



Diversity in habitat use by the East Asian fourfinger threadfin *Eleutheronema rhadinum* revealed by otolith Sr:Ca and Ba:Ca profiles

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ABSTRACT: Determining the movement and migration patterns of fish between different environments is crucial for understanding the distribution of fish populations and the ecological mechanisms underlying their spatial dynamics. This study is the first to employ otolith Sr:Ca and Ba:Ca profiles to elucidate habitat use by the commercially valuable estuarine species *Eleutheronema rhadinum*. Age 1+ fish were present in samples from the East China Sea and South China Sea, caught off China in October to December of 2019. Characterization of both otolith element profiles through a quantitative approach suggested migration plasticity for *E. rhadinum*, especially during the first year. However, the Ba:Ca profile revealed a more distinct pattern of habitat use compared with the Sr:Ca profile, suggesting that the Ba:Ca ratio is more appropriate for life-history reconstruction of this species. Most individuals appeared to be estuary-dependent, with some appearing to have entered fresh water for a short time during their first year of life. After their first winter, individuals tended to move into coastal waters, and most apparently overwintered in the marine environment. Knowledge of the diverse life-history strategies of this valuable species at different life stages should be incorporated into future conservation and management efforts.

KEY WORDS: Life history \cdot Winter period \cdot Migration plasticity \cdot Eleutheronema rhadinum \cdot Otolith chemistry

1. INTRODUCTION

Life-history characteristics are a critical aspect of the ecology of aquatic species; therefore, gaining an understanding these traits is key to implementing sustainable management strategies (Schindler et al. 2010). Aquatic organisms exhibit diverse life histories and commonly undergo ontogenetic migrations during their lifetime (Chapman et al. 2011, Hegg et al. 2015, Arai et al. 2020). Ontogenetic movements allow different life stages to find suitable habitats

and resources, such as for shelter from predators at early stages of life, different food requirements at various stages of life, and specific habitat types for reproduction (Appeldoorn et al. 2009, Ciannelli et al. 2015, Whitfield 2020).

The use of otolith chemistry is a powerful and effective means to reveal the movement, migration, and habitat use of individual fish (Campana 1999, Elsdon et al. 2008, Tanner et al. 2016, Arai et al. 2020). Fish otoliths are paired structures composed of biogenic calcium carbonate that grow continuously

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throughout life (Campana 1999, Elsdon et al. 2008). During calcium carbonate accretion, other elements potentially indicative of the surrounding environment can be incorporated and are not re-metabolized once deposited (Campana 1999, Campana & Thorrold 2001). The chronological properties and metabolic inertness of otoliths make them ideal natural markers to answer biological and ecological questions related to fish movements and habitat use (Campana & Thorrold 2001, Izzo et al. 2018).

It is possible to reconstruct the migratory history of diadromous fishes between freshwater, estuarine, and marine environments by examining different trace elements in calcified structures, such as the concentrations of Mg, Mn, Zn, Sr, or Ba (Campana 1999, Elsdon et al. 2008, Walther & Limburg 2012, Smith & Kwak 2014). Among these, Sr and Ba are the most commonly used elements to infer movements between habitats with different salinity levels (Elsdon et al. 2008). Sr and Ba are 2 elements generally incorporated into otoliths, and their concentrations are markedly positively influenced by the chemistry of the ambient water (Elsdon & Gillanders 2003, Izzo et al. 2018), which is the main source of these elements in fish otoliths (Webb et al. 2012, Doubleday et al. 2013). Levels of Sr are higher in marine water and lower in fresh water, and vice versa for elemental Ba, though with several exceptions (Secor & Rooker 2000, Kraus & Secor 2004, Yang et al. 2011). In general, higher Sr:Ca ratios are more indicative of marine habitat use, while higher Ba:Ca ratios are associated with exposure to fresh water, and an estuarine history is associated with medium Sr:Ca and Ba:Ca ratios (Yang et al. 2006, Jiang et al. 2019); this is the premise for the present study. The East Asian fourfinger threadfin Eleutheronema rhadinum (Jordan & Evermann, 1902) (family Polynemidae) was previously treated as a synonym of *E. tetradactylum* (Cheng & Zheng 1987). Motomura et al. (2002) redefined *E. rhadinum* as a valid species of the genus based on morphological characters (e.g. count of the pored lateral line scales and color of the pectoral-fin membrane). Similar to its congener *E. tetradactylum*, E. rhadinum is regarded as an estuarine fish and is typically harvested from coastal waters (Motomura 2004, Zhang et al. 2013, Su et al. 2020). As a subtropical species, it is endemic to East Asia, mainly distributed in China and occasionally reported in Japan, Vietnam, and Malaysia (Motomura et al. 2002, 2007, Motomura 2004, Atikah et al. 2020). In China, the larvae of E. rhadinum can be found in the surf zone of an estuary in Hangzhou Bay, Zhejiang province (Chen et al. 2011), and adults prefer to inhabit shallow and turbid areas (Su et al. 2020). *E. rhadinum* is a fast-growing fish, attaining almost 30 cm fork length (FL) in the first year of its life cycle (Su et al. 2020). It is a protandrous hermaphrodite, maturing first as a male and then becoming a female later in life, with abundant spawning occurring from May to August (Motomura 2004, Su et al. 2020). However, information on the habitat and biology of this species is scarce (Motomura 2004), and the size at maturity and time of sex change in this species are currently unknown. *E. rhadinum* is important in both commercial and recreational fisheries, commanding high auction prices in local fish markets (Motomura 2004) because of its good flavor and high nutritional value (Huang 2012).

Information on the migration ecology and behavior of *E. rhadinum* is needed to understand its population dynamics for the purpose of optimal resource management. In the present study, we provide the first analyses on the migration, environmental history, and habitat use by *E. rhadinum* in its main distribution area, i.e. the East China Sea and South China Sea, based on otolith chemistry, specifically the simultaneous use of Sr:Ca and Ba:Ca ratios.

2. MATERIALS AND METHODS

2.1. Sampling

A total of 22 *Eleutheronema rhadinum* individuals were collected from 2 sites (Fig. 1): Fuzhou in October 2019 (East China Sea, 26°07'N, 119°36'E), and Zhuhai in December 2019 (South China Sea, 21°56'N, 113°43'E) (Table 1). Samples from Zhuhai were collected from a fishing boat jetty, and samples from Fuzhou were collected from the local fish market. Fish were measured for FL and weighed. Saccular otolith pairs were extracted, cleaned using ultrapure water, air-dried, and stored in Eppendorf tubes. Sex was determined by observation of the gonads with the naked eye (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/b031p089_supp.pdf), followed by confirmation under a microscope.

2.2. Otolith preparation and microchemical analysis

Right saccular otoliths were embedded in epoxy resin in plastic tubes and then transversely sectioned to a thickness of 400–500 μ m using an IsoMet 1000 precision cutter double-bladed saw (Buehler) at low

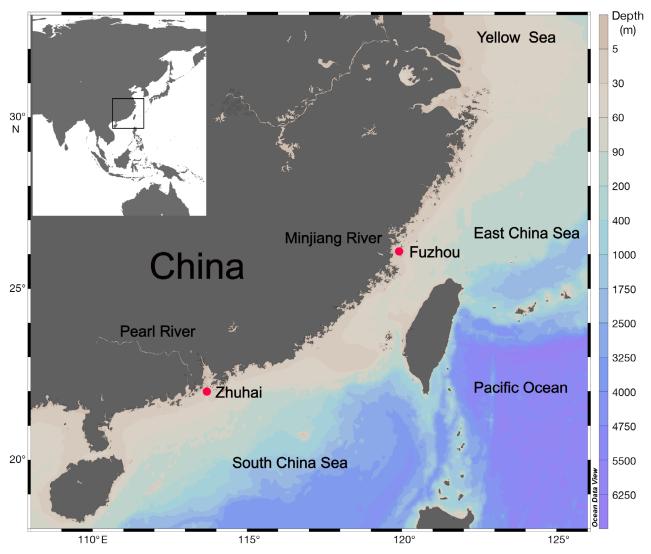


Fig. 1. Sampling sites at Fuzhou and Zhuhai, China, from which East Asian fourfinger threadfin *Eleutheronema rhadinum* were collected

speed. Otolith sections were polished on a polishing wheel with 600- and 1200-grit paper until the increments were clearly visible. Next, the thin sections were mounted on petrographic slides using crystal bond, sonicated for 8 min in ultra-pure water, and air-dried at room temperature.

Concentrations of the isotopes ⁸⁸Sr, ¹³⁸Ba, and ⁴³Ca were determined by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS), using a New Wave UP 193 LA system coupled to a Thermo Fisher Scientific iCAP RQ ICP-MS, at the Guangzhou Tuoyan Testing Technology Co., Ltd (Guangzhou, China). The laser was programmed to follow a transect path from the core to the dorsal edge of each otolith (Fig. 2), with a beam width of 20 µm, a pulse frequency of 10 Hz, and a

transect speed of 5 µm s⁻¹. Two National Institute of Standards and Technology standards (NIST612 and NIST610) were run at the beginning and end of each session. To convert elemental signals (intensity) to concentrations, NIST612 and Ca (38.3% weight; Sturgeon et al. 2005) were used for calibration and as internal standards, using the software ICPMSDataCal 10.8 (Liu et al. 2008) and Iolite 4 (Paton et al. 2011). Elemental concentrations are expressed as the ratios of elements to Ca mmol mol⁻¹ for Sr:Ca, and 10⁻² mmol mol⁻¹ for Ba:Ca. To smooth the transect-line data, data points more than 2 σ above or below the mean of the next 12 data points were removed, and the average of the 12 data points was calculated as the element concentration at that point (Heimbrand et

Table 1. Sampling information and cluster assignment based on otolith chemistry of East Asian fourfinger threadfin Eleutheronema rhadinum in this study. All specimens were females aged 1+. FZER and ZHER indicate samples from Fuzhou and Zhuhai, respectively. Clusters are illustrated in Figs. 3 & 4

Sample ID	Fork length (cm)	Weight (kg)	Sr:Ca profile	Ba:Ca profile
FZER_17	41.3	3.4	Cluster S1	Cluster B1
FZER_18	43.5	3.4	Cluster S5	Cluster B4
FZER_20	42.6	3.3	Cluster S1	Cluster B2
FZER_21	44.6	3.6	Cluster S4	Cluster B3
FZER_23	44.9	3.7	Cluster S2	Cluster B4
FZER_24	43.4	3.6	Cluster S1	Cluster B3
FZER_25	40.5	3.0	Cluster S5	Cluster B5
FZER_26	42.1	3.4	Cluster S5	Cluster B3
FZER_27	40.0	3.1	Cluster S3	Cluster B2
FZER_28	43.1	3.3	Cluster S4	Cluster B1
ZHER_5	47.4	4.3	Cluster S2	Cluster B5
ZHER_6	46.8	3.5	Cluster S1	Cluster B1
ZHER_7	45.0	3.7	Cluster S5	Cluster B5
ZHER_8	43.5	3.7	Cluster S2	Cluster B5
ZHER_9	42.0	3.4	Cluster S3	Cluster B4
ZHER_10	46.5	3.9	Cluster S3	Cluster B3
ZHER_11	49.0	4.4	Cluster S4	Cluster B4
ZHER_12	48.4	4.6	Cluster S3	Cluster B3
ZHER_13	47.2	4.2	Cluster S1	Cluster B3
ZHER_14	45.2	3.9	Cluster S5	Cluster B5
ZHER_15	50.5	4.2	Cluster S2	Cluster B5
ZHER_16	46.8	3.9	Cluster S2	Cluster B2

al. 2020). Fish age was determined by counting otolith annuli under an Olympus BX53 microscope and further estimated using age-length growth equations (Su et al. 2020).

2.3. Statistical analyses

A quantitative approach to characterize the lifehistory patterns of *E. rhadinum* was applied by using unsupervised hierarchical time-series clustering



Fig. 2. Right otolith section of an East Asian fourfinger threadfin *Eleutheronema rhadinum*. Black arrows, position of annual increment; white line and arrowhead, core-to-edge laser ablation transects; red circle, primordium.

Sample ID: FZER_20 (see Table 1)

algorithms of the Sr:Ca and Ba:Ca chronologies of groups of individuals. The chronology data were trimmed to the same lengths based on the individual with the shortest otolith transect-line length (2116 μm). Clusters of individuals were identified based on the Euclidean distance of the elemental transects, measured with an agglomerative hierarchical clustering algorithm with Ward's method, using the 'TSclust' package in R 4.1.3 (R Core Team 2022). The mean value of the annulus position for each cluster was averaged from the individuals belonging to the given cluster.

Changepoint analysis (CPA) automatically divides a lifetime profile with multiple change points to identify where a stable segment started, and then generates mean values for each segment (Killick & Eckley 2014, Killick et al. 2016). The 'cpt.mean' function in the 'changepoint' package was used with the Pruned Exact Linear Time (PELT) algorithm and modified Bayes information criterion (mBIC) as penalty (Killick et al. 2016).

3. RESULTS

3.1. Sr:Ca and Ba:Ca ratios

The estimated ages of the *Eleutheronema rhadinum* used in this study were in the same age 1+ class (Table 1; Table S1). Analysis of the otoliths along the transect lines showed that Sr:Ca ratios averaged (\pm SD) 4.8 \pm 0.7 (range: 2.7–8.1) (Fig. S2a), and Ba:Ca ratios averaged 2.5 \times 10⁻² \pm 2.6 \times 10⁻² (range: 0.4 \times 10⁻² to 23.1 \times 10⁻²) (Fig. S2b). Values of the Sr:Ca ratios were typically (>75%) in the range from 4 to 5.5 (Fig. S2a). Values of most of the Ba:Ca ratios (>60%) across the life history were <2 \times 10⁻² (Fig. S2b), and the point of the maximum value was typically achieved during the first year of life. Both the Sr:Ca and Ba:Ca ratios

varied significantly across the lifetime (see Figs. 3 & 4).

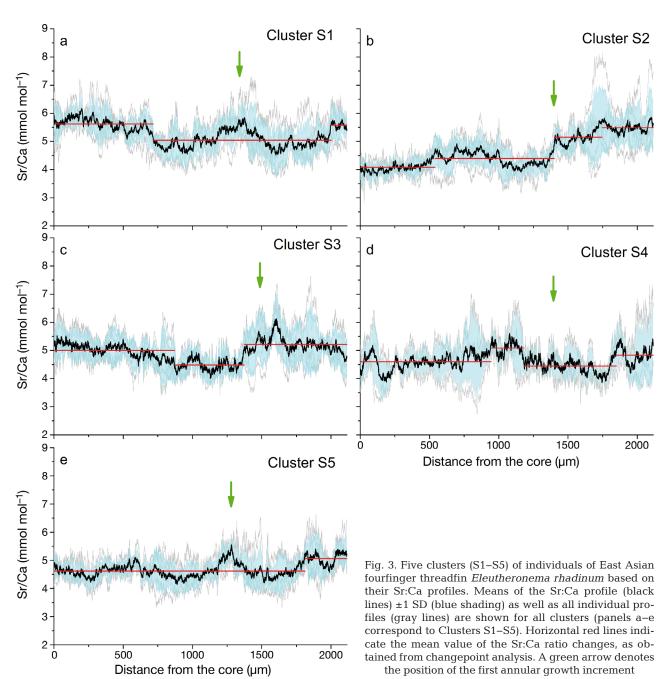
3.2. Summarized Sr:Ca profiles

In general, individuals of *E. rhad-inum* exhibited a high spike in the Sr:Ca ratio corresponding to the winter ring (annulus) (e.g. Figs. S3 & S4), with spikes typically larger than 6 (Figs. S3 & S4). In some fish, the highest Sr:Ca ratio in the otoliths did not

occur in the winter zone but during a later period of life (e.g. Fig. S4a).

Five clusters (S1–S5) of Sr:Ca profiles of *E. rhadinum* were statistically identified using hierarchical cluster analysis (Fig. 3). Significant changes in Sr:Ca ratios were observed for each cluster, with 1-3 change points based on the CPA results (Fig. 3). Individuals comprising Cluster S1 (n = 5, Fig. 3a) and Cluster S3 (n = 4, Fig. 3c) had a relatively high mean Sr:Ca ratio in their first year of life based on the CPA results, with an obvious spike in the winter period.

Individuals in Cluster S2 (n = 5, Fig. 3b) and Cluster S5 (n = 6, Fig. 3e) showed relatively low mean Sr:Ca values in their first year of life based on the CPA results, but higher values for the first winter period, and, thereafter, continuously increasing for the remainder of their lifetime in Cluster S2, and continuously decreasing in Cluster S5. Individuals in Cluster S4 distinctly differed from the other clusters in that their ratios did not peak during the winter period, although a specimen in this cluster showed an increase in the annulus (Fig. S3d).

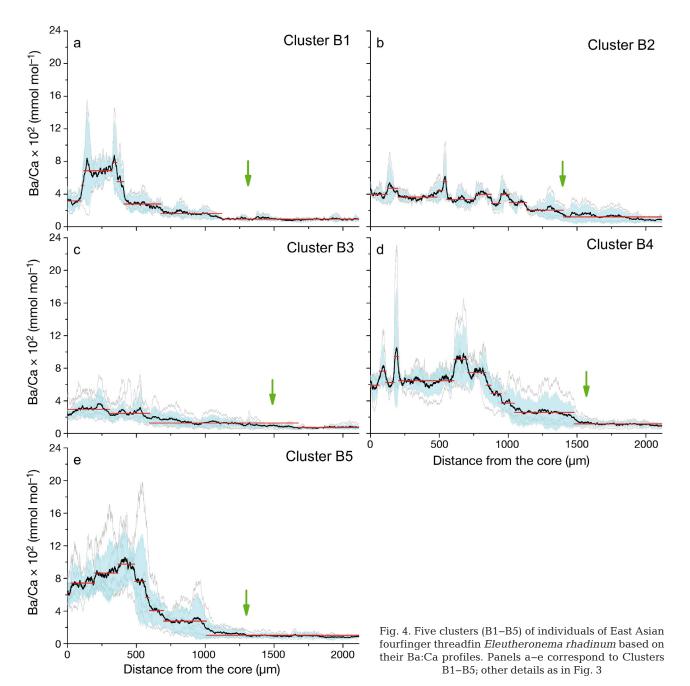


3.3. Summarized Ba:Ca profiles

In general, the otolith Ba:Ca ratios in the core region (mean value of the first segment) averaged 4.6 $\times~10^{-2}~\pm~1.8~\times~10^{-2}$ (range: $1.9~\times~10^{-2}$ to $8.5~\times~10^{-2}$) (Figs. S3 & S4). Most specimens displayed a high Ba:Ca ratio in their first year of life, with a high plateau, drastic fluctuations or an extremely high spike, and thereafter obvious decreases of the ratio in positions 500–1300 μm from the otolith core, to a low plateau (<2 $\times~10^{-2}$) by the end of the second year

(Figs. S3 & S4). During the lifetime after the winter period, the Ba:Ca ratios were typically low, averaging $0.9 \times 10^{-2} \pm 0.3 \times 10^{-2}$ (Figs. S3 & S4).

Five clusters (B1–B5) of Ba:Ca profiles of *E. rhad-inum* were likewise statistically identified using hierarchical cluster analysis (Fig. 4). Significant changes in the Sr:Ca ratios were observed for each cluster, with 3–11 change points based on the CPA results, especially during the first year of life (Fig. 4). All 5 clusters exhibited intermediate values of the Ba:Ca ratios (~4) in the core region, and



steady low values (~1) during the rest of the life after the first winter period. The individuals in Cluster B1 (n = 3, Fig. 4a), Cluster B3 (n = 6, Fig. 4c), and Cluster B5 (n = 6, Fig. 4e) had relatively high mean Ba:Ca ratios (>8) during their first year of life based on the CPA results, and the values sharply decreased to a low ratio at the last annulus. Individuals in Cluster B2 (n = 3, Fig. 4b) and B3 (n = 6, Fig. 4c) had relatively low Ba:Ca ratios during their whole lifetime, although several Cluster B2 individuals displayed spikes in their first year of life.

4. DISCUSSION

A lack of information on the relationship between otolith element ratios and freshwater versus saltwater environments meant that we were not able to completely classify the environmental history of *Eleutheronema rhadinum*. However, 5 clusters based on the Sr:Ca and Ba:Ca ratios of *E. rhadinum* arose across the life histories of the sampled fish, and obvious characteristics could be observed during particular ontogenetic stages, namely the first year of life and the overwintering period.

We found that *E. rhadinum* exhibits overwintering migration behavior in its first winter period, and likely migrates from estuarine waters into marine waters. As a subtropical species, E. rhadinum has possibly adopted a migration strategy that minimizes its exposure to thermal stresses in winter (Hurst 2007). Although the positive effect of water temperature on otolith Sr elemental incorporation has been widely documented (Martin & Thorrold 2005, Nelson et al. 2018, Tian et al. 2021), the high Sr:Ca ratios in the overwintering period would not necessarily have been caused by temperature, given the relatively low water temperatures in these sea areas in winter. Adults of E. rhadinum generally occur in coastal and inshore waters of continental shelves in China and are rarely caught in oceanic waters (Motomura 2004, Su et al. 2020), which might reflect a relatively short time in marine or oceanic waters during the winter period.

The otolith Ba:Ca profiles suggested that *E. rhadinum* in Chinese waters has a diversity of life-history strategies during the first year of life, typically with some estuarine experience. This is similar to other polynemids, such as juveniles of *E. tetradactylum* which frequently enter brackish waters (Motomura 2004). Estuaries are an important environment for many fish species, especially during their early life stages, providing food resources and refuge from

predation (Able 2005, Elliott et al. 2007). The extremely high Ba:Ca ratios (e.g. >15 \times 10⁻²) of E. rhadinum might suggest freshwater exposure, as juvenile specimens with a standard length of 22 cm were found in fresh water in the Yangtze River at Zhenjiang, China (Zhong et al. 2019). Laboratory studies have proved that E. rhadinum juveniles are euryhaline and can endure a salinity range of 0-30 psu (Zhang et al. 2013), which is consistent with the findings of the present study. However, a small portion of *E. rhadinum* might not enter estuarine waters during the first year of life. Diversity in migration has been documented within many fish species, and this is often reflected in diverse movement behavior during the juvenile stages (Kerr & Secor 2012, Hegg et al. 2015, Arai et al. 2020).

The low Ba:Ca ratios after the first winter period indicated that E. rhadinum might not be influenced by freshwater flow. Elemental Ba incorporated into otoliths is mainly absorbed from the surrounding water, although dietary sources can also contribute to its incorporation (Doubleday et al. 2013, Woodcock 2013). Even though studies on the feeding habits of E. rhadinum are scarce, we might deduce its habits from the congeneric E. tetradactylum, which shifts from feeding mainly on arthropods (e.g. mysids, shrimps, and prawns) as juveniles (range: 3-6 cm total length) to fish prey as adults (Motomura 2004). Therefore, the rapid decrease in the Ba:Ca ratio during the juvenile stage of *E. rha*dinum might suggest that not only the aquatic environment but also the dietary choice affects incorporation of the element, although the latter assumption will require confirmation.

The migration patterns of *E. rhadinum* from the different sampling sites appeared similar, although only individuals from the South China Sea showed low Ba:Ca ratios across the whole lifetime. Previous studies of phylogeny showed little genetic differentiation among *E. rhadinum* along the coast of China, indicating that this species is a single population (Deng 2014). Moreover, the species displays life-history diversity and possibly partial migration, which is a widespread phenomenon characterized by migrant and resident forms in the same population (Chapman et al. 2012).

The elements Sr and Ba incorporated from ambient water into fish otoliths are generally negatively correlated with each other (Campana 1999, Elsdon et al. 2008), yet this phenomenon was not observed in *E. rhadinum* in the present study. Moreover, 5 clusters of individuals were delineated based on cluster analyses of both the Sr:Ca and Ba:Ca pro-

files for this species. However, the individuals in the Sr:Ca profile clusters did not strictly correlate with those in the Ba:Ca profile clusters. This result might indicate that the elements Sr and Ba incorporated into fish otoliths of this species are not only influenced by water chemistry but are also directly or indirectly regulated by other factors, such as water temperature, food resources, or physiology (Bath et al. 2000, Sturrock et al. 2015, Izzo et al. 2018, Thomas & Swearer 2019, Hüssy et al. 2021). Moreover, the elements Sr and Ba might be regulated by different factors and to different extents; for instance, Ba incorporation was possibly more regulated by food resources than was Sr (Doubleday et al. 2013), and water temperature significantly affected Sr but not Ba incorporation in otoliths (Bath et al. 2000). To uncover the relationship between Sr and Ba absorption into otoliths for this species, a comprehensive laboratory experiment is necessary.

5. CONCLUSION

Otolith microchemistry can provide retrospective individual life-history information using only small samples of a species that might be difficult to obtain through traditional field investigation. To our knowledge, the current study provides the first data on otolith chemistry to describe the movements and life history of Eleutheronema rhadinum. The findings revealed various migration patterns with a preference for estuarine waters during the first year of life, and the potential to overwinter in marine waters. The findings also showed that an ontogenetic dietary shift might occur in this species during the juvenile stage. However, interpretations of geochemical markers in otoliths are strongly dependent on threshold values of the trace elements in different aquatic environments. We thus recommend validating the relationship between Sr:Ca and Ba:Ca ratios in otoliths and the elemental concentrations found in surrounding waters to improve the existing interpretation.

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