:Ca ratios that are chemically different between two adjacent zones (identified by regime shift analysis). (b) Two-dimensional Sr:Ca ratio maps (only two patterns are showed; all transverse sections, except the 1034-TP2: frontal section). See Appendix S3 for individual plots of Sr:Ca ratios and Ba:Ca ratios. Specimen codes and total length are indicated

et al., 2019). Previous studies mostly investigated causes of such migration (Brodersen et al., 2014; Chapman, Hulthén, et al., 2012), while the identification of consequences of these migration strategies was limited. Flexible migration can affect ecosystem functioning, such as nutrient and energy flow, the food chain, parasites and eco-evolution (Brönmark et al., 2014). Some species are semelparous (dying after spawning, such as Pacific salmon), and their carcasses contribute ocean-derived nutrients to freshwater food webs (Schindler et al., 2003). However, semelparous fish species have not yet been found in the Mekong River. Moreover, evolutionary effects are important for flexible migration and migratory fishes are necessarily adapted to different environmental conditions along migration routes (Corush, 2019). For example, climate change and other anthropogenetic impacts may contribute to flexible migration patterns in fish populations. In addition, growth rates or body sizes can differ between migrants and residents (Barrow et al., 2021; Gillanders et al., 2015), so decision-makers should manage these differently to maintain biodiversity and intraspecific diversity.

Migration strategies can vary among species and individuals within a species. Migration may be functional (e.g. reproduction, feeding and refuge-seeking) or habitat requirements (e.g. anadromy, catadromy, amphidromy, potamodromy and oceanodromy) to optimise growth or survival (Lucas & Baras, 2001; Myers, 1949; Northcote, 1978). Migration patterns differed among fish species and among individuals within the same species (this study; Vu et al., 2022). Migratory and resident individuals co-existed in the same species, with up to four migration strategies. Body length and capture location were significantly related to migration or residency strategy, while body condition did not differ significantly between migrants and residents (Figure 10). Elsewhere, migration was related to body condition (Brodersen et al., 2008), and smaller individuals tended to migrate more than larger individuals (Chapman, Hulthén, et al., 2012). Additionally, we found that Mekong fishes likely migrated between fresh and marine waters if they were near river mouths, but remained in fresh water if they were farther upstream (>150 km from the estuary).
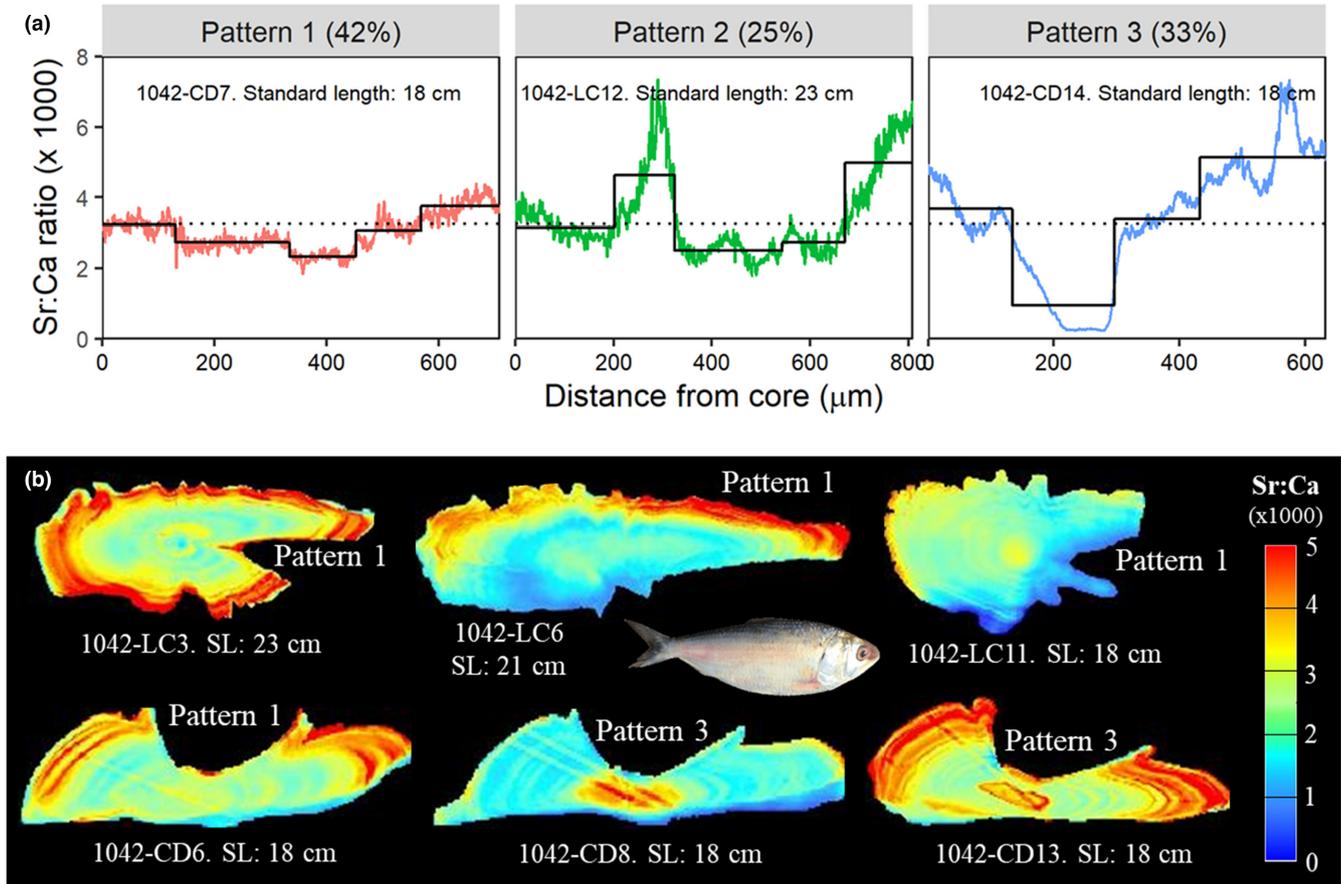
FIGURE 7 Variations of Sr:Ca ratios from core to edge of otoliths of *Hilsa kelee*. (a) Black solid lines indicate Sr:Ca ratios that are chemically different between two adjacent zones; dashed horizontal lines are environmental thresholds: freshwater residence if $y < 3.25$; brackish water residence if $3.25 ≤ y < 10.17$; and marine water residence if $y > 10.17$. Black lines indicate Sr:Ca ratios that are chemically different between two adjacent zones (identified by regime shift analysis). (b) Two-dimensional Sr:Ca ratio maps (only two patterns are showed; the top row are sagittal and the bottom row are transverse sections). See Appendix S3 for individual plots of Sr:Ca ratios and Ba:Ca ratios. Specimen codes and fork length are indicated

Diversity of migration tactics within species may reflect individuals with repeated migratory behaviour between generations, or individuals that are euryhaline opportunists that respond to competition and available food resources. An early and widely accepted explanation for diadromy is the productivity hypothesis, which proposes that predominance of anadromous species in temperate waters and catadromous species in tropical waters is due to the difference in productivity of marine and freshwater biomes at these latitudes (Gross et al., 1988). However, this theory was disputed as simplistic (McDowall, 2008). Anadromous and catadromous species likely represent equal proportions of fish species in the LMB (Vu et al., 2020).

Another explanation for anadromy is the "safe-site hypothesis" (Bloom & Lovejoy, 2014; Dodson et al., 2009) that proposes freshwater habitats provide a safe location for larvae and young fish. This helps explain anadromy in temperate river systems with low diversity, but does not inform anadromy in diverse tropical rivers, diadromous strategies with larvae in estuarine or marine waters (catadromy and freshwater amphidromy), or variable migrations in the present study.

Catadromy in temperate rivers and freshwater amphidromy on tropical oceanic islands are associated with low species diversity, which would favour adult growth. In these groups, tolerance of salinity is narrow in larvae within a species (Iida et al., 2010), possibly reflecting a marine ancestry (Bloom & Lovejoy, 2014), while plasticity within species appears uncommon (Augspurger et al., 2017; Smith & Kwak, 2014). Our results suggest another migratory pattern in tropical rivers, high plasticity within species with early life stages and adults in fresh water tolerating a range of salinities.

Most riverine species in the Mekong River that spawn in the main channel are pelagophils (have drifting larvae) (Cowx et al., 2015), which is a tactic shared by anadromous species in large tropical rivers (e.g. *Pangasius krempfi* in the Mekong River; *Hilsa* spp. in the Ganges River; *Brachyplatystoma* spp. in the Amazon River). In such rivers, the fast-flowing, lotic river channel might be a "mobile safe site," where larvae can obtain a critical first-feeding at very small spatial scales, while the broader lotic environment offers feeding opportunities and protection from predation at larger spatial scales. The potential risk of this strategy is that, depending on flow and location, drift can result in exposure to
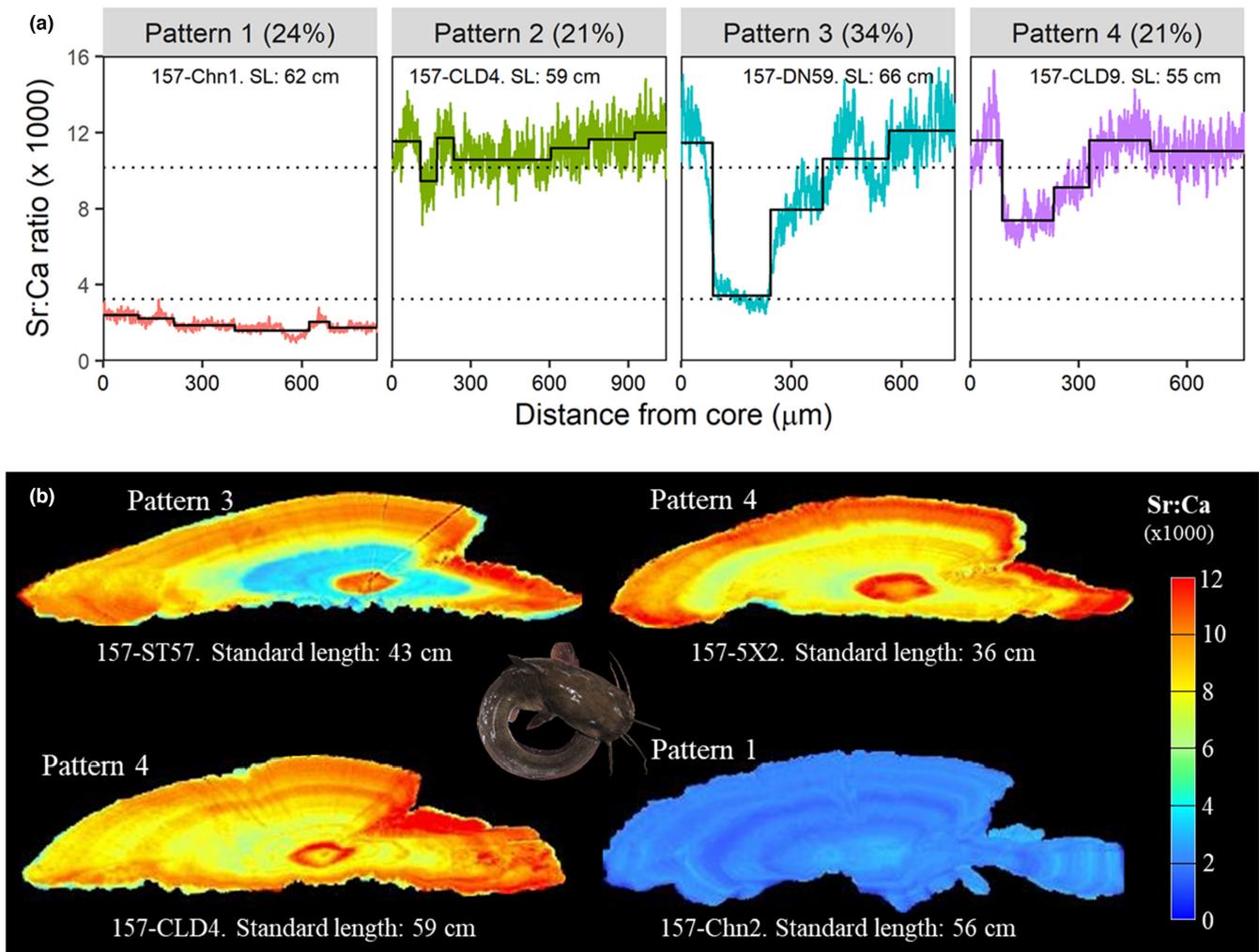
FIGURE 8 Variations of Sr:Ca ratios from core to edge of otoliths of *Plotosus canius*. (a) Black solid lines indicate Sr:Ca ratios that are chemically different between two adjacent zones; dashed horizontal lines are environmental thresholds: freshwater residence if $y < 3.25$; brackish water residence if $3.25 \leq y < 10.17$; and marine water residence if $y > 10.17$. Black lines indicate Sr:Ca ratios that are chemically different between two adjacent zones (identified by regime shift analysis). (b) Two-dimensional Sr:Ca ratio maps. See Appendix S3 for individual plots of Sr:Ca ratios and Ba:Ca ratios. Specimen codes and total length are indicated

brackish or marine salinities, so plasticity is an advantage. Goliath catfishes (*Brachyplatystoma* spp.) exhibit this migratory plasticity in the Amazon River (Hauser et al., 2020; Hegg et al., 2015), and our study provides further evidence to support plasticity. Indeed, in megadiverse tropical rivers, migratory plasticity within species may be the norm that provides diverse opportunities while spreading risk in a competitive environment akin to a "portfolio" strategy (Moran et al., 2016; Schindler et al., 2010).

Causes and consequences of migration or residency of an individual can be explained in terms of benefits and risks (Figure 11). Whether an individual migrates or remains resident may be explained by one of three questions: (1) What are the benefits of migration (increased growth, reproductive success, food availability, refuge and predation avoidance); (2) What are the risks of migration (increased fishing, predation, stress, parasite and disease); and (3) What are the costs of migration (energy availability, long or short migration route)? This framework shows that fishes tend

to migrate whether benefits outweigh risks, and costs associated with migration to maximise growth and survival; otherwise, they tend to stay. In a river like the Mekong, with its dynamic hydrology and high intra- and inter-annual variability, each of these situations may depend on prevailing conditions. Risks and benefits would change depending on whether it was a dry or wet year, for example. Previous studies found that migratory individuals tend to grow faster than residents (Gillanders et al., 2015; Milton et al., 2008). Hence, this framework is useful to explain why some individuals migrate while others may not. Similarly, trade-offs of growth predation or cost–benefit of migration were also used to examine causes of facultative migration elsewhere (Brodersen et al., 2008; Brönmark et al., 2014).

Migration versus residency can also be affected by natural and anthropogenic barriers, such as waterfalls or dams, which may also result in landlocked populations (McDowall, 1988). Areas sampled in our study do not have any barriers to migration (Khone Falls to
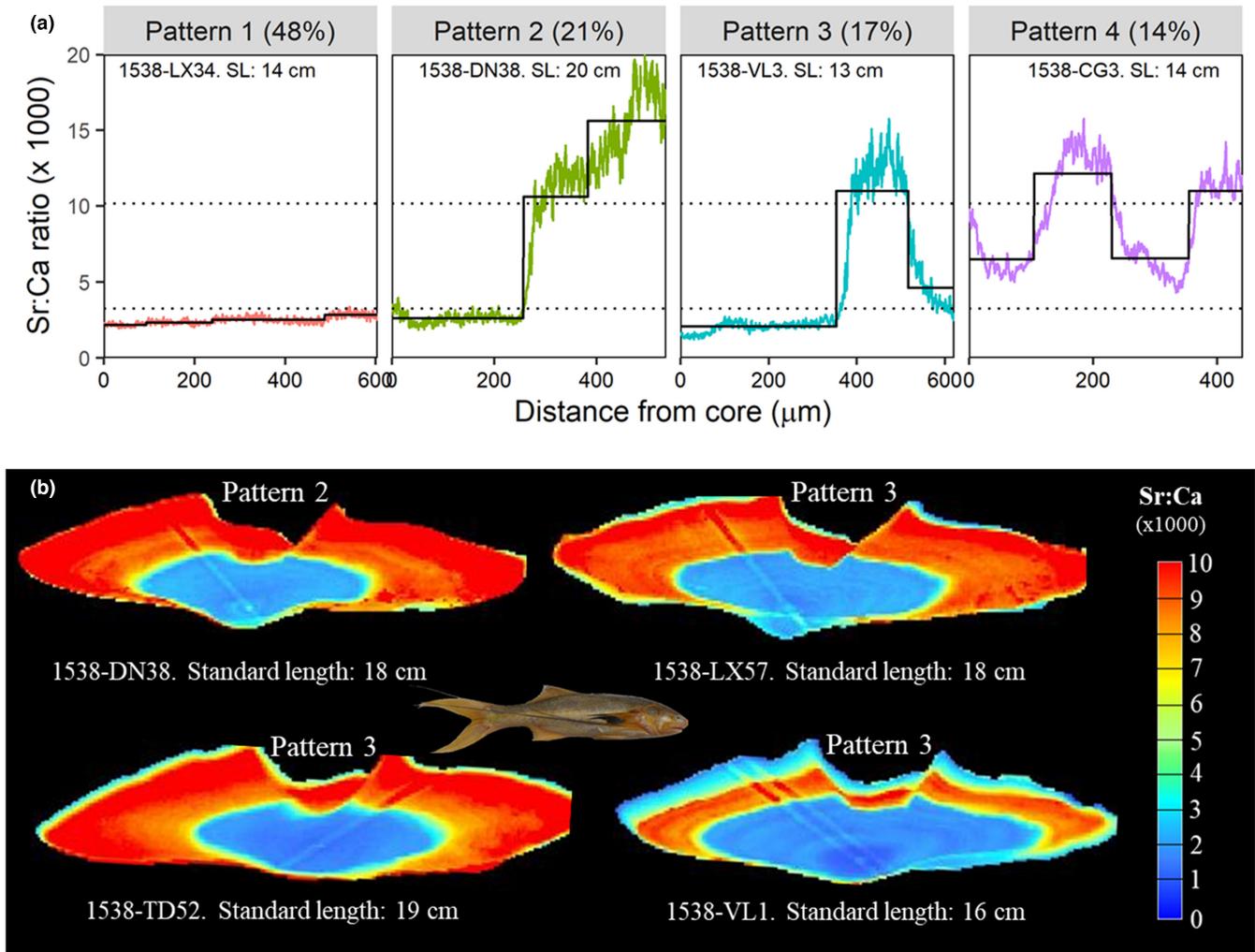
FIGURE 9 Variations of Sr:Ca ratios from core to edge of otoliths of *Polynemus melanochir*. (a) Black solid lines indicate Sr:Ca ratios that are chemically different between two adjacent zones; dashed horizontal lines are environmental thresholds: freshwater residence if $y < 3.25$; brackish water residence if $3.25 \leq y < 10.17$; and marine water residence if $y > 10.17$. Black lines indicate Sr:Ca ratios that are chemically different between two adjacent zones (identified by regime shift analysis). (b) Two-dimensional Sr:Ca ratio maps. See Appendix S3 for individual plots of Sr:Ca ratios and Ba:Ca ratios. Specimen codes and fork length are indicated

the Mekong estuary), but we showed that some individuals migrated while others did not. Therefore, barriers are unlikely to cause facultative migration, whereas other factors such as body condition and food availability may contribute to the diversity of Mekong fish migration tactics. Individuals of some Mekong fish species (e.g. *P. canius* and *P. melanochir*) may tend to stay whether they are safe from predators and have suitable food available. By contrast, some species (e.g. *P. krempfi* and *P. mekongensis*) require regular migrations between critical habitats to complete their life cycle (Vu et al., 2022). In this case, barriers along their migration routes can impact population sustainability.

4.2 | Options for barriers to fish migration

Populations of many migratory species in the Mekong have declined over time due to different factors, such as barriers and

fishing pressure (MRC, 2017; Ngor et al., 2018; Vu, Hortle, & Nguyen, 2021). To help manage and conserve these species, a sound understanding of life cycles of species of interest and diversity of migration strategies is required. Fishes require free-flowing migration routes to access critical habitats for spawning, feeding and refuge, and can be threatened if one habitat is degraded or becomes inaccessible. Facultative migrants are less vulnerable to river development because they comprise different components of populations that are distributed in different habitats (Chapman, Hulthén, et al., 2012). The Mekong River from the estuary to the reach upstream of Khone Falls, which is a complex waterfall system with natural, passable, channels, is the most important migration route for Mekong fish species. This is especially true for long-distance migratory species (including diadromous species) because 67% of Mekong fish species use this reach of the river (MRC, 2017). However, the main passable channel at Khone Falls was blocked by the Don Sahong hydropower dam in 2018 that

FIGURE 10 Comparison of Fulton index, standard length, and capture location between migrants and residents of *Plotosus canius* and *Polynemus melanochir*. "*" denotes significant difference at $p \leq 0.05$ while "ns" denotes not significant difference ($p > 0.05$)
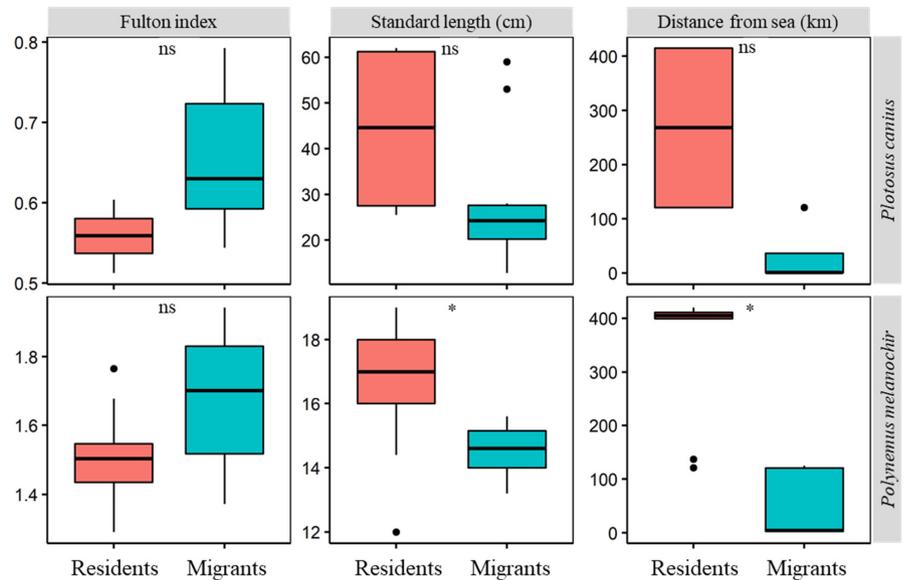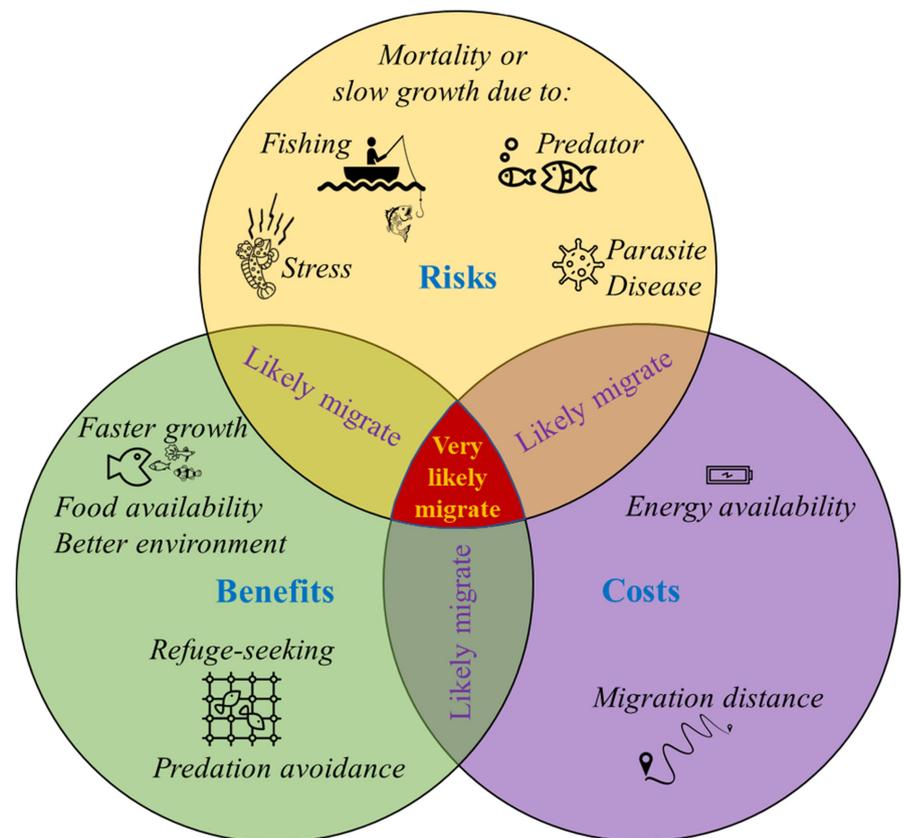

FIGURE 11 A conceptual model of competition pressure encouraging flexible migration strategies within a species

left hydraulically less desirable side channels with less discharge for fish migration. In addition, two dams may be built upstream of Khone Falls at Phou Ngoy (formally Lat Sua) and Ban Koum up and downstream of Pakse, and two dams (Stung Treng and Sambor) are planned downstream of Khone Falls (Campbell & Barlow, 2020). These dams will block fish migration to spawning and feeding habitats that may seriously impact Mekong fisheries and livelihoods of millions of people in the basin unless suitable fishways and downstream migration facilities are included in their designs (Baumgartner et al., 2014; Campbell & Barlow, 2020; Dugan

et al., 2010). Moreover, flood pulses are an important cue for fish migration that can be altered by barriers such as dams.

Fortunately, construction of the two planned mainstream dams (Stung Treng and Sambor) has been suspended pending further consideration of negative impacts on Mekong fisheries (Campbell & Barlow, 2020). Resumption of construction of these two dams and two dams above Khone Falls (Phou Ngoy and Ban Koum) would seriously threaten migration of all long-distance migrants between critical habitats in the LMB because critical spawning areas are around Khone Falls, including for anadromous species. The rate of

successful fish passage must meet a target of 60%–87% to maintain populations of smaller species with the presence of only one dam, but this increases to 80%–95% for the presence of two or three dams (Halls & Kshatriya, 2009). Such high passage efficiency will be difficult to meet in a tropical river system like the Mekong with over 1000 fish species. The technology used in current fishways cannot deal with migrations of such a large number of individuals and biomass through dams in the Mekong (Dugan et al., 2010). In addition, most long-distance migrants in the Mekong are pelagophils (have drifting larvae) that require a connected lotic (flowing) river and experience high mortality in lentic habitats upstream of dams where flow maintaining the drift is dissipated (Cowx et al., 2015; Dudley & Platania, 2007). Consequently, no fisheries of long-distance migratory fish are sustained upstream of dams in large tropical rivers (Winemiller et al., 2016). If sustaining food security and livelihoods of a capture fishery valued at $11 billion per annum (So et al., 2015) is considered a high priority, then no further dams should be built in the lower mainstem Mekong River.

CONFLICT OF INTEREST

We declare that we have no conflicts of interest. Mr. An V. Vu is an Australia Awards scholar but the viewa and opinions expressed in this paper do not represnent of the Australian Goverment.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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