



Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Functional approach reveals low niche overlap among common deep-sea fishes from the south-eastern Arabian Sea

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ARTICLE INFO

Keywords:

Functional traits

Niche overlap

Resource partitioning

Deep-sea fishes

South-eastern Arabian Sea

ABSTRACT

It is necessary to understand the resource partitioning among species, to describe the functioning of deep sea marine ecosystems. Functional morphology is an effective approach to understand and compare taxonomic units with different phenotypic characteristics related to swimming and foraging. In this study, our main objective was to delineate the functional traits with a view to determine the discrimination level and degree of functional niche overlap among seven common species inhabiting deep-sea waters in south-eastern Arabian Sea. Results indicated significant differences in the functional traits between species providing a low functional niche overlap. Although, the ecological and biological information of fishes were scarce, we demonstrated that functional analyses are effective to extrapolate the prey preferences, sizes and detection and propulsion efficiencies for their feeding and swimming strategies. Our study supports the hypothesis that in some environments with a limitation of resources, species coexisting is due to high resource partitioning. The present work is a first attempt to compare the morpho-functional characteristics and niche partitioning in the deep-sea fish assemblages from the Indian waters.

1. Introduction

The deep-sea ocean (> 200 m depth) began to be explored in the 19th century and still remains largely unexplored. In Indian coast, the studies were mainly exploratory during the 20th century (Birader, 1988; Bande et al., 1990; Nair and Reghu, 1990; Khan et al., 1996). In the last decades, an exhaustive Indian program of deep-sea benthos has been developed for the description of habitats and marine diversity (e.g., Venu and Kurup, 2002a; Kurup et al., 2005; Deepu et al., 2007; Wafar et al., 2011; Venu, 2013). In the Arabian Sea, scientific observations have revealed that the composition and abundance of fishes are intrinsically linked to the productivity of waters, which is associated with upwelling and a great flux of sediments transported by rivers during the monsoon rains (e.g., Rao et al., 1992; ; Nair et al., 1999; Madhupratap et al., 2001; Murtugudde et al., 2007; Karuppasamy et al., 2010). Notwithstanding, ecological information of fish assemblages is practically unknown (e.g., Vijayakumaran and Philip, 1988; Gopalakrishnan et al., 1988; Jayaprakash et al., 2006; Venu, 2013).

Hutchinson (1957) defined the niche as a volume in multidimen-

sional hyperspace in which species can maintain a viable population. An extension of this concept is the 'functional niche' where hyperspace axes are defined from functional traits (Rosenfeld, 2002). In fishes, these traits are combinations of morphological measurements (Webb, 1994; Langerhans et al., 2003; Collar and Wainwright, 2009) or categorical variables related to foraging and diet strategies, trophic level in food webs, size, locomotion, mobility, lifestyle, activity or distribution in habitat (Halpern and Floeter, 2008; Somerfield et al., 2008; Farré et al., 2016). One advantage of trait-based ecological approaches is that they may allow greater generalizations across systems, because traits are common to multiple ecosystems, even if those ecosystems do not share the same species (Mindel et al., 2015). By contrast, they have some limitations since species with similar traits may have a temporal (diel cycle) partitioning as a viable mechanism of coexistence (Gutman and Dayan, 2005; Colmenero et al., 2010), differ within life stages exploiting dissimilar ecological niches (Skúlason and Smith, 1995; Cucherousset et al., 2011; Zhao et al., 2014), acquire alternative traits for capturing same prey type (Wainwright et al., 2005) and have different hunting strategies providing trade-offs that would enable competitive coexistence on the same resource types (Kneitel and

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<http://dx.doi.org/10.1016/j.dsr.2016.11.011>

Received 20 June 2016; Received in revised form 28 November 2016; Accepted 28 November 2016

Available online xxxx

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Chase, 2004). Therefore, functional traits should be properties of organisms that strongly influence in their performance (McGill et al., 2006). They are commonly used to analyze the factors controlling biodiversity patterns (Mouillot et al., 2007; Mouchet et al., 2010; Bridge et al., 2016): competition between species (limiting similarity) and adaptation to local environmental conditions (environmental filtering). The limiting similarity of coexisting species (MacArthur and Levins, 1967) refers to the local exclusion of species that are too similar in their resource requirements, why species develop slight variations in their functional traits. By contrast, the niche filtering hypothesis (Zobel, 1997) assumes that coexisting species lead to a similar traits because environmental conditions act as a filter allowing only a narrow spectrum of species to survive. These ecological factors have been studied in species inhabiting freshwater ecosystems (rivers and lakes) (Mason et al., 2008; Blanchet et al., 2013; Pool et al., 2014) and marine coastal environments (estuarine, lagoons or reefs) (Halpern and Floeter, 2008; Brandl et al., 2015; Passos et al., 2016), and to a lesser extent on marine deep-sea communities (Langerhans and Reznick, 2010; Mindel et al., 2015; Farré et al., 2016).

Under the niche-based hypothesis, niche overlap modelling offers a useful tool for quantitatively assessing ecological similarity (limiting similarity) of species involved in partitioning resource (Mookerji et al., 2004; Silvertown, 2004). In this context, the deep-sea is usually characterized by a relatively high environmental stability below depths of 200 m (Hopkins, 1985; Gage and Tyler, 1991) and a decrease of productivity and food availability with depth (e.g., Cartes, 1998; Cartes et al., 2002; Rex and Etter, 2010; Papiol et al., 2012). These ecological conditions should promote the competition for limited resources, although species with similar niches may occur due to factors such as the habitat heterogeneity, disturbance and spatial mass (Dayton and Hessler, 1972; Mason et al., 2008). Even so, most studies have revealed a low dietary overlap in deep-sea fish species (e.g., Fock et al., 2002; Carrasón and Cartes, 2002; Preciado et al., 2016) indicating a high degree of resource partitioning.

A recent study on the functional diversity in marine ecosystem has revealed that in deep-sea communities the most abundant species tend to be separated within the functional space (Farré et al., 2016). In this theoretical framework, we performed an analysis of functional niche in common deep-sea fishes of south-eastern Arabian Sea, characterized by waters poor in nutrients and diversity (Robinson and Brink, 2005). Our initial hypothesis is that the spatial distribution of species into functional space is related to a high degree of specialization in the use of resources, partitioning resources, and life patterns; hence the functional niche overlap should be also low. For it, we selected functional traits related to structure of community such as food acquisition (Karpouzi and Stergiou, 2003; Sibbing and Nagelkerke, 2001; Albouy et al., 2011), swimming performance (Plaut, 2001; Ohlberger et al., 2006; Collar and Wainwright, 2009) and locomotion efficiency (e.g., Wainwright, 1991; Webb, 1994; Langerhans et al., 2003; Rice and Westneat, 2005; Collar et al., 2008). Our main goals were: (i) to analyze of the distribution of species within the functional space and to determine the separation degree between species; and (ii) to obtain the degree of niche overlap between species. In this case, we have used non-parametric indices developed by Mouillot et al. (2005) for estimating the niche overlap between two species based on functional traits (Mason et al., 2008; Thibault and Dodson, 2013; Laub and Budy, 2015).

2. Materials and methods

This study used the data from deep-sea fish assemblages in the south-eastern Arabian Sea (Fig. 1). Sampling was carried out in deep-sea fishing experiments conducted from FORV *Sagar Sampada* (71.5 m L_{OA} ; 2285 hp), during 2015, using a 38 m High Speed Demersal Trawl (HSDT; crustacean version), at a towing speed of 2.5–3.5 knots. Eight stations were surveyed (08°50'28"–12°57'55" N

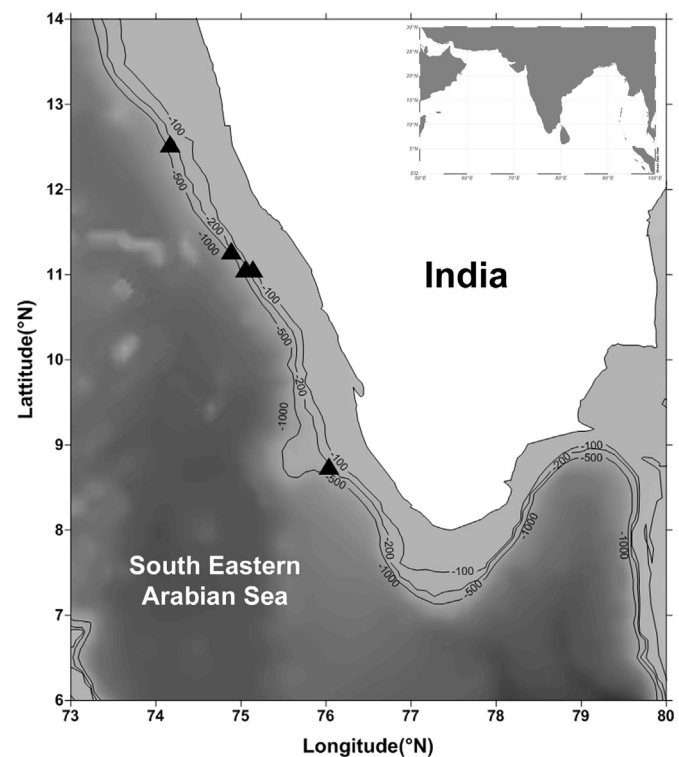


Fig. 1. Sampling stations in the south-eastern Arabian Sea.

lat., 73°51'57"–76°00'37" W long.) at a depth range of 210–352 m depending on the availability of suitable trawling grounds. The time of operation ranged from 9 am to 6 pm. The samples were identified up to species level using standard identification keys (Alcock, 1898, 1899; FAO, 1984), counted and weighed. Only adult individuals were selected for the subsequent analysis. A total of 17 fish species were recorded during the fishing operations (Table S1), although only 7 were considered common species (abundance > 1%, Magurran and Henderson, 2003; Hercos et al., 2012): *Psenopsis cyanea* (57%), *Bembrops caudimaculata* (15%), *Pterygotrigla hemisticta* (15%), *Chelidoperca investigatoralis* (4.5%), *Chlorophthalmus corniger* (2.9%), *Priacanthus blotchii* (2.5%) and *Hoplostethus rubellopterus* (2%).

2.1. Functional traits

Sixteen morphological measurements were directly taken on adult individuals (Fig. S1) and recorded to the nearest 0.01 mm using Vernier caliper. Over 20 individuals of similar fish length were analyzed in each species. Morphological measurements provided twelve functional traits related to the mode of food acquisition, position in the water column, swimming behaviour and preferred food type (Gatz, 1979; Webb, 1984; Dumay et al., 2004; Albouy et al., 2011). We included *Oral gape surface* (*Os_f*) which indicates the nature/size of items captured; *Oral gape shape* (*Osh*), which describes the method to capture food items; *Oral gape position* (*Ops*), which denotes the feeding position in the water column; *Eye size* (*Edst*), which helps to prey detection; *Eye position* (*Eps*), which displays the vertical position in the water column; *Body transversal shape* (*Bsh*), which denotes the vertical position in the water column and the level of hydrodynamism; *Pectoral fin position* (*PFps*), which represents the pectoral fin use in terms of maneuverability; *Caudal peduncle throttling* (*CPT*), which explains the caudal propulsion efficiency through reduction of drag; *Aspect ratio of the pectoral fin* (*ArPF*) and *Aspect ratio of the caudal fin* (*ArCF*), which are related to propulsion of pectoral and caudal fins, respectively; *Fins surface ratio* (*Fsr*), which indicates the type of

Table 1

Abbreviations and formulas for estimating the functional traits from morphological measurements (see Fig. S1) following Villéger 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 center along the head depth axis; *Hd*, head depth along the vertical axis of the eye; *Md*, mouth depth; *Mw*, mouth width; *PFb*, body depth at the level of the pectoral fin insertion; *PFl*, pectoral fin length; *PFI*, distance between the insertion of pectoral fin and the bottom of the body; *PFs*, pectoral fin surface.

Strategy	Functional trait	Abbreviation	Formula
Food acquisition	Oral gape surface	<i>Osf</i>	$[Mw \times Md]/[Bw \times Bd]$
	Oral gape shape	<i>Osh</i>	Md/Mw
	Oral gape position	<i>Ops</i>	Mo/Hd
	Eye size	<i>Edst</i>	Ed/Hd
Locomotion	Eye position	<i>Eps</i>	Eh/Hd
	Body transverse shape	<i>Bsh</i>	Bd/Bw
	Pectoral fin position	<i>PFps</i>	PFI/PFb
	Aspect ratio of the pectoral fin	<i>ArPF</i>	PF^2/PFs
	Caudal peduncle throttling	<i>CPt</i>	CFd/CPd
	Aspect ratio of the caudal fin	<i>ArCF</i>	CFd^2/CFs
	Fins surface ratio	<i>FSr</i>	$(2 \times PFs)/CFs$
	Fins surface to body size ratio	<i>FSb</i>	$[(2 \times PFs) + CFs]/(\pi/4 \times Bw \times Bd)$

propulsion between caudal and pectoral fins; and *Fins surface to body size ratio* (*FSb*), which is associated to the acceleration and/or maneuverability efficiency (see Table 1).

Functional traits were standardized to avoid an allometric effect. The biomass was selected because of the robust relationship between morphological or metabolic rates and body mass (Dumay et al., 2004; Mouillot et al., 2005). Since the allometric relationship between a trait (*X*) and mass (*M*) is $X = aM^b$ and the exponent coefficient were variant between species, the effect of body mass was removed using the residuals of the common within-group slopes of the linear regressions of each component on body mass.

2.2. Data analysis

To account for correlations between functional indices and to reduce dimensionality of the dataset, a principal-components analysis (PCA) was applied. We retained only PCs that cumulatively accounted for up to 95% of the total variation (Collar and Wainright, 2006). Multivariate analysis of variance (MANOVA) was used to test the hypothesis of significant differences between species and Bonferroni's correction for post-hoc pairwise multiple comparison (Marcus, 1993). A discriminant analysis was also performed to determine the ability to predict species using PC components (functional traits) as predictor variables. The hypothesis that the between group covariances was tested showing heterogeneity, thus a quadratic discriminant function was finally computed (Friedland and Reddin, 1994). The classification accuracy of this discriminant was evaluated by leave-one-out-cross-validation (Nishimoto et al., 2010). All statistical analyses were performed in XLStat 2012, a statistical plug-in for MS Excel 2011 spreadsheet program and PAST (Palaeontological Statistics, version v1.81) (Hammer et al., 2001). Significance level was set at 0.05 for all statistical tests used.

The estimation of niche overlap based on non-parametric kernel density functions (NO_K) on residual data was calculated as following (Mouillot et al., 2005):

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

being $NO_K(i, j, t)$ 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:

$$w_t = \frac{1}{2} + \sum_{i=1}^T \left(1 - \frac{r_{it}^2}{2}\right)$$

And r_{it} is the correlation coefficient of Pearson between traits *t* and *l* over all the species considered. To assess the statistical niche differences between species, permutation tests were performed to test whether the observed niche overlap was unusually low based on the potential distribution of niche overlap values generated by permutation of the data (Geange et al., 2011). Statistical null distributions (the distribution of the test statistic under the null hypothesis of no niche differentiation) were generated by calculating pseudo-values through randomly permuting species labels in the corresponding data set over 1000 runs. The distribution of the average niche overlap for the null model was then computed. To correct for multiple comparisons, we performed a Bonferroni adjustment of type I (Quinn and Keough, 2005). The niche overlap calculations and associated null model tests were performed using R version 3.0.2. (R Foundation for Statistical Computing, Vienna) using the density function and the source code provided as supporting information in Geange et al. (2011).

3. Results

3.1. Functional space analysis

The first 6 PCA components explained 96.4% of the total variation, where the first three components explained 76.9% of variance (Table S2). The first PC axis (46.5% variance explained) was correlated with food acquisition such as *Osf* ($r=0.803$, Table 2) and *Edst* ($r=0.323$). This axis clearly separated to fish groups associated to reduction in body size dorso-ventrally and big eyes: *C. corniger*-*P. hemisticta*-*B. caudimacula* and *H. rubellopterus*-*P. cyanea*-*C. investigatoris*-*P. blotchii* (Fig. 2). The second PC axis (18.8% variance explained) described variations in food acquisition (*Osf*, *Osh* and *Ops*) and locomotion (*PFps* and *CPt*) traits, although the variables better correlated were *Osh* ($r=0.522$) and *CPt* ($r=-0.410$) (Table 2). Thus, negative records represented species (mainly *P. hemisticta*, *B. caudimacula* and *H. rubellopterus*) with bigger mouths and faster swimming (Fig. 2). The third PC axis (11.7% variance explained) differentiated the positive values with locomotion traits (*Bsh*, $r=0.589$; *ArFP*, $r=0.430$), negative with food acquisition traits (*Ops*, $r=-0.362$; *Edst*, $r=-0.396$) (Table 2). The species *H. rubellopterus*, with a strong constriction body shape lateral, and *P. hemisticta*, with a large pectoral fin, showed the highest positive values; and *C. investigatoris*, with a bigger eye in relation to head size, presented the most negative value (Fig. 2). The remaining PC scores (19.5% variance explained) were mainly related to locomotion traits (Table 2).

The MANOVA analysis showed the existence of significant differences among species (Wilk's Lambda = 3.025×10^{-6} , $F_{36, 552} = 261.5$, $P <$

Table 2

Correlation between PC's components and functional traits. In bold, correlations higher abs (0.3).

Functional traits	PC1	PC2	PC3	PC4	PC5	PC6
<i>Osf</i>	0.802	0.383	0.104	-0.283	-0.081	0.144
<i>Osh</i>	-0.128	0.522	-0.037	-0.112	-0.015	0.121
<i>Ops</i>	-0.282	0.317	-0.362	-0.315	-0.012	0.028
<i>Edst</i>	0.323	-0.111	-0.396	0.180	0.015	0.046
<i>Eps</i>	0.019	-0.123	-0.094	-0.009	0.184	-0.041
<i>Bsh</i>	-0.253	0.155	0.589	-0.183	-0.429	0.018
<i>PFps</i>	-0.039	0.370	-0.002	0.774	-0.186	-0.144
<i>ArPF</i>	0.148	0.105	0.430	0.061	0.563	-0.548
<i>CPt</i>	0.015	-0.410	0.299	-0.065	0.083	0.311
<i>ArCF</i>	-0.061	0.134	0.162	0.280	0.425	0.723
<i>FSr</i>	0.034	0.159	0.187	0.096	-0.052	0.133
<i>FSb</i>	0.250	-0.266	0.096	0.221	-0.483	0.034

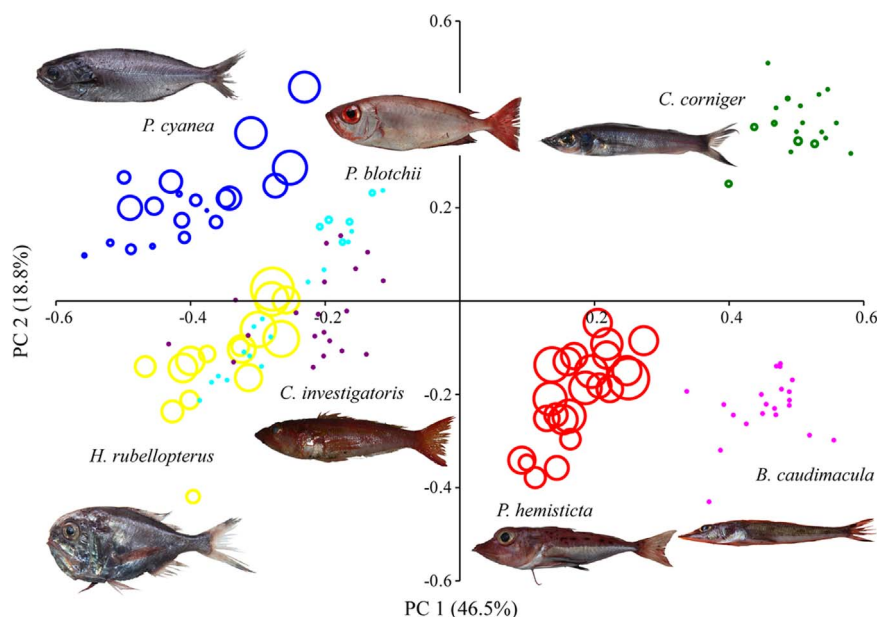


Fig. 2. Principal component analysis the functional traits of the common deep-sea fishes collected from the south-eastern Arabian Sea along the three major axes. The Z-axis is represented by the point size.

0.0001). Pair-wise comparison among species using sequential Bonferroni correction indicated significant differences ($P < 0.001$) among all species. The discriminant analysis revealed 100% classification success of cases for all species (Table S3).

3.2. Niche overlap

The analyses showed significant differences between species, hence functional niches were not overlapping (Table 3). The species *P. cyanea* showed the lowest values of overlap and *P. blotchii* the highest degree of overlapping. The overall niche overlap ranged between 0.13 for *P. cyanea*–*B. caudimacula* and 0.50 for *P. cyanea*–*H. rubellopterus*. Moreover, the niche overlap values for the twelve axes varied in relation to type of functional traits and species compared (Table S4, Figs. 3 and 4). The results indicated that *ArCF* was not significant for the most of comparisons, whereas *Edst*, *Eps*, *Bsh* and *PFps* provided differences in almost all cases.

4. Discussion

Our results revealed significant differences in the functional traits related to feeding and swimming mechanisms of common deep-sea fishes, which indicated low levels of overlap in functional niche between them. It supports a high partitioning of food resources promoting the coexistence of species in these communities (e.g., Fock et al., 2002; Carrassón and Cartes 2002; Preciado et al., 2016). Indeed, we found that overlap was less for the two most abundant species, *P. cyanea* and *B. caudimacula*, and higher for the least abundant species, *P. blotchii*, *H. rubellopterus* and *C. investigatoris*. In this sense,

Mason et al. (2008) showed that overlap of functional niche and species abundance tend to be related. Although the dominance of species may be enhanced by some particular traits (Loreau, 2000), rare species are also characterised by highly specialized forms of resource utilization supporting the functional richness, specialization and originality of assemblages (Leitão et al., 2016). Future studies that examine the functional niche overlap should include rare species to test the degree of overlap between common and rare species in deep-sea communities.

Studies in deep-sea fish species indicate that resource partitioning is related to prey size, and swimming capacity near the bottom (Cartes, 1998; Carrassón and Cartes, 2002; Papiol et al., 2013). Our study revealed variations in specialised functional abilities linked to the preference for food, manoeuvrability and foraging area, as well as the speed for catching the prey. Dissimilarities in the functional morphology of feeding between the species can help to determine the habitat where they live (Schoenfuss and Blobb, 2007). Numerous studies have also confirmed that mouth size and oral anatomy influence the trophic niche of species (e.g., Wainwright and Richard, 1995; Colborne et al., 2013). Several studies have connected the locomotory morphology and feeding strategy, noting the crucial role of fins in acceleration or deceleration while maintaining approach stability (Rice and Westneat, 2005; Higham, 2007a, 2007b). In our case, the four bathy-demersal species (*B. caudimacula*, *C. corniger*, *H. rubellopterus* and *P. cyanea*) and showed morphologies clearly differentiated and separated within the functional space. The main variations in the functional traits indicated that the species diverged in the prey preference, size and detection, and propulsion efficiency. *P. cyanea*, with a shape more adapted to epibenthic swimming, is basically a carnivore which feeds primarily on benthic and epibenthic organisms, such as myctophids

Table 3

Average (and standard deviation) weighted niche overlap for the functional traits considered (Table 1) between each pair of fish species. Statistically different niches are indicated in bold ($P < 0.05$).

Species	<i>B. caudimacula</i>	<i>C. corniger</i>	<i>C. investigatoris</i>	<i>P. blotchii</i>	<i>H. rubellopterus</i>	<i>P. hemisticta</i>
<i>P. cyanea</i>	0.13 (0.17)	0.35 (0.27)	0.38 (0.30)	0.46 (0.22)	0.50 (0.28)	0.17 (0.18)
<i>B. caudimacula</i>		0.20 (0.23)	0.30 (0.28)	0.25 (0.29)	0.27 (0.30)	0.34 (0.31)
<i>C. corniger</i>			0.25 (0.17)	0.25 (0.25)	0.30 (0.31)	0.27 (0.28)
<i>C. investigatoris</i>				0.46 (0.21)	0.41 (0.32)	0.22 (0.21)
<i>P. blotchii</i>					0.47 (0.21)	0.34 (0.26)
<i>H. rubellopterus</i>						0.32 (0.34)

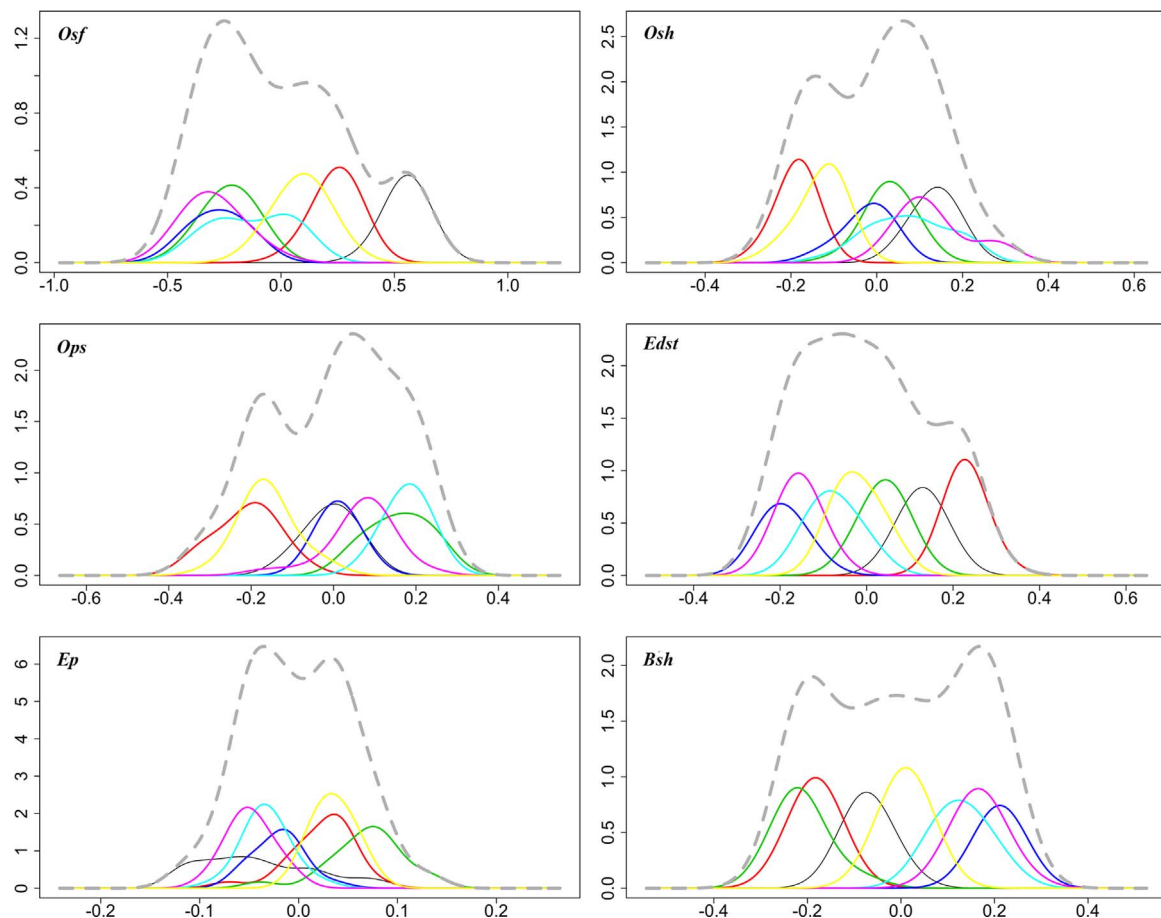


Fig. 3. Kernel densities estimate for functional traits distribution of the common deep-sea fishes from the south-eastern Arabian Sea. *Osf*, oral gape surface; *Osh*, oral gape shape; *Ops*, oral gape position; *Edst*, eye size; *Eps*, eye position; *Bsh*, body transversal shape.

and shrimps (*Aristeus* spp. and *Heterocarpus* spp.) (Venu and Kurup, 2002b). Although ecological and biological information is scarce, *H. rubellopterus*, could theoretically compete with *P. cyanea*. In general, the slimeheads are opportunist feeders with a feeding activity similar to mesopelagic fishes, which exploit from migrators (especially mesopelagic fishes) rising from mid-slope depths (Bulman and Koslow, 1995; Dunn and Forman, 2011). The high swimming capability and a big mouth would imply ability to capture prey in the column water. Bulman and Koslow (1995) suggested that adults of *Hoplostethus atlanticus* migrated up the slope from deeper water. This migration would entail a major energetic expenditure, which could be compensated by more efficient swimming. In this sense, this species is clearly different in the functional trait (*CPT*) with a very slim caudal peduncle and high aspect caudal fin whereas *B. caudimacula*, with a shape characteristic of fishes living on the bottom of the sea floor, feeds predominantly crustaceans (Hashim, 2012). Although no information is available on the food habits of *C. corniger*, the relative big eyes suggests that this species is an active predator adapted to low light availability (Boyle and Horn, 2006) which looks for small prey very close to the bottom. Probably, these could be fishes as in the case of *Chlorophthalmus agassizi* (Hashim, 2012).

Though no information on feeding is available on the three-demersal species (*P. hemisticta*, *P. blochii* and *C. investigatoris*) studied, we noted crustaceans and fishes (approximately, 60–40% for each item) in the gut of *P. hemisticta*, fishes and squids (approximately, 60–40% for each item) in *P. blochii*, and exclusively fishes in *C. investigatoris*. This information could help in understanding the functional differences noted between them and with the other species. *P. hemisticta*, which like all gurnards, use the paired fins (pelvic and pectoral fins) during “walking”, perching or probing for food items

(Gosline, 1994). This species living on the sea floor, like *B. caudimacula*, could capture more benthic crustaceans. Both species have similar functional characteristics, which explain why they were located in the same quadrant of the functional space (see Fig. 2). The priacanthids, including *P. blochii*, are usually epibenthic and found associated with rock formation or coral reefs (Starnes, 1988). The presence of squids in the gut content indicated that this species has a higher swimming speed for catching prey than other demersal species, including the bathy-demersal species such as *P. cyanea*. This enhanced swimming ability could allow both species to occupy close functional spaces (see Fig. 2). By contrast, *C. investigatoris* is a species with a serranid-like feeding mechanism allowing it to launch attacks on prey close to the sea floor, hence defined as an ambusher species (Hobson, 2006). Although the prey (fishes) could be similar to resource use by other species, the ecological strategy clearly differs.

In conclusion, differences in functional niches were observed between common species, likely as consequences of different mechanisms acting synergically to allow the coexistence of species. Future works would be needed to understand these mechanisms. In any case, the study shows the relevance of functional analysis of morphological features in an ecological frame, as has been anticipated in previous works on the ecology and morphology (e.g., Mouillot et al., 2005; Boyle and Horn, 2006; Collar and Wainwright, 2006; Farré et al., 2016).

Acknowledgments

The authors are deeply thankful to the Director, CMLRE for the encouragement and support during the study. Expressing sincere thanks to chief scientists, fishing master, participants and fishing hands of FORV Sagar Sampada for their courteous support and help

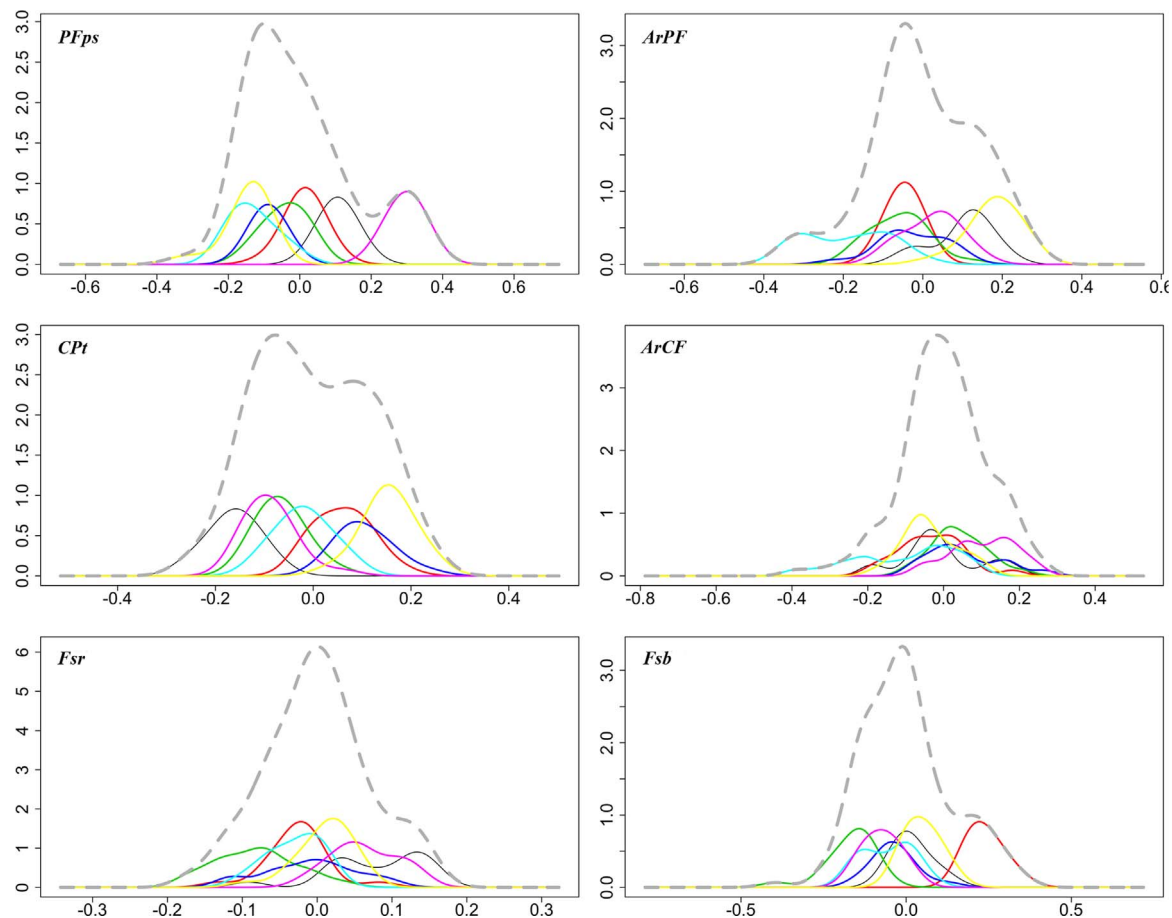


Fig. 4. Kernel densities estimate for functional traits distribution of the common deep-sea fishes from the south-eastern Arabian Sea. *PFps*, pectoral fin position; *ArPF*, aspect ratio of the pectoral fin; *Cpt*, caudal peduncle throttling; *ArCF*, aspect ratio of the caudal fin; *Fsr*, fins surface ratio; *Fsb*, fins surface to body size ratio.

during the sample collection and analysis. We would like to thank Dr M.R. Boopendranath and two anonymous reviewers for their constructive comments and suggestions which certainly improves the quality of the manuscript. The work is carried out as part of the Deep-sea and Distant water Fishery (DS & DWF) project under the Marine Living Resource Programme (MLR Programme) of CMLRE, Ministry of Earth Sciences (MoES). The financial and logistical support from the CMLRE (MoES), is appreciatively acknowledged. This is CMLRE contribution number 73.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dsr.2016.11.011](https://doi.org/10.1016/j.dsr.2016.11.011).

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