

Differentiating morpho-functional patterns of the five most common deep-sea benthic anglerfishes (Lophiiformes) from Andaman and Nicobar Islands (eastern Indian Ocean)

Meleppura Rajeeshkumar¹, Kannamkulathil Vijayan Aneesh Kumar¹, José Luí Otero-Ferrer², Antoni Lombarte³, Manjebayakath Hashim¹, Narayanane Saravanane¹, Velloorkirakathil Narayanan Sanjeevan⁴, Mallavarapu Venkata Ramana Murthy¹, Víctor Manuel Tuset³

¹ Centre for Marine Living Resources and Ecology, Ministry of Earth Sciences, Govt. of India, Kakknad, Cochin 682037, India.

(MR) E-mail: rajeeshmeleppura@gmail.com. ORCID iD <https://orcid.org/0000-0002-1223-2904>

(KVAK) (Corresponding author) E-mail: aneeshmenan12@gmail.com. ORCID iD: <https://orcid.org/0000-0002-0551-3505>

(MH) E-mail: hashimaqua@gmail.com. ORCID iD: <https://orcid.org/0000-0001-6556-7364>

(NS) E-mail: saravanane@cmlre.gov.in. ORCID iD: <https://orcid.org/0000-0003-3405-4923>

(MVRM) E-mail: mvrmana.m@cmlre.gov.in. ORCID iD: <https://orcid.org/0000-0001-6429-1511>

² Biostatech, Advice, Training and Innovation in Biostatistics (Ltd), Edificio Emprendia, Campus Vida s/n, 15782 Santiago de Compostela, Spain.

(JLO) E-mail: joseluis.oteroferrier@gmail.com. ORCID iD: <https://orcid.org/0000-0003-1078-4008>

³ Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Catalonia, Spain.

(AL) E-mail: toni@icm.csic.es. ORCID iD: <https://orcid.org/0000-0001-5215-4587>

(VMT) E-mail: vtuset@icm.csic.es. ORCID iD: <https://orcid.org/0000-0001-9032-2844>

⁴ Kerala University of Fisheries and Ocean Studies (KUFOS), Panangad, Cochin 682506 India.

(VNS) E-mail: sanjeevanmoes@gmail.com. ORCID iD: <https://orcid.org/0000-0002-8380-9934>

Summary: Anglerfishes are widely distributed from shallow to deep-water habitats occupying different ecological niches. To explain this adaptability, we performed a morpho-functional study on common benthic anglerfishes inhabiting the Indian deep-sea waters. Sensory capabilities of species were examined using the morphology and morphometry of *sagitta* otoliths (related to detection sound and hearing) and eye size (related to visual communication). We also performed an analysis of the degree of functional niche overlap using fish body traits to understand the coexistence of species. Otoliths showed a morphological pattern similar to that of other anglerfishes: an archaesusulcoid *sulcus acusticus* and variability in the irregularity of the dorsal margin. This last feature affected the allometric relationships between the otolith morphometry and fish length, as well as the otolith relative sizes of each species. The findings suggested that bigger otoliths are associated with the increase of depth distribution of species up to 1000 m, from which it decreases. Our hypothesis is that anglerfishes with irregular otolith shapes could be linked to more nocturnal feeding behaviour because they were characterized by greater eye sizes. The results also indicated interspecific significant differences in functional traits providing a low niche overlap. Therefore, our study supports the hypothesis of an environmental and ecological specialization of benthic anglerfishes.

Keywords: fish body traits; otolith shape; ecomorphology; Lophiiformes.

Diferenciando las características morfo-funcionales de las cinco especies más comunes de rapés de aguas profundas (Lophiiformes) de las islas de Andaman y Nicobar (Océano Índico oriental)

Resumen: Las especies del orden Lophiiformes habitan desde las aguas superficiales hasta las más profundas de los océanos ocupando diferentes nichos ecológicos. Con el fin de explicar esta adaptabilidad se llevó a cabo un estudio morfo-funcional de especies bentónicas comunes en aguas profundas del Océano Índico. La capacidad sensorial de las especies se analizó a partir de la morfología y morfometría del otolito *sagitta* (relacionado con la detección del sonido y la capacidad auditiva) y del tamaño del ojo (relacionado con la comunicación visual). Con el fin de comprender mejor la coexistencia entre especies, también se analizó el grado de solapamiento del nicho funcional usando atributos morfométricos del pez. Los otolitos presentaron una forma morfológica similar a otros lophiiformes: *sulcus acusticus* de tipo archaesusulcoide y variabilidad en la irregularidad del margen dorsal. Este último carácter afectó a las relaciones alométricas entre la morfometría del otolito y la talla del pez, así como los tamaños relativos del otolito de cada especie. Los resultados obtenidos sugieren que los otolitos más grandes estarían asociados con el incremento de la profundidad de distribución de las especies hasta los 1000 m, a partir de la cual disminuirían. La hipótesis que sustentamos es que las especies con otolitos más irregulares podrían tener un comportamiento nocturno asociado con la alimentación, ya que éstas tienen los ojos más grandes. Los resultados también indicaron diferencias interespecíficas significativas en los atributos funcionales de las especies, lo cual proporcionó un bajo solapamiento entre los nichos. En definitiva, el presente estudio apoya la hipótesis de una especialización ambiental y ecológica de las especies bentónicas de lophiiformes.

Palabras clave: atributos del pez; forma del otolito; ecomorfología; Lophiiformes.

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INTRODUCTION

The order Lophiiformes, commonly known as anglerfishes, is a diverse group of benthic and pelagic species inhabiting shallow to deep-sea waters. This order comprises approximately 358 extant species in five suborders (Pietsch and Grobecker 1987, Nelson et al. 2006): Lophioidei, Antennarioidei, Chaunacoidei, Ogcocephaloidei and Ceratioidei. Phylogenetic studies reveal that Lophioidei, the most primitive group, evolved independently of the remaining groups (Caruso 1985, Pietsch and Grobecker 1987, Pietsch and Orr 2007, Miya et al. 2010). Although some lophiiform morphological features are similar (Caruso 1983, Pietsch and Orr 2007), body shape differs between clades: dorso-ventrally flattened in Lophioidei (with rhomboidal head) and Ogcocephaloidei (with triangular or circular head) (Caruso 1985, Ho and Shao 2008), laterally compressed in Antennarioidei (Pietsch and Grobecker 1987, Arnold and Pietsch 2012) and globose in Chaunacoidei (Ho and Ma 2016). In Ceratioidei, species are characterized by specific morphologies adapted to mesopelagic and bathypelagic lifestyle, which has led to their rapid diversification (Miya et al. 2010). In general, lophiiforms are opportunistic (non-selective) ambushers, luring their prey by raising and moving the illicium, a modified first dorsal-fin spine with a terminal esca (bait) (Pietsch and Grobecker 1987, Afonso-Dias 1997). The Ogcocephaloidei species seem to be more adapted for the capture of small demersal prey (durophagy) such as gastropods, small crustaceans and polychaetes (Gibrán and Castro 1999, Nagareda and Shenker 2008). Indistinctly, all species are considered top-predators where the capture efficiency is favoured by a jet-propulsive locomotion, which is produced through pore-like gill openings behind the pectoral fin (Pietsch 1981).

The Indian Ocean, and especially the region around the Andaman and Nicobar Islands, is characterized by their rich deep-sea fishery resources (Venu and Kurup 2002, Jayaprakash et al. 2006, Hashim 2012, Sumod 2018, Rajeeshkumar 2018). Recent experimental surveys have reported 22 lophiiforms (Rajeeshkumar 2018). This eco-evolutionary scenario necessarily implies a high interspecific phenotypic variability leading to coexistence or segregation of species. It is known that this phenotypic variability is linked to multiple extrinsic

(Colborne et al. 2013, Aguilar-Medrano et al. 2016) and genetic factors (Pietsch and Orr 2007, Miya et al. 2010, Arnold 2015), avoiding direct competition for feeding resources (Bellwood et al. 2010, Frederick et al. 2016). For example, the distribution range or temporal segregation in the behavioural activity could play a key role in the coexistence for many sympatric species (Carothers and Jaksić 1984, Seehausen et al. 2008, Foster et al. 2015), as occurs between *Lophius budegassa* and *L. piscatorius* on the continental shelf and upper slope of the Mediterranean Sea. Both species have similar prey preferences (Preciado et al. 2006, Bohórquez-Herrera 2015), but they have developed sensory specialization in eye and otolith organs that allows *L. budegassa* to be more active at night, whereas *L. piscatorius* is more active during daytime (Hislop et al. 2000, Colmenero et al. 2010). Thus, sensory (visual and hearing) and morpho-functional features of an organism can be used to discern and understand the ecological segregation among species (Lombarte 1992, Arellano et al. 1995, Tuset et al. 2016). Overall ecomorphological studies on the ecology of lophiiforms are scarce (Carlucci et al. 2009, Colmenero et al. 2010), and there are none for the species inhabiting the Indian Ocean.

The aim of this work is to understand better the coexistence of the most common benthic species of lophiiforms occurring at the Andaman and Nicobar Islands (Rajan and Sreeraj 2013, Balakrishnan et al. 2008, Hashim 2012, Rajeeshkumar et al. 2016, 2017, Ho et al. 2016a): *Chaunax apus* Lloyd, 1909 and *C. multilepis* Ho, Rajeesh and Bineesh, 2016 (Chaunacidae), *Halieutaea coccinea* Alcock, 1894 and *Malthopsis lutea* Alcock 1891 (Ogcocephalidae), and *Lophiodes lugubris* (Alcock, 1894) (Lophiidae). To this end, we characterized the *sagitta* otolith (henceforth otolith) morphology for each species that may be essential for building marine food webs (Lombarte et al. 2010, Tuset et al. 2008, 2010, 2018), analysed the morphometric relationships of otoliths with fish length as an indirect factor of the range of spatial distribution in depth of the species (Tuset et al. 2010, Colmenero et al. 2010, Nazir and Khan 2019) and obtained functional traits as an indicator of ecological strategies and to detect the degree of functional niche overlapping between species (Gatz 1979, Sibbing and Nagelkerke 2001, Karpouzi and Stergiou 2003, Wainwright et al. 2007).

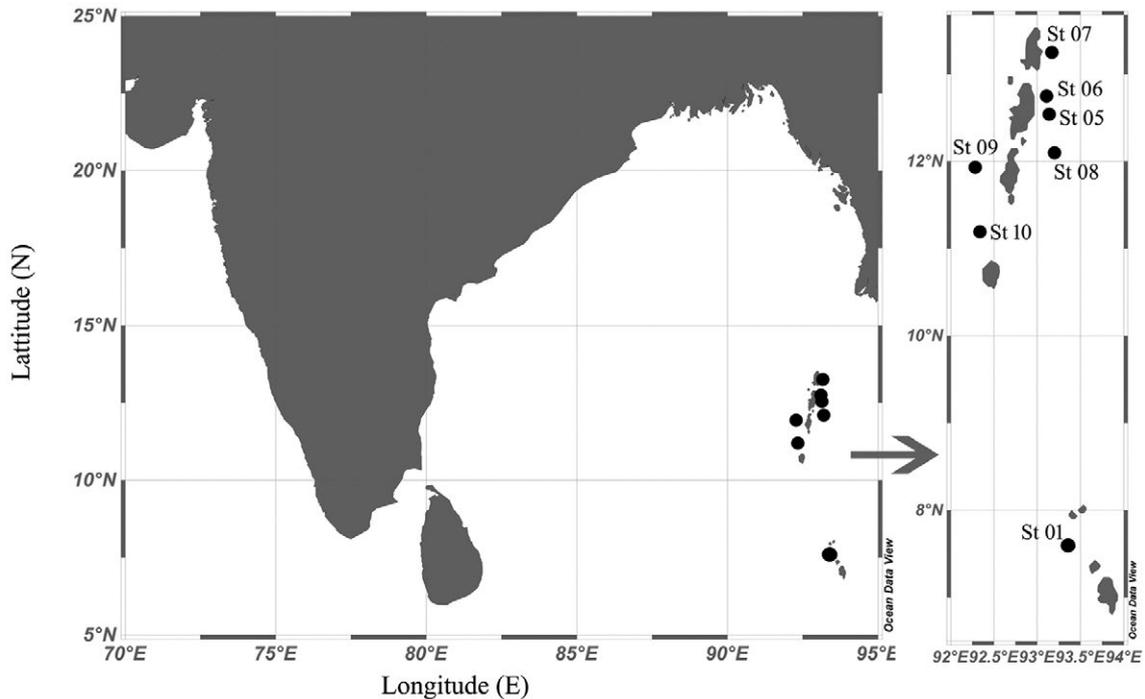


Fig. 1. – Geographical locations of the five most common deep-sea benthic anglerfishes sampled from the Andaman and Nicobar Islands (eastern Indian Ocean).

MATERIALS AND METHODS

Data collection

Specimens were collected during the deep-sea fishery exploratory surveys of the Fishery Oceanographic Research Vessel (FORV) *Sagar Sampada* (71.5 m L_{OA}: 2285 hp) (Cruise no 349) in Andaman and Nicobar waters in April 2016 using a High-Speed Demersal Trawl-crustacean version (HSDT-CV) at a towing speed of 2.5 to 3.5 knots. Eight stations were surveyed (one operation at each station) along the continental margins of the Andaman and Nicobar Islands (7.29-13.76°N and 92.14-93.11°E) at depths ranging from 300 to 650

m (Fig. 1). The locations were scanned using a SIMRAD EK60 echo sounder before trawling operations and stations were selected on the basis of the suitability of the grounds for trawling. The fishing operations were carried out from 6 am to 6 pm depending upon the weather conditions.

The lophiiforms were identified following standard identification keys (Alcock 1891, 1894, Rajeeshkumar et al. 2016, Ho et al. 2016a, b). Only non-damaged adult fishes were selected for meristic and morphological measurements and to extract the otoliths. The catch per unit effort (CPUE) and the spatial distribution of each species along with their geographical positions are given in the Figure 2.

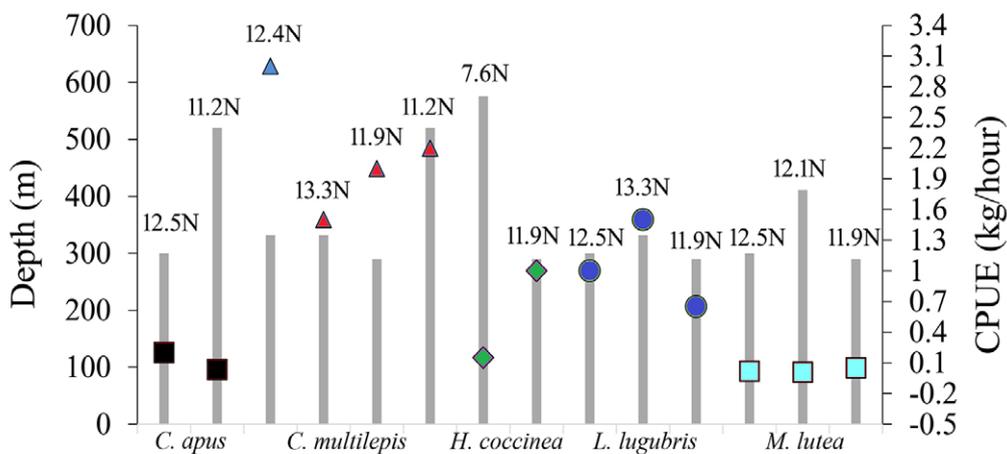


Fig. 2. – Catch per unit effort (CPUE) of the five most common deep-sea benthic anglerfishes at various stations (y-axis) of the Andaman and Nicobar Islands (eastern Indian Ocean). Station depth is indicated below the respective stations (x-axis). (N, north, indicating the geographical location).

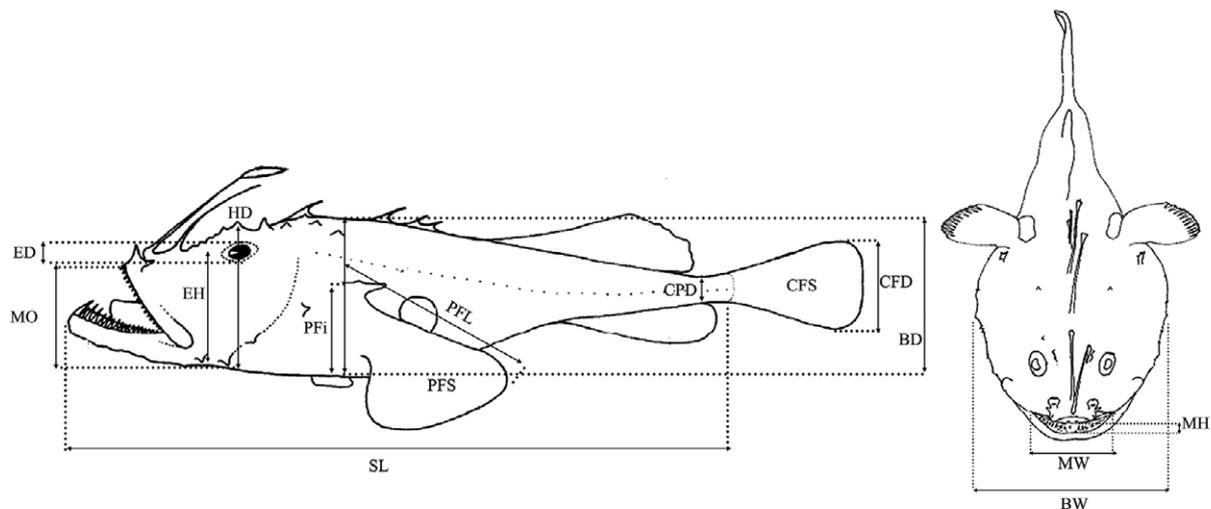


Fig. 3. – Illustration of the morphological traits of the fishes measured for estimating functional indices (after Albouy et al. 2011). *BD*, body depth; *BW*, body width; *CFD*, caudal fin depth; *CPD*, caudal peduncle minimal depth; *ED*, eye diameter; *EH*, distance between the bottom of the head and the eye centre along the head depth axis; *HD*, head depth along the vertical axis of the eye; *MH*, mouth height; *MO*, mouth opening; *MW*, mouth width; *PFB*, body depth at the level of the pectoral fin insertion; *PFi*, distance between the insertion of pectoral fin and the bottom of the body; *PFL*, pectoral fin length; *PFS*, pectoral fin surface; *SL*, standard length. Fish drawings after Caruso (1981, 2002).

Otolith morphology and morphometry

Otoliths were collected and washed with distilled water to remove exogenous matter, dried and kept in plastic vials for further analysis. Otoliths from the right side of each fish were oriented with the inner side (*sulcus acusticus*) uppermost on a slide in order to digitize their form using a microscope (S8APO Camera, Leica DFP-425). Otolith length (*OL*, mm), height (*OH*, mm), area (*OA*, mm²) and perimeter (*OP*, mm) were measured using ImageJ with magnification depending on otolith size. Otolith weight (*OW*, mg) was obtained using an electronic balance (Metler Toledo, ML 503) (see descriptive values in Appendix 1). The morphological characteristics of each species were described following Tuset et al. (2008).

Fish body morphological data

Sixteen morphological variables were measured on each specimen using a Vernier calliper (0.1 mm precision): total length (*TL*), standard length (*SL*), eye diameter (*ED*), mouth opening (*MO*), head depth (*HD*), eye height (*EH*), pectoral fin base (*PFB*), pectoral fin insertion, pectoral fin length (*PFL*), pectoral fin surface (*PFS*), caudal peduncle depth (*CPD*), caudal fin surface (*CFS*), caudal fin depth (*CFD*), body depth (*BD*), body length, body width (*BW*), mouth height (*MH*) and mouth width (*MW*) (Fig. 3). From these measurements, the following 11 ecomorphological attributes correlated with foraging, manoeuvrability and locomotion were selected for detailed studies. The formulas for estimating the functional traits are given in italicized letters.

– Oral gape surface (*Osf*) = $(MW \times MH) / (BW \times BD)$, which indicates the nature/size of the prey that can be captured. A large oral gape allows feeding on a wide size range including large prey (Karpouzi and Stergiou 2003).

– Oral gape shape (*Osh*) = MH / MW , which defines the method for capturing food items. A greater width allows species to capture highly mobile prey and have a more aggressive behaviour (Karpouzi and Stergiou 2003, Wainwright et al. 2007).

– Oral gape position (*Ops*) = MO / HD , which shows the feeding position in the water column. The position of the oral gape influences the retention of prey during ingestion (Kumar et al. 2017a, Villéger et al. 2017).

– Eye size (*Edst*) = ED / HD , which defines the prey detection efficiency. It also influences the feeding rhythms (nocturnal vs diurnal) and predator avoidance and indicates the availability of light in the microhabitat (Boyle and Horn 2006, Bellwood et al. 2014).

– Eye position (*Eps*) = EH / HD , which displays the vertical position in the water column. High values indicate dorsally located eyes (Watson and Balon 1984, Ribeiro et al. 2016).

– Body transversal shape (*Bsh*) = BD / BW , which indicates the vertical position of the fish in the water column as well as hydrodynamic efficiency (Villéger et al. 2017).

– Caudal peduncle throttling (*Cpt*) = CFD / CPD , which shows the caudal propulsion efficiency through the reduction of drag (Webb 1984, Zhao et al. 2014).

– Fin surface ratio (*Fsr*) = $(2 \times PFS) / CFS$, which indicates the type of propulsion between caudal and pectoral fins. Higher values denote a swimming driven by pectoral fins, whereas lower values correspond to a greater caudal fin propulsion (Mouillot et al. 2013, Zhao et al. 2014).

– Fin surface to body size ratio (*Fsb*) = $((2 \times PFS) + CFS) / (\pi / 4 \times BW \times BD)$, which indicates the acceleration and/or manoeuvring competence. Higher values indicate prolonged sustained swimming speed and fitness, which positively influence endurance, acceleration and manoeuvring capacities (Zhao et al. 2014, Kumar et al. 2017a).

– Aspect ratio of the pectoral fin ($ArPF$) = PFL^2/PFS , an indicator of swimming ability, which helps sustained swimming. Longer pectoral fins favour sustained swimming speed (Watson and Balon 1984, Casatti and Castro 2006).

– Aspect ratio of the caudal fin ($ArCF$) = CFD^2/CFS , which indicates the caudal fin use for propulsion and/or direction. A higher ratio produces the maximum thrust (Webb 1984, Bridge et al. 2016).

To estimate the functional traits, the morphological data were standardized to remove the allometric effect using the total weight (Mouillot et al. 2005, Kumar et al. 2017a). The allometric relationship between morphological data (X) and body mass (M) is $X = aM^b$, where ‘ b ’ varies with species. The effect of body mass was eliminated by using the residuals of the common within-group slopes of linear regressions for each component of body mass.

Statistical analysis

The Kolmogorov-Smirnov and Levene tests were used to check normality of the data distributions and variance homogeneity, respectively. The intraspecific variability was analysed considering the fish size-otolith measurement relationships as a tool in the feeding ecology to estimate fish size and biomass (Kumar et al. 2017b, c) and the otolith relative size as a resemblance to fish habitat and depth distribution (Lombarte and Cruz 2007). For the first analysis, the relationships between otolith morphometric variables (OL , OH , OA , OP , OW) were described using the allometric power equation ($Y = aX^b$) (Huxley 1924). Measurements were converted into logarithmic values (\log_{10}) to identify and exclude possible outliers in the data (Froese et al. 2011). Regression parameters a and b were estimated by the least square regression method, where b represents the constant of differential growth rate (Froese 2006). An analysis of covariance (ANCOVA) was performed to compare the regression slopes between species, treating the species as the main factor and fish size (SL) as a covariate. Specific difference was analysed using a post-hoc Tukey-HSD test. In the second analyses, the otolith measurements were standardized for each species by removing the effect of allometry (Lleonart et al. 2000). Different relative sizes were estimated for each otolith morphometric variable using the following criteria (Lombarte and Cruz 2007): OR_i = (otolith variable) $_i SL^b$, with $b=1$ for OL , OH and OP variables, $b=2$ for OA and $b=3$ for OW . An ANOVA was conducted for each variable on the relative size to test differences in the averages among species. A post-hoc test (Dunn’s test) was performed to elucidate the pairwise comparison of relative otolith sizes (Pohlert 2014). All statistical analyses were performed in PAST (PALaeontologicalSTATistics, version 3.26) (Hammer et al. 2001).

To order species in the functional space, a principal component analysis (PCA) based on the correlation matrix of the functional traits was performed. The choice of which principal components to interpret was based on a broken-stick model, which constructs a

null distribution of eigenvalues and compares it with observed ones (Collar and Wainwright 2006, Villéger et al. 2011). Our hypothesis of significant difference among the species and Bonferroni’s correction for post-hoc pairwise multiple comparisons were tested using multivariate analysis of variance (MANOVA) (Marcus 1993, Layman et al. 2005, Marrama and Kriwet 2017).

The degree of functional niche overlap among species was performed using a non-parametric kernel density function (NO_K) (Mouillot et al. 2005, Mason et al. 2008, Geange et al. 2011):

$$NO_{Kw}(i, j) = \frac{1}{\sum_{t=1}^T W_t} \sum_{t=1}^T w_t NO_K(i, j, t) \quad (1)$$

$NO_K(i, j, t)$ is the niche overlap between species i and j for the trait t , T is the number of functional traits and w_t is the weighting parameter, which is calculated as:

$$w_t = \frac{1}{2} + \sum_{l=1}^T (1 - \frac{r_{tl}^2}{2}) \quad (2)$$

r_{tl} is the Pearson correlation coefficient between traits t and l over all five species selected for the study. To understand the niche differences between the anglerfishes, permutation tests were performed to assess whether the observed niche overlap was significantly low based on the potential distribution of niche overlap values (Mouillot et al. 2005, Mason et al. 2008, Geange et al. 2011). Pseudo-values were calculated through randomly permuting species types in the corresponding data set for more than 1000 runs followed by computing the distribution of the average niche overlap for the null model to create the statistical null distributions. A Bonferroni adjustment of type I (Quinn and Keough 2002) was performed for the multiple comparisons. Density functions available in R (R Development Core Team 2017) were used to calculate niche overlap and for the subsequent null model tests. We followed the source code provided by Geange et al. (2011) for the above analysis in the R environment.

RESULTS

Otolith anatomical description

All species shared otolith features such as dorsal lobes and the lightly marked *sulcus acusticus*, with a well-defined crista inferior (Fig. 4). The otoliths of Chaunacidae (*C. apus* and *C. multilepis*) are characterized by a *sulcus acusticus* with undifferentiated *ostium* and *cauda* referred to as archaesulcoid. Indeed, they maintain an oval shape throughout growth with a smoothed and deep convex ventral margin. The dorsal margin has a variable number of lobes depending on species. In general, *C. apus* have more lobes (5 to 7) that are less angled than in *C. multilepis*. In Ogcocephalidae species, otoliths show a stronger differentiation in shape: *H. coccinea* has a semi-circular pattern (in the largest specimens), with a high number of deep lobes (6 to 10), some irregularities on the dorsal mar-

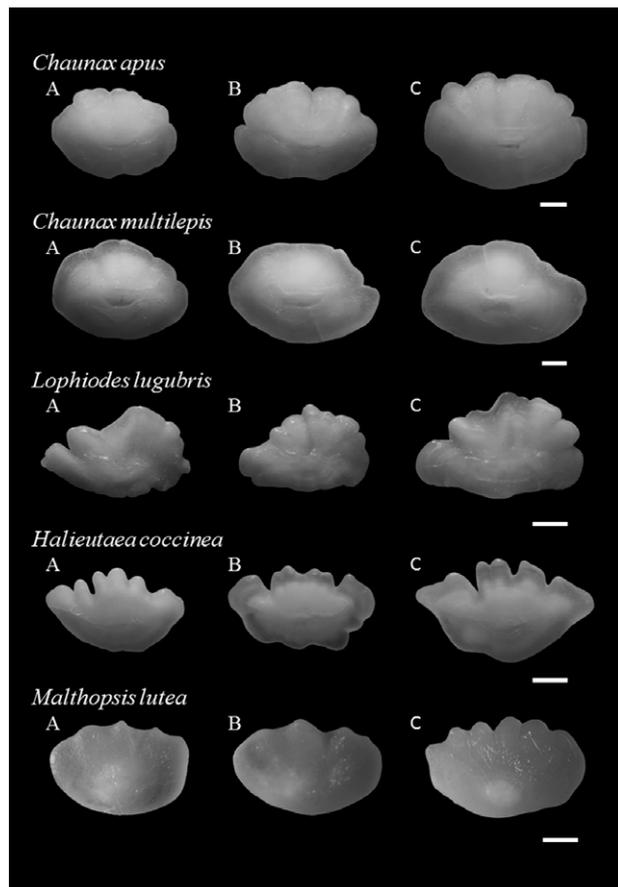


Fig. 4. – Left otoliths for the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). *Chaunax apus*: A, TL=9.1 cm; B, TL=9.5 cm; C, TL=12.0 cm. *Chaunax multilepis*: A, TL=9.0 cm; B, TL=12.1 cm; C, TL=13.0 cm. *Lophiodes lugubris*: A, TL=12.4 cm; B, TL=14.5 cm; C, TL=17.1 cm. *Halieutaea coccinea*: A, TL=8.5 cm; B, TL=11.2 cm; C, TL=11.5 cm. *Malthopsis lutea*: A, TL=7.4 cm; B, TL=7.5 cm; C, TL=8.2 cm. Scale bar = 1 mm.

gin, a smooth, convex ventral margin, a rounded to angled anterior margin, and an angled end at the posterior margin for the largest specimens, providing an oblong shape. In contrast, *M. lutea* has an oval shape, with a sinuous to lightly lobed dorsal margin (3 to 6 lobes) and a smooth, shallow, convex ventral margin, and the anterior margin is oblique, lacking a *rostrum*. In both

species the *sulcus acusticus* is archaesusulcoid, mesial and ascendant, with an oval *ostium* (poorly defined) and a *cauda* smaller than the *ostium*. In particular, the *sulcus acusticus* of *M. lutea* is placed in an inframedian position. Finally, the otolith of *L. lugubris* (Lophiidae) is characterized by a semi-circular to oblong shape (in the largest specimens), with a sinusoidal ventral margin and a deeply lobed (6 to 9) irregular dorsal margin, a blunt anterior margin and an undefined *rostrum* and pointed end of the posterior margin of the largest specimens. The *sulcus acusticus* is a homosulcoid type, with oval *ostium* and *cauda*.

Interspecific variability in the otolith morphometry

All otolith morphometric variables showed a statistically significant relationship with fish length for all species (Table 1, Appendix 2). However, otolith length and weight were the best variables correlated with fish size (r^2 ranges from 0.740 to 0.936 for *OL*, and between 0.708 and 0.959 for *OW*). The other variables showed a high intraspecific variation, and even attained very low values in the otolith height ($r^2=0.287$) for *M. lutea* and the otolith perimeter ($r^2=0.243$) for *H. coccinea* (Table 1). The ANCOVA exhibited no differences between species in the slopes of relationships *SL-OH* ($F=0.879$, $df=4$, $p=0.482$) and *SL-OA* ($F=2.158$, $p=0.085$), but it indicated interspecific variability for the *SL-OL* ($F= 4.764$, $df=4$, $p=0.002$), *SL-OP* ($F=2.705$, $df=4$, $p=0.039$) and *SL-OW* ($F=6.787$, $df=4$, $p<0.001$) relationships (Appendix 3). In particular, the slope (b) for the *SL-OW* relationship was higher in *M. lutea* than in *C. apus-H. coccinea*, and higher in *L. lugubris* than in *H. coccinea*. In fact, *H. coccinea* and *L. lugubris* also varied for the *SL-OP* and *SL-OL* relationships, and *L. lugubris* also showed differences with *C. apus* for the latter.

The ANOVA tests revealed significant differences for all relative variables (OA_R , $F=166.2$, $df=4$, $p<0.05$; OL_R , $F=120.1$, $df=4$, $p<0.05$; OH_R , $F=309.8$, $df=4$, $p<0.05$; OP_R , $F=46.6$, $df=4$, $p<0.05$; OW_R , $F=124.1$, $df=4$, $p<0.05$). Pairwise comparison using Dunn's test (Bonferroni, $p<0.05$) indicated significant inter-species differences, except between *Chaunax* spp. (Fig. 5, Table 2). The highest interspecific variability was ob-

Table 1. – Regression parameters of the relationships between otolith measurements and fish length of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). a , intercept; b , slope; n , number of specimens; OA , otolith area; OH , otolith height; OL , otolith length; OP , otolith perimeter; OW , otolith weight; r^2 , coefficient of determination; se , standard error of b ; SL , standard length. The b values following with superscript letters indicates significant differences ($p<0.001$).

Relationship	n	<i>Chaunax apus</i>				<i>Chaunax multilepis</i>				<i>Halieutaea coccinea</i>					
		a	b	$se(b)$	r^2	n	a	b	$se(b)$	r^2	n	a	b	$se(b)$	r^2
<i>SL-OA</i>	10	0.170	1.06	0.081	0.955	16	0.150	1.05	0.148	0.785	16	0.070	1.07	0.127	0.835
<i>SL-OH</i>	10	0.490	0.48	0.039	0.951	16	0.800	0.36	0.077	0.606	16	0.260	0.52	0.089	0.711
<i>SL-OL</i>	10	0.572	0.53 ^a	0.049	0.925	16	0.341	0.63 ^{ac}	0.075	0.833	16	0.337	0.58 ^a	0.069	0.838
<i>SL-OP</i>	10	0.220	0.59 ^{ab}	0.042	0.959	16	1.220	0.57 ^{ab}	0.083	0.768	16	3.370	0.33 ^b	0.169	0.240
<i>SL-OW</i>	10	0.049	1.50 ^{ac}	0.110	0.958	16	0.020	1.64 ^{ab}	0.281	0.708	16	0.047	1.24 ^a	0.109	0.902
		<i>Lophiodes lugubris</i>				<i>Malthopsis lutea</i>									
		n	a	b	$se(b)$	r^2	n	a	b	$se(b)$	r^2				
<i>SL-OA</i>	15	0.007	1.53	0.209	0.804	12	0.220	0.89	0.213	0.636					
<i>SL-OH</i>	15	0.238	0.53	0.098	0.690	12	1.220	0.29	0.147	0.287					
<i>SL-OL</i>	15	0.049	0.96 ^{bc}	0.121	0.829	12	0.300	0.53 ^{ac}	0.100	0.740					
<i>SL-OP</i>	15	0.270	0.82 ^a	0.111	0.805	12	1.680	0.46 ^{ab}	0.076	0.787					
<i>SL-OW</i>	15	0.001	2.01 ^{bc}	0.233	0.851	12	0.004	2.62 ^b	0.171	0.959					

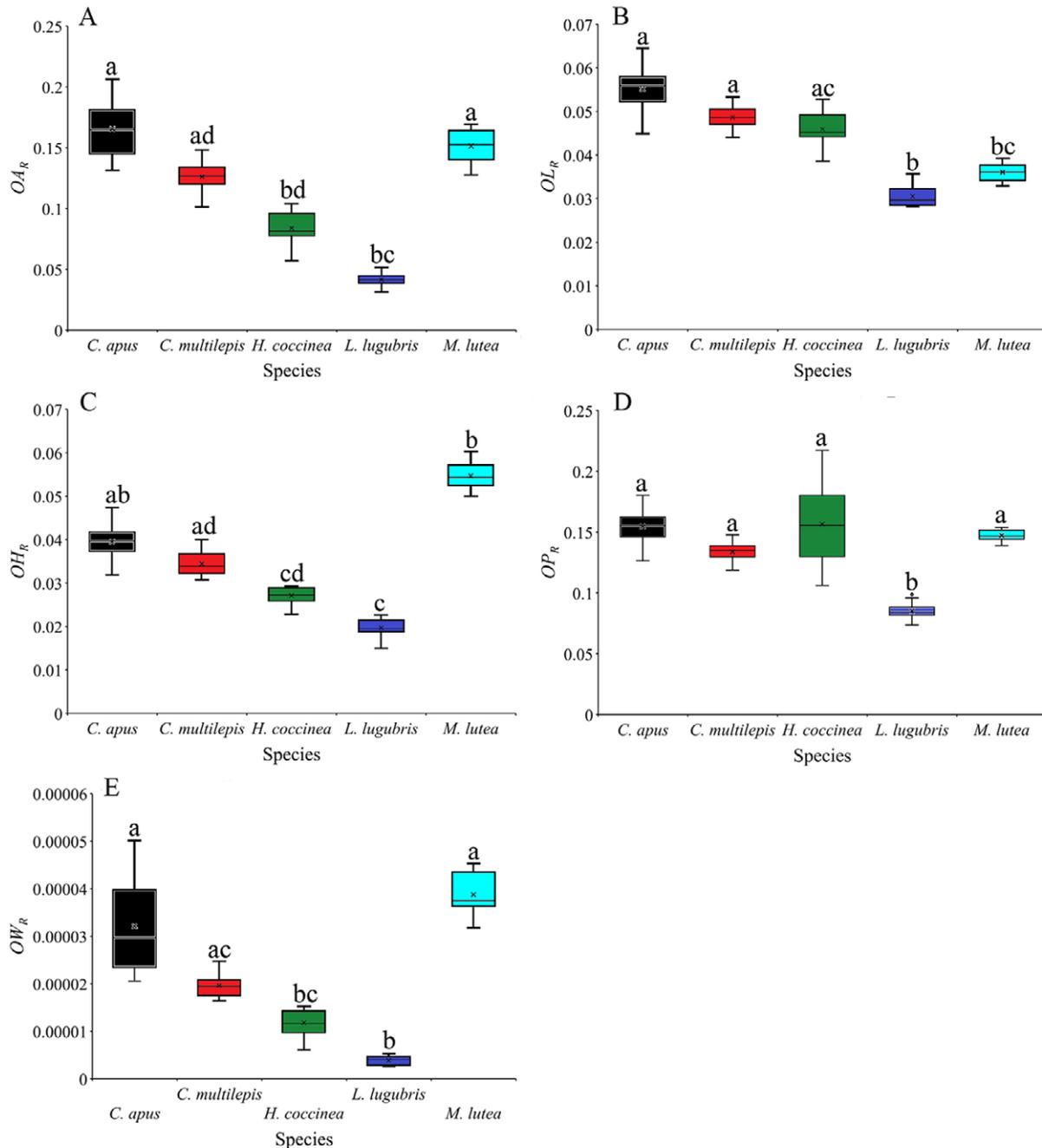


Fig. 5. – Boxplots (maximum, minimum, upper and lower quartiles) for the otolith relative size (OA_R , relative otolith area; OH_R , relative otolith height; OL_R , relative otolith length; OP_R , relative otolith perimeter; OW_R , relative otolith weight) for the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands. Results of the pairwise comparison using Dunn's post-hoc test (Bonferroni) indicated in different letters. Similar letters indicate no significant difference ($p < 0.05$).

tained for OH_R and the lowest for OP_R . No particular clustering was noted between species. In general, *L. lugubris* showed the lowest values for all relative sizes and *C. apus* the highest ones.

Comparing the functional niches

The first five PCA axes explained 97.9% of the total variance and the first three explained 93.8%. The PC1 axis alone contributed 63.7% of the total variance and was mainly correlated with *Fsb* ($r = 0.868$)

(Appendix 4). The positive values represented species with a more dorso-ventrally flattened body and higher swimming capabilities (*M. lutea*, *H. coccinea* and *L. lugubris*) versus species with higher body depth and lesser swimming abilities (*C. multilepis* and *C. apus*) (Fig. 6). The PC2 axis (19.1% of variance) was related to propulsion and acceleration capabilities (*ArCF*, $r = 0.893$), showing a similar pattern in all five species. The PC3 axis (10.9% of variance) was mainly related to swimming performance (*Arcf*, $r = -0.834$). The remaining PC scores (4 to 11) cumulatively ex-

Table 2. – Pairwise comparison of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean) using Dunn’s test (Bonferroni, $p < 0.001$). OA_R , relative otolith area; OH_R , relative otolith height; OL_R , relative otolith length; OP_R , relative otolith perimeter; OW_R , relative otolith weight. Statistically significant differences are indicated in bold ($p < 0.001$).

Variable	Species	<i>Chaunax multilepis</i>	<i>Haliutaea coccinea</i>	<i>Lophiodes lugubris</i>	<i>Malthopsis lutea</i>
OA_R	<i>Chaunax apus</i>	0.1333	0.000	0.000	1.000
	<i>Chaunax multilepis</i>		0.312	0.000	0.467
	<i>Haliutaea coccinea</i>			0.492	0.001
	<i>Lophiodes lugubris</i>				0.000
OH_R	<i>Chaunax apus</i>	1.000	0.018	0.000	1.000
	<i>Chaunax multilepis</i>		0.262	0.000	0.021
	<i>Haliutaea coccinea</i>			0.543	0.000
	<i>Lophiodes lugubris</i>				0.000
OL_R	<i>Chaunax apus</i>	0.969	0.156	0.000	0.000
	<i>Chaunax multilepis</i>		1.000	0.000	0.006
	<i>Haliutaea coccinea</i>			0.000	0.167
	<i>Lophiodes lugubris</i>				0.999
OP_R	<i>Chaunax apus</i>	0.066	1.000	0.000	1.000
	<i>Chaunax multilepis</i>		0.206	0.024	0.315
	<i>Haliutaea coccinea</i>			0.000	1.000
	<i>Lophiodes lugubris</i>				0.000
OW_R	<i>Chaunax apus</i>	0.443	0.002	0.000	1.000
	<i>Chaunax multilepis</i>		0.371	0.000	0.052
	<i>Haliutaea coccinea</i>			0.543	0.000
	<i>Lophiodes lugubris</i>				0.000

plained 6.2% of the variance and were related to locomotion traits (Appendix 4). MANOVA confirmed the occurrence of significant differences among these deep-sea anglerfishes (Wilk’s Lambda=00.0023, $F_{44,258,3}=22.88$, $p < 0.001$). The pairwise comparisons among species using sequential Bonferroni correction indicated significance differences among all species ($p < 0.001$) (Appendix 5).

The functional traits *Ops*, *Edst* and *Eps* showed the highest interspecific differences, whereas *Osf*, *Cpt* and *Fsr* showed the lowest (Table 3, Fig. 7). The overall

niche overlap ranged between 0.32 for *C. apus*-*M. lutea* and 0.65 for *H. coccinea*-*L. lugubris*. The species with highest niche partitioning was *M. lutea* due to its differentiation in the variables such as *Osf*, *Ops*, *Edst* and *Eps*. The analysis revealed significant differences between species, with *M. lutea* having a more differentiated functional niche, and both species of *Chaunax* showed more resemblance between them (Table 4). In any case, the findings indicated that functional niches did not overlap among the common five anglerfishes from the Indian Ocean.

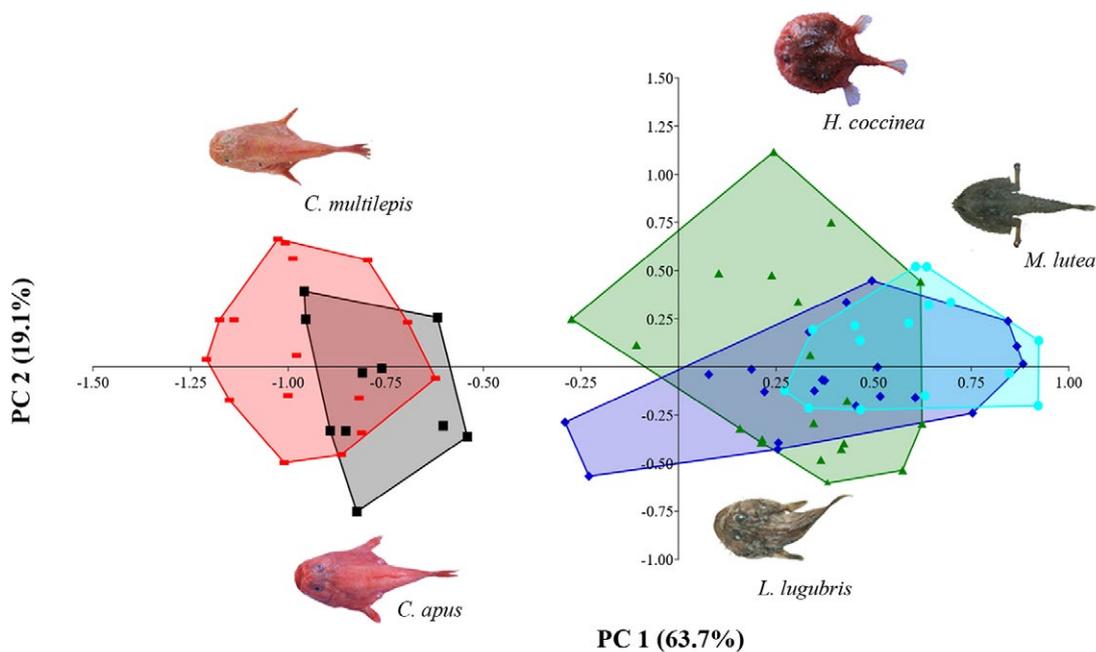


Fig. 6. – Functional space from principal component analysis for body shape of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean).

Table 3. – Estimation of niche overlap (NO) for the functional traits considered of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). Statistically different niches are indicated in bold ($p < 0.05$). The meaning of traits are explained in the text.

Traits	Species	<i>Chaunax multilepis</i>	<i>Halieutaea coccinea</i>	<i>Lophiodes lugubris</i>	<i>Malthopsis lutea</i>
ArCF	<i>Chaunax apus</i>	0.86	0.73	0.50	0.72
	<i>Chaunax multilepis</i>		0.69	0.45	0.62
	<i>Halieutaea coccinea</i>			0.54	0.61
	<i>Lophiodes lugubris</i>				0.66
ArPF	<i>Chaunax apus</i>	0.56	0.44	0.26	0.13
	<i>Chaunax multilepis</i>		0.82	0.64	0.48
	<i>Halieutaea coccinea</i>			0.75	0.57
	<i>Lophiodes lugubris</i>				0.81
Bsh	<i>Chaunax apus</i>	0.61	0.00	0.04	0.00
	<i>Chaunax multilepis</i>		0.00	0.00	0.00
	<i>Halieutaea coccinea</i>			0.80	0.47
	<i>Lophiodes lugubris</i>				0.45
Cpt	<i>Chaunax apus</i>	0.61	0.72	0.66	0.71
	<i>Chaunax multilepis</i>		0.77	0.40	0.47
	<i>Halieutaea coccinea</i>			0.61	0.67
	<i>Lophiodes lugubris</i>				0.82
Edst	<i>Chaunax apus</i>	0.28	0.48	0.10	0.00
	<i>Chaunax multilepis</i>		0.71	0.28	0.04
	<i>Halieutaea coccinea</i>			0.36	0.10
	<i>Lophiodes lugubris</i>				0.54
Eps	<i>Chaunax apus</i>	0.22	0.45	0.36	0.04
	<i>Chaunax multilepis</i>		0.67	0.53	0.40
	<i>Halieutaea coccinea</i>			0.80	0.47
	<i>Lophiodes lugubris</i>				0.51
Fsb	<i>Chaunax apus</i>	0.42	0.00	0.06	0.00
	<i>Chaunax multilepis</i>		0.00	0.01	0.00
	<i>Halieutaea coccinea</i>			0.78	0.52
	<i>Lophiodes lugubris</i>				0.62
Fsr	<i>Chaunax apus</i>	0.72	0.49	0.78	0.75
	<i>Chaunax multilepis</i>		0.74	0.91	0.91
	<i>Halieutaea coccinea</i>			0.68	0.72
	<i>Lophiodes lugubris</i>				0.90
Ops	<i>Chaunax apus</i>	0.20	0.83	0.57	0.25
	<i>Chaunax multilepis</i>		0.21	0.38	0.56
	<i>Halieutaea coccinea</i>			0.57	0.29
	<i>Lophiodes lugubris</i>				0.38
Osf	<i>Chaunax apus</i>	0.73	0.91	0.81	0.20
	<i>Chaunax multilepis</i>		0.75	0.74	0.27
	<i>Halieutaea coccinea</i>			0.76	0.14
	<i>Lophiodes lugubris</i>				0.22
Osh	<i>Chaunax apus</i>	0.65	0.71	0.64	0.68
	<i>Chaunax multilepis</i>		0.87	0.38	0.40
	<i>Halieutaea coccinea</i>			0.46	0.49
	<i>Lophiodes lugubris</i>				0.84

Table 4. – Average (and standard deviation) weighed niche overlap for the functional traits considered between each pair of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). Statistically different niches are indicated in bold ($p < 0.001$).

Species	<i>Chaunax multilepis</i>	<i>Halieutaea coccinea</i>	<i>Lophiodes lugubris</i>	<i>Malthopsis lutea</i>
<i>Chaunax apus</i>	0.53 (0.22)	0.52 (0.30)	0.44 (0.29)	0.32 (0.33)
<i>Chaunax multilepis</i>		0.57 (0.33)	0.43 (0.28)	0.38 (0.28)
<i>Halieutaea coccinea</i>			0.65 (0.15)	0.46 (0.20)
<i>Lophiodes lugubris</i>				0.62 (0.22)

DISCUSSION

Most studies performed on deep-sea fish species from Indian waters have focused on taxonomy and biology (Karuppusamy et al. 2008, Sreedhar et al. 2013,

Kumar et al. 2016, 2018), and only few have analysed interspecific competition (Narayani et al. 2015, Kumar et al. 2017a). The present study delved into this matter by analysing the differences in the sensory capability and functional niche of most common anglerfishes

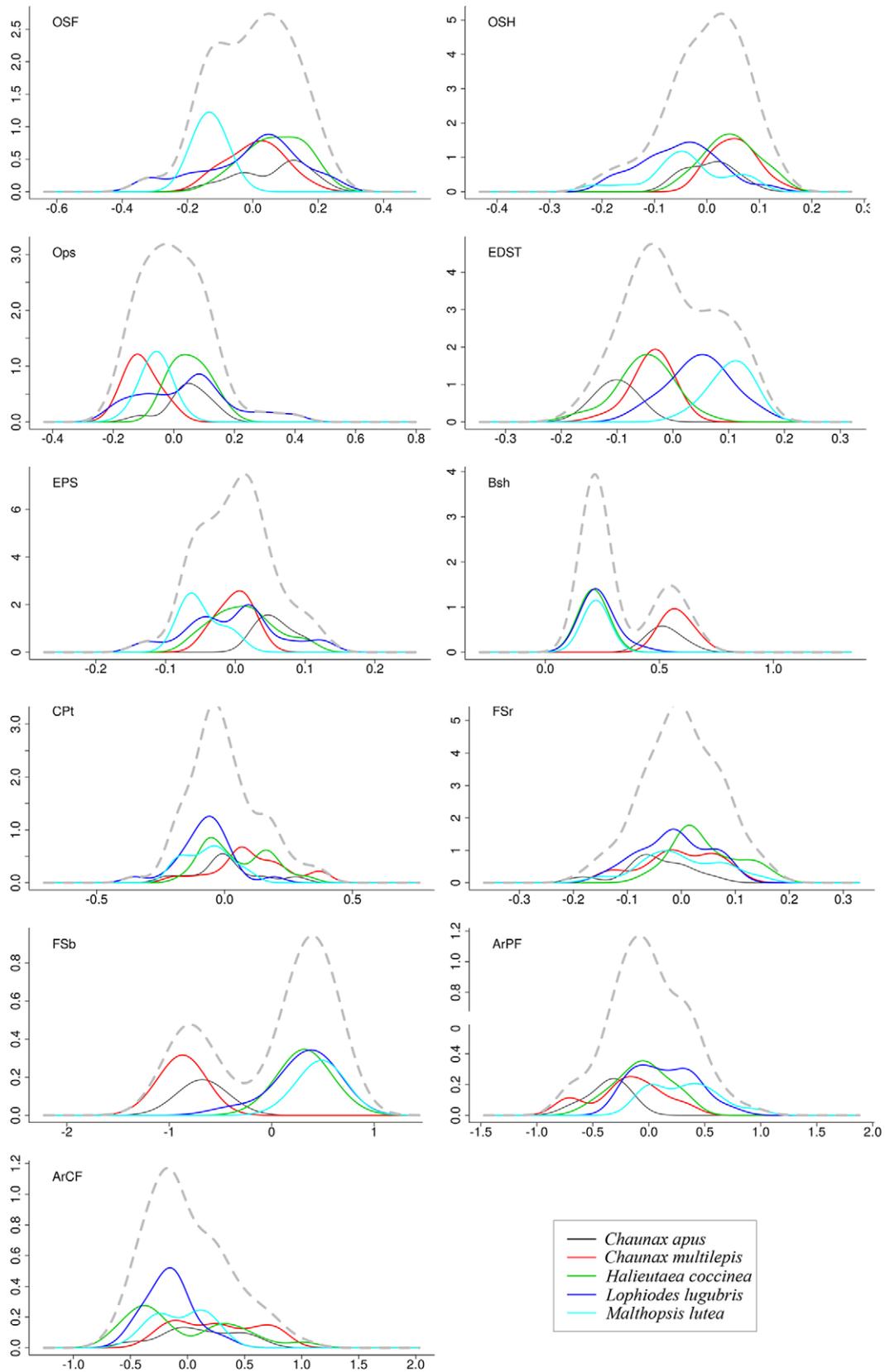


Fig. 7. – Species density distributions (y-axis) using kernel density models for each functional trait (x-axis) for the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). Grey dashed line indicates the total density for all species. *ARCF*, aspect ratio of the caudal fin; *ARPF*, aspect ratio of the pectoral fin; *Bsh*, body transversal shape; *Cpt*, caudal peduncle throattling; *Edst*, eye size; *Eps*, eye position; *Fsb*, fins surface to body size ratio; *Fsr*, fins surface ratio; *Osf*, oral gape surface; *Osh*, oral gape shape; *Ops*, oral gape position.

inhabiting these waters. In this context, our findings revealed a strong environmental adaptation of *sagitta* otolith shape to the depth distribution of species, confirming the ecomorphological pattern proposed by Colmenero et al. (2010) for *Lophius* spp. from the Mediterranean Sea. Moreover, the dissimilarity between the functional niches indicated a low interspecific niche overlap. Finally, no phylogenetic influence was inferred from the morpho-functional features analysed, as occurs in other fish species (Tuset et al. 2010, 2018, Kéver et al. 2014, Schwarzthans 2014), although a greater number of taxa should be necessary for this purpose.

The relative size of fish otoliths tends to increase with depth (Lombarte and Cruz 2007), improving their hearing capacities to compensate for the limitation in visual communication (Lychakov and Rebane 2000, Paxton 2000, Tuset et al. 2018). However, this trend is reversed due to carbonate under-saturation below 1000 m depth (Wilson 1985, Lombarte and Cruz 2007). This ecomorphological pattern was found in the present study: *Chaunax* spp. and *M. lutea*, characterized by a wide bathymetric distribution (200-700 m; Ho et al. 2016a, Rajeeshkumar 2018), had a greater relative otolith size in the area, height and weight; *L. lugubris*, the shallowest species (<250 m; Alcock 1894, Ho et al. 2016a, Rajeeshkumar 2018), had a smaller relative otolith size; and *H. coccinea*, which can inhabit over >1000 m (Rajeeshkumar 2018), also reached low values for some relative otolith sizes. Certainly, the set of relative otolith indices did not follow the same trend, which may be due to the high irregularity of sculpture of the dorsal margin in anglerfishes (see more examples in AFORO website, <http://aforo.cmima.csic.es/>; Lombarte et al. 2006; present study). It is known that this variability occurs at inter- and intraspecific levels and is a disadvantage for the automated separation of stocks (example in Cañas et al. 2012) and for the identification of species. Moreover, it would explain the low coefficients of determination and the interspecific similarity obtained in the slope value (*b*) of some morphometric relationships. Although some studies have demonstrated a morpho-functional correlation between the otolith and fish body shapes (Volpedo et al. 2008, Mille et al. 2016, Tuset et al. 2018), we found no evidence that the morphometry, relative otolith size and sculpture of the otolith margins were associated with the fish body morphotypes (globose versus dorso-ventrally flattened) or had any phylogenetic meaning in anglerfishes.

Given that common anglerfishes from the Indian Ocean had different functional niches and can coexist in some bathymetries, the slight variations in their functional traits suggest that functional variability is linked to competence for similar resource requirements (theory of limiting similarity, MacArthur and Levins 1967), as occurs in other fish groups such as cichlids (Winemiller et al. 1995), labrids (Wainwright et al. 2002), butterflyfishes (Bellwood et al. 2010), notothenids (Lombarte et al. 2010), rockfishes (Ingram 2011), damselfishes (Frederich et al. 2016) and lanternfishes (Tuset et al. 2018). Anglerfishes with a dorso-ventrally flattened body (*M.*

lutea, *L. lugubris* and *H. coccinea*) were characterized by a higher swimming efficiency in relation to species with globose body (*Chaunax* spp.). However, unlike *M. lutea* and *H. coccinea*, both *L. lugubris* and *Chaunax* spp. attract their prey with an angling apparatus (or illicium), which has a bait (esca) in the case of *Chaunax* spp. (Pietsch and Grobecker 1987, Armstrong et al. 1996, Ho et al. 2016a). This bait facilitates a predator behaviour based on slow movements by waiting for the potential prey very close to the mouth, whereas the greater swimming ability of *L. lugubris* would indicate the possibility of capturing prey more actively (i.e. at a greater distance from its prey).

Overall, anglerfishes with higher swimming capability and oral gape surface (e.g., *L. lugubris* and *H. coccinea*) seem to ingest more mobile and larger prey, including fishes (Zhao et al. 2014, Kumar et al. 2017a), whereas those with lesser swimming abilities or a smaller oral gape select crustaceans and gastropods as the main potentially preys (Gibrán and Castro 1999, Karuppasamy et al. 2008, Nagareda and Shenker 2008). Although the theory on the resource partitioning among the species in deep-sea habitats is essentially based on prey size and swimming capacity near the bottom (Papiol et al. 2013, Kumar et al. 2017a), species can also differentiate their feeding rhythms (nocturnal or diurnal). The ability to be more active at night is based on a higher sensory sensitivity from visual and hearing capabilities (Warrant 2004, Schmitz and Wainwright 2011, de Busserolles et al. 2013, Sadighzadeh et al. 2014). Colmenero et al. (2010) concluded that the eye size reflected the nocturnal phenotype between *Lophius* spp. from the Mediterranean Sea. Our findings suggest a similar behavioural ability in *M. lutea* and *L. lugubris* in relation to the remaining species.

In conclusion, anglerfishes have evolved functionally towards different ecological strategies to live in low-energy habitats. Hence, morpho-functional traits seem to be good ecological predictors for explaining the coexistence of species. Functional traits associated with feeding habits, locomotion and manoeuvrability help us to understand the ecology of these species (Bridge et al. 2016, Kumar et al. 2017a) and to predict their niches (Mouillot et al. 2005, Mason et al. 2008, Zhao et al. 2014). The eyes seem to be crucial for the differentiation of their feeding activity and the otolith for their hearing capabilities (Colmenero et al. 2010).

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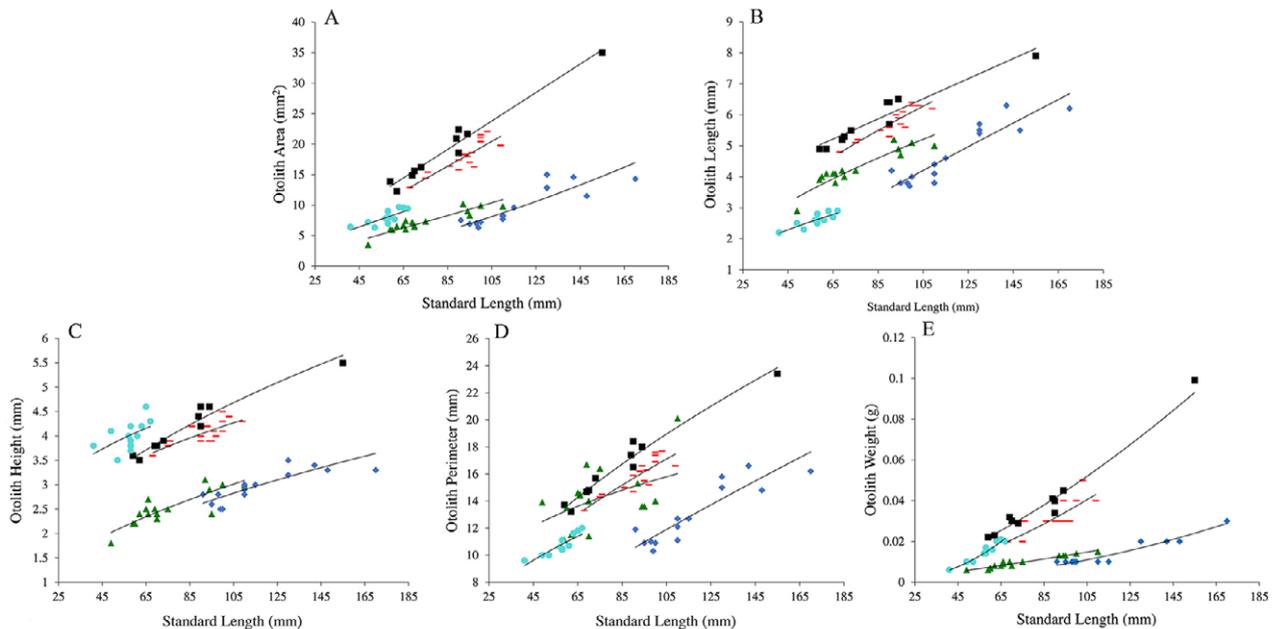
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APPENDICES

Appendix 1. – Descriptive values of fish length and otolith measurements of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). min, minimum; max, maximum; n, number of specimens; *OA*, otolith area; *OH*, otolith height; *OL*, otolith length; *OP*, otolith perimeter; *OW*, otolith weight; sd, standard deviation; *SL*, standard length.

Species	Variables	n	min	max	mean	sd
<i>Chaunax apus</i>	<i>OA</i>	10	12.3	35	19.15	6.54
	<i>OH</i>		3.47	5.53	4.19	0.62
	<i>OL</i>		4.86	7.93	5.88	0.94
	<i>OP</i>		13.2	23.4	16.58	2.98
	<i>OW</i>		0.022	0.099	0.0395	0.022
	<i>SL</i>		59	155	85.1	27.64
<i>Chaunax multilepis</i>	<i>OA</i>	16	12.9	22.1	17.83	2.64
	<i>OH</i>		3.59	4.53	4.07	0.24
	<i>OL</i>		1.62	4.81	5.76	0.5
	<i>OP</i>		13.3	17.7	15.86	1.28
	<i>OW</i>		0.021	0.048	0.0325	0.007
	<i>SL</i>		68	109	92	11.02
<i>Haliutaea coccinea</i>	<i>OA</i>	16	3.47	10.21	7.3	1.78
	<i>OH</i>		1.75	3.13	2.51	0.36
	<i>OL</i>		2.89	5.19	4.25	0.59
	<i>OP</i>		11.1	22.1	15.13	3.28
	<i>OW</i>		0.006	0.015	0.01	0.003
	<i>SL</i>		49	110	75.12	17.46
<i>Lophiodes lugubris</i>	<i>OA</i>	15	6.31	15	9.98	3.18
	<i>OH</i>		2.46	3.52	2.99	0.36
	<i>OL</i>		3.69	6.3	4.73	0.93
	<i>OP</i>		10.3	16.6	13.13	2.2
	<i>OW</i>		0.006	0.03	0.0134	0.007
	<i>SL</i>		91	170	118.5	22.6
<i>Malthopsis lutea</i>	<i>OA</i>	12	6.33	9.69	8	1.18
	<i>OH</i>		3.48	4.63	4.02	0.3
	<i>OL</i>		2.19	2.91	2.59	0.22
	<i>OP</i>		9.6	11.96	10.73	0.75
	<i>OW</i>		0.006	0.021	0.016	0.004
	<i>SL</i>		41	67	57.25	7.16



Appendix 2. – Relationship between fish size (*SL*, cm) and otolith morphometric variables (A, otolith area; B, otolith length; C, otolith height; D, otolith perimeter; E, otolith weight) for the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). *C. multilepis*, red dash; *C. apus*, black square; *L. lugubris*, blue diamond; *H. coccinea*, green triangle; *M. lutea*, blue circle.

Appendix 3. – Results of the ANCOVA for the relationship between fish size (*SL*) and otolith measurements of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). *OA*, otolith area; *OH*, otolith height; *OL*, otolith length; *OP*, otolith perimeter; *OW*, otolith weight; *SL*, standard length; *df*, degrees of freedom; *Sum Sq*, sum of squares; *Mean Sq*, mean sum of squares; *Pr*, significance level. Statistically significant differences indicated in bold.

Variable	df	Sum Sq	Mean Sq	F value	Pr(>F)
<i>OA</i>					
<i>SL</i>	1	0.760	0.760	371.152	<0.001
Species	4	1.873	0.470	229.436	<0.001
<i>SL</i> : Species	4	0.018	0.004	2.158	0.085
Residuals	59	0.121	0.002		
<i>OH</i>					
<i>SL</i>	1	0.011	0.101	15.474	<0.001
Species	4	0.657	0.164	238.848	<0.001
<i>SL</i> : Species	4	0.002	0.001	0.879	0.482
Residuals	59				
<i>OL</i>					
<i>SL</i>	1	0.660	0.660	1074.370	<0.001
Species	4	0.531	0.133	216.269	<0.001
<i>SL</i> : Species	4	0.012	0.003	4.764	0.002
Residuals	59	0.036	0.001		
<i>OP</i>					
<i>SL</i>	1	0.157	0.157	127.371	<0.001
Species	4	0.240	0.060	48.657	<0.001
<i>SL</i> : Species	4	0.013	0.003	2.706	0.039
Residuals	57	0.070	0.001		
<i>OW</i>					
<i>SL</i>	1	0.957	0.957	350.515	<0.001
Species	4	3.746	0.936	343.147	<0.001
<i>SL</i> : Species	4	0.074	0.019	6.787	<0.001
Residuals	59	0.161	0.003		

Appendix 4. – Correlation between principal components and functional traits (see text for acronyms) of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). In bold, higher absolute correlation values ($r > 0.3$).

Traits	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6
<i>Osf</i>	-0.030	-0.068	0.153	0.739	0.253	0.306
<i>Osh</i>	-0.034	0.019	0.012	0.120	0.653	-0.101
<i>Ops</i>	0.050	-0.084	0.168	0.499	-0.548	-0.066
<i>Edst</i>	0.075	0.037	-0.051	-0.149	-0.302	0.041
<i>Eps</i>	-0.018	-0.022	0.039	0.233	-0.166	0.061
<i>Bsh</i>	-0.236	-0.012	-0.169	0.056	-0.077	0.215
<i>CPt</i>	-0.084	0.274	0.162	0.182	0.160	-0.686
<i>FSr</i>	0.013	0.021	0.137	-0.139	0.212	0.570
<i>FSb</i>	0.868	0.130	0.360	-0.045	0.041	0.035
<i>ArPF</i>	0.350	0.309	-0.834	0.236	0.028	0.026
<i>ArCF</i>	-0.225	0.893	0.212	-0.014	-0.109	0.205

Appendix 5. – Results of the inter-species classification using canonical variate analysis for fish body shape of the five most common deep-sea benthic anglerfishes from the Andaman and Nicobar Islands (eastern Indian Ocean). Predicted group membership in each group are in bold letters and percentage of classification is in parenthesis.

Species	<i>Chaunax apus</i>	<i>Chaunax multilepis</i>	<i>Halieutaea coccinea</i>	<i>Lophiodes lugubris</i>	<i>Malthopsis lutea</i>	Total
<i>Chaunax apus</i>	10 (100)	0	0	0	0	10
<i>Chaunax multilepis</i>	0	16 (100)	0	0	0	16
<i>Halieutaea coccinea</i>	0	0	19 (95)	1	0	20
<i>Lophiodes lugubris</i>	0	0	1	17 (89.5)	3	21
<i>Malthopsis lutea</i>	0	0	0	1	14 (82.3)	15