Billfish resources of India with special reference to the fishery and biology of blue marlin *Makaira nigricans* caught from the Eastern Arabian Sea

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Abstract

Billfish, comprising sailfishes, marlins, spearfishes, and swordfishes, are highly migratory and large pelagic predators distributed globally across tropical and subtropical oceans. Along the Indian coast, the estimated landings of billfishes have shown a rising trend, reaching 21,321 tonnes in 2024. The major species contributing to landings during 2009–2024 include *Istiophorus platypterus* (50%), *Istiompax indica* (23%), *Makaira nigricans* (12.5%), *Xiphias gladius* (15%), and *Kajikia audax* (<1%). Mechanized gillnetter cum hook-and-line units were the primary gears responsible for billfish capture. Molecular identification using cytochrome oxidase I (COI) gene barcoding successfully differentiated four billfish species occurring in Indian waters. Mitochondrial DNA control region (mtDNA-CR) based phylogenetic analysis revealed two well-supported sub-clades within the major clades I and II, further aiding in species-level differentiation. The reproductive and feeding biology of *M. nigricans* (blue marlin) was studied using 764 specimens (237 females, 364 males, and 163 unidentified) collected between 2017 and 2024, with lower jaw fork lengths (LJFL) ranging from 130 to 305 cm. Among females, 23.2% measured <200 cm LJFL, while 76.8% were >200 cm LJFL. In contrast, 61% of males were <200 cm LJFL and 39% were >200 cm LJFL. The length at first maturity (L_{m50}) was estimated at 185 cm LJFL for females and 179.56 cm LJFL for males. Gonadosomatic index (GSI) values ranged from 0.6 to 3.9 in females and 0.6 to 3.1 in males, with peak values observed in May, indicating peak spawning during the pre-monsoon and monsoon months (April–June). Oocytes within the size range of 0.2–0.9 mm were included in fecundity estimations, which ranged from 1.67 to 11.1 million eggs. The spatial distribution of billfish resources from 2018-2023 collected by the Fishery Survey of India, Tuna Longline survey vessels MFV YellowFin and MFV Matsya Vrushti along the Indian EEZ of Arabian sea reveals that the spatial distribution of billfish hooking rates (0.01–2.0) in the Arabian Sea within India's EEZ off the west coast, showing low to moderate rates (0.01–1.12) across most areas and distinct high-intensity hotspots (1.12–2.0) southwest of the mainland near the Lakshadweep Islands. Histological evidence also confirmed that the eastern Arabian Sea, particularly the Lakshadweep region, serves as a significant spawning ground for blue marlin, with the presence of matured and spent females. The feeding strategy estimated from the diet matrix revealed the BUM as a specialist predator that feeds on specific prey species or groups of individuals specialized on selective prey types.

Keywords: Billfish, mtDNA-CR, reproductive biology, hooking rate, feeding strategy

Introduction

Billfishes are large, predatory fish that migrate extensively and can be found in all oceans worldwide, except for the Arctic and Southern Ocean (Surya *et al*., 2023). A total of 10 species of billfish *Xiphias gladius* under family Xiphidae and *Istiophorus platypterus, Kajikia audax, K. albida, Tetrapturus angustirostris, T. belone, T. georgii, T. pfluegeri*, *Makaira nigricans* and *Istiompa indica* under family Istiophoridae have been identified (Surya *et al*., 2022; 2023). The WoRMS includes two more species in the Istiophoridae family: *Istiophorus albicans* and *Makaira mazara*, which Eschmeyer's Catalog of Fishes regards as synonyms of *Istiophorus platypterus* and *Makaira nigricans*, respectively (ECoF, Fricke *et al*., 2025). The ITIS (2008) and followed Collette *et al*., (2006) classification placed *Istiophoridae* together with Xiphiidae under the suborder Xiphioidei.

In most countries, billfishes are typically not the primary targets of large-scale fisheries. In India, billfish fisheries occur as bycatch in longlines, troll, and oceanic gillnet fishery, which generally target oceanic tunas, although they contribute substantially to the total large pelagic landings in India (Bishnupada and Ansy, 2014; Surya *et al*., 2021a; 2021b; 2023). Billfish landings have increased over the years due to the expansion of fishing grounds and improved fishing capacity. As a pelagic fish resources billfishes play a vital role in maintaining the ecological balance of the marine environment (Rohit *et al*., 2024). The most common billfishes that landed along the Indian coast are *I. platypterus* (Indo-Pacific Sailfish), *X. gladius* (Swordfish), *I. indica* (Black marlin), *M. nigricans* (Blue marlin), *K. audax* (Striped marlin) and rare landings of *T. angustirostis* were also reported. The landings are mainly contributed by mechanised gillnetter cum hooks and lines (Surya *et al.,* 2023).

The blue marlin, *Makaira nigricans*, is a highly migratory species found worldwide, important for both commercial and recreational fishing. Among all billfish, blue marlins have the widest tropical distribution, though their density varies seasonally and annually due to changes in oceanic conditions. They show dimorphic growth, with females growing faster and reaching a larger size than males. (Su *et al*., 2011; 2013). Blue marlins are multiple spawners with asynchronous oocyte development. The spawning occurs once every 2-3 days on average (Sun *et al*., 2009). They show a sexual difference in the migration, mainly associated with spawning and feeding regions (Shimose *et al*., 2012). Several studies have been reported from the Indian, Atlantic and Pacific oceans on the fishery, habitat preference, biology and stock structure of billfish (Hoolihan, 2004; Ganga *et al*., 2008; Chang *et al*., 2012; Bruno *et al*., 2014; Rathnasuriya *et al*., 2016; Bandaranayake *et al*., 2018; Kadagi *et al*., 2022) (Bruno *et al*., 2018; Ganga *et al*., 2012; Surya *et al*., 2021a; 2021b; 2022; 2023). The distribution, species composition and environmental preferences of billfishes landed along the Indian coast have also been reported (Varghese *et al*., 2005; Varghese *et al*., 2013; Bishnupada and Ansy, 2014). Some aspects of biology, movement patterns, habitat use, and stock assessment of blue marlin have been studied by several researchers worldwide (Ortega-Garcia *et al*., 2006; Shimose *et al*., 2009; Sun *et al*., 2009; Kraus *et al*., 2011; Veiga *et al*., 2011; Su *et al*., 2011; 2012; Fan *et al*., 2019; Freitas *et al*., 2022; Andrzejaczek *et al*., 2023; Crespo-Neto *et al*., 2025).

The demand for billfish is steadily increasing, making it essential to manage these resources with effective management plans to prevent future overexploitation (Surya *et al*., 2023). The hooking rate of billfishes was observed to be gradually declining in the Andaman Sea, resulting in a lower contribution to the overall species composition (Jacob *et al*., 2024). The fishing pressure on females (blue marlin) is greater than that on males, emphasising the need to consider sexual dimorphism in stock assessments for sexually dimorphic species (Su *et al*., 2013). Although billfish are highly resilient to fishing pressure due to their high fecundity, migratory behaviour, and ability to inhabit tropical and subtropical oceans, management strategies must be adapted to ensure their sustainability (Surya *et al*., 2023).

The present study provides details on the catch and species composition of billfishes landed along the Indian coast with a special emphasis on the fishery and biology of blue marlin *Makaira nigricans*.

Methodology

The annual estimates of billfish landings recorded by the National Marine Fisheries Data Centre (NMFDC) of ICAR-Central Marine Fisheries Research Institute for the years 2009-2024. Genomic DNA was extracted from fin tissues of five specimens per species using the Qiagen DNeasy Blood and Tissue Kit following standard protocol. Briefly, tissue samples were finely cut, lysed with Buffer ATL and Proteinase K at 56°C, and subsequently treated with Buffer AL and ethanol before being loaded onto a DNeasy Mini spin column. After sequential washes with Buffer AW1 and AW2, DNA was eluted in Buffer AE and stored at –20°C for further use. The integrity of isolated gDNA was verified by electrophoresis on 0.8% agarose gel prepared in 1X TBE buffer with ethidium bromide, and visualized under UV illumination using a gel documentation system (BIO-RAD, USA). Data on length, weight, sex, and gonads were collected from processing units at with gonads preserved for laboratory analysis. Maturity stages and spawning season were studied by assessing ova diameter, fecundity, and histological sections of preserved gonads, with developmental stages classified following Brown- Peterson et al. (2011). Gonado-somatic index (GSI) was calculated monthly, and length at first maturity (Lm) was estimated using logistic regression of maturity proportion against length. Fecundity was determined gravimetrically from 12 mature ovaries, with absolute and relative fecundity estimated from subsample counts. Stomachs with gut contents were preserved, dissected, and analyzed in the laboratory. Prey items were identified to the lowest possible taxon using diagnostic hard parts and reference collections, measured, and weighed to determine seasonal, ontogenic, and spatial variations in diet. Diet composition was analyzed using frequency of occurrence (%F), percentage by weight (%W), and the Index of Preponderance (Ii), while feeding preference was quantified through the Index of Relative Importance (IRI), with month- and size-based variations analysed in PRIMER v.6 using multivariate methods (Bray-Curtis similarity, cluster analysis, SIMPROF, and MDS). Trophic niche breadth was estimated using Levin's Standardised Niche Breadth Index (BA), and feeding strategy was interpreted through Amundsen's graphical method, plotting prey-specific abundance against frequency of occurrence to distinguish between specialist, generalist, and mixed feeding modes.

Results and discussion

Study was conducted on the billfish samples caught from the Eastern Arabian Sea (Fig. 1). Along the Indian coast, the estimated landings of billfishes have shown a rising trend (Fig. 2), reaching 21,321 tonnes in 2024. The major species contributing to landings during 2009–2024 include *Istiophorus platypterus* (50%), *Istiompax indica* (23%), *Makaira nigricans* (12.5%), *Xiphias gladius* (15%), and *Kajikia audax* (<1%) (Fig.3). The spatial distribution of billfish resources from 2018-2023 collected by the Fishery Survey of India Tuna Longline survey vessels MFV Yellow Fin and MFV Matsya Vrushti along the Indian EEZ of Arabian sea reveals that the Spatial distribution of billfish hooking rates (0.01–2.0) in the Arabian Sea within India's EEZ off the west coast, showing low to moderate rates (0.01–1.12) across most areas and distinct high-intensity hotspots (1.12–2.0) southwest of the mainland near the Lakshadweep Islands (Fig. 4).

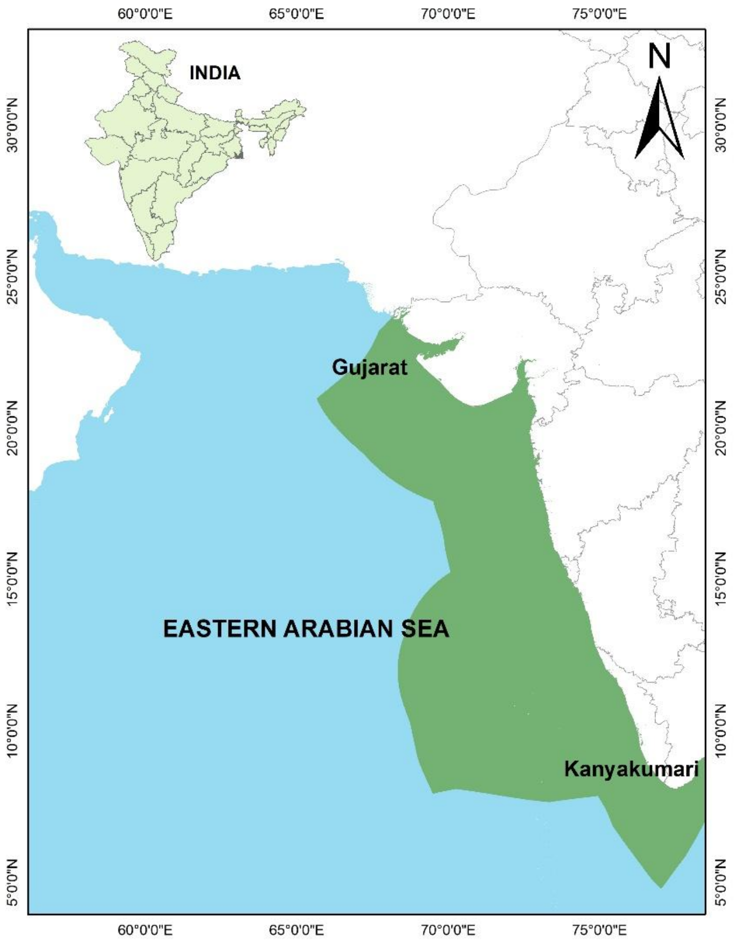

Fig. 1. Sampling location (Eastern Arabian Sea)

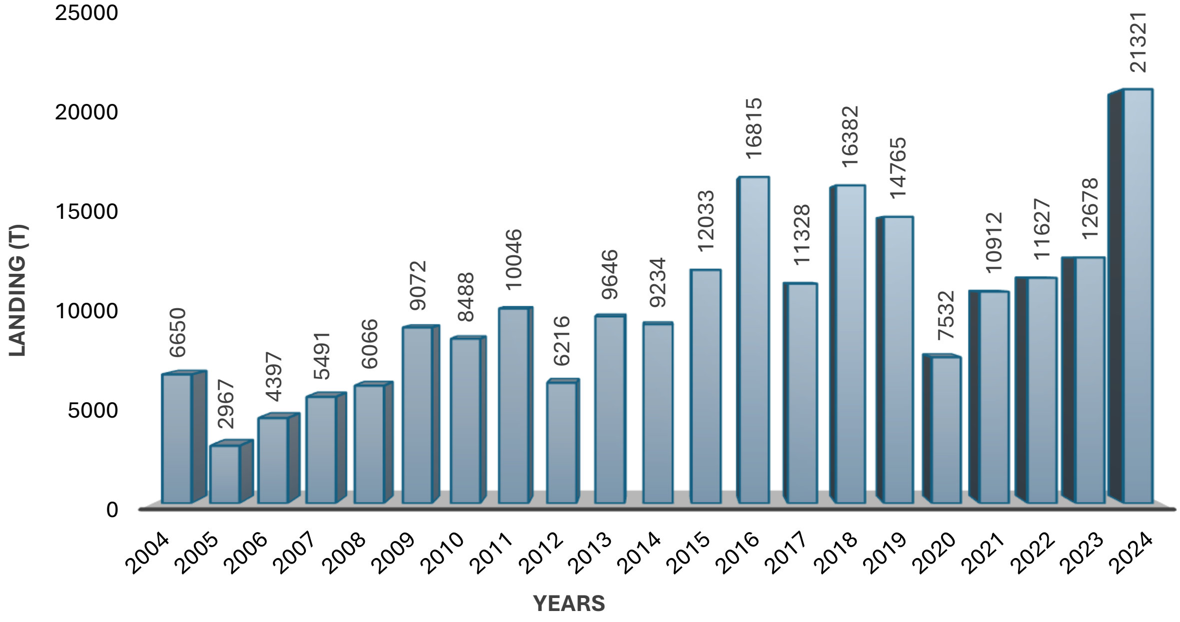

Fig. 2. Landings of billfish along the Indian coast in tonnes (2004-2024)

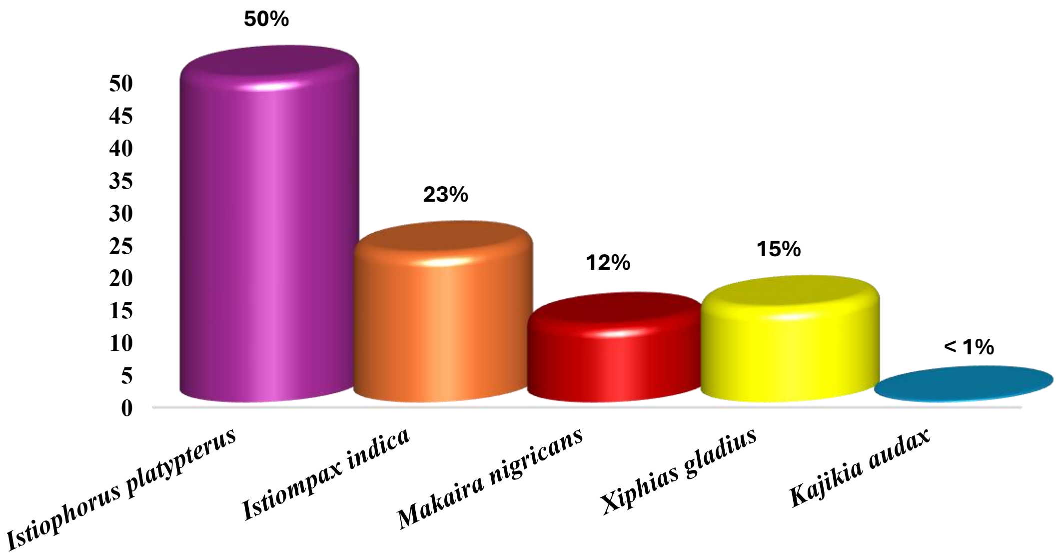

Fig.3. Percentage contribution of billfish species landed along the Indian coast (2009–2024)

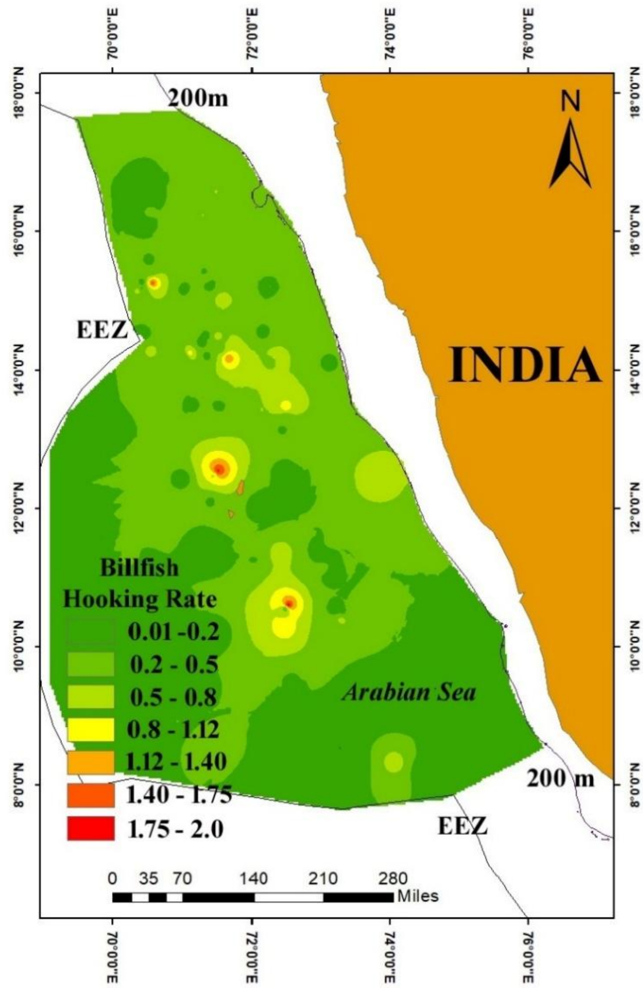

Fig. 4. Billfish distribution and its hooking rates

Billfishes caught from the Eastern Arabian Sea and were generally caught by multiday gillnetter cum longliners. Depending on the availability of fish, the fishers switched to varied gears like gillnet and hook and line. However, most fishers mentioned their difficulties when operating both gears in one trip, and if they were operating long lines, they continued to focus only on the longline operation. The accurate fishery details of billfishes were unavailable from the commercial catches owing to its non-targeted fishery. Longlines are the most preferred gear to catch billfishes than gillnets as per the fishers. Usually, Hook No. 4 and 5 are used for catching billfishes. *Selar crumenophthalmus* is the most preferred live bait used to hook billfishes and hook no. 14 is used to catch the bait fishes and the captured fishes are kept alive on board the gillnetters. The live baits are hooked manually and then the lines are deployed to capture billfishes.

Five billfishes were identified from the eastern Arabian Sea during the present study and the identified billfishes are *Istiophorus platypterus* (Indo-Pacific Sailfish), *Kajikia audax* (Striped marlin), *Istiompax indica* (Black marlin), *Makaira nigricans* (Blue marlin) and *Xiphias gladius* (Swordfish). All the five species of billfishes available in Indian waters showed near or higher values of the 2% divergence threshold adopted for species delimitation (Hubert *et al*., 2008) and were identifiable by barcodes, whereas global results suggested that only 50% of billfishes are readily distinguishable by standard COI barcodes and the rest falls into complexes. Though COI is the standard marker of choice in various organisms, the marker alone does not provide conclusive evidence of species delineation in relatively young or recently diverged species (Hickerson *et al*., 2006) due to the insufficient time for the accumulation of mutations. *K. audax* and *K. albida* were found to be in one complex in this study, similar to previous reports (Graves 1998; Shivji *et al*., 2006; Collette *et al*., 2006) primarily due to their recent divergence. The homologous sequences of COI and Control Region (CR) sequences from billfishes and their closely related groups as outgroups were downloaded for phylogenetic analysis. A total of 40 sequences of COI and 32 sequences of D-loop/CR were used for phylogenetic analysis. Sequence data from GenBank generated in this study for phylogenetic analysis are shown in Table 1.

Table 1. Details of sequences generated from billfishes used in this study and those downloaded from GenBank.

Sl. No	Species	Marker amplified and GenBank accession number	
		COI	CR/D-loop
		(Sequence generated-Downloaded)	(Sequence generated-Downloaded)
1.	*I. platypterus*	MZ562767- MZ562770	MZ579524
2.	*M. nigricans*	MZ562772- MZ562776	MZ579528- MZ579531
3.	*K. audax*	MZ562777- MZ562782	MZ579525- MZ579527
4.	*I. indica*	MZ572970- MZ572971	-------------
5.	*X. gladius*	MZ562883	-------------

Gonads of the Indo-pacific Blue marlin, *M. nigricans* (n=764) of which 364 males, 237 female fishes, and 163 ID with LJFL ranging from 130 cm- 305 cm exploited from Eastern Arabian Sea during March 2017 to February 2019 were used for the study. Majority of the fishes (86%) landed with LJFL 160-269 cm (Females 238.5±19 cm and males 182.5±15 cm). Out of 237 female fishes, 23.2% of individuals were <200cm LJFL and 77% were > 200cm LJFL. Out of 364 male fishes, 61% were <200 cm LJFL and 39 % were >200 cm LJFL. Of the total 601 individuals analysed, 276 individuals were less than 200 cm LJFL, in which 221 male fishes (80%) and 55 female fishes (20%). The remaining 325 fishes with LJFL greater than 200 cm were males (44%) and females (56%).

The length at first maturity (L_m) was analysed for the male and female stocks separately because of the sex based size differences in the stock. The study was based on the examination of 201 females and 294 males in the maturity stages of III and above. The L_m for the female stock was estimated at 185 cm LJFL while for the male stock, it was estimated at 179.56 cm LJFL. A maturity curve was plotted by taking the percentage of matured proportion of females and males against their length groups at 10 cm class intervals (Fig.5). The GSI values fluctuated from 0.6 - 3.9 in females and 0.6 - 3.1 in males. Month-wise prominent peak was observed during May in both males and females (Fig.6). This denotes the peak spawning to occur during the Pre-monsoon and monsoon season from April-May-June. The L_m estimated in the present study was comparable to others studies, with small variations that could be due to environmental or genetic effects or errors in sampling. Females of blue marlins sampled from Lakshadweep islands during April- June with a GSI >3 indicated the fish to be reproductively active and also indicated the spawning ground. The fecundity was analysed from the matured gonads of 12 female specimens ranging from 197.5 to 297.2 cm LJFL and 79.6 – 280 kg TW. The total number of eggs in the mature ovary weighing 6.02 – 22.12 kg was 1.67 million to 11.1 million eggs (ova-diameter 0.2 mm to 0.9 mm only were considered). The relative fecundity of the species ranged from 21 - 50 eggs/g of body weight.

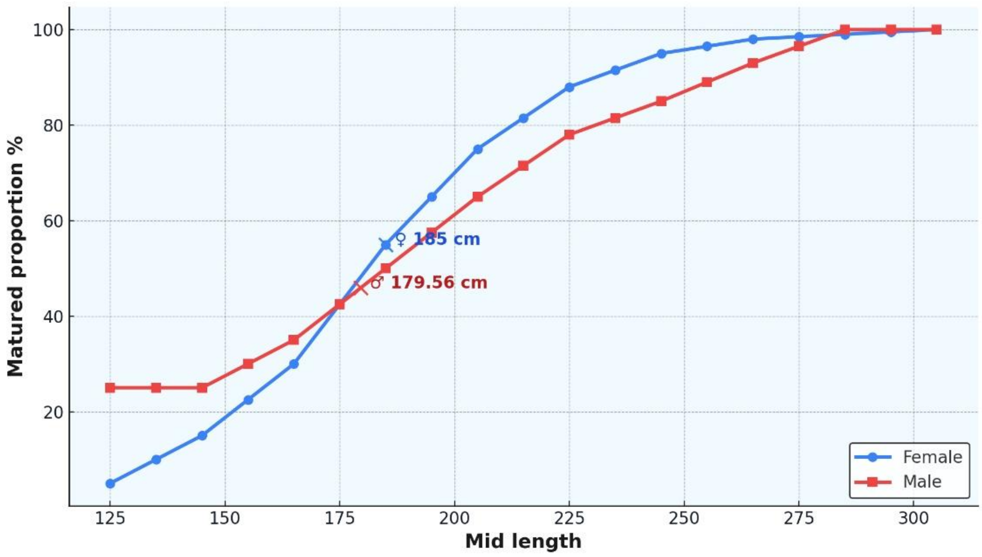

Fig.5. Length at first maturity (L_m) of *M. nigricans* (Male and female)

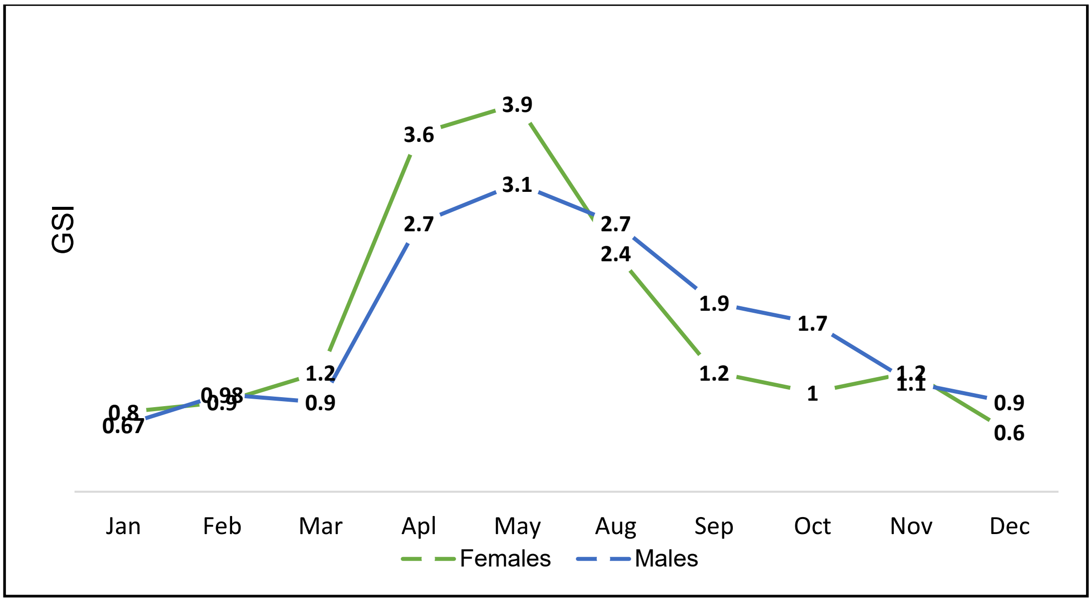

Fig.6. Month-wise Gonado-Somatic Index of *M. nigricans* (male and female)

The maturity stages were studied with the help of simple five-point standardized scale for maturity stages as described by Brown-Peterson *et al*. 2011. The mature ovaries were seen peak from April-June. Spent stages were observed during September, October and November. This indicated that *M. nigricans* spawns during the late pre-monsoon and monsoon months. In the case of male fishes, gonads look similar and oozing milt was seen in the testicular duct during most of the months. The photograph of female and male gonad of *M. nigricans* was given in Plate.1 and Plate 2. The ova diameter frequency polygons in ovaries of successive maturity stages are given in Fig.7.

Plate.1. Photograph of female gonads of *M. nigricans*

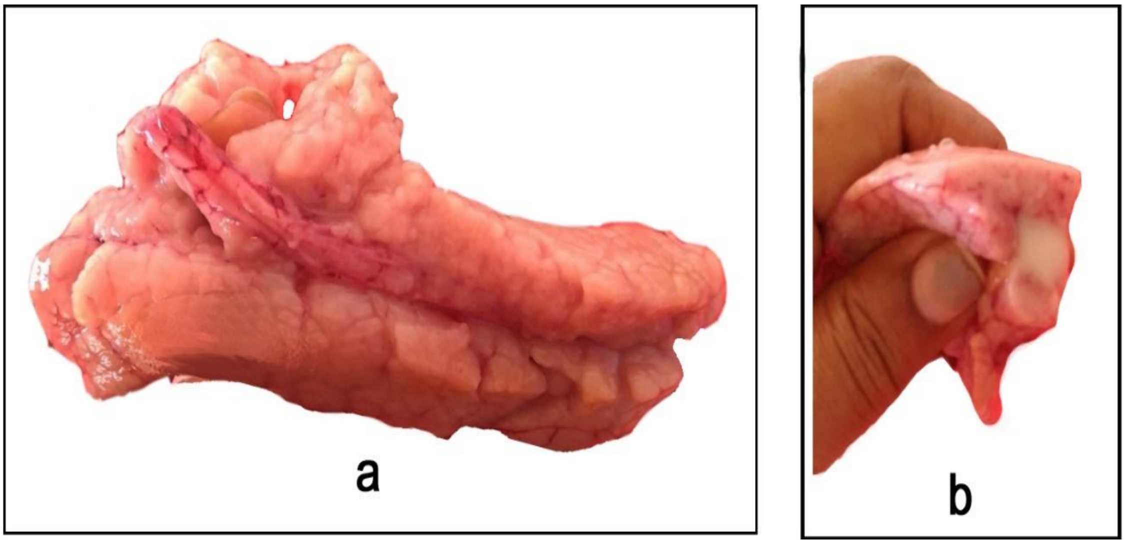

Plate.2. (a) Photograph of male gonads of *M. nigricans (*b) Oozing milt from the testicular duct

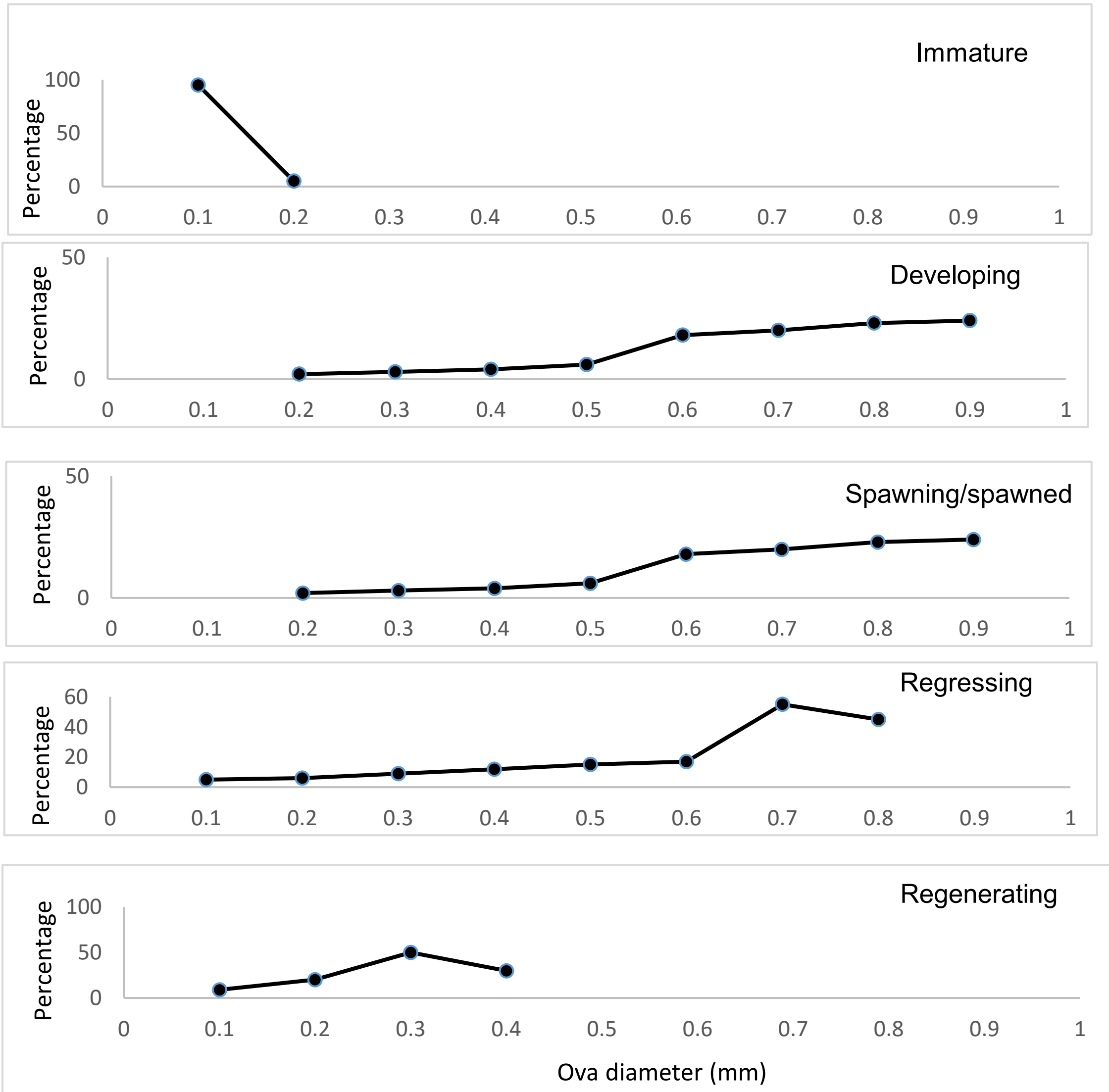

Fig. 7. Ova diameter frequency of *M. nigricans*

In stage I, only immature (0.1 to 0.2mm) ova were observed. In stage I, about 95% of the gonad was occupied by immature ova. By stage II, the ova diameter had increased up to 0.6 mm, with approximately 60% consisting of medium-sized maturing eggs and 40% of mature eggs. In stage III, about 95% of the gonad was filled with mature ova (0.6–0.9 mm), while the remaining 5% comprised medium-sized eggs. Stage IV represented the regressing phase, where very few eggs were present, as most of the mature eggs had already been released. In the subsequent regenerating phase, about 70–80% of the gonad was occupied by small-sized ova, with the rest consisting of medium-sized eggs. The studies on the reproductive biology of BUM (Sun *et al*., 2009; Shimose 2005; Shimose *et al*., 2009; Shimose *et al*., 2012; Sun *et al*., 2013) explained the maturity stages using histological studies but the classification of stages varied as compared to the present study. In the current study, it was seen that the matured ova formed more or less two modes in each stage and they are distinctly separated from the rest of the stock of eggs and concluded that the species is a fractional spawner releasing the ripe ova in batches during the spawning season. Different reproductive strategies of BUM such as asynchronous oocyte development, partial spawning, extended spawning season, indeterminate fecundity, and frequency of spawning and duration enhance the probability of progeny survival of BUM.

A total of 520 stomach samples of the *M. nigricans* were collected from landing centres and processing units and the analysis revealed that 53% of stomachs contained undigested or partially digested food, 33% had digested material, and 13% were empty. A total of 27 fishes, three crabs, three shrimps, two squids, one cuttlefish and one species of mantis shrimp were identified from the stomach contents. Feeding intensity revealed notable seasonal variations, with gorged stomachs peaking in November, full stomachs in August, half-full in October and March, and the highest proportion of empty stomachs in May. Index of Relative Importance (IRI) confirmed carangids as the primary food group (Fig.8), with seasonal shifts in dominance of specific species, while multivariate analyses indicated significant dietary similarity across months with notable variations during October to December (Fig. 9). Feeding strategy analysis indicated that *M. nigricans* is a specialist predator, with high prey-specific abundances for tunas, mahi mahi, pufferfishes, cephalopods, and carangids, the latter being the only group showing both high PSA and frequency of occurrence (Fig.10). Feeding was comparatively specialized with a limited niche width in fishes during most of the months and supporting the estimated feeding strategy above

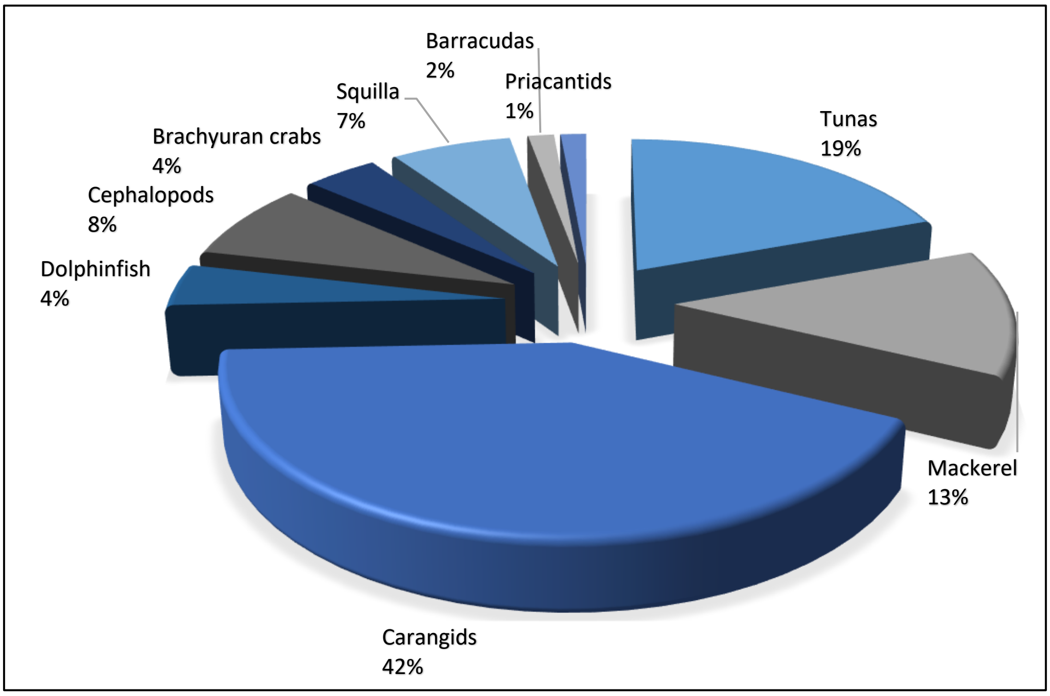

Fig. 8. IRI of different prey items of *M. nigricans*

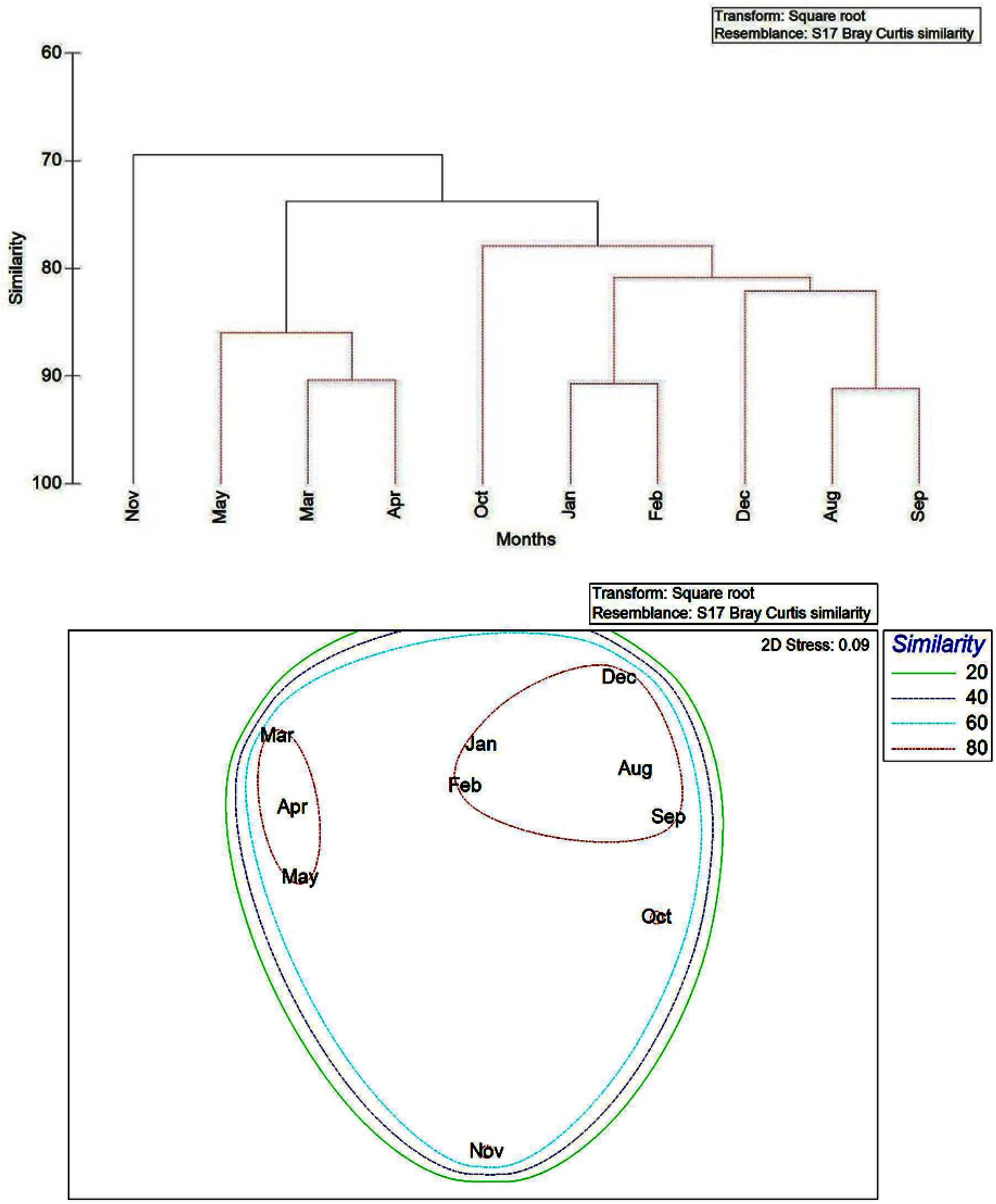

Fig. 9. Prey abundance similarity (a) and Multidimensional Scaling (MDS) of prey abundance (b) of BUM for different months for group wise prey item.

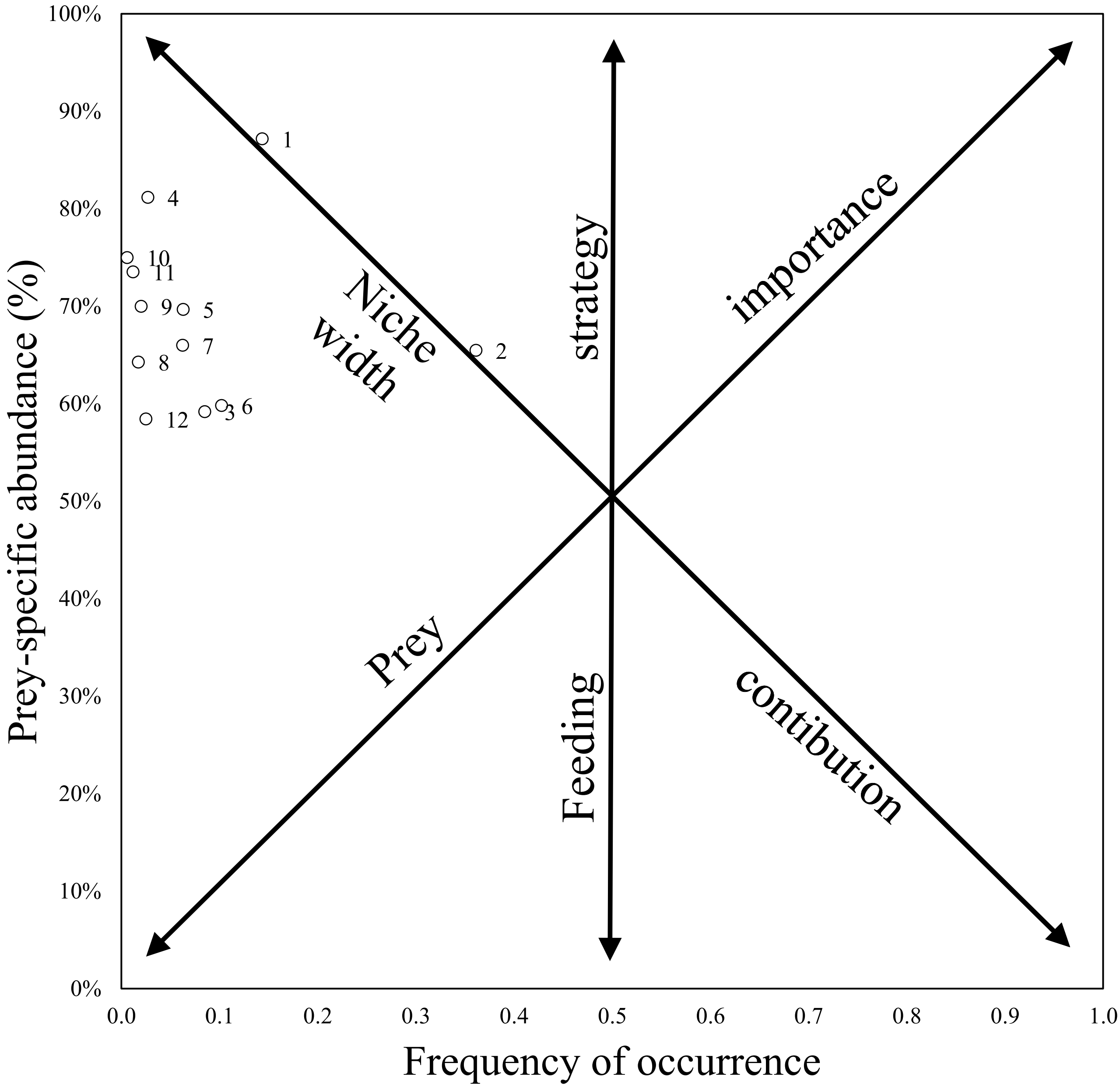

Fig. 10. Feeding strategy of BUM depicted by plotting the prey-specific abundance (%) against frequency of occurrence (%) for dominant prey groups. The two diagonal axes represent the importance of prey and the contribution to niche width and the vertical axis defines the predator feeding strategy. Where: 1 – Tuna; 2 – Carangid; 3 –Mackerel; 4- Dolphinfish; 5 – Cephalopod; 6 – Squilla; 7 – Crabs; 8 - Barracudas; 9 – Priacanthids; 10 – Billfishes; 11 – Pufferfish; 12 – *Acetes* sp.

Billfishes form a bycatch in the tuna longline and gillnets fleets operating in the Eastern Arabian Sea and it is largely seen as a non-target species of industrial and artisanal fisheries. The demand for billfish is increasing daily; hence, managing the resources with proper plans is supreme to avoid overexploitation. In India, basic information on biological aspects and stock assessments for billfishes are scarce and management plans considering genotypic peculiarities and physiological vulnerability to capture are non-existent. The pronounced aggregation of elevated hooking rates near Lakshadweep indicates that this area may serve as a potential ground for billfishes. This zone is characterized by enhanced oceanographic productivity driven by monsoon-induced upwelling and island-induced mixing, which support high prey availability. In addition, the presence of warm tropical waters (>26 °C) and the complex bathymetry of atolls creates favourable conditions for spawning activity, larval retention, and reproductive aggregations. The present study sheds light on the food, trophodynamics and reproductive biology of BUM's. The acquisition of basic biological data, such as feeding and reproduction, which are scarce for the group, is a necessary input for conducting stock assessments which in turn provides important inputs to formulate suitable plans for its management. The reproductive strategies identified in the present study are in response to environmental preferences for feeding or spawning; hence ecosystem-based or habitat-based standardization models can be developed by incorporating reproductive characteristics and environmental preferences for the assessment of billfishes in the future. From the diet contents analysis, it is inferred that, BUMs are specialist feeder that feeds on the most preferred prey in a geographic area. Understanding the unique feeding behaviour of marlins a fast swimming oceanic fish, holds the key to their effective management. The limited research on the food and feeding nature of marlins shows that the diet can vary greatly between species and geographic regions. Nonetheless, the present findings are the first to show the feeding preference and strategy of BUM in the Eastern Arabian Sea and contribute to the global understanding of how marlins feed across oceans and how they adapt to their trophic niches regionally. While the present findings have revealed trophic differences that have important implications for the conservation and management of these species, more research is needed in the trophic studies to effectively manage and protect these keystone predators.

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