

Pilot study to reconstruct life history of *Diaphus thiollierei* from the Arabian Sea by otolith microstructure and microchemistry

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Abstract

The lanternfishes are mesopelagic fish that are highly productive as common bycatch of deep-sea shrimp trawlers, but they are often neglected or discarded. Despite being one of the dominant lanternfish species in the Arabian Sea, little is known about the life history of *Diaphus thiollierei* and its role in marine ecosystems. In this study, 103 *D. thiollierei* were collected in the Arabian Sea during October–November 2020 to study population growth based on sagittal otolith daily ages; and 10 fish collected during April–May 2021 were subjected to otolith microchemistry analysis to reconstruct the vertical migration in their life history using LA-ICP-MS technique. The standard length–dry weight (SL–DW) relationships for *D. thiollierei* revealed both negative allometric growth and a significant difference between the sexes. Using daily growth annuli counts on the sagittal section of otoliths, the von Bertalanffy growth equation for *D. thiollierei* was determined. The pattern of four elemental ratios (Sr to Ca, Mg to Ca, Li to Ca, and Ba to Ca) in sagittal otolith suggested that, in general, *D. thiollierei* descended continually after hatching until the post-larval (PL) stage when they reached a depth of approximately 200 m. Subsequently, from the PL stage to the post-metamorphosis II (PM II) stage, *D. thiollierei* likely further sank from 200 m to a depth of approximately 300 m, and then in the daytime they were at a depth of approximately 300–800 m to take refuge from predators. This pilot study explored to unravel the vertical migration during life history in *D. thiollierei* from sagittal otoliths, whereas further investigation on otolith is needed to better delineate the population ecology in detail, and thus to provide basic information for the exploitation of the lanternfish resource and the understanding of their ecological roles.

Key words: lanternfish, *Diaphus thiollierei*, sagittal otolith, vertical migration, population growth, microchemistry

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1 Introduction

Lanternfishes (Myctophidae) are a major group of mesopelagic fish biomass (5–15 billion metric tons) (Caiger et al., 2021). The catch biomass of lanternfishes was approximately 20–100 million tonnes in the Arabian Sea (Catul et al., 2011), and furthermore, the overall myctophid catch over the years has exhibited an increasing trend (Sebastine, 2014). In marine ecosystems, lanternfishes mainly feed on primary consumers such as copepods and euphausiids, and in turn they are also the food of high-level consumers such as squids, tuna, whales and other marine organisms (Eduardo et al., 2021). Therefore, the lanternfishes, as an integral link between meso- and macrozooplankton and top predators in the marine food chain, play an important role in maintaining the stability of the marine ecosystem (Shotton, 1997; Catul et al., 2011; Milligan and Sutton, 2020). Moreover, at least 73% of lanternfishes observed in this study vertically migrate to the surface to feed at night (Eduardo et al., 2021). Thus, they might contribute substantially to the export of organic carbon

from the euphotic zone to the deep ocean through their diurnal vertical migrations and the large quantities of fast-sinking feces they produce (Pakhomov et al., 1996; Robinson et al., 2010). However, these fish, which are frequent bycatch in deep-sea shrimp trawlers, are mostly underutilized and primarily used for fishmeal or manure production.

The large stocks of lanternfishes have attracted increasing research attention, while many aspects of the lanternfish ecology still remain poorly known (Sebastine, 2014; Eduardo et al., 2021). There remains a lack of research on the population dynamics and diurnal vertical movement of specific lanternfish species, including the habitat depth at a given life stage (Eduardo et al., 2021). *Diaphus* is a genus with higher species richness and abundance within the family Myctophidae. *Diaphus thiollierei* Fowler is one of the dominant species in mid-deep fishes in the Indian Ocean–Arabian Sea (Sebastine et al., 2013). Thus, understanding the population fluctuation and habitat depth movements of *D. thiollierei* is crucial for assessing the stock status of important com-

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mercial fish species in the sea area, as well as their impact on the ocean carbon cycle. Therefore, studying the population dynamics and movements in habitat depth would contribute to further exploitation and utilization of mesopelagic fishery resources, as well as to a better understanding of their role in the ocean carbon cycle process.

Fish otoliths serve as objective chronicles of fish life history and have been widely used for studies on individual age and growth as well as ecological information due to their stable structure, corrosion resistance and irreversible daily increments (Campana, 2001; Izzo et al., 2018; Petursdottir et al., 2006; Smith, 1992; Sun et al., 2020). Generally, a ring is usually formed on the otolith every day in common conditions, although the deposition rate may be influenced by environmental factors (Alhossaini and Pitcher, 1988; Wright et al., 1992; Taubert and Coble, 1977). Thus, they are widely used to shed light on biological and ecological questions concerning population growth, movements and habitat.

Otolith microchemical analysis is a useful tool to reveal the environmental conditions experienced by the fish population and to trace the key habitats (e.g., spawning site, nursery ground, and growing area) throughout their life cycle, based on the understanding that the composition and content of otolith elements are closely related to the bioavailability of elements in the ambient water (Campana, 1999; Sturrock et al., 2015; Izzo et al., 2018; Liu et al., 2018; Soeth et al., 2020; Xiong et al., 2021; Xuan et al., 2023). Laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS), as a powerful and effective technique for microchemical analysis, has become the main technical means for reconstructing the life history and environmental history of fish. Thus, this approach offers significant advantages in studying the temporal and spatial histories of fish populations and assessing the formation mechanism and spatial structure of fish stocks (Sturrock et al., 2015; Izzo et al., 2018; Soeth et al., 2020; Duan et al., 2021).

The present study focused on the population ecology of *D. thiollierei* in the Arabian Sea based on sagittal otolith information. This paper mainly aims to achieve the following two research goals: (1) to identify the age of individuals using sagittal otoliths and analyze the population's growth characteristics and (2) to infer depth changes during certain life stages using otolith microchemistry.

2 Materials and methods

2.1 Sample collection and measurement

A total of 150 *D. thiollierei* were collected by light falling nets to study otolith daily ages during October–November 2020, and 10 fish were collected for otolith microchemistry analysis during April–May 2021. The vessel was 54.6 m in length, 10.5 m in width and 4.7 m in draught. Biological samples were collected using a light falling-net; 110 attracting lamps (4 kW per lamp) were arranged along the sides of vessel in two rows. Net dimensions were 800 m circumference and 1 200 m stretched length, with a cod-end mesh of 20 mm, and mesh at the net mouth of 35 mm. The maximum working depth of net was 50 m. The vessel stopped sailing and drifted at night. All the lamps were turned on to lure fish between about 20:00 and 22:00 (local time). After the fish are lured into the net set up in advance, fishing operations were carried out and the net was emptied on deck for sampling. The survey area was in the Arabian Sea (15.5°–18.5°N, 62.5°–67.5°E, Fig. 1).

Both temperature and salinity showed similar profiles of vari-

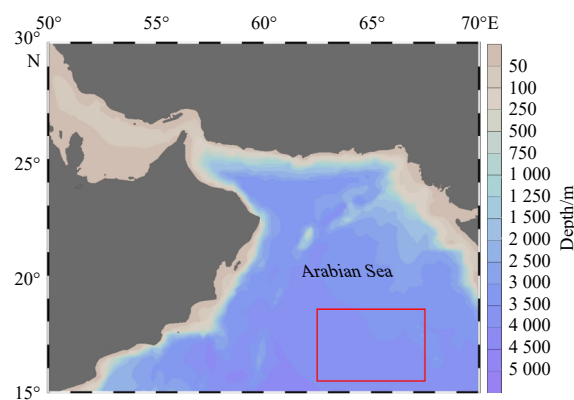


Fig. 1. Sampling area in the Arabian Sea.

ance with depth in the study area (data from World Ocean Atlas, shown in Fig. S1). Salinity decreased rapidly with depth in 0–200 m, gradually fell slowly down with depth, and then increased rapidly after 1 000 m; the temperature went down with depth in 0–300 m, decreased rapidly after 300 m, and then remained stable until the deep sea.

Samples were quickly separated based on morphological characteristics, wrapped in tin foil paper and preserved in 100% alcohol or in liquid nitrogen for otolith microchemistry analysis. Then, the alcohol was renewed three times every day to prevent samples from degrading. For each specimen, the standard length (SL: 0.1 mm) and dry weight (DW: 0.01 g) were measured with vernier caliper (433 digital caliper; MNT, Shanghai, China) and microbalance (JJ300Y; G&G, Changshu, China), respectively. Well, just a note that the wet weights of the specimens were not recorded due to the limitations in storage conditions on board. Dry weight measurements were made after the fish were placed in a fume hood for 1–2 h and the alcohol had completely evaporated. Sex was then identified by inspection of the gonads, and their photos of the male and female gonads were shown in Fig. S2. Both sagittal otoliths from each specimen were removed and then rinsed with ultrapure water to remove any attached tissue under a dissecting microscope. The otoliths were weighted to the nearest 0.000 1 g with microbalance (CP214; OHAUS, USA) after drying with alcohol. The average value of the mass of the left and right otoliths was used to represent the otolith mass of each fish, since there was no significant differences between left and right otoliths (paired *t*-test, $p > 0.05$).

2.2 Sagittal otolith preparation

The right or left sagittal otolith was randomly selected for ring counting. Each otolith was embedded in epoxy resin with the sulcus side upward. The mounted otoliths were ground by a grinding machine (Discoplan-TS; Struers, Denmark) to expose the cores and polished using an automated polishing machine (Roto Pol-35; Struers, Denmark) with a polishing solution (OP-S Non-Dry; Struers, Denmark) to remove scratches on the surface. Since the nucleus and growth rings on the ventral axis were more clearly observed along the longitudinal planes in the initial examination of the sagittal otolith, the longitudinal sections were selected for grinding. Following this, the nucleus and growth rings in each otolith section were clearly visible for age determination and elemental analysis.

2.3 Ring counting

All otolith growth rings were counted and measured along the

same axis from core to postrostrum under microscope (BX53; Olympus, Japan). All otoliths were read three times every two weeks by the same reader to ensure the accuracy and consistency of ring counting. The order of the otoliths was randomized during each counting run. Then the hatching dates were back-calculated with the date of capture and daily ages. A total of 103 sagittal otoliths with clear rings were finally obtained.

2.4 Otolith microchemical analysis

Right sagittal otoliths were embedded in transparent epoxy resin (Struer) and cut into longitudinal sections using Struers Discoplan-TS to preserve the nucleus region. Sections were ground by Struers Roto Pol-35 until the nucleus and daily annuli were clearly visible. All rings were counted and measured as 2.3 ring counting. The polished otolith sections were washed in ultrapure water for 10 min to avoid other elements interfering with the detected result and then oven-dried at 38°C overnight.

Otoliths were analyzed using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) at the Laboratory of Fishery Microchemistry at the Freshwater Fisheries Research Center, Wuxi, China. Laser sampling was performed using a NW213 laser ablation system (New Wave Research, excimer laser: wavelength of 213 nm and time of 5 s), and a 7500ce ICP-MS instrument (Agilent Technologies, Wilmington, USA) was used to acquire ion-signal intensities. A mixture of helium and argon was applied as a carrier gas. The laser beam diameter and frequency were set to 40 μm and 10 Hz, respectively. The distance between the centers of two adjacent punched holes was 50 μm. The laser ablation route was set along the axis of the ventral edge of the sagittal otolith section, from core to edge, with the spots being continuous and in the same direction.

Otoliths were analyzed for ⁴³Ca, ²⁴Mg, ⁵⁵Mn, ⁸⁸Sr, and ¹³⁷Ba. All results were expressed as the molecular weight ratio (mmol/mol) of the element to Ca. NIST612 and USGS MACS-3 were used as the standard reference materials. One hundred seconds of blank data were measured before and after the analysis to calculate the limits of detection (LOD).

2.5 Data analysis

2.5.1 Daily age reading and population growth analysis

The precision of daily ages for reading the same otolith at three counting runs was calculated using the coefficient of variation (CV) and average percentage error (APE) (Beamish and Fournier, 1981).

The length-weight relationship (LWR) of *D. thiollierei* was described by the following equation: $DW = aSL^b$, where DW is dry weight (0.01 g), SL is standard length (0.1 mm) and *a* and *b* are constants. The difference between the regression coefficients (*b*) in males and females was tested using analysis of covariance (ANCOVA, standard length as covariate, after natural logarithmic transform). *T* tests were used to compare the difference between regression coefficients (*b*) and the isometric growth index (*b*=3).

The von Bertalanffy model, $SL = L_{\infty} \{1 - \exp[-K(t - t_0)]\}$, was used for determining the daily-age-standard length relationship, where SL is the body length at daily age *t*, L_{∞} is the theoretical asymptotic length, *K* is the growth coefficient, and t_0 is theoretical age when body length equals 0. The difference between males and females was tested using ANCOVA.

2.5.2 Otolith chemistry analysis

The available elements for microchemical analysis were de-

termined based on the limits of detection (LOD) and the relative standard deviation (RSD, <10%) between the specimen and the standard sample.

The sample mean (*X*), standard deviation (SD), range, and coefficient of variation ($CV = [SD/X] \times 100\%$) were used to describe the elements measured and their variability. All the data were checked for normality and homoscedasticity using Kolmogorov-Smirnov tests and presented as average and median values. Spearman's rank correlation coefficients were used to calculate correlations between the four ratios of elements (Sr, Li, Mg and Ba) to calcium. The ratios of four elements to calcium were compared using Kruskal-Wallis test (nonparametric one-way ANOVA) with all pairwise comparison to find out the significant ($p < 0.05$) differences among six life stages.

Statistical analysis was performed using SPSS 26.0 (IBM SPSS Statistics Inc.).

3 Results

3.1 Body length and body dry weight

Otolith growth ring analysis was conducted on 103 specimens, including 56 females and 47 males, caught in the Arabian Sea from October to November 2020. The standard length (SL) of the examined specimens ranged from 36.2 mm to 57.4 mm [mean±SD; (47.6 ± 4.6) mm], while the body length of males was the same range and averaged (45.8 ± 5.2) mm. The females had a body length between 41.2 mm and 56.8 mm and an average of (49.1 ± 3.3) mm. The body dry weight (DW) of the examined specimens ranged from 0.52 g to 2.13 g and averaged (1.38 ± 0.35) g. The body dry weight range of the females was 1.06–2.13 g and averaged (1.52 ± 0.27) g, while the body dry weight of the males was 0.52–2.10 g and averaged (1.21 ± 0.37) g. The length-weight (SL-DW) relationships derived are as follows (Fig. S3):

$$\text{for males: } DW = 0.000145 SL^{2.357} (R^2 = 0.821, p < 0.01),$$

$$\text{for females: } DW = 0.000219 SL^{2.269} (R^2 = 0.719, p < 0.01),$$

$$\text{for combined: } DW = 0.000127 SL^{2.401} (R^2 = 0.803, p < 0.01).$$

There were significant differences in the length-weight relationship between males and females (ANCOVA, DWs and SLs transformed by natural logarithm, $p = 0.002$). The growth patterns of both males and females were significantly less than the theoretical value of isometric growth (*b*=3) (*t*-test, male $p < 0.0001$, female $p < 0.0001$, combined $p < 0.0001$).

3.2 Growth and age

The left and right sagittal otoliths of *D. thiollierei* are visually symmetrical in shape, and nearly elliptical [photo in Zhuang et al. (2023)]. The daily growth increments were clearly and well-defined in sagittal otolith of *D. thiollierei* (Fig. 2a). Ages determined by daily annuli ranged from 69 d to 153 d, with a main distribution in 71–100 d accounting for 76.7% of the total (Fig. 3a). The hatching dates of the 103 specimens were back-calculated, ranging from June to September 2020, and the fish were mainly spawned in September (Fig. 3b). The coefficient of variation (CV) and average percentage error (APE) of each specimen were all less than 5%.

The von Bertalanffy growth functions for this species were as follows (Fig. 4):

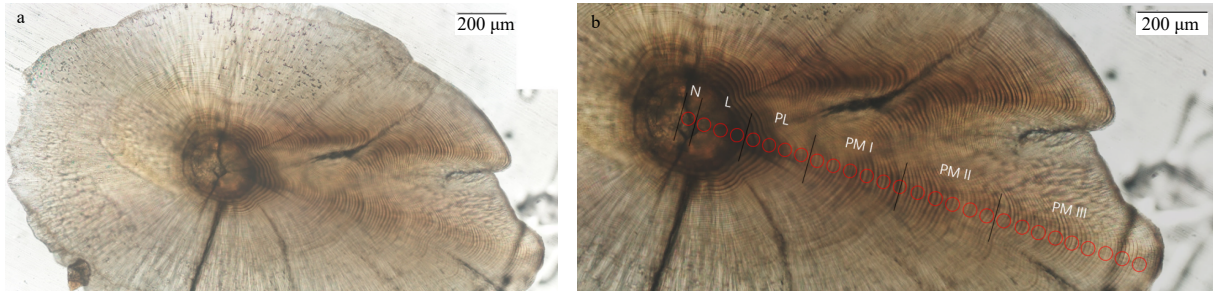


Fig. 2. Light micrographs of sagittal otolith from a female *Diaphus thiollierei* with 55.4 mm SL and 139 d age. a. Longitudinal section in which dark and light bands suggesting daily increments; b. the same otolith showing schematic diagram of laser ablation for chemistry analyses and six life history stages: primordium (nucleus, N), larval (L), postlarval (PL), postmetamorphic I (PM I), PM II, and PM III stages. The red circles represent spot raster for LA-ICP-MS.

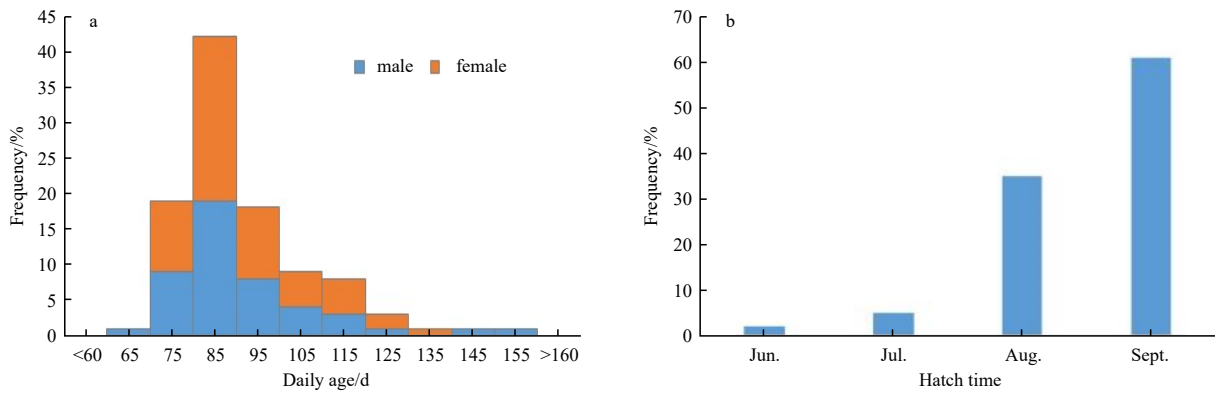


Fig. 3. Frequency distributions of daily age (a) and hatch time (b) of *Diaphus thiollierei* caught in the Arabian Sea from October to November 2020.

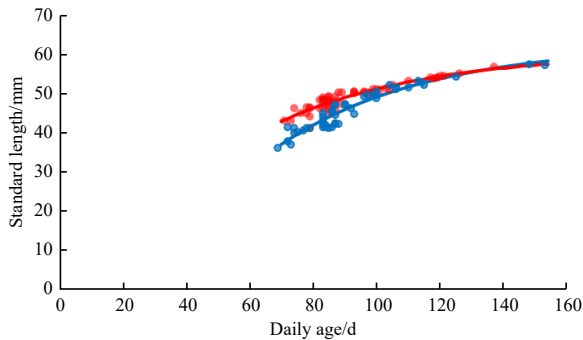


Fig. 4. The von Bertalanffy growth function fitted to the relationship between daily age and standard body length. Blue for male and red for female.

$$\text{for female: } SL = 60.46(1 - e^{-0.021(t-11.33)}), R^2 = 0.875,$$

$$\text{for male: } SL = 62.39(1 - e^{-0.021(t-27.60)}), R^2 = 0.915,$$

$$\text{for combined: } SL = 59.826(1 - e^{-0.025(t-27.18)}), R^2 = 0.780,$$

where t is age (d) determined by otolith daily annuli, and SL is standard body length (mm).

Since the two K values of females and males were the same in the VB growth curve, the growth functions were combined. Estimates of growth parameters L_{∞} and K were 59.83 cm and 0.025 per day, respectively. The age of the species at zero length (t_0)

was estimated as 27.2 d. And otolith microstructure analysis confirmed that the development time of *D. thiollierei* was approximately 25–30 d before postlarval stage (Fig. 2b).

The sagittal otolith weight of each specimen ranged from 0.001 5 g to 0.005 2 g and averaged (0.003 3 ± 0.000 7) g. The sagittal otolith weight range of the females was 0.002 4–0.005 2 g and averaged (0.003 5 ± 0.000 6) g, while the sagittal otolith weight of the males was 0.001 5–0.004 8 g and averaged (0.003 0 ± 0.000 7) g. Logarithmic relationships between daily age (t) and sagittal otolith weight (M) were observed.

$$\text{For female: } M = 0.002 8 \ln t - 0.008 9, R^2 = 0.432 6, p < 0.01,$$

$$\text{for male: } M = 0.003 2 \ln t - 0.011 5, R^2 = 0.580 5, p < 0.01,$$

$$\text{for combined: } M = 0.003 0 \ln t - 0.010 4, R^2 = 0.454 1, p < 0.01.$$

There were significant differences in the daily age and otolith weight relationship between males and females (ANCOVA, $p = 0.002$).

The exponential functions for the relationship between sagittal otolith weights (M) and body standard length (SL) were as follows:

$$\text{for female: } M = 0.000 6e^{0.035SL}, R^2 = 0.456 9, p < 0.01,$$

$$\text{for male: } M = 0.000 5e^{0.037SL}, R^2 = 0.655 5, p < 0.01,$$

for combined: $M = 0.0005e^{0.038SL}$, $R^2 = 0.6059$, $p < 0.01$.

There were no significant differences in the standard length and otolith weight relationship between males and females (ANCOVA, $p=0.092$).

3.3 Otolith chemistry analysis

The fish, 10 specimens, were aged between 120 d and 158 d, with a range of 54.8–57.5 mm in standard length. Their hatching dates were back-calculated, ranging from January to February 2021, and thus the fish were mainly spawned in January.

3.3.1 Microstructure of sagittal otolith

The sagittal sections of otoliths in *D. thiollierei* were examined under an optic microscope with reflected light, and the annuli were discernible from concentric rings in otoliths. According to Greely et al. (1999) the section was subdivided into six zones on the basis of alternately clear and dark bands, which represented six life history stages: primordium (nucleus, N), larval (L), postlarval (PL), postmetamorphic I (PM I), PM II, and PM III stages (Fig. 2b and Table 1). The nucleus of the otolith was the central region with an annulus width of 50 μm , and it represented the hatching stage, the initial growth point, on which the first laser ablation was carried out. The range of laser ablation numbers on each specimen was 24–28.

3.3.2 Microchemical analysis

Elemental concentrations were measured from the core to the edge region of the right sagittal otoliths of 10 *D. thiollierei* by means of LA-ICP-MS. Seven elements (Na, Sr, Mg, Li, Mn, Ba, Cu) were well above the lowest detection limits with relative standard deviation (RSD) less than 10% (Table S1), given as concentration relative to calcium content (ratio of element to calcium, mmol/mol). Four elements, i.e., Sr, Mg, Li and Ba, were selected as the main elements for microchemical analysis in this study in view of their low coefficient of variation. In addition, the deposition of Na in otoliths is also susceptible to environmental factors and individual fish physiology, but it was not selected for easy loss during the grinding and sectioning process.

The ratios of the four elements fluctuated in different life stages (Fig. 5). The $K-S$ tests showed that the ratios of all four elements in Ca^{-1} significantly deviated from a normal distribution; thus, the median was more representative in delineating the central tendency in each stage. The ratios of Sr to Ca, Li to Ca, and Mg to Ca in otoliths showed similar fluctuations with ontogenetic process, high values from hatching to postlarval stage, followed by a marked decline and then tendency to flatten out (Fig. 5 and Table 2). The ratios of the three elements were significantly positive correlated in a pairwise manner (Spearman correlation, in Table 3). In contrast to the aforementioned profiles of ratios of Sr to Ca, Li to Ca, and Mg to Ca, the ratios of Ba to Ca were low from the hatching to postlarval stages and increased during the three post stages (Fig. 5). Thus, negative correlations

were found between otolith Ba to Ca vs. Li to Ca ratios and otolith Ba to Ca vs. Mg to Ca ratios (Table 3).

4 Discussion

4.1 Accuracy of age determination of sagittal otoliths

At present, there is no specific research on the daily ring deposition rate of *D. thiollierei*. Due to sampling limitations and other factors, this study was unable to verify the daily ring deposition rate of *D. thiollierei*. However, studies on other lanternfishes have demonstrated that the deposition rate is one ring a day in common conditions (Gartner, 1991; Suthers, 1996; Hayashi et al., 2001; Moku et al., 2001, 2005; Wang et al., 2019; Zhang et al., 2021). Moku et al. (2005) concluded that in mesopelagic fishes, sagittal otolith increments in larvae, juveniles and adults are formed daily, based on the marginal increment analysis of sagittal otoliths. Since the daily growth annuli in other species in the same genus have previously been shown, such as *D. kapalae* (Suthers, 1996), and *D. brachycephalus* (Tian et al., 2022), the rings observed in *D. thiollierei* otoliths were assumed to be formed daily and could be used to estimate age and hatching date. In this study, the CVs (coefficient of variations) and APEs (average percent error) of the estimated daily ages of each *D. thiollierei* were all less than 5%, i.e., 4.74% and 3.92%, respectively, indicating reliable aging results (Campana, 2001).

4.2 Population growth characteristics

In this study, the best functional relationship (SL-DW) between the standard length and dry weight of *D. thiollierei* was described by a power function, consistent with other lanternfish species (Greely et al., 1999). The allometric coefficient (b) in this study indicated negative allometric growth, as the growth coefficient of dry weight relative to standard length was less than 3 ($b = 2.401$), implying that the length gain was faster as they grew. The results were also consistent with findings for other lanternfishes such as *Myctophum asperum* (Wang et al., 2019) and *Benthosema pterotum* (Karuppasamy et al., 2008), but there are also some lanternfishes that undergo isometric growth, such as *D. watasei* (Sebastine et al., 2013) and *Ceratoscopelus warmingii* (Zhang et al., 2021). There was a significant difference in the SL-DW functions between female and male *D. thiollierei*. Factors such as gonad maturity, growth phase, sampling season, stomach fullness, size range, and preservation techniques can all affect SL-DW relationships (Zhang et al., 2021). In this study, the body weight of fish was expressed in body dry weight due to the preservation method of samples, and consequently, the power exponent (b) of the length-weight function was not likely to be the same using wet weight measurements as the ratios of dry to wet weight vary across different life stages (Pakhomov et al., 1996). Since linear relationship between dry weight and wet weight were both highly significant, and no statistical differences were found between the slopes of the regression (Schaafsma et al., 2022). Thus, our results could provide reliable information concerning allometric

Table 1. Annulus width, number of LA-ICP-MS points, and estimated ages in day for six life stages

Life stage	Annulus width/ μm	Number of LA-ICP-MS points	Estimated daily age/d
Primordium = Nucleus (N)	about 50	1	
Larval (L)	about 150	3	about 25–30 (including N and L)
Postlarval (PL)	about 200	4	about 30–40
Postmetamorphic I (PM I)	about 300	6	about 40–70
Postmetamorphic II (PM II)	about 250/200	5/4	about 70–100
Postmetamorphic III (PM III)	>250	>5	about 100 to >130

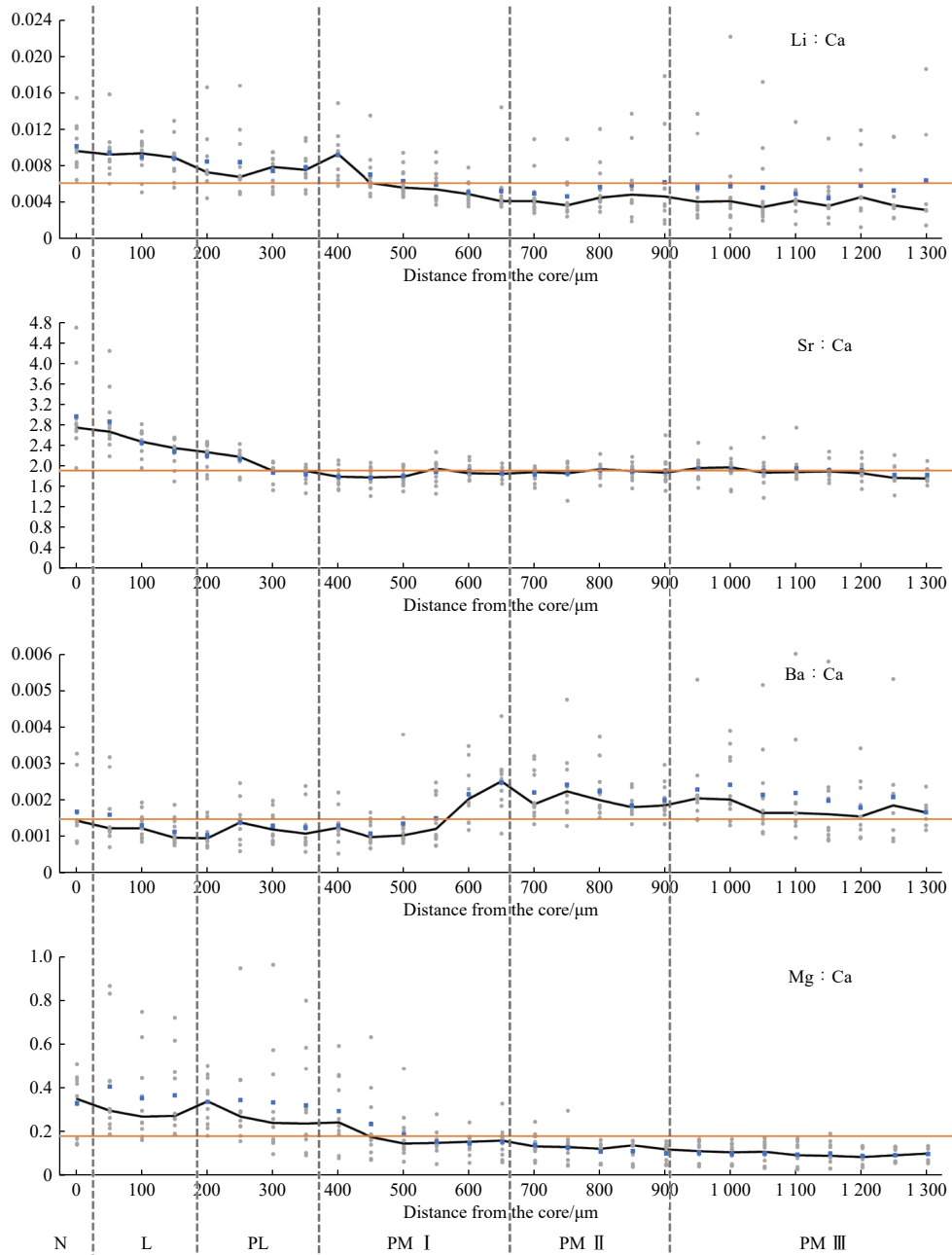


Fig. 5. The ratios of each otolith element to Ca concentration along the line transects from the core (0 μm) to the edge of the sagittal plane of *D. thiollierei*. The gray dots indicate the ratio point value of each otolith element to Ca, while the solid black line and blue block indicate the median and average values of all specimens, respectively. The vertical dashed lines separate the six life history stages. N, nucleus (primordium); L, larval; PL, postlarval; PM I, postmetamorphic I; PM II, postmetamorphic II; and PM III, postmetamorphic III stages.

Table 2. Median ratios of element to calcium in sagittal otolith of *Diaphus thiollierei* during six life stages

Life stage	Li to Ca	Mg to Ca	Sr to Ca	Ba to Ca
N	0.009 47 a	0.339 ab	2.73 a	0.001 37 ab
L	0.008 98 a	0.276 a	2.50 a	0.001 14 a
PL	0.007 18 a	0.265 a	1.95 b	0.001 03 a
PM I	0.005 65 b	0.150 b	1.81 b	0.001 30 ab
PM II	0.004 10 bc	0.111 c	1.86 b	0.001 83 b
PM III	0.003 65 c	0.081 c	1.82 b	0.001 67 b

Note: The different letters indicate significant differences ($p < 0.05$, Kruskal-Wallis test with all pairwise comparisons).

Table 3. Spearman’s correlation coefficients between ratios of element to calcium

	Mg to Ca	Sr to Ca	Ba to Ca
Li to Ca	0.855**	0.533**	-0.625**
Mg to Ca		0.535**	-0.523**
Sr to Ca			-0.223

Note: ** Correlation is significant at the 0.01 level (2-tailed).

growth of *D. thiollierei*.

It was showed that females were generally larger than males in the samples based on the standard length and dry weight data

(Fig. 4). Similar conclusions were reported for other myctophid species, such as *D. danae* (Flynn and Paxton, 2012), *D. adenomus* (Braga et al., 2008), and *M. asperum* (Wang et al., 2019). However, in von Bertalanffy growth functions, there was no significant difference in growth coefficients between males and females, which differed from other lanternfish species, e.g., *Ceratoscopelus warmingii* (Zhang et al., 2021). Chen and Mello (1999) suggested that small sample sizes and unbalanced age compositions might introduce biases, especially when there were insufficient numbers of older and younger individuals. Thorson and Simpfendorfer (2009) suggested that 200 specimens were required to consistently achieve good accuracy for growth parameters. With a small sample size of 103 individuals with a wider range of body lengths in males, the accuracy of the growth parameters might have been impacted.

Lombarte and Leonart (1993) proposed that changes in sagittal size were synchronized with the growth of body length. Some studies have shown that the otolith weight can be used to estimate the age of certain fish with long lifespans and slow growth rates, such as *Lethrinus mahsena*, *Epinephelus chlorostigma*, *L. lentjan*, *L. nebulosus*, *Scarus ghobban* and *S. rubroviolaceus* (Pilling et al., 2003), while this might not be the case for fish with fast growth rates, e.g., *Sardinella aurita* (Pawson, 1990). In this study, logarithmic relationships were observed between sagittal otolith weight (M) and daily age (t) for male, female and combined *D. thiollierei* specimens, while exponential relationships were observed between sagittal otolith weight (M) and body standard length (SL) for these specimens. More studies involving a broader daily age range of *D. thiollierei* are needed to establish more robust relationships between daily age and sagittal otolith weight on account of the small lanternfish size and short life history. Nevertheless, considering the current lack of research on the basic biology of *D. thiollierei*, the data from this study contribute to understanding of the population dynamics of this species.

4.3 Sagittal otolith microchemistry associated with vertical location in life history

Ambient environmental factors, such as temperature, salinity, and habitat depth could also have some effect on otoliths, in addition to individual biological characteristics such as sex, age, and body length (Campana, 1999). And in turn, the life history might be reconstructed based on the microchemistry of otoliths, especially in cases where there were significant environmental differences among different areas of fish migration (Duan et al., 2021). Elemental analyses have mostly been performed using the sagittal otolith, the largest of the three otoliths, because it has the longest growth axis and is the easiest to locate (Thresher, 1999). A strong relationship has been observed between ambient salinity and the concentration ratios of certain elements (e.g., Sr, Ba) to calcium (Ca) in fish otoliths (Brown and Severin, 2009; Yang et al., 2011; Taddese et al., 2019; Xuan et al., 2023), since the concentration changes of macro- and minor elements in seawater are typically consistent with changes in salinity.

Some myctophid adults exhibit diurnal vertical migration, ascending to the upper 100 m layer at night, while of course, some others remain in deep waters (200–350 m). During the daytime their habitat is presumed to be near the bottom, since the species are commonly captured in the daytime by commercial deep-sea shrimp bottom trawls at a depth range of 250–500 m (Gjøsaeter, 1984; Sebastine, 2014). Lanternfish assemblages are not strongly affected by the thermohaline structure and current systems of the region (Eduardo et al., 2021). In our survey area, salinity and temperature fluctuated less at the horizontal scale than at the depth

scale, i.e., the coefficients of variation (CV) of salinity in the horizontal direction was significantly lower than that in the vertical direction within 1 000 m (t -test, $p < 0.01$), and same for the variation of temperature (t -test, $p < 0.01$). Due to being located in the tropics, even in the surface, the fluctuant range of temperature and salinity was small, so the gradient profiles of water temperature and salinity are similar in each month (Fig. S1). Considering the migration distance of lanternfishes with weak horizontal structuring (Eduardo et al., 2021), the microchemical elements recorded in the sagittal otoliths of *D. thiollierei* might predominantly reflect vertical movement during their life history.

Currently, the concentration ratio of Sr to Ca is the most commonly used indicator for analyzing the microchemistry of sagittal otoliths in marine fish. This ratio could accurately predict environmental changes occurring in the life history, as a positive correlation has been confirmed between the otolith ratio of Sr to Ca and habitat salinities (Secor and Rooker, 2000; Yang et al., 2011). In our results, the rapid decline in the ratios of Sr to Ca from the N to PL stages suggested that these fish mostly hatched in the high-salinity zone associated with surface or very shallow water. As larvae grow after hatching, they start to possess the ability of diel vertical movement and migration to deeper layers. The fastest decline in the ratio of Sr to Ca was observed during the PL stage, corresponding to approximately 30–40 daily annuli in the otolith, and it was compatible with the great variations in salinity at depths of around 100–200 m (Fig. S1). This result suggested that *D. thiollierei* might likely rapidly descend during the PL and PM I stages to depths of approximately 100–200 m, and then the sinking rate began to slow down at a certain depth. The fluctuations in salinity in deeper water (200–800 m) and ratios of Sr to Ca after the PM I stage were both no longer obviously observed, so it was impossible to reliably determine the location depth using the ratio of Sr to Ca. Below 800 m, the decreasing rate of salinity with depth was getting faster, and in contrast, the ratio of Sr to Ca varied only slightly after the PM II stage. Therefore, we assumed that *D. thiollierei* after the PM II stage continued to descend from a depth of approximately 300 m with a depth range of 300–800 m, and their location depth is not likely to exceed 800 m throughout their life history.

In addition to Sr, Mg has also been used to reconstruct the habitat histories of marine fish (Xiong et al., 2015). Unlike Sr, the ratio of Mg to Ca in sagittal otoliths is not significantly related to salinity or Mg content in seawater (Elsdon and Gillanders, 2002; Martin and Thorrold, 2005; Woodcock et al., 2012), and moreover, the relationship between temperature and the ratio of Mg to Ca is species-specific (Miller, 2011). In our study, a general downward trend in the ratio of Mg to Ca was observed along with increasing distance from the core within 400 μm in sagittal otoliths (i.e., before the PM I stage). As stated above, *D. thiollierei*, from the N to PL stages, inhabited a depth range of 0–200 m, where the temperature also decreased rapidly (Fig. S1). Therefore, it could be inferred that there was a positive correlation between water temperature and the ratio of Mg to Ca in the sagittal otoliths. After the PL stage, the ratio of Mg to Ca continued to exhibit a noticeable decline until the PM II stage, i.e., the daily age of 100, indicating that their location depth could be around 200–300 m during the PM I to II stages according to the temperature-depth curve. The seawater temperatures below 300 m remained relatively constant, as did the ratios of Mg to Ca in otoliths after PM II. Thus, the habitat depth could not be inferred from the ratios of Mg to Ca after the PM II stage.

The ratio of Li to Ca showed a general downward trend in sagittal otoliths throughout the life history. The ratios of Li

to Ca, and Mg to Ca in otoliths showed significantly similar fluctuations during the ontogenetic process ($r_{sp} = 0.855$, $p < 0.01$). Thus, the profile of the Li to Ca ratio in sagittal otoliths confirmed the vertical distribution of *D. thiollierei* inferred from the ratio of Mg to Ca.

Ba in the otoliths of marine fishes is mainly deposited from seawater (Walther and Thorrold, 2006), therefore Ba would be expected to be another potential element to reconstruct fish habitat histories. Before that, however, it might be necessary to carry out species-specific Ba deposition models involving environmental conditions. Yet the relationships between temperature, the water ratio of Ba to Ca, and salinity are very complex and species-dependent (Fowler et al., 1995; Miller, 2011). Thus, in this study, the ratio of Ba to Ca in otoliths was not used to estimate the inhabit depth of *D. thiollierei* owing to the lack of the ambient environmental information for each specimen.

In summary, this study concluded that *D. thiollierei* could continually descend after hatching until PL stage reaching depths of approximately 200 m, and then from the PL to PM II stages they might further sink to depths of approximately 200–300 m and spend the daytime at depths of 300–800 m to take refuge from predators. Although the results of microchemical analysis in this study only revealed the vertical migration pattern of fish populations born in January, our results still provided some clues for understanding the vertical movement of lanternfishes born in other months. These findings are generally consistent with other observations on lanternfish vertical migration detected with acoustic means by Sassa et al. (2004). It is important to note that throughout the life history of lanternfishes, the rate of migration to the deep layer is not constant but is sometimes fast and sometimes low, and many factors, such as light intensity, reproductive status, predation and prey pressure, can all influence vertical migration activity. The general pattern of vertical migration of lanternfishes remains to be investigated more and further.

5 Conclusions

As one of the dominant species in the Indian Ocean, *D. thiollierei* plays a crucial role in the oceanic food chain, and fluctuations in its resources significantly impact the Indian Ocean ecosystem. However, there is a lack of research on aging, growth, and population characteristics. In this study, *D. thiollierei* exhibited negative allometric population growth characteristics and significant male-female differences. While there were no significant differences in growth coefficients between males and females in von Bertalanffy growth functions, further studies involving a broader daily age range of *D. thiollierei* are necessary to establish more robust relationships. Based on otolith microchemistry analysis, we can speculate on the vertical migration of *D. thiollierei* during developmental stages. *Diaphus thiollierei* could continually descend after hatching until the post-larval (PL) stage, reaching depths of approximately 200 m. From the PL to post-metamorphic stage II (PM II), they might further sink to depths of approximately 200–300 m and spend the daytime at depths of 300–800 m to take refuge from predators. Although the results of microchemical analysis in this study only revealed the vertical migration pattern of fish populations born in January, they still provide some clues for understanding the vertical movement of lanternfish born in other months. Further investigation on otoliths is needed to better delineate population ecology in detail, thereby providing basic information for the exploitation of lanternfish resources and understanding their ecological roles.

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Supplementary information:

Fig. S1. Salinity and temperature with depth in sampling area.

Fig. S2. The gonads of male and female *Diaphus thiollierei*.

Fig. S3. The length-weight (SL-DW) relationships in male and female. Blue for male and red for female.

Table S1. Precision parameters of elemental ratios in sagittal otolith.

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