



Population variations of Opal fish, *Bembrops caudimacula* Steindachner, 1876 from Arabian Sea and Andaman Sea: Evidence from otolith morphometry

K.P. Deepa^a, K.V. Aneesh Kumar^{b,*}, Oxona Kottanis^a, R. Nikki^a, K.K. Bineesh^c, M. Hashim^b, N. Saravanane^b, M. Sudhakar^b

^a Kerala University of Fisheries and Ocean Studies (KUFOS), Panangad PO, PIN 682506, Kochi, Kerala, India

^b Centre for Marine Living Resources and Ecology (CMLRE), CMLRE, Ministry of Earth Sciences, 6th Floor, C- Block, Kendriya Bhavan, PB No 5415, CZEZ P. O., Kochi 682037, India

^c Zoological Survey of India, Andaman & Nicobar Regional Centre (ANRC), Haddo, Port Blair-744 102, Andaman & Nicobar Islands, India

ARTICLE INFO

Article history:

Received 1 February 2018

Received in revised form 29 November 2018

Accepted 5 December 2018

Available online 10 December 2018

Keywords:

Bembrops caudimacula

Arabian sea

Andaman sea

Otolith

ABSTRACT

Bembrops caudimacula dominates the deep-sea trawl catch in the exploratory surveys and as bycatch in the commercial trawling targeting deep-sea shrimps, in the Indian Exclusive Economic Zone. The intra-species variability in the bathy-demersal fish *Bembrops caudimacula* collected from two different ecosystems in the Indian Ocean were studied using otolith morphometric analysis. Five otolith size parameters (ferret length, ferret width, area, perimeter and weight), and five shape indices (roundness, rectangularity, ellipticity, form factor and circularity) were taken from forty-seven otoliths collected from two regions. Principal component analysis (PCA) and non-parametric PERMANOVA successfully differentiate the fishes from two regions based on the otolith morphometry. PCA indicated that ellipticity and otolith weight were the major factor responsible for the variation. The study indicated that otoliths of the fishes collected from Andaman Sea (part of Bay of Bengal) were more elliptic and massy compared to those collected from the Arabian Sea. This is the first work on the differentiation of *B. caudimacula* population from these two unique ecosystems, using otolith morphometry which is highly imperative to understand its population structure. Our study confirmed the suitability of otolith morphometric studies as an easiest and inexpensive method for differentiating the fish populations.

© 2018 Elsevier B.V. All rights reserved.

1. Introduction

The genus *Bembrops* (Opal fish), coming under the family Percophidae, includes 17 species (Eschmeyer, 2017; Smith and Heemstra, 1986; Das and Nelson, 1996). These fishes are mainly distributed in the continental shelf and slope areas of tropical and warm temperate regions of the Indo-West Pacific and Atlantic between depths of approximately 50–700 m (Das and Nelson, 1996; Venu, 2009; Hashim, 2012). *Bembrops caudimacula* (Steindachner, 1876), *B. platyrhynchus* (Alcock, 1894), and *B. curvatura* (Okada and Suzuki, 1952) were reported from Andaman and Nicobar water whereas *B. caudimacula* and *B. platyrhynchus* are distributed in the Arabian Sea (Das and Nelson, 1996; Hashim, 2012). The genus *Bembrops* has an elongated body, sub-cylindrical, head depressed anteriorly, posteriorly compressed and smaller in size (Smith and Heemstra, 1986; Das and Nelson, 1996) with a maximum length of 350 mm. (Knapp, 1981; Das and Nelson, 1996; Venu, 2009;

Hashim, 2012). *B. caudimacula* is known to be one of the most dominant deep-sea fish species caught during the exploratory fishery operations as well as a major by-catch during commercial deep-sea trawling targeting deep-sea shrimps (Venu, 2009; Hashim, 2012). However, little information is available on their economic value. These species can be considered as a potential alternative fishery resource which certainly would reduce fishing pressure on other fishery resources.

Studies on *B. caudimacula* from Indian waters are restricted to their basic biological characteristics such as food and feeding and length–weight relationships (Venu, 2009; Hashim, 2012). No efforts have been made to understand their stock structure and population characteristics from these regions as these data are essential for their accurate assessment of stock and formulating sustainable managements policies and strategies for the responsible utilization of this resource. Each stock is characterized by unique features which are influenced by their genetic as well as environmental factors (Cadrian and Friedland, 1999). Phylogeny associated otolith shape variability has been reported in many teleost fishes (Gaemers, 1984; Monteiro et al., 2005), with some conflicting results (Lombarte et al., 2010).

* Corresponding author.

E-mail address: aneeshmenan12@gmail.com (K.V.A. Kumar).

Table 1

Otolith sample size (n), ranges of mean values, standard lengths and otolith size parameters and shape indices of *Bembrops caudimacula* collected from Arabian Sea and Andaman Sea, India.

n	SL (cm)	OW (g) ^a	FL (mm) ^a	FW (mm) ^a	Area (mm ²) ^a	Perimeter (mm) ^a	Ellipticity ^b	Roundness ^b	Rectangularity ^b	Form factor ^b	Circularity ^b
<i>Arabian Sea</i>											
27	12.9–18.0	0.004–0.022	4.41–5.54	2.43–3.8	7.74–14.0	11.69–17.24	11.38–18.49	0.48–0.60	0.62–0.72	0.53–0.66	17.62–23.94
mean ± SD	16.1 ± 1.30	0.0158 ± 0.004	5.04 ± 0.37	3.14 ± 0.37	10.67 ± 1.68	14.70 ± 1.57	15.54 ± 1.95	0.53 ± 0.03	0.67 ± 0.03	0.61 ± 0.04	2.34 ± 1.77
<i>Andaman and Nicobar waters</i>											
20	13–20.52	0.012–0.034	4.59–6.39	2.49–4.02	13–20.52	12.02–18.22	17.80–28.61	0.45–0.53	0.61–0.75	0.52–0.70	17.85–22.46
mean ± SD	18 ± 1.95	0.02345 ± 0.00664	5.84 ± 0.48	3.31 ± 0.38	18.3 ± 1.95	15.98 ± 1.57	23.22 ± 3.78	0.48 ± 0.02	0.67 ± 0.03	0.63 ± 0.05	19.75 ± 1.27

SL, Standard Length; OW, Otolith Weight; FL, Feret Length; FW, Feret Width.

^aOtolith size parameters.

^bOtolith shape indices.

Shape analysis of sagittal otoliths are found to be more accurate than fish morphology for differentiating the population as these objects are species specific, highly sensitive to short term variability in feeding, spawning and environmental condition of the ecosystem (Vieira et al., 2014; Zischke et al., 2016; Libungan et al., 2016). The shape analysis of otoliths are effective alternate methods to differentiate the population/stocks over genetic analysis as these methods are time consuming and much more expensive (Wakefield et al., 2014; Zhuang et al., 2015; Libungan et al., 2016; Zischke et al., 2016). Otolith morphological variations which are highly influenced by sex, age, year class and stock, are considered as potential tools and are extensively used in the food and feeding studies (Vignon and Morat, 2010; Zischke et al., 2016; Kumar et al., 2017a,b). Morphological characteristics are species specific and extensively used to identify fish species in palaeoichthyology, stock discrimination, for testing the function and ecological significance, and for systematic research on teleost fish (Aguirre and Lombarte, 1999; Tuset et al., 2010; Bostanci et al., 2015). The differentiation of species/stocks using otolith morphometry from the Indian waters are either unavailable or very limited (Kumar et al., 2012).

The objective of the present work is to study the feasibility of the use of the otolith morphometry to differentiate the stocks of *B. caudimacula* collected from the Arabian Sea and the Andaman Sea.

2. Materials and methods

2.1. Sampling and otolith collection

Experimental fishing operations were carried out in the Arabian Sea (AS) (April 2015, cruise no. 338, 11° 07'43" N, 75° 25' 82"E, depth 238 m) and the Andaman Sea (AN) (April 2016, cruise no. 349, 12° 44' 480" N 93° 08'204" E, depth 332 m) onboard FORV Sagar Sampada of Ministry of Earth Sciences, Government of India using high speed demersal trawl (HSDT, Crustacean version) for studying the deep-sea fishery resources of Indian Exclusive Economic Zone. Trawl catches were sorted and morphometric measurements of the fishes were taken onboard. Fishes were identified to species level using standard identification keys (Alcock, 1898, 1899; FAO, 1984). Otoliths were removed by making an incision on the cranium and were cleaned with distilled water, dried and stored in plastic vials for the subsequent analysis. A total of 47 otoliths (right side) were taken for the morphometric analysis (20 and 27 from AN and AS, respectively). The images of the otolith (sulcus side) was taken using stereo zoom trinocular microscope (Leica model No. S8APO; Camera, Leica DFP-425). Five parameters indicating the size of the otoliths (feret length, FL, the longest dimension between rostrum and post rostrum; feret width, FW, the dimension from dorsal to ventral edge of otolith taken at right angles to the FL through the focus of the otolith; area, perimeter, weight) and five shape indices (roundness, rectangularity, ellipticity, form factor, and circularity) were calculated using the image analyzing software *ImageJ*. The shape indices were calculated

based on specific mathematical equations (Leguá et al., 2013). The otolith weight was measured using an electronic balance (Metler, Toledo, ML 503) with an accuracy of 0.0001 g (Kumar et al., 2017a,b). The summary of the statistics of five otolith size parameters and five shape indices of *B. caudimacula* is provided in Table 1. All the otolith size parameters selected for the analysis give the two-dimensional representations of the otolith. The curvature and thickness of the otoliths were not considered for the study (Zischke et al., 2016).

2.2. Statistical analysis

The otolith size variables showed significant relationship with fish size (Table 2) (Battaglia et al., 2010; Kumar et al., 2017a,b) and were scaled up with fish size (SL) using linear regressions (Zischke et al., 2016; Tuset et al., 2018). The slope (*b*) was calculated using the linear regressions to standardize (scaling) otolith size parameters for removing the allometric influence data (Zischke et al., 2016). The allometry corrected data was used for the subsequent analysis. The allometric correction of the data was achieved by using the following equation.

$$M_s = M_o \left(\frac{\bar{x}}{x} \right)^b$$

M_o is the original otolith size parameter, $\bar{x}$ is the mean of the size parameter (SL) for all specimens, x is the size parameter (SL) of each specimen. The slope value (*b*) was estimated for each otolith size parameter as the slope of the regression between $\log M_o$ and $\log x$ (Elliott et al., 1995; Leonart et al., 2000; Zischke et al., 2016). The shape indices, which were also found to have a significant correlation with standard length, usually invariant with fish size (Duarte-Neto et al., 2008) were also scaled following the same protocol. Later, a data matrix was created with allometry corrected and non-corrected (size parameters which not related with fish size) size parameters for the further statistical analysis.

The principal component analysis (PCA) was performed on allometry corrected data to determine the intra-species otolith morphological variability among *B. caudimacula* collected from AS and AN based on five otolith size parameters (area, perimeter, width, height, weight) and five shape indices (roundness, rectangularity, ellipticity, form factor and circularity). We also tried to determine the major variables responsible for these variations (Nielsen et al., 2010; Gauldie and Crampton, 2002).

All the otolith size parameters and shape indices were examined by checking the normality and homoscedasticity using Shapiro-Wilk test and Levene test (R Core Team, 2014). Since the data set was non-normal and heteroscedastic in nature, a non-parametric multivariate test (One-way PERMANOVA, based on Bray-Curtis Similarity Index) (Anderson, 2001, 2005) was performed using PAST (Paleontological Statistics, version v1.81) (Hammer et al., 2001) to understand the intra-specific variation in otolith morphometry of *B. caudimacula*.

Table 2

Correlation between various otolith size parameters and shape indices with fish size of *Bembrops caudimacula* collected from Arabian Sea and Andaman Sea, India (statistically significant relationships are marked in bold) during 2015–2016.

	Relationship between	R ²	Significance level
Arabian Sea	SL X Feret length	0.68	p < 0.05
	SL X Feret width	0.74	p < 0.05
	SL X Area	0.76	p < 0.05
	SL X Perimeter	0.74	p < 0.05
	SL X Otolith weight	0.72	p < 0.05
	SL X Roundness	0.11	P > 0.05
	SL X Rectangularity	0.31	p < 0.05
	SL X Ellipticity	0.33	p < 0.05
	SL X Form factor	0.32	p < 0.05
Andaman Sea	SL X Feret length	0.91	p < 0.05
	SL X Feret width	0.76	p < 0.05
	SL X Area	0.9	p < 0.05
	SL X Perimeter	0.83	p < 0.05
	SL X Otolith weight	0.77	p < 0.05
	SL X Roundness	0.001	P > 0.05
	SL X Rectangularity	0.09	P > 0.05
	SL X Ellipticity	0.73	p < 0.05
	SL X Form factor	0.08	P > 0.05
	SL X Circularity	0.09	P > 0.05

R², correlation coefficient.

Table 3

Results of principal component analysis depicting of percentage variance in first five axes.

PC	Eigenvalue	% variance
1	11.2509	52.447
2	7.17911	33.466
3	2.45969	11.466
4	0.540898	2.5214
5	0.0120235	0.056049

3. Results

The representative otolith images of *B. caudimacula* collected from two regions are shown in Fig. 1. The results of the morphometric analysis are summarized in Table 2. Otoliths from both regions were visually very similar in appearance and shape. Linear regression showed significant correlations between fish size (SL) and otolith size parameters and shape indices (Fig. 2A). Five otolith size parameters (FL, FW, area, perimeter, weight) and four shape indices (rectangularity, ellipticity, form factor and circularity) showed significant correlation with fish size (SL) (r^2 ranges 0.32–0.75) for the otoliths collected from AS. All the five otolith morphometric measurements (FL, FW, area, perimeter, otolith weight) (r^2 ranges 0.76–0.91) and one shape index (ellipticity) showed significant correlation with fish size ($r^2 = 0.73$, $P < 0.05$) for the otoliths collected from AN. Shape indices such as roundness, rectangularity, form factor and circularity for the fishes collected from AN waters did not show any significant relationship with the

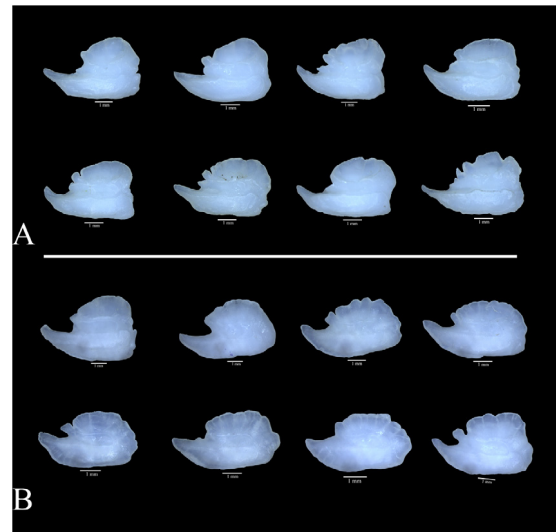


Fig. 1. Representative otolith images of *B. caudimacula* collected from Arabian Sea (A) and Andaman Sea (B), India collected during 2015–2016.

fish size ($P > 0.05$) and were not considered for allometric scaling. Subsequent scaled otoliths variables had no correlation with fish size, indicating that the effect of fish size on otoliths measurements was successfully removed (Fig. 2B).

The fishing operations carried out in AN (cruise no 349) were deeper compared to AS (332 m and 238 m for AN and AS, respectively). The temperature and salinity recorded from AN and AS were 11.5 °C and 13.4 °C, and 35.03 and 35.17, respectively.

3.1. Multivariate analysis

In the PCA analysis, first five PCs account for 100% of the variation. The first and second PC axes described 52.4% and 33.5% of the total variation in otolith morphometry (Table 3). The *B. caudimacula* collected from AN and AS falls on the positive and negative axes of the PC1, respectively (Fig. 3). PC1 clearly differentiates the fishes based on ellipticity ($r = 0.77$) and otolith weight ($r = 0.61$) (Table 4). Otolith weight ($r = 0.75$) and ellipticity ($r = 0.57$) are responsible for the major variation in the PC2. The otoliths of *B. caudimacula* collected from AN were more elliptic and massy compared to the specimens collected from AS (see Fig. 3).

The One-Way PERMANOVA using all scaled otolith morphometric variables were found to be very effective in differentiating *B. caudimacula* collected from the two regions (9999 Permutations, $F = 44.3$, $p = 0.0001$) indicating a significant difference in the otolith morphometry of *B. caudimacula* between the two regions.

Table 4

Correlation coefficient values between PC's components and otolith morphometric variables. In bold, correlations higher abs (0.3).

	PC 1	PC 2	PC 3	PC 4	PC 5
Area	0.10742	0.14241	0.088228	0.79744	−0.11088
Perimeter	0.0060753	0.18575	0.37136	0.44186	−0.16351
Feret length	0.061301	−0.016387	0.040594	0.10023	0.50149
Feret width	−0.016971	0.061802	0.022819	0.15636	0.79336
Otolith weight	0.60912	0.75111	−0.16331	−0.19516	−0.0019335
Roundness	−0.0061251	0.0089933	−0.0044758	0.01382	−0.094524
Rectangularity	−0.0009418	−0.0011507	−0.0041756	0.0061832	−0.26027
Ellipticity	0.76891	− 0.56922	0.27838	−0.024298	0.0010571
Form factor	−0.0025861	−0.0060999	−0.023133	0.016598	−0.047616
Circularity	−0.14864	0.22987	0.86452	− 0.30851	0.033339

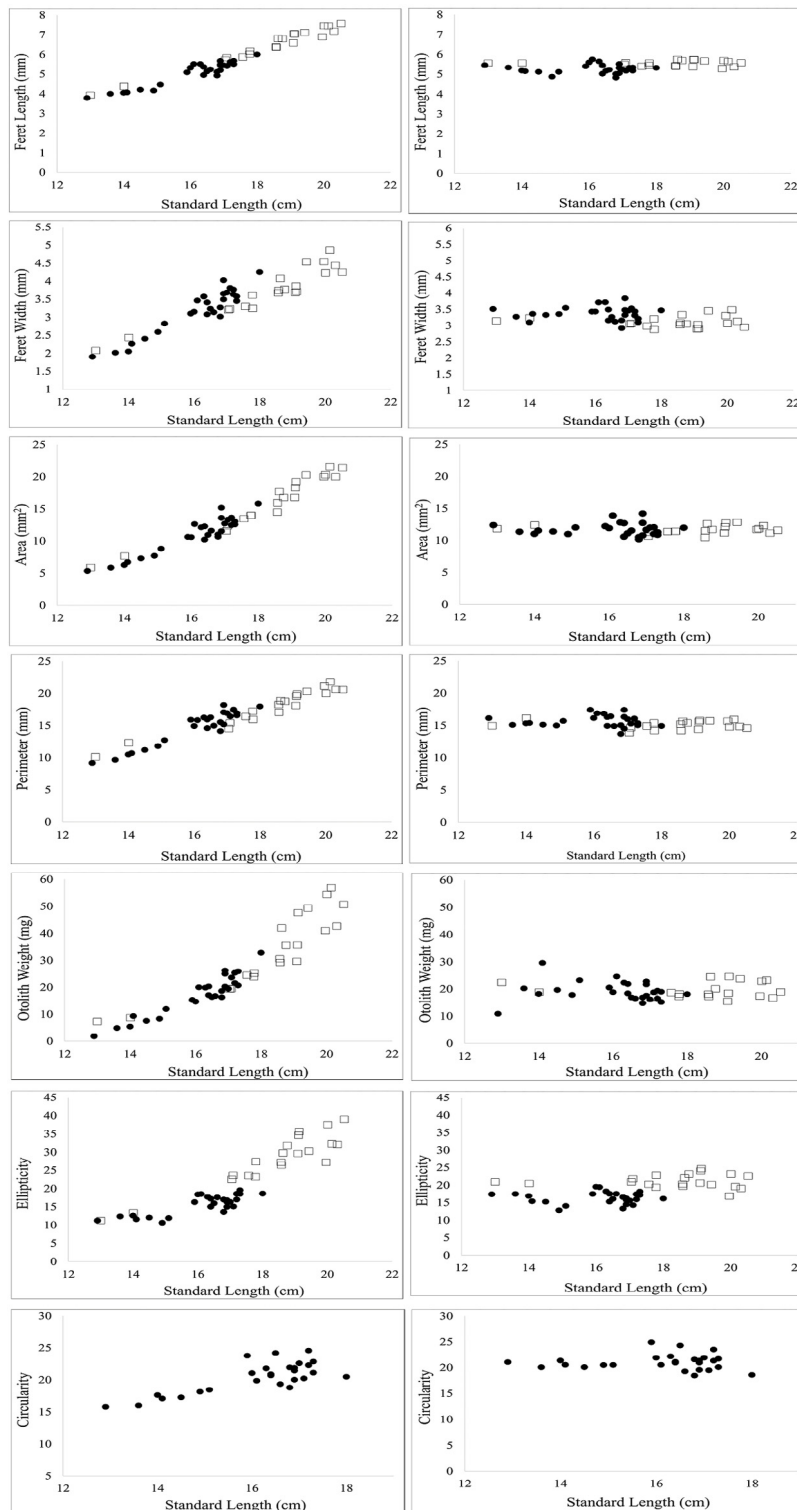


Fig. 2. Scatter plots of original otolith measurements (A) and scaled up otolith measurements (B) with standard length for *B. caudimacula* collected from Arabian Sea (black circles) and Andaman Sea (open squares), India during 2015–2016.

4. Discussion

B. caudimacula contributed a major share to the total catch during the exploratory deep-sea trawling surveys onboard FORV Sagar Sampada at depth ranges found both in both Arabian Sea and Andaman Sea and forms the major by-catch during commercial trawling operations for deep-sea shrimps along west coast of India (Venu, 2009; Hashim, 2012). The accurate identification of

stocks of these species are very essential for their management and sustainable utilization of resources. The molecular methods are always time consuming and expensive and are often not highly reliable when the fishes exhibit ecomorphological adaptations (Zischke et al., 2016). Our studies confirmed the suitability of otolith morphometry in differentiating the populations of *B. caudimacula* found at AS and AN. Otolith morphology and morphometric measurements can differ among populations of the same species

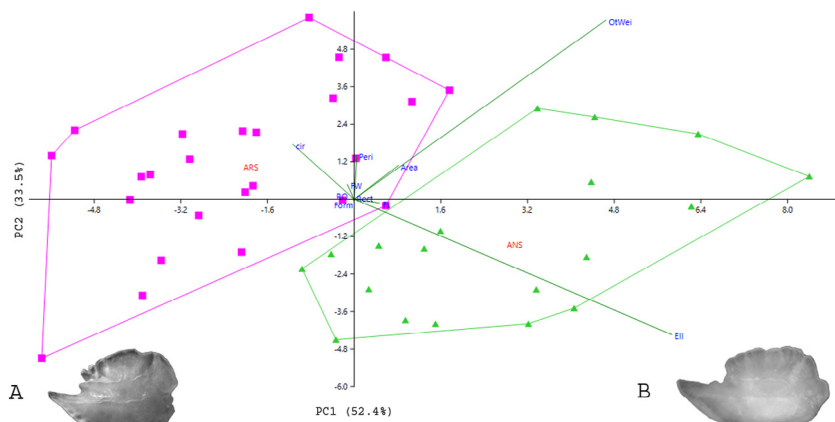


Fig. 3. Principal component analysis showing the differentiation of *Bembrops caudimacula* collected from Arabian Sea and Andaman Sea based on their otolith morphometry (A: Arabian Sea, B: Andaman Sea).

in different locations (Reichenbacher et al., 2009). Our study indicated that otolith weight and ellipticity are the major variables responsible for the differentiation between the *B. caudimacula* inhabiting in two different ecosystems. Fishes from AN possess more heavy and elliptic otoliths compared to those collected from the AS. Previous studies reported that otolith shape varies with the habitat the fish inhabits (Parmentier et al., 2001). Physico-chemical characteristics of the region (viz., salinity, temperature and depth) greatly influence the otolith accretion rates (Kumar et al., 2012; Cardinale and Arrhenius, 2004; Zischke et al., 2016). It is highly evident from various studies that both AS and AN are very unique in their oceanographic characteristics (Kumar et al., 2002; Gauns et al., 2005; Madhupratap et al., 2001). The fishes collected from AN were from deeper waters (332 m) compared to those from AS (238 m). The habitat complexity and depth where the fish inhabits might have profound influence on the otolith accretion rates and its morphology as confirmed by previous researchers (Lombarte and Leonart, 1993; Gaudie and Crampton, 2002; Bani et al., 2013). Further studies have to be conducted on the otolith morphometric variations at different depths from the same geographical area to discern these relationships clearly. AN was found to be cooler (11.5 °C) than AS (13.4 °C) at fishing depths during the sampling period. The influence of water temperature on otolith accretion rates was reported by previous researchers (Lombarte and Leonart, 1993; Gaudie et al., 1980; Kalish, 1989; Jones, 1992). The decline of temperature with increasing depth was reported to be an important factor for the otolith growth (Lombarte and Leonart, 1993; Gagliano and McCormick, 2004; Mérigot et al., 2007; Hüsey, 2008). It was observed that AN was less saline compared to AS (Madhupratap et al., 2001; Kumar et al., 2002). The influence of salinity on the otoliths accretion rates were confirmed by research carried out elsewhere (Mazloumi et al., 2017; Diouf et al., 2006; Elsdon and Gillanders, 2002). Hence, it is well understood that the changes in physical and chemical parameters in different habitats are responsible for differences in calcareous concrescence formation in fishes.

The present study observed a high *b* value for the relationship between feret length and otolith weight for the fishes collected from AS ($b = 3.38$) compared to AN ($b = 3.29$). This indicated that relative length of the otolith, compared to its weight, is higher in AS. Vermeij (1978) and Lombarte and Leonart (1993) reported the lower temperature negatively influences the accretion of calcium carbonate incorporation in the otolith. The relationship between otolith size and fish size of *B. caudimacula* from AS were reported by Kumar et al. (2017a,b). No previous estimations are available on the relationship between otolith size and fish size of *B. caudimacula* from AN. The availability of preferred food items may differ

between the locations also expected to play a role in the otolith morphological variability among species (Cardinale and Arrhenius, 2004; Gagliano and McCormick, 2004; Hüsey, 2008; Limburg, 1995; Gallahar and Kingsford, 1996; Buckel et al., 2004). The rebuilding of body size and prey biomass from otolith measurement is possible by applying a back-calculation (Battaglia et al., 2010). The Arabian Sea is biologically more productive than the Bay of Bengal which differs greatly in their oceanographic characteristics (Kumar et al., 2002; Gauns et al., 2005). The uniqueness of these two ecosystems with their physico-chemical characteristics regulates the otolith accretion rates. These factors are also expected to influence their diet preferences and availability, and are reflected in the intra-species otolith morphometric variations.

B. caudimacula can be considered as a promising resource for the commercial exploitation at a depth range of 50–700 m when most of the conventional fishery resources of the country are either depleted or there is no scope for the further expansion (Das and Nelson, 1996). Better understanding about the otolith morphology/morphometry and their intra-species variability would be very useful in understanding population structure and for accurate yield estimations in the future. The present study further confirms the ease, speed and relatively low cost of this method, to differentiate populations.

Acknowledgments

We would like to express our sincere thanks and gratitude to the Secretary, Ministry of Earth Sciences (MoES), and the Director, Centre for Marine Living resources and Ecology (MoES), Government of India, for their wholehearted support and encouragement during the study. Thankful to Captain, fishing master, scientific participants and all the crew members of FORV *Sagar Sampada* for their support and assistance during the sample collections. The work has been carried out as part of DSDWF project under the Marine Living Resource programme of CMLRE. Sincere thanks to Ministry of Earth Sciences, India for the financial and logistic support provided. We are very much thankful to the Editor and anonymous reviewers for their constructive comments and advice which certainly improved the quality of the manuscript. This is CMLRE contribution no. 98.

References

- Aguirre, H., Lombarte, A., 1999. Ecomorphological comparisons of sagittae in *Mullus barbatus* and *M. surmuletus*. J. Fish Biol. 55, 105–114.
- Alcock, A.W., 1898. Natural history notes from H.M. Indian marine survey ship "Investigator". Ser. II., No. 25. A note on the deep-sea fishes, with descriptions of some new genera and species, including another probably viviparous ophioid. Ann. & Mag. Nat. Hist. (Ser. 7) 2, 136–156.

- Alcock, A.W., 1899. A Descriptive Catalogue on the Indian Deep-Sea Fishes in the Indian Museum: Being a Revised Account of the Fishes Collected by the Royal Indian Marine Survey Ship Investigator III. Indian Museum, Kolkata.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Aust. Ecol.* 26, 32–46.
- Anderson, M.J., 2005. PERMANOVA Permutational Multivariate Analysis of Variance. Department of Statistics, University of Auckland, Auckland, New Zealand.
- Bani, A., Poursaeid, S., Tuset, V.M., 2013. Comparative morphology of the sagittal otolith in three species of south Caspian gobies. *J. Fish Biol.* 82, 1321–1332.
- Battaglia, P., Malara, D., Romeo, T., Andaloro, F., 2010. Relationships between otolith size and fish size in some mesopelagic and bathypelagic species from the Mediterranean Sea (Strait of Messina, Italy). *Sci. Mar.* 74, 605–612.
- Bostanci, D., Polat, N., Kurucu, G., Yedier, S., Konaş, S., Darçin, M., 2015. Using otolith shape and morphometry to identify four *Alburnus* species (*A. chalcoides*, *A. escherichii*, *A. mossulensis* and *A. tarichi*) in Turkish inland waters. *J. Appl. Ichthyol.* 31, 1013–1022.
- Buckel, J.A., Sharack, B.L., Zdanowicz, V.S., 2004. Effect of diet on otolith composition in *Pomatomus saltatrix*, an estuarine piscivore. *J. Fish Biol.* 64, 1469–1484.
- Cadrin, S.X., Friedland, K.D., 1999. The utility of image processing techniques for morphometric analysis and stock identification. *Fish. Res.* 43, 129–139.
- Cardinale, M., Arrhenius, F., 2004. Using otolith weight to estimate the age of haddock (*Melanogrammus aeglefinus*): a tree model application. *J. Appl. Ichthyol.* 20, 470–475.
- Das, M.K., Nelson, J.S., 1996. Revision of the percophid genus *Bembrops* (Actinopterygii: Perciformes). *Bull. Mar. Sci.* 59, 9–44.
- Diouf, K., Panfili, J., Labonne, M., Aliaume, C., Tomás, J., Do Chi, T., 2006. Effects of salinity on strontium: calcium ratios in the otoliths of the West African black-chinned tilapia *Sarotherodon melanotheron* in a hypersaline estuary. *Environ. Biol. Fish.* 77, 9–20.
- Duarte-Neto, P., Lessa, R., Stosic, B., Morize, E., 2008. The use of sagittal otoliths in discriminating stocks of common dolphin-fish (*Coryphaena hippurus*) off north-eastern Brazil using multi shape descriptors. *ICES J. Mar. Sci.* 65, 1144–1152.
- Elliott, N.G., Haskard, K., Koslow, J.A., 1995. Morphometric analysis of orange roughy (*Hoplostethus atlanticus*) off the continental slope of southern Australia. *J. Fish Biol.* 46, 202–220.
- Elsdon, T.S., Gillanders, B.M., 2002. Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. *Can. J. Fish. Aquat. Sci.* 59, 1796–1808.
- Eschmeyer, W.N., Fricke, R., van der Laan, R. (Eds.), 2017. Catalog of fishes: genera, species, references. (<http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>). (accessed 24 2017).
- FAO, 1984. FAO species identification sheets for fishery purposes. In: Ficher, W., Bianchi, G. (Eds.), Western Indian Ocean (Fishing Area 51) Rome: Food and Agricultural Organization of the United Nations, Vol. 1–4.
- Gaemers, P.A.M., 1984. Taxonomic position of the Cichlidae (Pisces, Perciformes) as demonstrated by the morphology of their otoliths. *Neth. J. Zool.* 34, 566–595.
- Gagliano, M., McCormick, M.I., 2004. Feeding history influences otolith shape in tropical fish. *Mar. Ecol. Prog. Ser.* 278, 291–296.
- Gallahar, N.K., Kingsford, M.J., 1996. Factors influencing Sr/Ca ratios in otoliths of *Girella elevata*: an experimental investigation. *J. Fish Biol.* 48, 174–186.
- Gauldie, R.W., Crampton, J.S., 2002. An eco-morphological explanation of individual variability in the shape of the fish otolith: comparison of the otolith of *Hoplostethus atlanticus* with other species by depth. *J. Fish Biol.* 60, 1204–1221.
- Gauldie, R.W., Graynoth, E.J., Illingworth, J., 1980. The relationship of the iron content of some fish otoliths to temperature. *Comp. Biochem. Physiol. A: Physiol.* 66, 19–24.
- Gauns, M., Madhupratap, M., Ramaiah, N., Jyothibabu, R., Fernandes, V., Paul, J.T., Kumar, S.P., 2005. Comparative accounts of biological productivity characteristics and estimates of carbon fluxes in the Arabian Sea and the Bay of Bengal. *Deep Sea Res. II* 52, 2003–2017.
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4, 9.
- Hashim, M., 2012. Distribution, Diversity and Biology of Deep-Sea Fishes in the Indian EEZ (Ph.D. thesis), Cochin University of Science and Technology.
- Hüssy, K., 2008. Otolith shape in juvenile cod (*Gadus morhua*): Ontogenetic and environmental effects. *J. Exp. Mar. Biol. Ecol.* 364, 35–41.
- Jones, C.M., 1992. Development and application of the otolith increment technique. In: Stevenson, D.K., Campana, S.E. (Eds.), Otolith Microstructure Examination and Analysis, Vol. 117. Can. Spec. Publ. Fish. Aquatic Sci, pp. 1–11.
- Kalish, J.M., 1989. Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. *J. Exp. Mar. Biol. Ecol.* 132, 151–178.
- Knapp, L.W., 1981. Percophidae. In: Fischer, W., Bianchi, G., Scott, W.B. (Eds.), FAO Species Identification Sheets for Fishery Purposes. Eastern Central Atlantic; Fishing Areas 34, 47 (in part), Vol. 3. Dept. of Fisheries and Oceans Canada and FAO.
- Kumar, P., Chakraborty, S.K., Jaiswar, A.K., 2012. Comparative otolith morphology of sciaenids occurring along the north-west coast of India. *Ind. J. Fish.* 59, 19–27.
- Kumar, K.V.A., Deepa, K.P., Hashim, M., Vasu, C., Sudhakar, M., 2017a. Relationships between fish size and otolith size of four bathydemersal fish species from the south eastern Arabian Sea, India. *J. Appl. Ichthyol.* 33, 102–107.
- Kumar, S.P., Muraleedharan, P.M., Prasad, T.G., Gauns, M., Ramaiah, N., De Souza, S.N., Madhupratap, M., 2002. Why is the Bay of Bengal less productive during summer monsoon compared to the Arabian Sea? *Geophys. Res. Lett.* 29 (24).
- Kumar, K.V.A., Nikki, R., Oxona, K., Hashim, M., Sudhakar, M., 2017b. Relationships between fish size and otolith size of nine deep-sea fishes from the Andaman and Nicobar waters, North Indian Ocean. *J. Appl. Ichthyol.* 33, 1187–1195.
- Leguá, J., Plaza, G., Pérez, D., Arkhipkin, A., 2013. Otolith shape analysis as a tool for stock identification of the southern blue whiting, *Micromesistius australis*. *Lat. Am. J. Aquat. Res.* 41 (3).
- Libungan, L.A., Slotte, A., Otis, E.O., Pålsson, S., 2016. Otolith variation in Pacific herring (*Clupea pallasii*) reflects mitogenomic variation rather than the subspecies classification. *Pol. Biol.* 39, 1571–1579.
- Limburg, K.E., 1995. Otolith strontium traces environmental history of subyearling American shad *Alosa sapidissima*. *Mar. Ecol. Prog. Ser.* 25–35.
- Leonart, J., Salat, J., Torres, G.J., 2000. Removing allometric effects of body size in morphological analysis. *J. Theoret. Biol.* 205, 85–93.
- Lombarte, A., Leonart, J., 1993. Otolith size changes related with body growth, habitat depth and temperature. *Environ. Biol. Fish.* 37, 297–306.
- Lombarte, A., Palmer, M., Matallanus, J., Gómez-Zurita, J., Morales-Nin, B., 2010. Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nothoenidae. *Environ. Biol. Fish.* 89, 607–618.
- Madhupratap, M., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., 2001. Mesozooplankton biomass, composition and distribution in the Arabian Sea during the Fall Intermonsoon: implications of oxygen gradients. *Deep-sea Res. II* 48, 134–1368.
- Mazloui, N., Doubleday, Z.A., Gillanders, B.M., 2017. The effects of temperature and salinity on otolith chemistry of King George whiting. *Fish. Res.* 196, 66–74.
- Mérigot, B., Letourneur, Y., Lecomte-Finiger, R., 2007. Characterization of local populations of the common sole *Solea solea* (Pisces, Soleidae) in the NW Mediterranean through otolith morphometrics and shape analysis. *Mar. Biol.* 151, 997–1008.
- Monteiro, L.R., Di Benedetto, A.P., Guillermo, L.H., Rivera, L.A., 2005. Allometric changes and shape differentiation of sagitta otoliths in sciaenid fishes. *Fish. Res.* 74, 288–299.
- Nielsen, J.R., Methven, D.A., Kristensen, K., 2010. A statistical discrimination method using sagittal otolith dimensions between sibling species of juvenile cod *Gadus morhua* and *Gadus ogac* from the Northwest Atlantic. *J. Northwest Natl. Fish. Sci.* 43, 27–45.
- Parmentier, E., Vandewalle, P., Lagardère, F., 2001. Morpho-anatomy of the otic region in carapid fishes: eco-morphological study of their otoliths. *J. Fish Biol.* 58, 1046–1061.
- R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reichenbacher, B., Feulner, G.R., Schulz-Mirbach, T., 2009. Geographic variation in otolith morphology among freshwater populations of *Aphanius dispar* (Teleostei, Cyprinodontiformes) from the southeastern Arabian Peninsula. *J. Morphol.* 270, 469–484.
- Smith, M.M., Heemstra, P.C., 1986. Smith's Sea Fishes. Smith Institute of Ichthyology, Grahamston, South Africa.
- Tuset, V.M., Olivar, M.P., Otero-Ferrer, J.L., López-Pérez, C., Hulley, P.A., Lombarte, A., 2018. Morpho-functional diversity in *Diaphus* spp. (Pisces: Myctophidae) from the central Atlantic Ocean: Ecological and evolutionary implications. *Deep Sea Res. I* 138, 46–59.
- Tuset, V.M., Piretti, S., Lombarte, A., González, J.A., 2010. Using sagittal otoliths and eye diameter for ecological characterization of deep-sea fish: *Aphanopus carbo* and *A. intermedius* from NE Atlantic waters. *Sci. Mar.* 74, 807–814.
- Venu, S., 2009. The Systematics, Distribution and Bionomics of Deep-Sea Fishes beyond Depth 200 M Along the South West Coast of India (Ph. D. thesis), Cochin University of Science and Technology, India.
- Vermeij, G.J., 1978. Biogeography and Adaptation Patterns of Marine Life. Harvard University Press, Cambridge.
- Vieira, A.R., Neves, A., Sequeira, V., Paiva, R.B., Gordo, L.S., 2014. Otolith shape analysis as a tool for stock discrimination of forkbeard (*Phycis phycis*) in the Northeast Atlantic. *Hydrobiol.* 728, 103–110.
- Vignon, M., Morat, F., 2010. Environmental and genetic determinant of otolith shape revealed by a non-indigenous tropical fish. *Mar. Ecol. Prog. Ser.* 411, 231–241.
- Wakefield, C.B., Williams, A.J., Newman, S.J., Bunel, M., Dowling, C.E., Armstrong, C.A., Langlois, T.J., 2014. Rapid and reliable multivariate discrimination for two cryptic *Eteline* snappers using otolith morphometry. *Fish. Res.* 151, 100–106.
- Zhuang, L., Ye, Z., Zhang, C., 2015. Application of otolith shape analysis to species separation in *Sebastes* spp. from the Bohai Sea and the Yellow Sea, northwest Pacific. *Environ. Biol. Fish.* 98, 547–558.
- Zischke, M.T., Litherland, L., Tilyard, B.R., Stratford, N.J., Jones, E.L., Wang, Y.G., 2016. Otolith morphology of four mackerel species (*Scomberomorus* spp.) in Australia: Species differentiation and prediction for fisheries monitoring and assessment. *Fish. Res.* 176, 39–47.