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RESEARCH ARTICLE

Observations on feeding habits of the common dolphinfish, *Coryphaena hippurus* (Linnaeus 1758) from the western Bay of Bengal

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Abstract – *Coryphaena hippurus* is a large pelagic species and constitutes an important by-catch in drift gillnet, trolling and long-line fishing gears operated along the Bay of Bengal, northeastern Indian Ocean. The present study, first from the region, is aimed at deciphering the feeding dynamics from 1150 individuals collected from 2017 to 2019. 32.17% of the fishes had empty stomachs or was with food traces, 45.57% had partially-full stomachs and 22.26% had full stomachs. The feeding intensity was inferred through stomach filling and predator-prey weight ratio, which was higher in May and lower in January, and increasing as increase in the fish size. *Coryphaena hippurus* is considered a piscivorous pelagic predator as pelagic teleosts contribute more than half of the prey species. Major prey species were big-eye scad (27.3%), squid (10.3%), crabs (9.3%), Indian mackerel (7.2%), Indian scad (5.9%), whitebaits (5.7%) and sardines (5.4%). Scads and crabs were abundantly preyed during summer and winter, while clupeids and engraulids in monsoon; however, no significant variations were observed in prey composition between sizes. Trophic Level was 4.22 ± 0.15 and Levins Standardized Niche Breadth Index was 0.30. Dietary niche breadth was higher during summer (0.48) and monsoon (0.33) and in fishes measuring 60.0–74.9 cm (0.51) and below 45.0 cm (0.48) indicating generalised feeding. This primary study from Bay of Bengal is the first comprehensive report on trophodynamics for the species and would contribute to its management using trophic interactions.

Keywords: Bay of Bengal / *Coryphaena hippurus* / feeding intensity / prey composition / feeding strategy

1 Introduction

The Bay of Bengal Large Marine Ecosystem (BOBLME) in the northeastern Indian Ocean is bordered by India in the west, Bangladesh in the north, Myanmar and Andaman and Nicobar Islands in the east and by Sri Lanka and Indonesia at both ends in the south. It is the largest Bay in the world and is one of the most productive ecosystems ($>300\,g\,C\,cm^{-2}\,y^{-1}$) influenced by marked seasonal fluctuations of oceanographic parameters caused by monsoons (Dwivedi and Choubey, 1998). Fishery in this region is characterized by its multi-gear and multi-species nature. In the nearshore waters of the Bay, small pelagic finfishes and shrimps at lower trophic levels are targeted. Further offshore, catches are dominated by oceanic tunas and other mid or large sized pelagic carnivores belonging to higher trophic levels. Mean trophic level of the catch along the northern region of the Bay is greater than 3 (Das et al., 2018). Among the large pelagics landed as by-catch in the drift gillnet and the line gears (trolling and long-lines) targeting tuna and Spanish mackerel, the two coryphaenidae species, *Coryphaena hippurus* (Linnaeus 1758) (Common dolphinfish/mahimahi) and *Coryphaena equiselis* (Linnaeus 1758) (Pompano dolphinfish) are found to occur. Though *C. equiselis* is sparsely landed, the contribution of *C. hippurus* (common dolphinfish) to the fishery, particularly in the southern region along the western Bay of Bengal, is considerable. Over the last decade, landings in the western Bay of Bengal have decreased

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Table 1. Fleet and fishing gears characteristics of the *Coryphaena hippurus* fishery in the western Bay of Bengal.

Gears	Vessels (Overall Length) (m)	Mesh Size (mm) / Hook Number and Type (total number of hooks/vessel)	Dimensions (m): Length X Depth or Main Line and Branch Line	Distance between sinkers and floaters / branch lines (m)	Depth of Operation (m)
Drift gillnets	Mechanised (12–14)	140–150	4000–6000 × 12–15	30; 6	>50
Drift gillnets	Motorised (10–12)	70–80	1800–2500 × 12	9; 6	30–60
Troll-lines	Motorised (10–12)	1 / 2 / 7 / 8 (Single hook X 5–6 lines)	45–50; no branch line	–	>30
Long-lines	Mechanised (12–14)	3 J (500–650 hooks)	14000–15000; 25–30	35–40	>30
Long-lines	Motorised (12)	4 J (1000 hooks)	3200; 3	6	>30

from 3838 tonnes in 2011 to 3126 tonnes and 3092 tonnes during 2014 and 2015 respectively, and to 2438 tonnes in 2018 (personal communication from Pelagic Fisheries Division, Central Marine Fisheries Research Institute, Kochi, India). A detailed description of the fishing activity and gears capturing this species is presented in Table 1.

Coryphaena hippurus, distributed in the tropical and temperate waters, is an oceanic migratory pelagic species and is an active and opportunistic top predator (Palko et al., 1982). The distribution in the nearshore waters is limited to 30 m depth (Palko et al., 1982) and the species feeds continuously to maintain higher metabolic rates which are paramount for life in pelagic environment (Benetti et al., 1995). The trophodynamics of the targeted catch along the Bay of Bengal, mainly yellowfin tuna (*Thunnus albacares* Bonnaterre 1788) and narrow-barred Spanish mackerel (*Scomberomorus commerson* Lacepede 1800) has been studied (Satishkumar and Ghosh, 2020; Mahesh et al., 2018). However, no information regarding dietary composition or the trophic status exists for other large pelagic predators landed as by-catch. Ecosystem models, widely adopted for management of apex predators, are data intensive requiring detailed information on trophic linkages, energy transfer and consumption and production at different trophic levels of the ecosystem, for which a thorough understanding on prey species composition and trophic level is essential (Pauly et al., 2002).

Food and feeding aspects of *Coryphaena hippurus* for over half a dozen decades have been studied in most marine ecosystems; northwestern, eastern, central and southern Pacific; Mediterranean Sea; northwestern, central and southern Atlantic (Molto et al., 2020). Compared to the other oceans and seas, the Indian Ocean is the least studied with respect to the diet of *C. hippurus*, with only four studies focusing on the Arabian Sea (Varghese et al., 2013; Rajesh et al., 2016; Kumar et al., 2017; Saroj et al., 2018). No information exists on the feeding dynamics and the trophic role of *C. hippurus* from any other parts of the Indian Ocean, including the Bay of Bengal. Along the Bay of Bengal, as the trophic interactions for the species is largely unknown, it is essential that the trophic ecology is studied for providing information on trophic relationships, facilitating development of management or conservation strategies. Again, for understanding the prey resource partitioning and competition with cohabiting predators for available prey, it is essential to know the dietary niche and the trophic organisation. Also, all dietary studies on *Coryphaena hippurus* performed globally and mentioned above, have not captured the feeding strategy and the trophic level of this predator. The present study was therefore, attempted to provide a detailed and comprehensive information on the feeding habits of the common dolphinfish from the Bay of Bengal. This first attempt on determining the feeding ecology of *C. hippurus* for understanding the trophic interactions at the top of the food web, would contribute to the ecosystem-based fisheries management in the Bay of Bengal region.

2 Materials and methods

2.1 Sample collection

Samples of *Coryphaena hippurus* were randomly collected at fortnight intervals from the landings of drift gillnets, trolling and long-lines at Visakhapatnam (17.696^{0}N; 83.301^{0}E) and Kakinada (16.984^{0}N; 82.279^{0}E) fishing harbours, along the western Bay of Bengal (Fig. 1) during the three year study period from January 2017 to December 2019. Fishing details were obtained on enquiry from the vessels landing the species at both locations. The collected iced samples were placed in insulated ice boxes, immediately on landing and were transported to the laboratory of Visakhapatnam Regional Centre of Central Marine Fisheries Research Institute to be analysed on the same day for negating the impact of digestion on stomach size and content. The fork length (L_F) of each individual was measured to the nearest millimeter (mm) and total weight to 0.1 g precision. Sex was identified on visual examination of the gonads and a five-stage maturity scale was used to classify the gonads of females and males following the maturity scale proposed by Brown-Peterson et al. (2011). A total of 1150 individuals; 274 in 2017, 420 in 2018 and 456 in 2019 ranging in L_F and weight from 25.0 cm to 110.0 cm and 167 g to 9863 g were analysed during the study period. Individuals analysed in each month, pooled for the three years are indicated in parenthesis in Table 1.

The trophic interactions of apex predators such as *Coryphaena hippurus* vary spatially and temporally due to the species looking for favourable feeding conditions to take advantage of seasonal prey pulses. Therefore, it is essential to study the seasonal variations in prey composition and niche width for comprehensively understanding the feeding behavior. Moreover, for maximising the intake of energy and nutrients, ontogenic switches in prey types and sizes are common. Therefore, all aspects on food and feeding were examined with respect to months or seasons (summer from March–June, monsoon from July–October and winter from

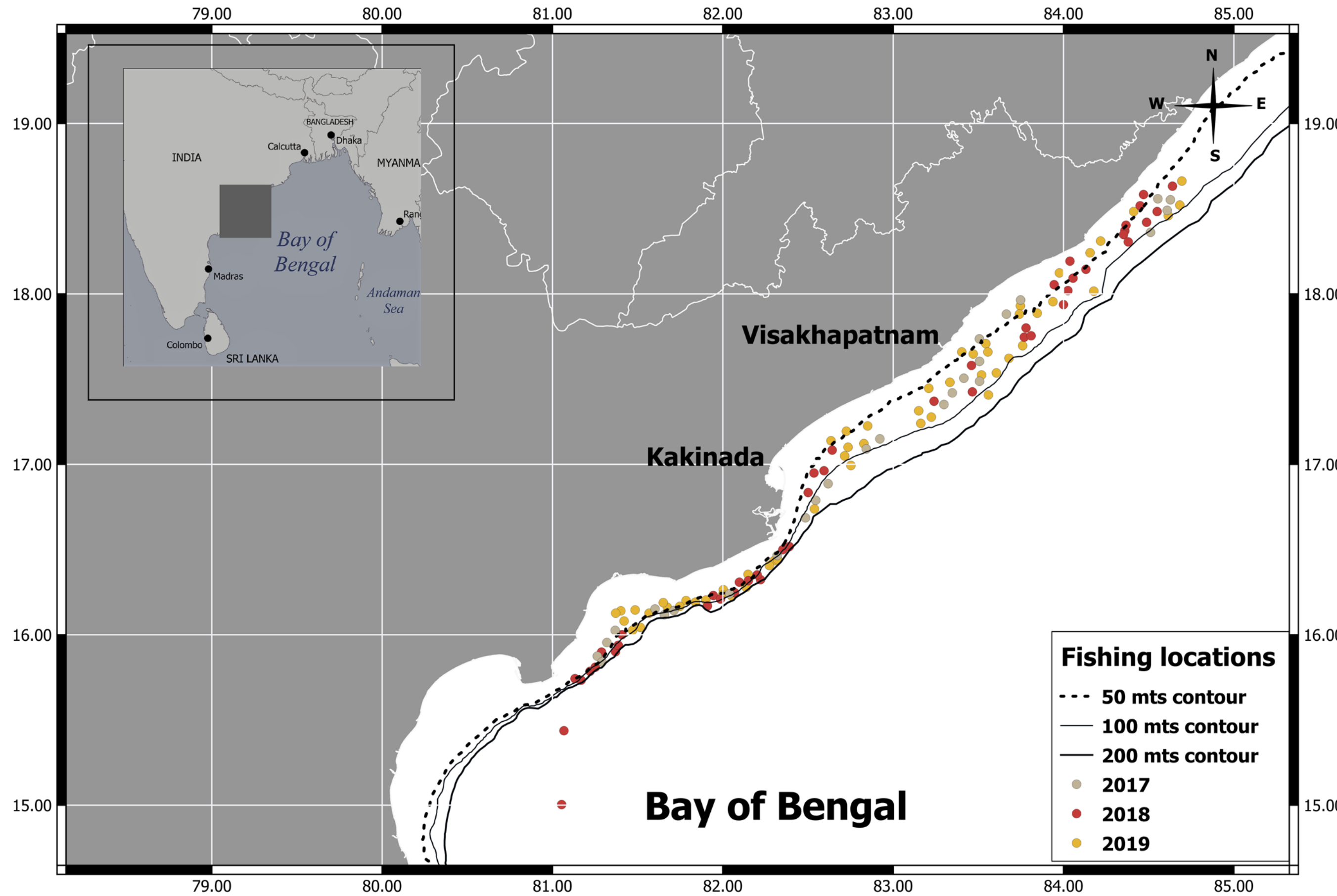

Fig. 1. Map of western Bay of Bengal with sampling locations.

November–February) and sizes based on reproductive capacities (<45.0 cm L_F, 45.0–59.9 cm L_F, 60.0–74.9 cm L_F and 75 cm and above L_F). Stomachs from the individual fish were cut open, all prey contents were sorted and identified to the lowest taxon possible, and prey numbers were recorded and individually measured (finfish in fork length, cephalopod in mantle length and crustacean in carapace length) and weighed to 1.0 mm and 0.01 g precision. Prey identification was performed visually following Fischer and Whitehead (1974) and Fischer and Bianchi (1984) methodologies and aided by a trinocular microscope when required. Unidentifiable semi-digested (half or more digested) finfishes were expressed as such, whereas for identifiable prey individuals in low or moderate states of digestion, weight was reconstituted from length measurements. Accumulated non-assimilated items (fish scales, hard parts including fish bones and otoliths, eye-balls, crustacean shells, cephalopod beaks, etc) and non-animated objects (plastics and artificial baits) were discarded. Cumulative prey curve was constructed for assessing the adequacy of sampling in describing the diet (Ferry and Cailliet 1996).

2.2 Feeding intensity

Feeding intensities were studied by the degree of fullness of the stomach in relation to the size of the fish. Stomach state was assessed based on the distension and the degree of fullness and was classified on a six-point scale; empty (0% full), trace (<5% full), 25% full, 50% full, 75% full and 100% full. However, the stomach states were subsequently reduced to three categories for analysis; empty and trace, partially-full (25% and 50% full) and full (75% and 100% full). Stomach filling was assessed by month, by sex and by size. For additional assessment of feeding intensity, predator-prey weight ratio was estimated following the log-transformed equation proposed by Hahm and Langton (1984).

2.3 Prey composition

The Index of Relative Importance (IRI%) (Pinkas et al., 1971) was used to assess the prey contents. IRI% was calculated by summing the numerical and gravimetric percentage values and multiplying by the frequency of occurrence percentage value. IRI% was evaluated for seasons, sexes and sizes. IRI% was square root transformed and the Bray-Curtis similarity index was estimated for measuring prey overlap or similarity. Nonmetric multidimensional scaling (nMDS) was employed to describe and compare dietary relationships between seasons and between sizes. Similarity percentage (SIMPER) was applied to identify prey species that could discriminate between seasons, sexes and sizes. One-way analysis of similarity (ANOSIM), a non-parametric and

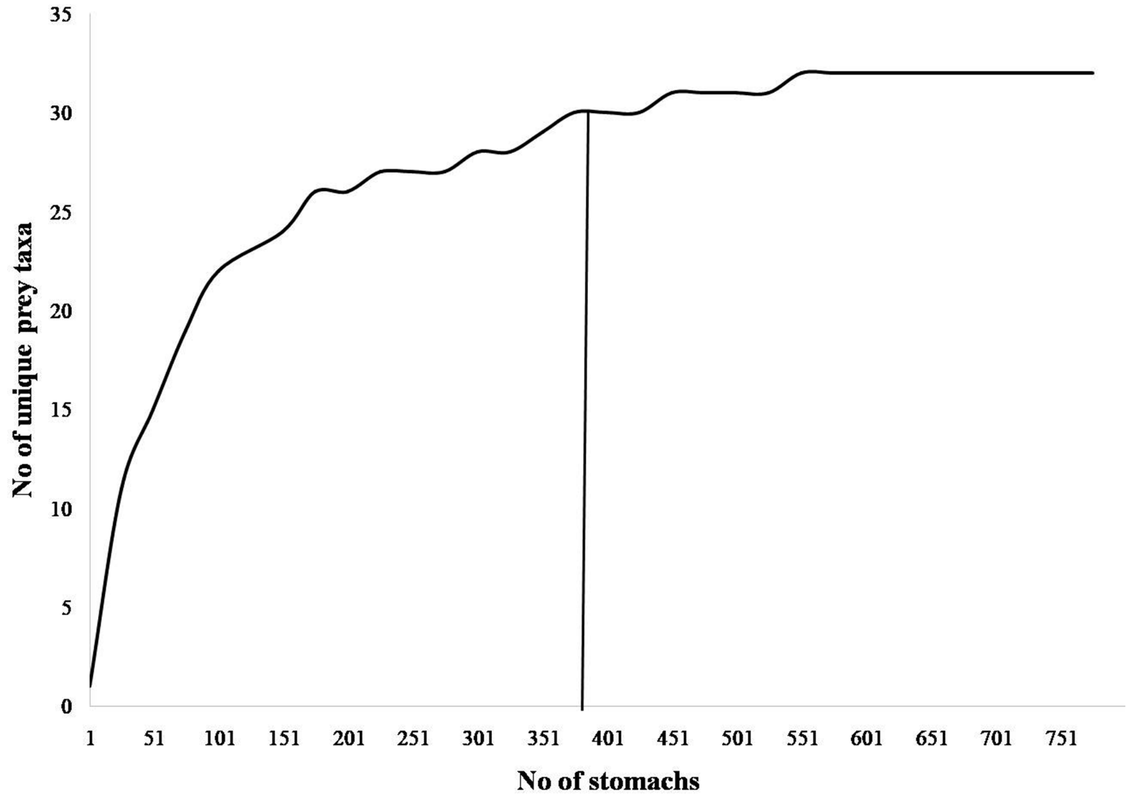

Fig. 2. Cumulative prey curve exhibiting the relationship between the number of unique prey taxa and the sampled stomachs for *Coryphaena hippurus*; vertical line indicates the asymptote of the curve.

multivariate analysis of variance, was used to evaluate significant differences in prey similarities. ANOSIM uses a R test statistic ranging from -1 to $+1$, where greater positive values indicate significant dissimilarity between groups than within groups. For determining ANOSIM's Global R statistic size-wise and season-wise, data were randomly permuted 999 times and 280 times respectively for a distribution; whereas for ANOSIM's Pairwise R statistic, for both sizes and seasons, 10 random permutations in data were performed. SIMPER, ANOSIM and nMDS were based on Bray-Curtis similarity values. Multivariate analyses were carried out using PRIMER v. 6 (Clarke and Gorley, 2006) and PAST 2.17 (Hammer et al., 2001).

2.4 Feeding strategy

Predators with a diverse diet or broad dietary niche are considered as generalists and that with a low prey diversity or narrow niche width as specialists (Amundsen et al., 1996). *Prey specific abundance*, the percent numerical *abundance* of a prey item averaged over the stomach samples in which it occurs, was estimated following the methodology in Amundsen et al. (1996). Feeding strategy was determined from the plot of percentages of prey-specific abundance against frequency of occurrence. Specialists have prey points positioned in the upper part of the plot, whereas generalists have all prey points in the lower part; with preys located in the upper left indicating specialisation by subgroups of the predator population and preys in the upper right indicating specialisation by the whole predator population. Dietary niche breadth was estimated using the Levins Standardized Niche Breadth Index (B_A): $B_A = (B - 1)\,(n - 1)^{-1}$; where B is Levins Niche Breadth Index and n is the total number of prey species. Levins Niche Breadth Index was calculated as $B = (\sum P^2{}_j)^{-1}$; where P_j is the proportion of prey species j in the diet. The index ranges from 0 to 1, with 0 meaning that the species consumes a single prey and 1 meaning that the species consumes available preys in equal proportions. To estimate prey-specific abundance and dietary niche breadth index, unidentified semi-digested (half or more digested) prey items were excluded. Trophic level of *C. hippurus* was calculated from the proportion and trophic level of each prey species in the diet following the equation of Christensen and Pauly (1992). The trophic level values for each prey species were adopted from Das et al. (2018) and for species where the values were not available, the value of the group was assigned to the species.

3 Results

3.1 Feeding intensity

The cumulative prey curve (Fig. 2) approached the asymptote, pointing to the fact that the number of stomachs analysed were adequate to describe the diet diversity and breadth in *Coryphaena hippurus*. The stabilization occurred at around 375 stomachs and 30 prey species. From the 1150 individuals (772 females and 378 males) analyzed, 32.17% had

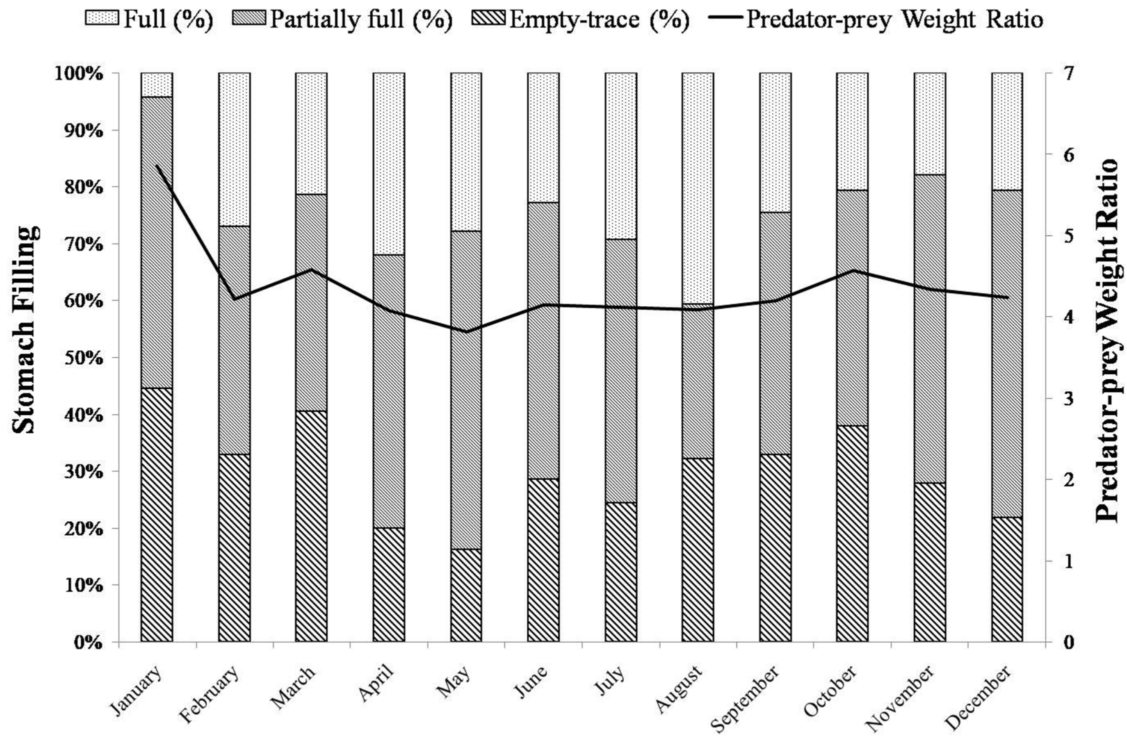

Fig. 3. Seasonal feeding intensity of *Coryphaena hippurus* (Sample size: 137 in January, 170 in February, 84 in March, 25 in April, 43 in May, 70 in June, 82 in July, 59 in August, 155 in September, 116 in October, 122 in November and 87 in December).

empty stomachs or contained traces of food, 45.57% had partially-full stomachs and 22.26% had full stomachs. During 2017, 2018 and 2019; stomachs either empty or with traces of food and predator-prey weight ratios were 37.23% and 4.27, 31.43% and 4.06 and 29.82% and 4.49. Partially-full and full stomachs were 34.31% and 28.47% in 2017, 41.43% and 27.14% in 2018 and 56.14% and 14.04% in 2019. In females and males, empty stomachs or stomachs with traces of food were 33.42% and 29.63%. Partially-full stomachs were 45.60% in females and 48.68% in males and full stomachs were 20.98% in females and 21.70% in males. Predator-prey weight ratio was 4.28 in males and 4.39 in females. Stomach filling and predator-prey weight ratio in various months is presented in Figure 3. Highest feeding intensity, with maximum stomach filling and smallest predator-prey weight ratio, was in May. Lowest feeding activity was in January with minimum stomach filling and largest predator-prey weight ratio. Spawning capable individuals were observed (26.19–57.38%) throughout the year, with higher values in the months of August (53.33%), September (53.85%), October (50.86%), November (57.38%) and December (44.19%), indicating that August-December comprises the spawning peak for the species in this region. Feeding intensity in *C. hippurus* increased with an increase in the body size (Fig. 4). Empty stomachs or stomachs with traces of food and predator-prey weight ratio was highest in fishes below 45.0 cm L_F, and decreased henceforth, with lowest predator-prey weight ratio and highest proportion of full stomachs observed in fishes measuring 60.0 to 74.9 cm L_F.

3.2 Prey composition

Coryphaena hippurus was found to prey on 32 species; from which 25 were teleosts, 4 were crustaceans and 3 were cephalopods (Tab. 2). Additionally, unidentified fish eggs, shells of gastropods (*Trochus niloticus* and *Babylonia spirata*) and brown seaweeds (*Sargassum vulgare*) were occasionally observed in the stomach contents. Teleosts were the most abundant, contributing 56.20% (IRI) to the diet, followed by cephalopods and crustaceans, which contributed 10.36% and 9.50% (IRI) respectively. Unidentified semi-digested finfishes accounted for 23.95% (IRI) of the diet. Prey species by sexes, sizes and seasons are presented in Table 3. Predator-prey size ratio increased from 2.44 ± 0.19 in fishes <45.0 cm L_F to 2.55 ± 0.07, 2.58 ± 0.07 and 3.03 ± 0.22 in fishes measuring 45.0–59.9 cm, 60.0–74.9 cm and ≥ 75.0 cm L_F.

Sex-based analysis using SIMPER revealed disimilarity in prey species composition to the tune of 27.34% between males and females. Between various body sizes, the average dissimilarity in prey composition ranged from 28.18% to 47.50%; however, size-wise ordination using nMDS revealed this variation in feeding preferences to be insignificant (ANOSIM Global $R - 0.065$, $p - 0.257$) (Fig. 5a). With respect to seasons, prey composition differed significantly as evident in the nMDS ordination (ANOSIM Global $R - 0.605$, $p - 0.011$) (Fig. 5b). Average disimilarity in prey between summer and monsoon was 32.43% (ANOSIM Pairwise $R - 0.459$, $p - 0.020$), summer and winter was 26.98% (ANOSIM Pairwise $R - 0.481$, $p - 0.010$) and monsoon and

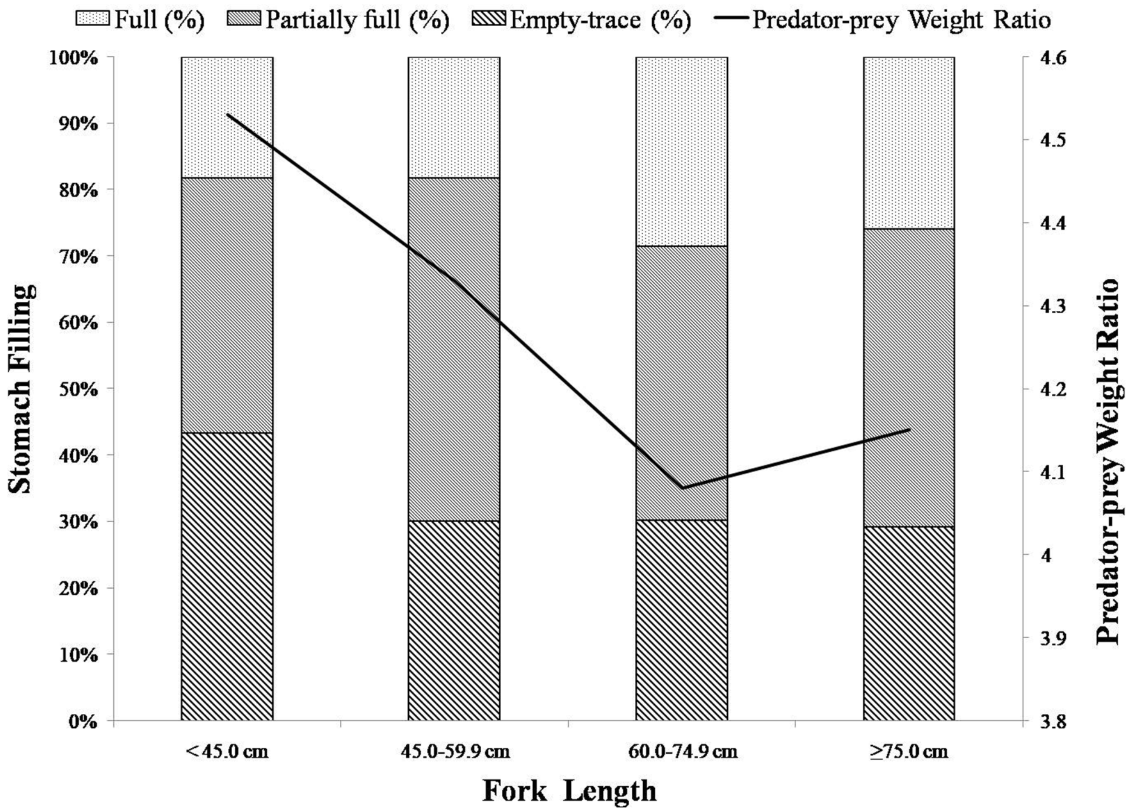

Fig. 4. Feeding intensity by size for *Coryphaena hippurus* (Sample size: 187 in <45.0 cm, 472 in 45.0–59.9 cm, 344 in 60.0–74.9 cm and 147 in ≥75.0 cm).

Table 2. Summary of the quantifiable dietary composition of *Coryphaena hippurus* in the western Bay of Bengal.

Prey Family	Prey Species	% Weight	% Number	% Frequency	% IRI
Carangidae	Big-eye scad (*Selar crumenophthalmus*)	26.28	7.94	14.31	27.282
	Unidentified semi-digested finfishes	13.12	10.32	18.35	23.945
Loliginidae	Squid (*Uroteuthis duvauceli*)	6.69	8.93	11.90	10.349
Portunidae	Crabs (*Charybdis cruciata* and *C. natator*)	1.53	22.92	6.85	9.333
Scombridae	Indian Mackerel (*Rastrelliger kanagurta*)	12.08	4.76	7.66	7.185
Carangidae	Indian scad (*Decapterus russelli*)	8.77	4.76	7.86	5.927
Clupeidae	Sardines (*Sardinella fimbriata*, *S. gibbosa* and *Dussumieria acuta*)	6.08	13.10	5.04	5.382
Engraulidae	Whitebaits (*Stolephorus commersonnii*, *S. indicus* and *Thryssa setirostris*)	2.83	8.63	8.87	5.660
Exocoetidae	Flyingfish (*Cheilopogon cyanopterus*)	5.61	2.48	3.43	1.544
Scombridae	Tunas (*Euthynnus affinis* and *Auxis thazard*)	4.68	1.39	2.82	0.955
Carangidae	Torpedo scad (*Megalaspis cordyla*)	3.95	1.59	3.02	0.933
Tetraodontidae	Pufferfish (*Lagocephalus inermis*)	1.56	3.77	1.81	0.539
Carangidae	Shrimp scad (*Alepes djedaba*)	1.62	2.48	2.02	0.460
Trichiuridae	Ribbonfish (*Trichiurus lepturus*)	1.63	1.19	1.41	0.222
Penaeidae	Speckled shrimp (*Metapenaeus monoceros*)	1.13	2.18	0.81	0.149
Balistidae	Triggerfish (*Abalistes stellatus*)	0.79	0.99	0.60	0.060
Sciaenidae	Sciaenids (*Nibea maculata* and *Pennahia anea*)	0.10	0.69	0.40	0.018
Clupeidae	Tardoore (*Opisthopterus tardoore*)	0.30	0.40	0.40	0.016
Squillidae	Squilla (*Oratosquilla nepa*)	0.13	0.30	0.60	0.014
Sepiidae	Cuttlefish (*Sepiella inermis*)	0.54	0.10	0.20	0.007
	Unidentified Fish eggs	0.02	0.20	0.40	0.005
Triacanthidae	Tripodfish (*Triacanthus biaculeatus*)	0.10	0.30	0.20	0.005
Ariidae	Thinspine Catfish (*Plicofollis tenuispinis*)	0.27	0.10	0.20	0.004
Narcinidae	Numbfish (*Narcine timlei*)	0.03	0.20	0.20	0.003
Mullidae	Goatfish (*Upeneus vittatus*)	0.06	0.10	0.20	0.002
Fistulariidae	Pipefish (*Fistularia petimba*)	0.06	0.10	0.20	0.002
Octopodidae	Octopus (*Octopus membranaceus*)	0.03	0.10	0.20	0.001

Table 3. Sex, size and season based prey importance in *Coryphaena hippurus*.

Prey Species	Sex-wise		Size-wise (fork length)				Season-wise		
	Males (n = 266)	Females (n = 514)	< 45.0 cm (n = 106)	45.0–59.9 cm (n = 330)	60.0 – 74.9 cm (n = 240)	75 cm and above (n = 104)	Summer (n = 156)	Monsoon (n = 278)	Winter (= 346)
Big-eye scad	20.238	33.173	8.336	20.700	33.223	24.645	17.958	18.735	26.925
Unidentified semi-digested finfishes	11.148	26.303	14.959	25.148	11.575	33.269	24.047	16.251	23.445
Squid	12.360	9.028	10.930	9.656	18.197	0.955	10.860	9.763	10.172
Crabs	5.448	11.090	5.577	24.189	4.721	0.164	8.144	5.196	14.069
Indian Mackerel	16.470	3.933	4.592	2.387	10.462	13.308	8.069	4.750	9.994
Indian scad	10.463	4.084	3.902	7.726	5.707	3.887	0.801	0.621	11.161
Sardines	9.499	3.685	0.527	4.501	4.251	13.169		24.074	0.096
Whitebaits	8.550	3.408	45.133	3.552	1.084	1.477	9.658	16.363	1.091
Flyingfish	2.805	1.030		0.106	6.614	4.730	1.024	1.726	0.680
Tunas	1.723	0.138	0.471	0.030	0.385	2.920	4.012	0.345	0.026
Torpedo scad	0.047	1.718	1.923	0.372	2.752		6.590		1.634
Pufferfish		1.122	1.202	0.508	0.026		5.425	0.105	0.416
Shrimp scad	0.040	0.793	0.713	0.136	0.634	0.842	0.131	1.282	0.159
Ribbonfish	1.011	0.032	1.365	0.435		0.156	1.489		0.010
Speckled shrimp		0.311		0.237	0.129	0.186	0.370	0.464	0.027
Triggerfish	0.014	0.079		0.154	0.104		0.541	0.083	0.007
Sciaenids	0.075	0.004		0.040	0.017		0.535		0.009
Tardoore	0.027	0.011	0.369		0.027		0.348		
Squilla	0.019	0.012		0.089					0.073
Cuttlefish		0.016				0.180		0.070	
Unidentified Fish eggs		0.010			0.013	0.050		0.041	
Tripodfish	0.046			0.028				0.039	
Thinspine Catfish		0.009			0.036			0.040	
Numbfish		0.005			0.027			0.022	
Goatfish	0.018				0.017			0.015	
Pipefish		0.004				0.061		0.015	
Octopus		0.003		0.009					0.007

winter was 33.50% (ANOSIM Pairwise $R - 0.763, p - 0.010$). Prey species contributing to the above observed dissimilarities between sexes, sizes and seasons are depicted in Table 4.

3.3 Feeding strategy

Despite higher prey-specific abundances observed for most major prey species, frequency of occurrences was low (Fig. 6). Therefore, it is likely that *Coryphaena hippurus* is an opportunistic predator, with groups of individuals within the population specialising on few dominant selective prey species. The two most dominant preys, big-eye scad and squid, showed relatively higher occurrences indicating predation by large number of individuals. Apart from few other prey species; Indian mackerel, Indian scad, whitebaits and crabs, the rest exhibited low occurrences, indicating them to be an occasional preys.

Levins Standardized Niche Breadth Index for *Coryphaena hippurus* was 0.30. Feeding was comparatively specialised with niche breadth index of 0.20 in fishes measuring 45.0–59.9 cm L_F. The niche breadth index increased to 0.35 in fishes of 75.0 cm L_F and above, and generalised feeding with index values of 0.48 and 0.51 was observed in fishes <45.0 cm L_F and 60.0–74.9 cm L_F. During summer and monsoon, feeding was generalised with niche breadth index of 0.48 and 0.33; whereas in winter, relative specialisation in feeding was reported with index value of 0.21. The trophic level value was 4.22 ± 0.15, signifying the species to be a top-level carnivore with predatory nature.

4 Discussion

The trophic studies up to date, from various parts of Pacific and Atlantic Oceans and from Mediterranean and Arabian Seas have reported the diet composition and preferences based on a sample size ranging from 28 (Sinopoli et al., 2017) to 575 (Sakamoto and Taniguchi, 1993). In the present study, we analyzed 1150 specimens and the prey curve (Fig. 2) reached the asymptote, indicating that the data generated on the trophodynamics was robust in providing a detailed and comprehensive analysis. *Coryphaena hippurus* is a diurnal visual predator, feeding actively in the morning hours in the presence of sunlight (Massuti et al., 1998). Six distinct foraging strategies have been observed for the species; with 'active chasing' the most frequent due to greater visibility avalable near the surface of tropical waters and the ability to swim at high speeds (Nunes et al., 2015). Stomach emptiness from the Bay of Bengal was 32.17%, lower than 40% to 64% reported from the Arabian Sea of the Indian Ocean

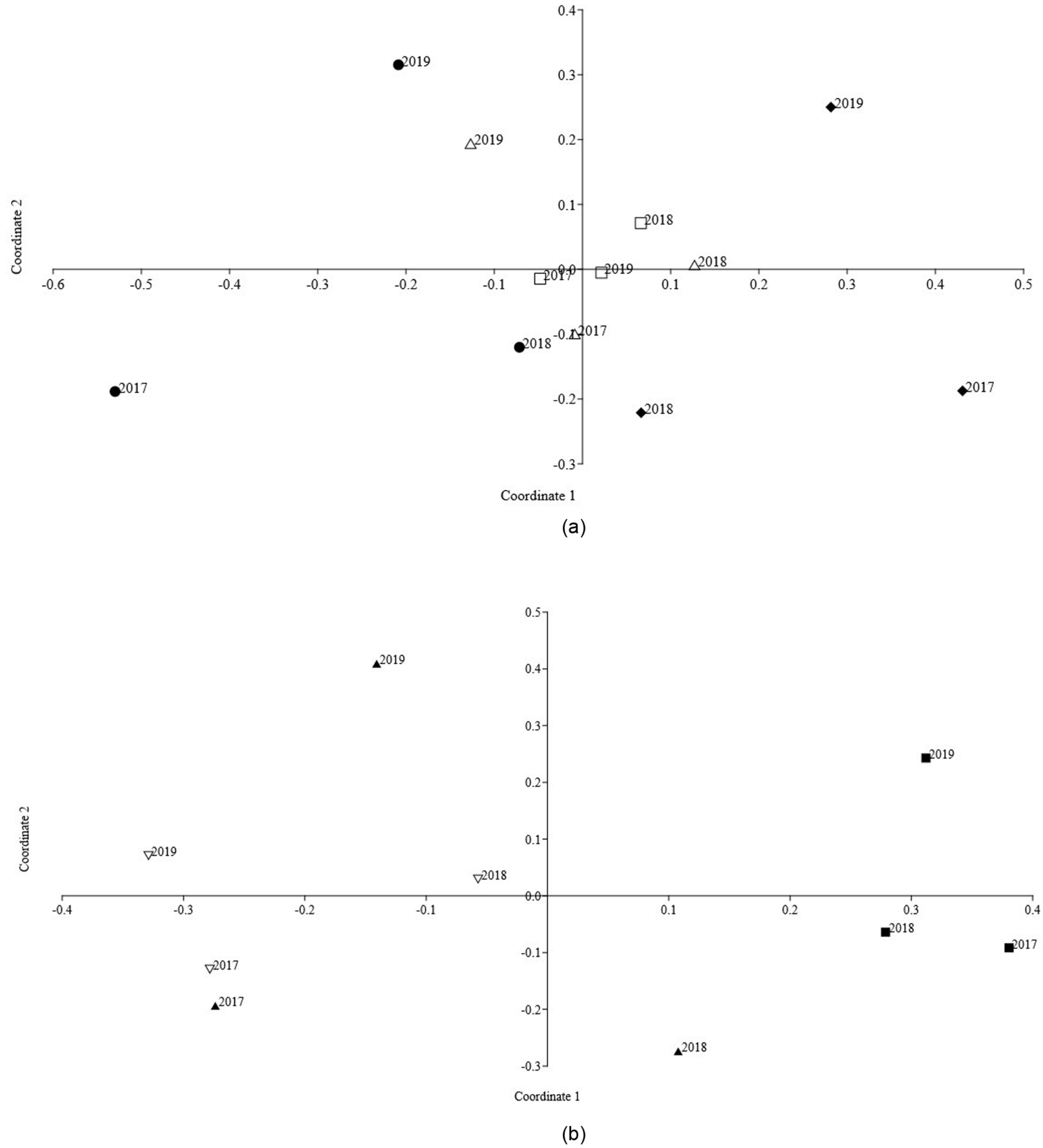

Fig. 5. nMDS ordination of prey composition in *Coryphaena hippurus* using Bray–Curtis similarities calculated on square-root transformed Index of Relative Importance%; on (a) sizes (● – <45.0 cm, Δ – 45.0–59.9 cm, □ – 60.0–74.9 cm and ♦ – ≥75.0 cm) and (b) seasons (▲– summer, ▽ – monsoon and ■ – winter), with numerals indicating the sampling year.

(Rajesh et al., 2016; Kumar et al., 2017; Saroj et al., 2018). In the Arabian Sea, the species is mostly exploited by mechanised gillnetters which are operated in the late night hours; whereas along the Bay of Bengal, it is indistinctly exploited by drift gillnets, trolling and long-lines which are set by late morning or noon capturing actively fed individuals. From other oceans, Rose and Hassler (1974), Manooch et al. (1984), Massuti et al. (1998), Oxenford and Hunte (1999), Castriota et al. (2007) and Pimenta et al. (2014) have all, recorded lower stomach emptiness ranging from 11% to 24% in purse seine and long line caught individuals which were operated and retrieved during morning and afternoon. From the present study and in comparison with earlier reports, it can be inferred that variations in feeding intensity for the species reflects the differences in the time of the day when the individuals were caught rather than any real differences in the feeding habits. Feeding intensity for *C. hippurus* in the Bay of Bengal was highest in May and lowest in January, and it is probably related to the reproductive activity. Gonadal development in the species along the Bay of Bengal starts from April onwards and continues till August with a substantial energy demand for gonadal maturation apart from somatic growth. Feeding activity was at its peak during April-August and lower during the peak spawning months of September–December. Enhanced feeding intensity during post-spawning was also because, when gonads were in spent state, maximum space was available for the stomachs to expand and be fully gorged with the food material. Feeding activity increased with an increase

Table 4. Contribution of major prey species (90% cut-off for low contribution) to the observed average dissimilarities between sizes (a, b, c and d indicate sizes <45.0 cm L_F, 45.0–59.9 cm L_F, 60.0–74.9 cm L_F and 75.0 cm and above L_F), seasons (1, 2 and 3 resemble summer, monsoon and winter) and sexes (M and F depict male and female) based on one-way SIMPER; values in parenthesis indicate the average total dissimilarity percentage.

Prey Species	Sizes						Seasons			Sexes
	a & b (32.37)	a & c (33.65)	b & c (31.29)	a & d (47.50)	b & d (39.75)	c & d (28.18)	1 & 2 (32.43)	1 & 3 (26.98)	2 & 3 (33.50)	M & F (27.34)
Big-eye scad	2.78	4.54	2.01	3.43	0.72	1.31		1.47	1.43	1.96
Unidentified semi-digested finfishes	1.92	0.73	2.67	3.14	1.31	3.87	1.30		1.34	2.78
Squid		1.51	1.92	3.85	3.71	5.38				0.79
Crabs	4.28		4.55	3.23	7.86	2.90	0.86	1.39	2.44	1.55
Indian Mackerel	1.00	1.72	2.80	2.49	3.66	0.68	0.98		1.63	3.22
Indian scad	1.34	0.65	0.65		1.41	0.68		3.78	4.23	1.88
Sardines	1.21	2.11	3.42	4.79	6.32	2.57	7.31		7.63	1.80
Whitebaits	10.40	11.14	1.40	11.38	1.17		4.50	4.99	4.98	1.71
Flyingfish		4.06	3.73	3.59	3.22	0.65			0.81	1.02
Tunas	0.63		1.05	2.06	2.78	2.83	2.15	3.06	0.88	1.34
Torpedo scad	1.30		1.74	2.29	1.06	2.72	3.83	1.99	2.12	1.70
Pufferfish	0.64	1.48	0.92	1.81	1.24		2.99	2.60	0.53	1.64
Shrimp scad	0.80		0.71		0.96		1.15		1.22	1.07
Ribbonfish	0.85	1.84	1.09	1.28		0.65	1.82	1.73		1.28
Speckled shrimp	0.81							0.69	0.86	0.87
Triggerfish	0.66					0.53	0.66	1.01		
Sciaenids							1.09	0.99		
Tardoore	1.02	0.70					0.88	0.91		
Squilla									0.45	
Cuttlefish					0.74	0.69				

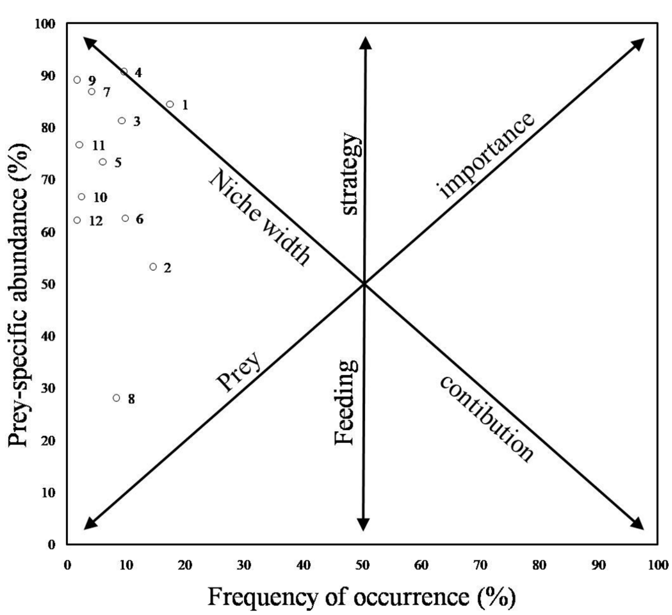

Fig. 6. Graphical representation of feeding startegy in *Coryphaena hippurus* following Amundsen et al. (1996). Feeding strategy depicted by plotting the prey-specific abundance (%) against frequency of occurrence (%) for dominant prey groups. The two diagonal axes represent the importance of prey and the contribution to niche width and the vertical axis defines the predator feeding strategy. Where: 1–big-eye scad; 2–squid; 3–Indian mackerel; 4–Indian scad; 5–sardines; 6–whitebaits; 7–flyingfish; 8–crabs; 9–tunas; 10–shrimp scad; 11–pufferfish; 12–ribbonfish.

in fish size. Higher feeding intensity observed in large sized individuals is consistent with other large pelagic resources and it is because of enhanced prey catching efficiency caused by increasing mouth gape and improved locomotive ability.

Similar to other tropical pelagic species, *Coryphaena hippurus* is an opportunistic pelagic predator with mostly piscivory habit, also consuming crustaceans and molluscs. Preference for teleosts as prey have earlier been observed from Arabian Sea, with finfishes forming from 60% (Kumar et al., 2017) to around 85% (Varghese et al., 2013; Rajesh et al., 2016) of the dietary constituents, and the same was noted in the present study. Species belonging to Carangidae, Loliginidae, Portunidae, Scombridae, Clupeidae and Engraulidae formed the dominant prey in the Bay of Bengal. Among teleosts, the big-eye scad formed the major share of the prey species, followed by the Indian mackerel and the Indian scad. From the Arabian Sea however, diet was dominated in different studies by Indian scad (40% by IRI) (Rajesh et al., 2016), tuna (26% by IRI) (Saroj et al., 2018) and flyingfish (17% by IRI) (Varghese et al., 2013). Carangids, as one of the major prey in *C. hippurus*, were also earlier observed by Gibbs and Collette (1959), Rose and Hassler (1974) and Manooch et al. (1984). Squids and crabs contributed substantially to the dietary contents along the western Bay of Bengal, as had been reported from Arabian Sea, wherein they constituted from more than 10% (Varghese et al., 2013; Rajesh et al., 2016) to around 30% (Kumar et al., 2017) of the prey. Given that squids and crabs dwell in deep waters, they perform nictemeral diel vertical movements to the water surface (Anusha and Fleming, 2014), and this is when they were preyed upon by *C. hippurus*. Occasional feeding in deeper waters has earlier been reported

(Oxford and Hunte, 1999; Olson and Galvan-Magana, 2002; Varghese et al., 2013) for the species and could also explain the occurrence of squids and crabs in the stomach contents. Pimenta et al. (2014) had observed that ribbonfish and scad, individually contributed around 20% and squids around 15% to the diet of *C. hippurus* from the Pacific waters. Various other authors (Oxenford, 1985; Massuti et al., 1998; Oxenford and Hunte, 1999; Olson and Galvan-Magana, 2002; Vaske and Lessa, 2004; Varela et al., 2016) had reported dominance of other families (Dactylopteridae, Exocoetidae, Monacanthidae and Polynemidae) in the diet. *C. hippurus* is a non-selective feeder, foraging on whatever prey organisms that is locally available. These differences in prey species are due to the variations in the availability of the prey species in their respective habitat, rather than any prey preferences. With feeding primarily on epipelagic prey, the species is a surface water feeder. Dolphinfishes uses different visual and active foraging strategies; however, 'active chasing' involving detection of prey from a distance followed by an increase in the swim speed until prey capture is preferred (Nunes et al., 2015). Presence of actively swimming prey species belonging to the families Carangidae, Scombridae, Clupeidae and Engraulidae in the diet in large amounts suggests similar feeding behaviour, and confirms the species to be a fast swimming and an aggressive feeder, in chasing and pursuing its prey. The occurrence of seaweeds in the diet indicates foraging near floating objects and feeding on prey associated with the seaweeds. Negative phototropism in smaller individuals, on preference to shadows created by floating objects is an opportunistic strategy; with these floating objects used for food source on the associated prey and for shelter against predators (Nunes et al., 2015). However, global assessments have indicated that the species do not use floating objects as their main feeding grounds because prey availability would then deplete very rapidly (Molto et al., 2020). Unidentified semi-digested finfishes were observed in large amounts in the stomach contents and this could either be due to the rapid prey digestion rate in the species or to the fact, that in individuals caught using drift gillnets, wherein the nets are retrieved after 3–4 hrs of setting, the digestive enzymes started digesting and dissolving the prey species in gilled and entangled individuals. From the present study and in comparison to adjacent regions; though teleosts formed the major prey with considerable contribution by cephalopods and crustaceans in both, the Bay of Bengal and Arabian Sea; however, spatial differences in prey constituents with variations in prey species are evident between different parts of the Indian Ocean.

Significant differences in prey species between seasons were due to variations in the biomass of the available prey in each season. Seasonal resource pulses are important components of annual energy budgets for many large pelagic species, and the same was observed in *Coryphaena hippurus* along the Bay of Bengal. According to Oxenford and Hunte (1999), when prey distribution is spatio-temporally uneven, the species forages on what is present and is easier to catch. Abundance of clupeids and engraulids during monsoon was a result of higher productivity caused due to enhanced nutrient availability (Kumar et al., 2010) in the coastal waters of the Bay. During summer and winter seasons, the species preyed upon scads and opportunistically on squids and crabs. Similar reports on prey dissimilarities between seasons due to different faunal assemblages have earlier been reported by Manooch et al. (1984) and Massuti et al. (1998). With earlier studies from Arabian Sea not elucidating the seasonal dissimilarity in prey constituents, the present study is the first from Indian Ocean to demonstrate seasonal variations in prey for *C. hippurus*. Contrarily to the findings of Varghese et al. (2013) from the Arabian Sea, prey species did not vary between sexes. Ontogenetic shifts in prey species to reduce intraspecific competition between juveniles and adults have been recorded for *C. hippurus* by Sakamoto and Taniguchi (1993), Oxenford and Hunte (1999), Benseddik et al. (2015) and Varela et al. (2017). From the Bay of Bengal, predator-prey size ratio increased with predator size for the species indicating no length-based prey selection with advancement in body size. Though prey selectivity is influenced by prey size in piscivores, no such ontogenetic switches in prey were observed presently.

Coryphaena hippurus is one of the top predators in the Bay of Bengal as evident in the high trophic level (4.22 ± 0.15) values. According to Vivekanandan et al. (2009), in large predatory piscivorous fishes which predates on other predators, the trophic level varies between 4.0 and 4.5. Similarly, with *C. hippurus* preying abundantly on mid-trophic level carnivores, it occupied a comparatively higher trophic level. Present information on trophic level is the first from the Indian Ocean. Predators exhibit intra-population behavioral differences and move and forage differently from conspecifics, and therefore, individuals or groups within a population vary considerably in their usage of habitat and resources (Jaeger et al., 2010). Again, in large predators, individual or group specialization within a population is a means to reduce intraspecific competition (Bolnick et al., 2003). In *C. hippurus*, foraging depends on body size and is influenced by experience and social interactions. Large and mature individuals exhibit more complex active feeding strategies, while juveniles prefer opportunistic foraging near floating objects (Nunes et al., 2015). With prey species exhibiting low percentage occurrences, inspite of higher prey-specific abundances, sub-group specialisation on few dominant selective prey taxa is apparent in *C. hippurus*. However, as significant seasonal variations in prey species were observed, their influence on feeding strategy cannot be negated and it could be that, temporal differences in the prey resource availability and abundance provided a false sense of group specialisation in feeding.

Dietary niche breadth is a measure of trophic specialisation (Amundsen et al., 1996) and the intermediate value (0.30) in the Bay of Bengal indicate the species to be an opportunistic predator, preying on a substantial number of prey species. Earlier, Varela et al. (2016) from Pacific Ocean had reported on a narrow niche width (0.10) for the species with large number of individuals feeding on the dominant taxa, which contributed more than half of the diet. This variation is because of the differences in the variety of prey species between regions. Feeding was relatively generalised during summer and monsoon with higher niche breadth due to higher diversity of prey items during these seasons. Predator dietary breadth is strongly influenced by predator body size (Cohen et al., 1993) and the same appeared true, to an extent for *C. hippurus*. Feeding was specialised in fishes measuring 45.0–59.9 cm L_F

with dependence on few dominant prey species which were consumed in abundance.

Traditional stomach content analysis is often confounded by variations in prey assimilation efficiencies and hence, provides only a snapshot of prey consumed over a limited time frame. Non-assimilated materials often tend to accumulate over a short time frame, which results in an overestimation of the concentration of these materials. Therefore, estimates on trophic interactions are not as accurate as that obtained from isotopic ratios of carbon and nitrogen within predator tissues that reflects those of their preys (Williams and Martinez, 2004). Also, temporal variability in the diet can only be ascertained accurately by comparing the isotopic values of multiple tissues with different turnover rates (Bearhop et al., 2004). Isotope analysis provide a proxy for the assimilated diet at greater precision than conventional studies. Therefore, minimising biases between ingested and assimilated prey, by combining or complementing traditional approaches with the stable isotope analysis (Tripp-Valdez et al., 2015) is paramount.

5 Conclusion

Coryphaena hippurus, being an apex piscivorous predatory carnivore, plays a very important role in the energy transfer of pelagic ecosystems in major oceans. Present study is the first from the Bay of Bengal, northeastern Indian Ocean providing maiden knowledge on its role in the food web in this marine ecosystem. Some aspects; size-wise feeding intensity, trophic level, feeding strategy and size-wise and season-wise dietary niche are primary information for the species globally. Information generated on the diet along the Bay of Bengal would be crucial in understanding the species ecology and the trophic interrelationships required for trophic ecosystem modelling, thus facilitating ecosystem-based fishery management of the region. Future research in the Bay of Bengal on seasonal changes in prey availability and biomass would help to complement the present study and confirm on the feeding strategy and the extent of prey specialisation for the species. This is important because, for tropical ecosystems, generalist predators exert strong top-down control on the highly diverse prey communities. Also, prey-resource partitioning between *C. hippurus* and its competitors, yellowfin tuna and narrow-barred Spanish mackerel, needs to be critically and carefully evaluated in the future.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Ethics approval

Not Applicable, as previously captured and killed specimens from commercial fisheries were used as samples in the present study.

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