

Feeding habits of the longfin goatfish *Upeneus supravittatus* Uiblein and Heemstra, 2010, along Chennai coast, south India

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Abstract

Recognising the need to understand the feeding habits of marine fishes, a study was undertaken on the longfin goatfish *Upeneus supravittatus* Uiblein and Heemstra, 2010, which contributed to trawl fisheries along Chennai coast (south-east coast of India). Data on trophic attributes such as mouth gape area, gill raker counts, stomach and intestine lengths; and gut condition and contents were collected and analysed to determine condition index, index of relative importance (IRI), niche breadth and trophic level (TrL) with reference to two variables, namely, body size (small, medium and large) and season (post north-east monsoon (PNE); summer (SUM); south-west monsoon (SW); north-east monsoon (NE)). The mouth gape area of *U. supravittatus* was 129.3 mm². The maximum body depth-total length ratio was 1:5.0; gill rakers in lower arch was 29 and the relative intestine length was 0.48. Empty stomach contributed 56.1% of the samples. *U. supravittatus* fed on prey belonging to 25 Orders and >40 Genera. Decapods such as shrimps and crablets were the main prey followed by fishes. The IRI of decapods was 6474 and that of fishes was only 193. The maximum prey size predated by the fish was 33.5 and 9.8% in terms of the predator's length and weight, respectively. Higher prey diversity was noticed in small size group and during south-west monsoon season. The narrow niche breadth of 0.20 showed the selective nature of the fish to feed on decapods. The fish is a benthic carnivore with a mean trophic level of 3.58. The trophic level decreased with body size. Diet similarity was evident between north-east and post north-east monsoon and between summer and south-west monsoon seasons. Diversity indices showed marginal variation in prey diversity among size groups and among seasons. This study paves way for estimating production efficiency of *U. supravittatus*.



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Keywords:

Diet composition, Index of relative importance, Trophic level, Trophic morphology, *U. supravittatus*

Received : 21.07.2023

Accepted : 12.08.2024

Introduction

Study on feeding habit of fish helps to determine diet composition and trophic role of the selected fish in the ecosystem; assess ontogenetic and seasonal changes in diet; evaluate predatory diversity, competition and production efficiency; map the dynamics of ecological relationships between co-existing species; estimate prey abundance in an ecosystem and to determine the habitat of the species (Hyslop, 1980).

Goatfishes are common marine fish of high economic value in many coastal areas. They play an important role in tropical and temperate marine ecosystems. Being at an intermediate trophic level, they are

involved in a large number of interactions in the marine food web (Uiblein, 2007; Uiblein and Randall, 2023). Goatfishes are characterised by a pair of typical chin barbels that are unique and are very efficient tools for food search and location. Due to their very active foraging behaviour with vigorous stirring up of sediments by their barbels and mouth, goatfishes are known to provide important ecosystem services (Ng *et al.*, 2021). In the Indian seas, several studies on food and feeding habits of goatfishes are available (Jayaramaiah *et al.*, 1996; Mohanraj, 2000; Shanthi Prabha and Manjulatha, 2008; Gomathy, 2013). Goatfishes are midlevel benthic carnivores, and they play an important role in the

ecosystem as predators of organisms lower in the food web and as prey to higher level predators. As food selection may vary between goatfish populations in different habitats, seasons and age groups, it is important to investigate the stomach content of this key species to understand their role in food web models.

In spite of many publications on food and feeding of a number of goatfish species, there are no estimates on the quantitative aspects of feeding of any goatfish species in the Indian seas. Among the goatfishes occurring along the Chennai coast, *Upeneus supravittatus* Uiblein and Heemstra, 2010, is reported to be common (Gomathy *et al.*, 2023). The objectives of the study are to understand feeding habits of *U. supravittatus* qualitatively and quantitatively along the Chennai coast; to assess changes in the feeding habits of different size groups and seasons and to suggest future advanced studies on feeding habits of the fishes.

Materials and methods

About 550 bottom trawlers of 12 to 18 m overall length (OAL) and engine horsepower of 100 to 200 based at Chennai Fisheries Harbour (CFH, 12°80'N; 80°20'E) operate in fishing grounds at a depth of 10 to 100 m extending from Pudupatnam in the south to Nizampatnam in the north, a coastal stretch of about 400 km (Fig. 1). These trawlers land goatfish among other species regularly at CFH. Weekly fresh samples of *U. supravittatus* were collected from trawl landings at CFH for two years from 2008-2010.

The fish samples were washed and analysed in the laboratory at the Madras Regional Station of ICAR-Central Marine Fisheries Research Institute (ICAR-CMFRI). The total length (TL) of all specimens was

measured to the nearest mm on a measuring board from the tip of the snout to the tip of the upper caudal fin. The weight of each fish was determined in an electronic balance (Make:Mira, Sartorius Mechatronics India; Accuracy: 1 g) after blotting the whole fish to remove the adhering water. The total length and body weight of males ($n = 402$) ranged from 95 to 199 mm and from 9 to 109 g and that of females ($n = 699$) from 96 to 196 mm and from 8 to 103 g, respectively.

The samples were subjected to the following measurements and analyses. Upper and lower jaw lengths were measured and dentition pattern and teeth count were recorded. Mouth gape area was measured employing the formula used for elliptical shape as $\pi 0.5A \times 0.5B$, where A is mouth height and B is mouth width (Ward-Campbell *et al.*, 2005). Gill raker counts were made using a hand-held lens (Froese and Pauly, 2000). Stomach and intestine lengths were measured and relative stomach length ($RSL = \text{stomach length} / \text{fish total length}$) and relative intestine length ($RIL = \text{intestine length} / \text{fish total length}$) were calculated (Ribble and Smith, 1983). Condition index was determined by allotting points to stomach condition from empty to gorged (Pillay, 1952). In the present study, the following points were allotted to the percentage of each stomach condition to the total number of stomachs: Empty: 1, Trace: 2, Quarter-full: 3, Half-full: 4, three-quarter full: 5, Full: 6 and Gorged: 7. The percentage of each stomach condition was multiplied with the allotted points and averaged to arrive at stomach condition index (SCI) for each body size and season. Detailed quantitative and qualitative analysis of stomach contents up to the level of family/genus/species was made, (vii) Data on all trophic attributes were collected and analysed.

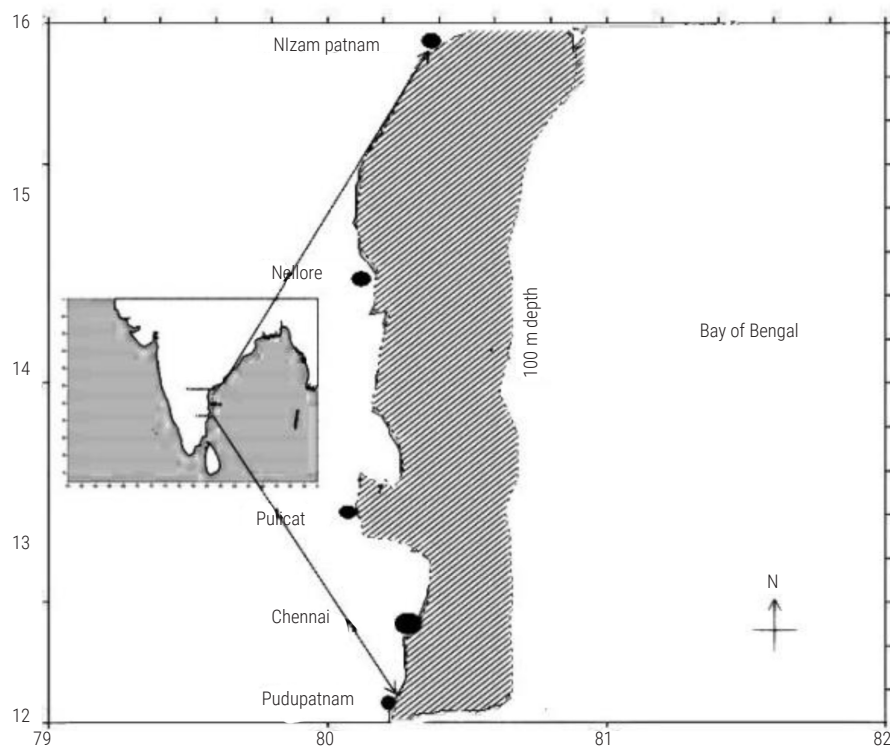


Fig. 1. Fishing ground (shaded portion) of trawlers based at Chennai Fisheries Harbour

To find out the relative importance of prey items, dietary overlap, trophic position, similarities and dissimilarities within and between groups and diversities of prey types, indices such as IRI (Pinkas *et al.*, 1971; Cortes, 1997; Alonso *et al.*, 2000), Prey specific abundance (PSA) (Amundsen *et al.*, 1996), niche breadth (Levins, 1968), trophic level (TrL) (Odum and Heald, 1975; Christensen and Pauly, 1992; Froese and Pauly, 2000), cluster analysis (Bray and Curtis, 1957), multidimensional scaling (MDS) (Sheppard, 1962; Kruskal, 1964), Shannon index, Simpson index and Pielou's evenness index were calculated. The similarity indices were estimated using PRIMER version 6 (Clarke and Gorley, 2006) and SPSS version 17. The details on the analysis of these parameters are explained by Gomathy and Vivekanandan (2017).

All the trophic attributes were tested with reference to two variables, namely, three body sizes (small, medium and large), and four seasons (post north-east monsoon season (PNE): January - March; summer (SUM): April - June; south-west monsoon season (SW): July - September; north-east monsoon season (NE): October - December). For comparison of different size groups, the samples were categorised into 10 mm length groups such as 80-89 mm, 90-99 mm and so on, up to 190-199 mm. For further analysis, the fishes between 80-119 mm were grouped as small, 120-149 mm as medium and 150-199 mm as large. Statistical analyses such as standard deviation (SD), standard error (SE), coefficient of variation (CV), regression, correlation coefficient (r^2) Student's t test and Analysis of Co-variance (ANCOVA) were performed following Snedecor and Cochran (1967).

Results

Trophic morphology

The mouth of goatfish is small and low with two chemosensory barbels in the lower side of the chin (Fig. 2a). The lower jaw is inferior and shorter than the upper jaw, measuring 11.5 and 13.5 mm

respectively for a fish of 150 mm total length. Villiform teeth are present in both jaws in a single row, vomer and palate. Teeth are not enlarged as canines. When fully open, the mouth gape is elliptical in shape (Fig. 2b) with extended maxilla on the upper jaw. The mouth height is 1.6 times the mouth width. The mouth height and width were 16.5 and 10.0 mm, respectively and the gape area was determined as 129.3 mm². The gape area increased linearly with the length of the fish. The maximum body depth (MBD) of *U. supravittatus* was 28 mm for a fish of 150 mm length. It increased linearly with increasing fish length. The MBD-fish length ratio was 1: 5.03.

Gill rakers were present along the entire length of the lower arch, but were absent from the middle of the upper arch for 3 mm towards the end (Fig. 2c). They were of medium length, thick, strong and moderately spaced with three rakers within a distance of every 2 mm in the gill arch. The length of each gill raker ranged from 0.1 to 4 mm. The longest ones (4 mm) were found at the junction of both the gill arches and the length gradually reduced towards the middle of the upper arch (2 mm) and at the end of lower arch (0.1 mm). For a fish of 150 mm length, 29 gill rakers were present.

The gut of *U. supravittatus* is distinctly demarcated into stomach, pyloric caeca and intestine (Fig. 3a). The stomach is divided into two compartments, namely cardiac and pyloric stomachs. The cardiac stomach is drawn out into a caecum. Pyloric stomach starts at the junction of cardiac stomach and caecum. It is very short and thick-walled with a narrow proximal part and a wide distal part. The cardiac stomach is comparatively thin-walled and becomes membranous when expanded, to hold large volume of prey (Fig. 3b, c), whereas the pyloric stomach did not stretch to hold any prey. The pyloric stomach is followed by the duodenum, which extends forward as the ileum, ends in rectum and opens outside by anus.

The intestine is moderately long and the length linearly increased with

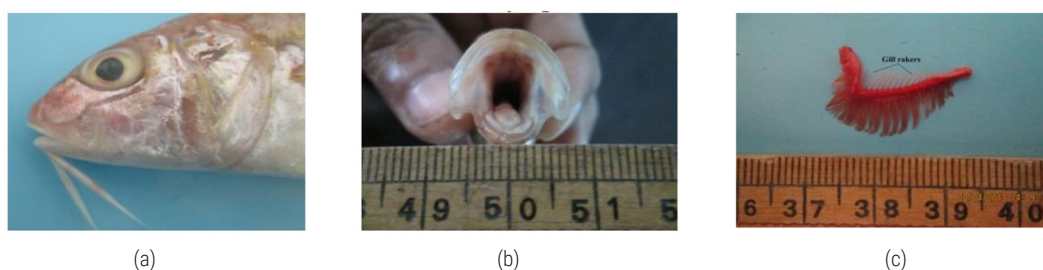


Fig. 2. (a) Image of head (side view); (b) fully open mouth; and (c) gill arch of *U. supravittatus*

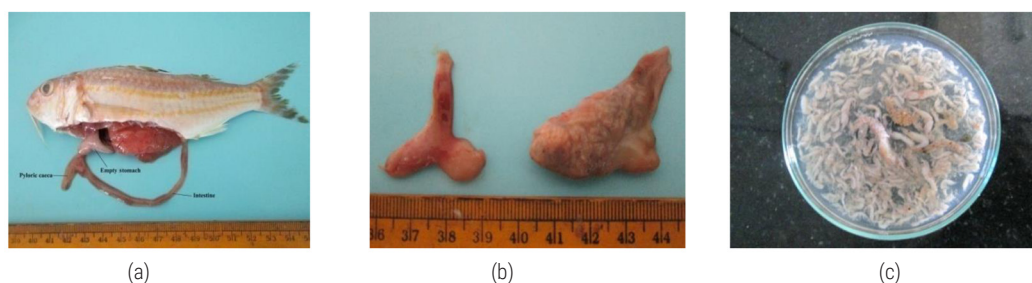


Fig. 3. (a) Gut, (b) Empty and gorged cardiac stomachs and (c) Contents of gorged stomach of *U. supravittatus*

increase in fish length. The relative intestine length (RIL) was 0.48. The stomach length also increased linearly with increasing fish length and the relative stomach length (RSL) was 0.15.

\ln stomach length (mm) = $[(0.9891 * \ln \text{ fish length (mm)}) - 1.8441]$ ($r^2 = 0.404$; $n = 902$)

\ln intestine length (mm) = $[1.4612 * \ln \text{ fish length (mm)}] - 166.5$ ($r^2 = 0.9905$; $n = 8$)

Feeding intensity

A large number of individuals in the sample had empty stomach (56.1%). Among size groups, the percentage of empty stomach was high (50.5%) and that of full stomach low (10.4%) in small size group. The condition index (CI) estimated by allotting points to the percentage of different stages of stomach condition showed that the small size group had marginally higher CI (251.7 ± 25.1) (Fig. 4a). The CI was significantly higher during SUM (276.9) than during NE monsoon (209.5) (Fig. 4b). It could be inferred that the feeding intensity was higher during summer.

Prey types

The food of *U. supravittatus* consisted of a wide variety of prey items. The prey belonged to several Orders of invertebrates, cephalochordates and teleosts, all together comprising 10 Classes, 25 Orders and > 40 Genera (Table 1). The major components of prey were Arthropods (11 Orders) followed distantly by teleosts (5 Orders). Polychaetes, ophiurids, planktonic mysids, copepods and hooded shrimp (cumaceans) were frequent in occurrence. Several other groups like foraminiferans, bivalves, gastropods, ostracods, euphausiids, amphipods, stomatopods and amphioxus were found in the stomach occasionally.

Index of relative importance (IRI)

Among the prey groups, occurrence of decapods was by far the highest, occurring in 423 (69.9% of the total) stomachs (Table 2). The decapods showed importance in terms of numerical abundance (43.5%) as well as biomass (68.9%).

The IRI of decapods was significantly higher (6474) than all other prey groups. The IRI of the next dominant prey, the teleosts, was considerably low (193). The $\ln\%$ value of IRI was positive for

decapods, teleosts and polychaetes only (Fig. 5a). Comparison of $\ln\%$ IRI for the three size groups (Fig. 5b, c, d) showed that the values were positive for more number (5) of prey types in the large size groups. This indicates that during ontogenetic development, the large fish fed on relatively more varieties of prey in higher quantities.

The decapods remained as the major prey in all the seasons. Importance of teleosts was the second highest during NE and PNE seasons, but their importance reduced in the other two seasons. Polychaetes were the second most dominant prey during SW season. These changes show the differences in the importance of secondary prey groups between seasons.

Prey specific abundance (PSA)

U. supravittatus population is specialised to feed on decapods as indicated by its position on the right side of the plot (Fig. 6a). A few individuals of the predator fed specifically on ostracods, polychaetes and gastropods. The remaining 11 prey types (except teleosts) were rare and unimportant as they clustered on the left lower side of the plot.

During ontogenetic development also, the decapods remained as the specialised prey of the population. However, ophiurids in the small size group, ostracods and polychaetes in the medium and polychaetes and gastropods in the large size group were fed specifically by a few individuals in the population. It appears that, as the fish grows, individuals in the population diversify their feeding habit by ingesting more number of specific prey types. Notably the foraminiferans which were lowermost on the left lower corner (PSA: 5%) of small size group (Fig. 6b), moved up on the left side in the medium size group (PSA: 40%; Fig. 6c) and further up to 80% in the large size group (Fig. 6d).

Cephalochordates were also consumed specifically by several individuals of large size group (PSA: 70%) which was not evident in the small (18%) and medium (10%) size groups. Several individuals in the medium size group preferred to feed on ostracods, unlike the small and large size groups. These differences in the PSA between the size groups show the ontogenetic changes in food preference by a few individuals in the population, but the decapods were the dominant prey type in all the size groups.

Decapods remained as the specialised prey of *U. supravittatus*

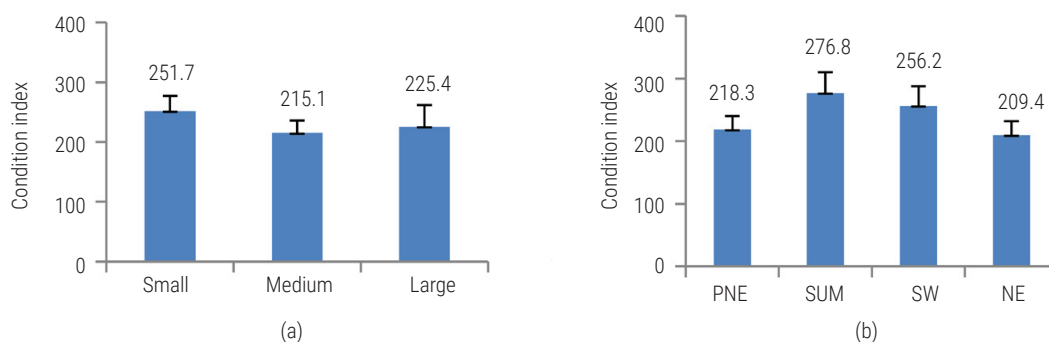


Fig. 4. Condition index of *U. supravittatus* ($n = 1377$) for (a) three size groups and (b) four seasons during July 2005 - December 2008. Vertical lines indicate standard deviation

Table 1. Taxonomic classification of prey types of *U. supravittatus*

Phylum	Class	Order	Genus/species/common names
Foraminifera	Rotalidia	Rotaliida	<i>Elphidium</i> sp.
Annelida	Polychaeta	Phyllodocida	<i>Nereis</i> sp.
		Canalipalpata	<i>Polydora</i> sp., <i>Spiophane</i> sp.
		Terebellida	<i>Cirratulus</i> sp.
Mollusca	Bivalvia	Veneroidea	Clam shell
	Gastropoda	Littorinimorpha	<i>Natica subcostata</i>
Arthropoda	Ostracoda	Littorinimorpha	Punctulimporcupinae
		Podocopa	Ostracods
		Calanoida	Calanoids
		Harpacticoida	Harpacticoids
		Cyclopoida	Cyclopoids
	Malacostraca	Mysida	Mysids
		Cumacea	Cumaceans
		Amphipoda	<i>Amphilocus neapolitanus</i>
		Amphipoda	<i>Gammarus</i> sp.
		Euphausiacea	Euphausiids
		Decapoda	<i>Acetes indicus</i>
			<i>Lucifer</i> sp.
			<i>Solenocera</i> sp.
			<i>Penaeus indicus</i>
			<i>P. monodon</i>
			<i>Metapenaeus dobsoni</i>
			<i>Alpheus</i> sp.
			<i>Pontocaris</i> sp.
			Crab juveniles, <i>Persephona</i> sp.
Echinodermata	Ophiuroidea		Megalopa
			Zoea
			Mysid
Cephalochordata	Leptocardii	Mysida	Mysid
		Stomatopoda	<i>Squilla mantis</i>
Chordata	Actinopterygii	Ophiurida	<i>Amphipholis squamata</i> (Brittle-star)
		Amphioxiformes	<i>Branchiostoma lanceolatum</i> (Amphioxus)
		Gadiformes	<i>Bregmaceros maclellandii</i>
		Anguilliformes	<i>Leptocephalus</i>
		Scorpaeniformes	<i>Grammolites scaber</i>
		Scorpaeniformes	<i>Scorpaena</i> sp.
		Perciformes	<i>Leiognathus lineatus</i>
			<i>Secutor insidiator</i>
			<i>Secutor ruconius</i>
			<i>Sphyraena</i> sp.
		Clupeiformes	<i>Stolephorus</i> sp.
			Unidentified fish larvae and eggs

Table 2. Frequency of occurrence (FO), Abundance (A, number) and Biomass (B, g) of prey types of *U. supravittatus* (n = 605) during July 2005 - December 2008

Prey	FO	A	B	IRI
Foraminifera	6	25	0.223	1
Polychaeta	33	740	8.410	144
Bivalvia	12	12	0.128	1
Gastropoda	6	89	0.473	3
Ostracoda	1	29	0.087	0
Copepoda	36	193	0.756	35
Mysida	37	193	2.136	42
Cumacea	5	39	0.340	1
Amphipoda	13	26	0.753	3
Euphausiacea	13	84	0.364	6
Decapoda	423	1263	89.084	6474
Stomatopoda	19	20	2.805	7
Ophiurids	46	61	4.429	35
Amphioxiformes	7	18	0.640	1
Teleostei	77	113	18.736	193
Total	605	2905	129.364	6945

population in all the seasons. Foraminiferans during PNE, ostracods, polychaetes and gastropods during SUM, polychaetes during SW and foraminiferans during NE were the specialised prey of a few individuals. The major difference in the PSA between size groups and seasons was that the foraminiferans emerged as the specialised prey of a few individuals during PNE and NE, whereas they were rare and unimportant in all the size groups except in the large individuals.

Relationship between fish size and prey size

To find out the relationship between fish size and prey size, the length and weight of prey was compared with that of fish. For this, the stomachs with single prey alone were considered.

The maximum prey size consumed was 33.5% in terms of fish length, but only 9.8% in terms of weight. No relationship was found between fish length and prey length in all the stomachs (Fig. 7a), or in full and gorged stomachs (Fig. 7b). Similarly, there

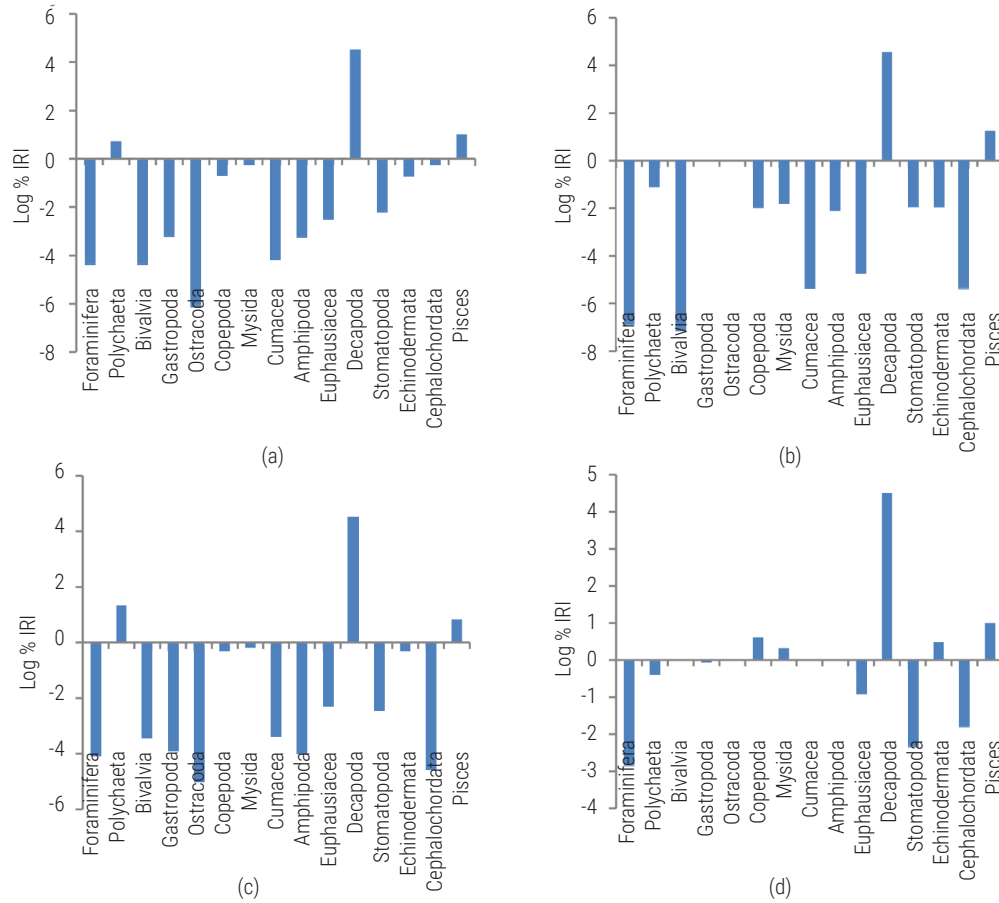


Fig. 5. Index of relative importance (Ln% IRI) of prey groups of *U. supravittatus* (n = 605) of different size groups during July 2005 – December 2008. (a) Pooled; (b) Small; (c) Medium and (d) Large

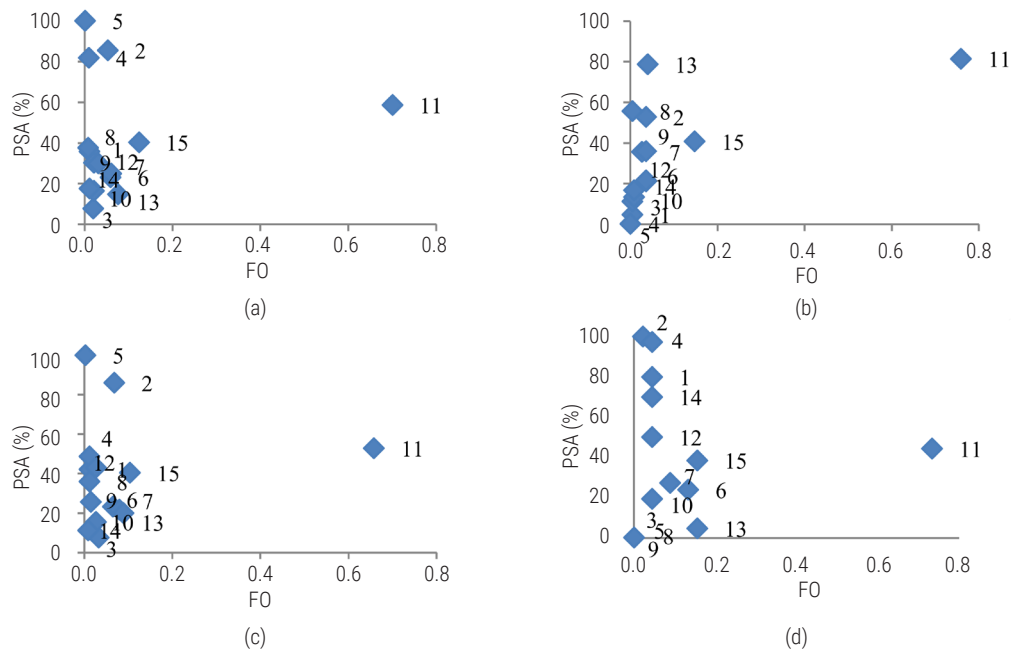


Fig. 6. Prey specific abundance (%) in relation to Frequency of occurrence (FO) of *U. supravittatus* (n = 605) in the three size groups; (a) Pooled; (b) Small; (c) Medium and (d) Large. 1 = Foraminifera; 2 = Polychaeta; 3 = Bivalvia; 4 = Gastropoda; 5 = Ostracoda; 6 = Copepoda; 7 = Mysida; 8 = Cumacea; 9 = Amphipoda; 10 = Euphausiacea; 11 = Decapoda; 12 = Stomatopoda; 13 = Ophiurida; 14 = Cephalochordata; 15 = Teleostei

was no relationship between stomach length and prey length (Fig. 7c) as well as fish weight and prey weight (Fig. 7d). This random distribution of prey size in relation to fish size shows that the fish did not select any particular prey size and randomly ingested prey of different sizes within a maximum threshold.

Niche breadth

For *U. supravittatus*, the B and BA values were higher ($B = 5.78$; $BA = 0.34$) for the large size group than in small and medium size groups (Table 3). Among the seasons, the B and BA values were the highest during summer ($B = 5.37$; $BA = 0.31$). The B and BA values of *U. supravittatus* as a whole were 3.75 and 0.20 respectively. As the BA of *U. supravittatus* was only 0.20 which is near 0 than to 1, Levins measure shows that *U. supravittatus* is more towards a specialist feeder. This is because the fish is feeding predominantly on a single prey group namely, the decapods. Ontogenetic and seasonal data on niche breadth shows that the small size group ($B = 1.99$) is relatively more specialised on prey preference than the other groups ($B = 3.68$ and 5.78) and the fish is strictly a specialist feeder during NE season ($BA = 0.04$).

Trophic level (TrL)

For determining the TrL, information on the food of prey of *U. supravittatus* was gathered from different sources. *U. supravittatus* ingested prey types with a wide variety of feeding habits such as herbivores (ostracods), detritivores (bivalves),

Table 3. Levins measure of niche breadth (B) and standardised measure of niche breadth (BA) for *U. supravittatus*

Size /Season	B	BA
Small	1.99	0.07
Medium	3.68	0.19
Large	5.78	0.34
Post north-east	2.42	0.10
Summer	5.37	0.31
South-west	3.38	0.17
North-east	1.63	0.04
All	3.75	0.20

scavengers (polychaetes), filter feeders (bivalves and euphausiids), omnivores (mysids) and carnivores (decapods and teleosts). The predominant prey, namely, the decapods consisted of a wide variety of organisms such as penaeid and non-penaeid shrimps, crablets, alpheid, cumaceans and crangonid; each prey type showed different feeding habits with mean TrL of 2.5. The mean TrL of the teleost prey was 3.15. The TrL of all the prey types of *U. supravittatus* were within the range of 2.0 to 3.2. From the biomass and assigned trophic level of each prey type, the TrL of *U. supravittatus* was determined as 3.58 (Table 4). Information on the TrL of *U. supravittatus* is not available in literature. Vivekanandan et al. (2009) reported the mean trophic level of different species of goatfishes as 3.54 ± 0.15 .

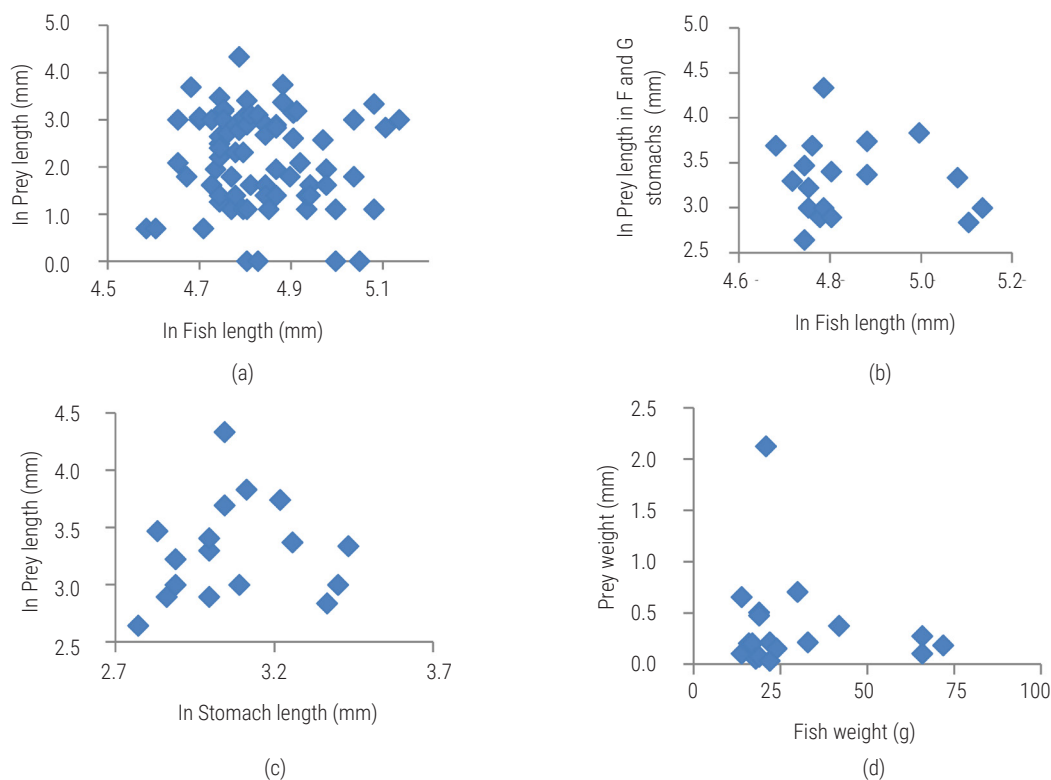
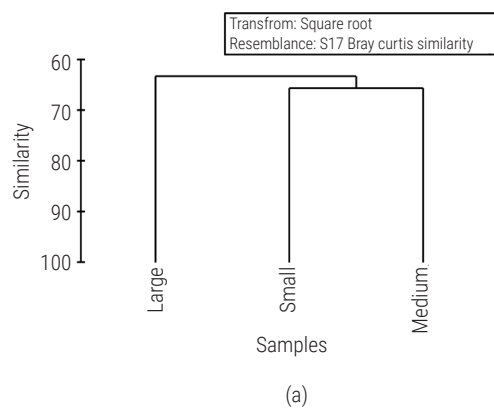


Fig. 7. Relationship between (a) fish length and prey length in ($n = 79$); (b) fish length and prey length in full and gorged stomachs ($n = 18$); (c) stomach length and prey length in full and gorged stomachs ($n = 18$) and (d) Fish weight and prey weight in full and gorged stomachs ($n = 18$) of *U. supravittatus*

Table 4. Trophic level of *U. supravittatus*

Size / season	Trophic level
Size group	
Small	3.63
Medium	3.58
Large	3.56
Season	
Post north-east	3.93
Summer	3.49
South-west	3.55
North-east	3.63
All	3.58

The TrL of *U. supravittatus* marginally reduced from 3.63 to 3.56 with increasing body size. The large *U. supravittatus* ingested relatively less biomass of teleosts (which had a higher TrL of 3.15). The TrL was higher during NE and PNE seasons (October - March) than during SUM and SW (April - September). This is also because *U. supravittatus* ingested larger biomass of teleosts during PNE and NE.



Diet similarity

Cluster analysis

The dendrogram based on the prey abundance showed grouping of small and medium size groups at 65.51% similarity to which the large group joined at 63.15% (Fig. 8a). The dendrogram for seasons showed grouping of SUM and SW at 62.35% similarity and that of PNE and NE at 56.55% (Fig. 8b). Both the groups got linked at 42.8%.

Multidimensional scaling (MDS)

The MDS ordination graph showed overlapping of all size groups (Fig. 9a) as well as seasons (Fig. 9b) with very few outliers indicating homogeneity in food preference among all size groups as well as seasons. The 2D stress value of 0.01 indicates the goodness of fit of MDS.

Diversity indices

In Shannon diversity index, though the range and quartile values of prey diversity were narrow for small size group compared to

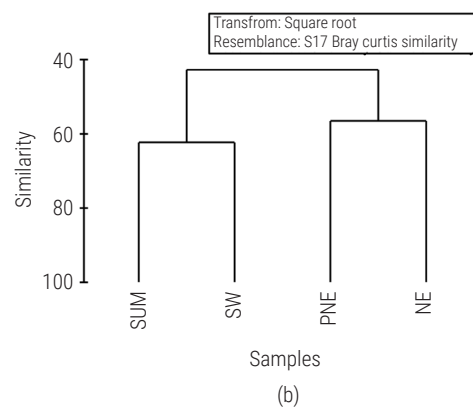


Fig. 8. Dendrogram showing group average similarity (%) of prey of *U. supravittatus* for (a) small, medium and large size groups and (b) during PNE, SUM, SW and NE seasons (8b)

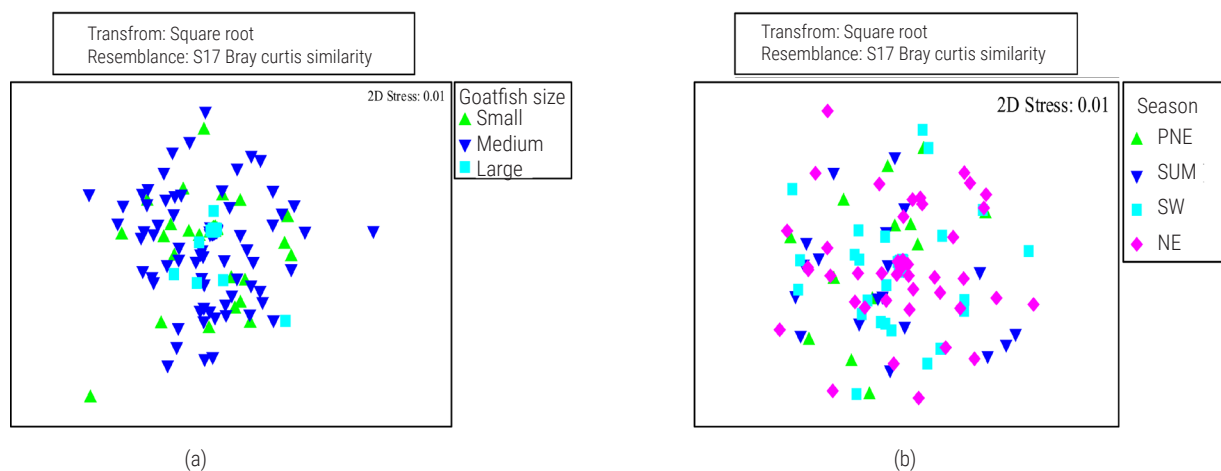


Fig. 9. MDS ordination graph of *U. supravittatus* prey types for (a) small, medium and large size groups and (b) during PNE, SUM, SW and NE seasons

medium and large size groups, the median diversity values were almost equal (0.67-0.69) between size groups (Table 5) showing that the diversity of prey types and number of individuals of prey are equal between size groups. The species dominance (Simpson index) and evenness of prey (Pielou's index) showed relatively more dispersion of data for medium size group, but almost equal median values, indicating that the abundance within prey type is relatively evenly distributed.

The median values of Shannon diversity index remained at around 0.69 among seasons (Table 5). Simpson dominance median value was higher for PNE, but the evenness value was almost equal at around 0.9 for the seasons. These indices showed differences in the range of dispersion of prey diversity, dominance and evenness among size groups as well as seasons, but the median values were almost equal (except for Simpson's richness index for seasons), suggesting that the mean prey diversity, dominance and evenness did not differ within the two variables (size group and season), but there were differences in the outliers.

Discussion

In the trawling grounds off Chennai, the longfin goatfish *U. supravittatus* is primarily a bottom-living mid-level carnivore. Its diet mainly consists of a wide variety of benthic organisms and pelagic invertebrates, with a preference for decapod crustaceans followed by teleost fish. The relative proportions of these prey changed with the size of the predator and seasons. Overall, a vast diversity of prey types such as penaeid and non-penaeid shrimps, crabs, polychaetes, amphipods, copepods, bivalves, gastropods and teleosts such as silverbellies and whitebaits were found in the stomach. Twenty five prey groups (Orders) and more than 40 genera were recorded in the stomach of the goatfish. The wide choice of food indicates the potential of the fish to shift its diet when a particular prey becomes scarce.

Though no specific studies have been conducted on the diet of *U. supravittatus*, there are a number of publications on other species of goatfishes distributed in different regions of world oceans. Uiblein (2007) recorded 66 species of goatfishes, widely distributed across tropical, subtropical and temperate habitats ranging from the upper littoral zone to the upper slope. Considering their wide distribution, Uiblein (2007) suggested that goatfishes play a significant ecological role and may serve as indicators of natural habitat conditions. All goatfishes are zoobenthivores foraging primarily on crustaceans and polychaetes found in soft sediments such as sand and mud. They rely largely on their tactile and chemosensory barbels to detect the prey (Gosline, 1984; Labropoulou *et al.*, 1997; Cherif *et al.*, 2011). Goatfishes employ an efficient foraging strategy playing an important role in the benthic ecosystems. Using their highly sensitive chemo-sensory barbels,

they skim the sea floor, shoveling and turning over the substrate to locate and capture prey. By disturbing the substratum, goatfishes alter the bottom topography and redistribute benthic organisms. This activity attract other carnivorous fish, which prey on the small organisms that are flushed out during the substratum disturbance (Soares *et al.*, 2020). Additionally, goatfishes are known to function as nuclear species, often followed by other carnivorous fish that take advantage of small preys flushed out during substratum disturbances caused by their foraging activities (Gosline, 1984). Of the 20 species of goatfishes reported to occur in the Indian seas (Thomas, 1969), studies on the food and feeding habits are available for 10 species. In all of these species, crustaceans have been identified as the primary component of their diet (Chacko, 1949; Kuthalingam, 1955, 1956; Rabindranath, 1966; Thomas, 1969; Jayaramiah *et al.*, 1996; Hamsa and Rao, 1997; Mohanraj, 2000; Shanti Prabha and Manjulatha, 2008). Despite their overall morphological similarity and their exclusive bottom foraging behaviour, the distribution and abundance of sympatric goatfish species vary across different regions of the Indian seas. This variation probably helps minimise competition and reduces dietary overlap between species. Stergiou and Karpouzi (2002) suggested that the diet may vary significantly between goatfish populations leading to variations in their trophic levels between habitats. The trophic level of *U. supravittatus* in the present study ranged from 3.49 to 3.93 during different seasons. Consolidating the available data, Stergiou and Karpouzi (2002) showed that the trophic level of the red mullet *Mullus barbatus* ranged widely from 2.79 to 3.57 in the Mediterranean Sea due to combined effects of habitat, age and season. Due to these reasons, and considering the wide variety of prey types ingested by goatfishes, Krajewski *et al.* (2006) concluded that these fishes should not be simply generalised as bottom foragers.

In the present study, a large number of stomachs were empty (56.1%) irrespective of the date and time of sampling. Regurgitation of ingested food was not noticed as the stomachs were in shrunken condition, probably for a long duration. The high percentage of empty stomachs may be attributed to the ability of the fish to become satiated quickly and rapidly digest their food. Similar suggestion was made by Labropoulou *et al.* (1997) for the striped red mullet *Mullus surmuletus* in north-eastern Mediterranean.

The feeding behaviour of *U. supravittatus* is aided by morphological adaptations to prey on small benthic invertebrates and occasionally on more mobile fishes. The tactile and chemosensory barbels, short jaw (upper jaw = 9.0% of fish length) and small mouth gape area (129.3 mm²), are adaptations to shovel by burrowing with snout and move the snout against the substratum, dislodging the top layer and capture the invertebrate prey using jaw movement. The small teeth without canines, moderate maximum body depth (fish length ratio of 1: 5.0) and moderate gill raker length (0.1 to 4.0 mm) and numbers (3 gill rakers in 2 mm length) are adaptations for short distant chase of mobile prey like small fishes. The goatfishes are capable of shifting their foraging strategy depending upon the prey type available (Krajewski *et al.*, 2006). *U. supravittatus* has a short stomach (RSL: 0.15) with a capacity to hold and digest small prey. The small stomach and intestine (RIL = 0.48) also indicate that the time for digestion may be short. Overall, *U. supravittatus* may be characterised as a versatile bottom predator, specialised with different feeding modes to forage on soft and hard substrata as well as on moving fishes and crustaceans.

Table 5. Shannon, Simpson and Pielou's index median values for various size groups of *U. supravittatus* and seasons

Index	Size			Season			
	Small	Medium	Large	PNE	SUM	SW	NE
Shannon	0.69	0.67	0.69	0.69	0.69	0.69	0.67
Simpson	0.67	0.67	0.75	0.83	0.67	0.67	0.60
Pielou's	0.92	0.92	0.88	0.95	0.92	0.92	0.93

Minor changes in feeding strategy with ontogenetic development of *U. supravittatus* were evident. Morphologically, the mouth gape area, maximum body depth, gill raker count and stomach length increased linearly with size of the fish. While the decapods, followed distantly by teleosts, were the major food of all size groups, the large fish ingested relatively less number of prey types (10) than the small fish (13), but in large quantities, which is evident from IRI and PSA analyses. Nevertheless, the relative importance of decapods and teleosts was high and that other food types were of minor importance in the small size group. There was no difference in the size of ingested prey with ontogenetic development, indicating no prey size selection. Thus, ontogenetic differences in feeding habit were not evident in all the attributes on which data were collected. However, one of the most important ontogenetic changes in the food was the difference in prey types within decapods. Smaller fishes tended to eat small non-penaeid shrimps like *Acetes indicus* whereas larger fishes preyed on larger penaeid shrimps and crabs. However, as large fishes ingested smaller prey also along with larger prey, a clear prey size-related feeding pattern could not be established for large fishes. Nevertheless, as the diet of all the three size groups was primarily from the same prey taxa, MDS analysis showed homogeneity in diet between size groups. The mean values of diversity indices (Shannon, Simpson and Pielou) were almost equal between size groups. The fish matures at 135 mm (63.7% of L_{∞} ; age: 9 months) (Gomathy, 2013), which was grouped as medium size in this study. It appears that the feeding habit of the fish did not change conspicuously after attaining maturity.

Many earlier researchers have reported a shift in feeding habit with increase in body size for several species of goatfishes (Kuthalingam, 1955; Thomas, 1969) and several other marine fish species (Rios *et al.*, 2019). Mohanraj (2000) reported that small *U. bensasi* and *U. moluccensis* preyed mainly on shrimps and larger ones on other crustaceans and fishes off Chennai. Golani and Galil (1991) observed that well-developed upper jaw dentition of large *U. moluccensis* enables it to prey more efficiently upon organisms of relatively larger size in the eastern Mediterranean. N'Da (1992) inferred that smaller predators cannot move swiftly to prey upon fast moving organisms. These differences in the conclusions of the earlier publications may be due to the fact that these studies were based on the frequency of occurrence and numerical abundance of prey items only and not on prey biomass and hence are influenced markedly by small food items that may occur in higher numbers, but constitute a low biomass. This bias is more evident in fish ingesting small-sized prey (Cailliet and Barry, 1978). In the present study, the feeding habits were determined by IRI which combines all the three measures, into a presumably less biased statistic for the dietary importance of various prey items (Carrasson *et al.*, 1992). It is important that the factor of prey biomass or volume in the gut should be considered in dietary studies especially those related to fish feeding on small prey types.

Similar to minor ontogenetic differences in the diet, season was another factor, which accounted for a few changes in the diet. Decapods followed distantly by teleosts were the major prey types in all the seasons. Cluster analysis showed aggregation of NE and PNE seasons, when the fish fed more on selective prey with high trophic level. As stomach emptiness was more during NE and PNE, the feeding intensity was low during these two seasons. These results showed differences in the diet of NE and PNE from that of other two seasons. The spawning season of *U. supravittatus*

extended for nine months from October to June, with peak during NE (October-December) (Gomathy, 2013), which coincided with the differential seasonal diet composition. During peak spawning, fishes are known to feed less or starve as the large ovaries occupy a substantial portion of the body cavity. Due to the extended spawning season, it is difficult to conclude whether the feeding intensity of the goatfish was influenced by spawning activity. Nevertheless, low feeding intensity and prey types clustered the NE and PNE seasons together, which coincided with peak spawning, indicating at least indirectly, the possible influence of spawning activity on the feeding intensity and diet of the fish. However, as the fish was feeding predominantly on the same prey taxa (decapods) in all the seasons, the MDS and diversity indices did not show heterogeneity in the diet of the fish.

Extensive removal of decapods indicates that the fish play an important role at the middle level of the food web of the coastal ecosystem off Chennai. The goatfish controls the population of benthic organisms low in trophic level, and perhaps may form food of organisms higher in trophic level (for example, ribbonfish and lizardfish) thereby playing an important role in linking the organisms at different trophic levels.

Several challenges were encountered when visually examining the stomach contents, including difficulties in identifying the food composition at the species level. Technological advancements have significantly improved stomach content analysis in fishes in recent decades, particularly through methods such as fatty acid analysis, stable isotope analysis, and genetic techniques (Brodeur *et al.*, 2017; Soares *et al.*, 2020). Given the importance of precisely estimating fish feeding habits, application of these advanced methods for evaluating feeding ecology and trophodynamics is highly warranted.

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