Estuarine, Coastal and Shelf Science 87 (2010) 601–610

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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

# Trophic organisation and predator–prey interactions among commercially exploited demersal finfishes in the coastal waters of the southeastern Arabian Sea

K.P. Abdurahiman*, T.H. Nayak, P.U. Zacharia, K.S. Mohamed

*Central Marine Fisheries Research Institute, P.B. No.: 1603, Cochin 682 018, Kerala, India*

ARTICLE INFO

*Article history:*
Received 15 September 2009
Accepted 4 March 2010
Available online 10 March 2010

*Keywords:*
demersal finfishes
trophic level
cluster analysis
diet breadth
trophic guilds
southeastern Arabian Sea

ABSTRACT

Trophic interactions in commercially exploited demersal finfishes in the southeastern Arabian Sea of India were studied to understand trophic organization with emphasis on ontogenic diet shifts within the marine food web. In total, the contents of 4716 stomachs were examined from which 78 prey items were identified. Crustaceans and fishes were the major prey groups to most of the fishes. Based on cluster analysis of predator feeding similarities and ontogenic diet shift within each predator, four major trophic guilds and many sub-guilds were identified. The first guild 'detritus feeders' included all size groups of *Cynoglossus macrostomus*, *Pampus argenteus*, *Leiognathus bindus* and *Priacanthus hamrur*. Guild two, named 'Shrimp feeders', was the largest guild identified and included all size groups of *Rhynchobatus djiddensis* and *Nemipterus mesoprion*, medium and large *Nemipterus japonicus*, *P. hamrur* and *Grammoplites suppositus*, small and medium *Otolithes cuvieri* and small *Lactarius lactarius*. Guild three, named 'crab and squilla feeders', consisted of few predators. The fourth trophic guild, 'piscivores', was mainly made up of larger size groups of all predators and all size groups of *Pseudorhombus arsius* and *Carcharhinus limbatus*. The mean diet breadth and mean trophic level showed strong correlation with ontogenic diet shift. The mean trophic level varied from $2.2 \pm 0.1$ in large *L. bindus* to $4.6 \pm 0.2$ in large *Epinephelus diacanthus* and the diet breadth from $1.4 \pm 0.3$ in medium *P. argenteus* to $8.3 \pm 0.2$ in medium *N. japonicus*. Overall, the present study showed that predators in the ecosystem have a strong feeding preference for the sergestid shrimp *Acetes indicus*, penaeid shrimps, epibenthic crabs and detritus.


## 1. Introduction

Studies on demersal fish communities, which sustain many fisheries, are important for ecosystem-based fishery management (Mathews et al., 1973; Perez-Espana et al., 2005). Tropical marine ecosystems have a large number of species and consequently the food web is more complex than in other ecosystems. It includes a high number of interactions in the sense that they are different when compared with those of subtropical, temperate and high latitude food webs (Larkin et al., 1984; Pauly, 1998; Souter and Linden, 2000). Demersal fish fauna in the tropics is remarkably consistent and complex with many of the same families represented in similar areas and ecosystems (Longhurst and Pauly, 1987). Knowledge of the type of prey and food partitioning among demersal fishes is essential in order to identify their potential impact on prey survival and their role in structuring populations at lower trophic levels. This is particularly important for any ecosystem approach to fisheries management where knowledge of interactions is critical. Trophic groupings, which integrate a large amount of information of predator–prey interactions based on diet data are of immense use in such cases. Even though single specie models are still dominant worldwide for the management of commercially valuable fish stock, an emerging consensus has developed among fishery scientists and managers to consider the multispecies trophic interactions for sustainable fisheries and management (Christensen and Pauly, 1997; Walters et al., 1997).

The concept of trophic guild, which basically groups fish based on feeding similarity, has become increasingly important in fish community studies as it offers the possibility of dividing the community into functional groups (Livingston, 1982; Gerking, 1994; Garrison and Link, 2000; Cartes et al., 2002). Analysis of diet relationships within fish assemblages is of great value in enabling identification of the impact of each predator species on prey resource sharing (Ross, 1980). Although there are a number of studies on food and feeding of finfishes from the Indian coasts, most of these are qualitative in nature (Dhulked, 1962; Kagwade,

* Corresponding author. Present address: King Fahd University of Petroleum and Minerals, P.B. No.: 1454, Dhahran 31261, Saudi Arabia.
*E-mail address:* arahimankp@yahoo.com (K.P. Abdurahiman).

0272-7714/$ – see front matter 
doi:10.1016/j.ecss.2010.03.002

1964; Pati, 1978; Rao, 1980; Sivakami, 1995; Devaraj, 1998). Furthermore, the meagre quantitative information available is inadequate to explain the complex food chain interaction between them, and the methodological approach and application of statistical tests to analyze the results are inconsistent. The traditional diet measurements used by many earlier researchers from the region provided varied information into the feeding habits of predators and included different expressions of stomach contents with counts, weight or volume and frequency of occurrence. Different diet items were grouped as 'very common', 'common', 'frequent' and 'rare' rather than quantitatively. Stomach contents with counts may give the impression that a specific prey item that occurs very frequently in stomachs represents one of the most important prey items. However, if this prey is small they may represent only a small proportion of the total food consumed. If diet is expressed in terms of weight or volume, consumption of a single large prey item would imply that this prey is a major component of the diet, when in fact, very few individuals may have consumed it. Frequency of occurrence can provide information on how often (or not) a particular prey item was eaten, but it provides no indication of the relative importance of prey to the overall diet. To overcome such limitations of individual diet measurements, and to promote consistency in estimation of the relative importance of each prey, the methods developed by Pinkas et al. (1971) have been widely used to facilitate comparison of diets between different predators and within size groups of each predator (Michael et al., 1996; Abdurahiman et al., 2006, 2007; Ellis and Musick, 2006; Stergiou and Fourtouni, 2006). This compound index is an integration of measurement of number, volume and frequency of occurrence to assist in evaluating the relationship of the various food items found in the stomach.

The vast complexity of food web data can be summarized in simplified models consisting of a network of compartments connected by trophic links. Aggregation of species into trophically similar groups is a desirable goal for food web modellers (Yodzis and Winemiller, 1999). Various notions have been suggested for aggregating taxa into trophic groups including guilds which include taxa that exploit similar prey groups (Root, 1973). Many earlier workers have effectively used diet data for guild structuring and trophic interactions within fish communities (Garrison and Link, 2000; Cartes et al., 2002; Hajisamae et al., 2003). Recently, Chambers and Dick (2005) studied the trophic structure of the deep-sea fish community of the eastern Canadian Arctic Sea and suggested that guild formation is an effective method of trophic evaluation in fish communities. Garrison and Link (2000) studied dietary guild structuring and emphasized that ontogenic diet shifts are an important factor in trophic guild determination within fish communities. Moreover, ignoring ontogenic diet shifts in prey resource use probably increases the diet overlap and reduces the usefulness of trophic guilds within fish communities. In the present study, multivariate techniques have been used to explore ontogenic diet shifts and to define groups of species that share similar prey (trophic guilds). The southeastern Arabian Sea, due to its high productivity, is well known as one of the most important commercial fishing zones in the Arabian Sea. This zone, though comprising only about 16% of the Indian coastline, contributed 31.7% (0.74 million tonnes) annually to the marine fish production in India (Vivekanandan et al., 2003).

Therefore, the objectives of this study were: (1) to organize commercially exploited demersal finfishes into trophic guilds in a tropical marine ecosystem, while considering the possible ontogenic driven changes in feeding; (2) to understand prey resource sharing by trophic guilds; (3) to identify high-ranking prey groups in the demersal habitat.

## 2. Materials and methods

### 2.1. Study area

The study was conducted along the southeastern Arabian Sea situated between 11°31′ and 18°45′N latitude and 74°12′ and 78°40′E longitude (Fig. 1). This area, off the maritime state of Karnataka, is well known for coastal fisheries and more than a dozen rivers, which carry nutrient rich waters, open to this Arabian Sea Coast. Most of the rivers form large estuaries which are important both from an ecological and biological point of view. The area is characterized by strong seasonal upwelling with the onset of summer monsoon (June–September) (Madhupratap et al., 2001) which lasts up to the end of August/early September. The coastal upwelling of nutrients occurring during the southwest monsoon supports the rich fisheries in this region, mainly during the post monsoon season (Vivekanandan et al., 2003).

### 2.2. Sample collection

Fish samples were collected biweekly from commercial catches in boats at the fishing ports from August 1999 to July 2001. Demersal finfishes are exploited by two types of trawlers from this coast: small trawlers (Single Day Fleet – SDF), and larger trawlers (Multi Day Fleet – MDF) (Zacharia et al., 1996). The former operate within the 25 m depth zone (average annual catch amounts to 31,000 tonne) and the latter between the 25 and 200 m depth zone (estimated average annual catch amounts to 87,000 tonne). Sample collection from MDF trawlers, which usually operate for 6–7 days, was done with extra care due to the possible chance of stomach contents being decayed during long storage in ice. Since stomach contents will continue to digest (different prey taxa digest at different rates) even after fish are caught from the sea (Sutela and Huusko, 2000; Kim and DeVries, 2001), particular care was taken to avoid samples of highly decomposed and spoiled fishes. Similarly, fishes with regurgitated and inverted stomachs, which could be observed during sampling, were rejected. Commercially exploited demersal species were selected for the study based on their relative abundance in the trawls. It was presumed that this would be an adequate representation of the demersal finfishes of this ecosystem.

Table 1 shows the species selected for the study together with their common name, sample number ($n$) and size groups. The total length of specimens was measured from the tip of the snout to tip of caudal fin (to the nearest mm) and weighed (accuracy: 0.1 g). After measuring length and weight of each specimen, the sex and maturity stages were recorded. Each species was divided into small (when in immature stage), medium (matured large), and large (matured largest) groups to understand the possible ontogenic shifts in diet. The stomachs of all species were carefully removed to prevent loss of the contents and were preserved with 10% buffered formalin. In cases of *Pampus argenteus*, the stomach was pulpy and flabby and hence was not separated from the remaining visceral mass and was preserved wholly. Using a binocular microscope, gut contents were identified up to genus/species level depending upon the state of digestion. For some predators, as in cases of *Pseudorhombus arsius*, fish prey identification was easy. However, in most of the other predators as in *Carcharhinus limbatus*, many fish prey were in a high state of digestion and were identified mainly from the partially digested parts such as scutes (as for carangids), scales (as cycloid or ctenoid fish), beaks (as for cephalopods) and slender bones and fish flesh as unidentified fishes. Although a number of fish families were recorded from different predators, in the present study they were broadly grouped as teleosts. Foraminiferans, mainly from Malabar tonguesoles, and were identified as small

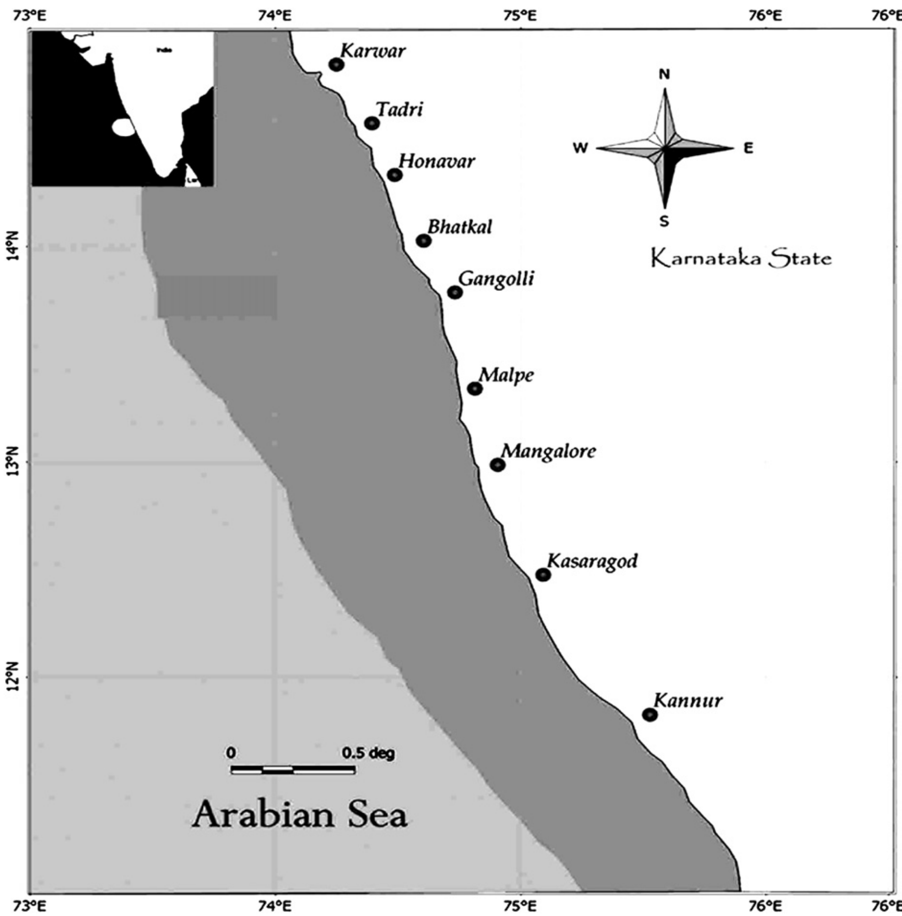


**Fig. 1.** Map of the study area, showing major fishing harbours along Karnataka coast in southeastern Arabian Sea. Fish samples were collected from the area shaded white along the southwest coast of India from August 1999 to July 2001. One degree equals 60 nm.

circular whorls of crystalline materials. Many small crustaceans, other than copepods, were grouped as crustacean zooplankton. Detritus were found as digested or dark flocculent amorphous material. A fraction of diet in most of the fishes was identified as 'digested matter', which is more solid in nature and different from loose amorphous detritus, and was generally made up of bits of unidentified flesh and other animal remains. The net weight of each prey was measured to the nearest milligram using an electronic balance.

### 2.3. Data analysis

The diet was quantified to evaluate the importance of each prey, by percentage frequency of occurrence (%FO), percentage of number (%$N$) and percentage of weight (%$W$) or volume (%$V$) and by one compound index – index of relative importance (IRI) (Pinkas et al., 1971). The IRI was calculated for each prey as:

$$\text{Index of relative importance, } \mathrm{IRI}_i = (\%N_i + \%W_i) \times \%\mathrm{FO}_i$$

**Table 1**
Commercially exploited demersal finfishes, their size ranges, trophic level and diet breadth sampled for the study; $n$ = number of stomachs analysed, TrL = trophic level and $B$ = diet breadth.

| Species | Common name | $n$ | Mean TrL | Mean $B$ | Size groups (total length-mm) | | |
|---|---|---|---|---|---|---|---|
| | | | | | Small | Medium | Large |
| *Epinephelus diacanthus* | Spinycheek grouper | 550 | 4.11 ± 0.29 | 4.85 ± 1.2 | 101–180 | 181–260 | 221–300 |
| *Grammoplites suppositus* | Spotfin flathead | 581 | 3.78 ± 0.14 | 5.41 ± 2.2 | 141–190 | 191–240 | 241–290 |
| *Priacanthus hamrur* | Moontail bullseye | 216 | 3.40 ± 0.44 | 3.16 ± 1.53 | 151–190 | 191–250 | 251–290 |
| *Johnieops sina* | Drab jewfish | 470 | 3.60 ± 0.37 | 2.28 ± 0.24 | 101–120 | 121–150 | 151–180 |
| *Otolithes cuvieri* | Lesser tigertooth croaker | 364 | 3.96 ± 0.28 | 2.81 ± 1.1 | 91–150 | 151–210 | 211–270 |
| *Nemipterus japonicus* | Japanese threadfin bream | 329 | 4.09 ± 0.15 | 5.58 ± 1.8 | 131–180 | 181–255 | 256–305 |
| *Nemipterus mesoprion* | Mauvelip threadfin bream | 555 | 4.14 ± 0.29 | 4.58 ± 2.2 | 76–135 | 136–195 | 196–255 |
| *Leiognathus bindus* | Orangefin ponyfish | 241 | 2.29 ± 0.20 | 3.86 ± 1.19 | 76–87 | 88–99 | 100–111 |
| *Cynoglossus macrostomus* | Malabar tonguesole | 241 | 2.71 ± 0.34 | 1.74 ± 1.2 | 106–125 | 126–145 | 146–165 |
| *Pseudorhombus arsius* | Largetooth flounder | 285 | 4.38 ± 0.17 | 4.58 ± 2.2 | 136–195 | 196–255 | 256–315 |
| *Pampus argenteus* | Silver pomfret | 228 | 2.56 ± 0.37 | 1.99 ± 0.88 | 91–150 | 151–240 | 241–300 |
| *Lactarius lactarius* | Bigjawed jumper | 293 | 3.91 ± 0.36 | 3.68 ± 1.2 | 91–130 | 131–170 | 171–210 |
| *Carcharhinus limbatus* | Blacktip shark | 193 | 4.11 ± 0.19 | 3.98 ± 1.2 | 310–500 | 501–700 | 701–900 |
| *Rhynchobatus djiddensis* | Giant guitarfish | 170 | 3.96 ± 0.26 | 3.76 ± 0.93 | 226–375 | 376–600 | 601–750 |

where $N_i$, $W_i$ and $FO_i$ represent percentages of number, weight and frequency of occurrence of prey *i*, respectively.

This IRI is a modified version of the index where the original term of percentage by volume was replaced by the %*W* term (Alonso et al., 2000) and this index was used to describe predator diets in this study. However, for fishes such as *Leiognathus bindus*, *Cynoglossus macrostomus*, and *Pampus argenteus*, IRI was calculated based on the volume (%*V*) due to the difficulty in estimating the weight of very small prey organisms. In such cases, the volumetric point method suggested by Hynes (1950) was used. In case of fishes such as *C. macrostomus* and *P. argenteus*, which feed largely on detritus, IRI for detritus was calculated based only on volume (%*V*) and frequency of occurrence (%FO). Although detritus cannot be counted, a value of one was given for their number (%*N*) when they were present in the diet to offset distortions in the index. In order to improve interpretation of the IRI, this index was expressed as a percent basis (%IRI) (Cortés, 1997).

Chi-square or non-parametric two-way contingency analysis (Sokal and Rohlf, 1995) was performed to test the independence between the numbers of major prey groups among the predators (Cortés, 1997). Trophic level expresses the position of organisms within the food webs (Odum and Heald, 1975). Following Cortés (1999), the trophic level for each predator was calculated as:

$$\text{Trophic level (TrL)} = 1 + \left(\sum_{j=1}^{n} W_i \times T_i\right)$$

where $W_i$ is the percentage contribution by weight of *i*th prey item, $T_i$ is the trophic level of the *i*th prey item and *i* is the number of prey categories. The values of trophic level for prey species and other taxa were obtained from Vivekanandan et al. (2005) and from the FishBase (Froese and Pauly, 2000).

To establish the level of specialization of each demersal predator and to identify whether they are generalists or specialists (Krebs, 1989) in feeding, Levins (1968) index of diet breadth was calculated for each species as,

$$B = \left(\frac{1}{n-1}\right)\left(\left(\frac{1}{\sum_{i\cdot j=1}^{n} P_{ij}^2}\right) - 1\right)$$

where $B$ = diet breadth; '$p_{ij}$' = the proportion diet of predator '*i*' that is made up of prey item '*j*'; '*n*' = number of prey categories.

### 2.4. Multivariate statistical methods

For creation of trophic guilds, multivariate methods of classification and ordination of diet data were performed using the software package Primer-5 (Clarke and Warwick, 2001). For classification, cluster analysis using the Bray–Curtis similarity coefficient (Bray and Curtis, 1957) was adopted while for ordination, non-metric Multi Dimensional Scaling (MDS) was applied for graphical representation of trophic grouping. Since after square transformation, the difference between the values of IRI and %IRI was negligible, the Bray–Curtis similarity coefficient was calculated with %IRI of prey for each predator. Although 78 different preys were identified, for ease in analysis and interpretation they were grouped as teleosts, penaeid shrimps, benthic crabs, copepods, cephalopods, diatoms etc. (Table 2).

ANOSIM (Analysis of similarities) was employed to test the differences in prey similarity between groups. To identify which prey groups primarily account for observed differences in predator assemblages, the similarity percentage (SIMPER) routine in Primer-5 was used. The BVSTEP routine of the same package was used to determine which prey groups were most influential for predators in the demersal fish community studied.

## 3. Results

### 3.1. General dietary features

A total of 4716 demersal finfish stomach contents from 14 fish species were observed for the trophic guild analysis. Table 2 shows the diet matrix of predators selected in the study. Altogether, 78 different prey taxa were positively identified from the guts of all species. Out of these, fishes (35 prey taxa) and crustaceans (27 prey taxa) were the most important prey resources. Generally, the sergestid shrimp *Acetes indicus*, penaeid shrimps such as *Solenocera choprai*, benthic crabs and copepods were the most important crustaceans. Among fishes, a major proportion could not be identified and were grouped as unidentified fishes. Detritus, diatoms, worms, bivalves and gastropods were also important in the diet of some predators. Two-way contingency table analysis showed that there were significant variations in the number of major prey groups among predators ($\chi^2$ test, df = 65, $P < 0.001$). Among the prey groups, variation was mainly in the number of diatoms, fishes and worms. Among predator groups, *Leiognathus bindus* followed by *Cynoglossus macrostomus* and *Priacanthus hamrur* were the main sources of variation.

### 3.2. Ontogeny and trophic guilds

Cluster analysis, based on the predator's feeding preference and ontogenic shifts in feeding, showed definite trophic guilds having clear separation among different predators (Fig. 2). MDS of different prey taxa supports the results of cluster analysis as the points represented by each predator-formed guild were either entirely or almost entirely discrete from each other (Fig. 3). Subsequent ANOSIM revealed that the diet of many fishes were significantly different among size groups (ANOSIM, Global $R = 0.891$, $P = 0.001$), and fishes with similar feeding habits formed four distinct trophic guilds at a similarity level of 50%. The first guild is 'detritus feeders', which included all size groups of *Cynoglossus macrostomus*, *Pampus argenteus*, *Leiognathus bindus* and small *Priacanthus hamrur*. Guild two is 'shrimp feeders', the largest guild identified, and it included all size groups of *Rhynchobatus djiddensis* and *Nemipterus mesoprion*, medium and large *Nemipterus japonicus*, *P. hamrur* and *Grammoplites suppositus*, small and medium *Otolithes cuvieri* and small *Lactarius lactarius*. Guild three, 'crab and squilla feeders', consisted of small and medium sized *Epinephelus diacanthus*, *N. japonicus* and *G. suppositus*, medium and large *Johnieops sina*. The fourth trophic guild is 'piscivores', which constituted all size groups of *Pseudorhombus arsius* and *Carcharhinus limbatus*, large *O. cuvieri* and *E. diacanthus* and medium and large *L. lactarius*. Again, based on cluster analysis, several (9 in total) sub-guilds (Fig. 2) were identified within the guilds.

### 3.3. Trophic level and diet breadth

With ontogeny, distinct changes in both trophic level and diet breadth were observed for most of the predators. The mean trophic level varied from 2.2 ± 0.1 in large *Leiognathus bindus* to 4.6 ± 0.2 in large *Epinephelus diacanthus*. Diet breadth ranged from 1.4 ± 0.3 in medium *Pampus argenteus* to 8.3 ± 0.2 in medium *Nemipterus japonicus*. The mean trophic level and the mean diet breadth of medium and large predators had a positive correlation ($R^2 = 0.7$). However, for small predators, the correlation was weak between trophic level and diet breadth (Fig. 4).

**Table 2**
Diet matrix of commercially exploited demersal finfishes with their prey arranged as groups (summarized from78 prey types) based on the % values of index of relative importance.

| | *Johnieops sina* | | | *Otolithes cuvieri* | | | *Leiognathus bindus* | | | *Pseudorhombus arsius* | | | *Priacanthus hamrur* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large |
| Teleosts | 21.9 | 14.0 | 3.6 | 2.9 | 15.7 | 75.7 | 6.9 | 6.8 | 2.2 | 99.2 | 73.8 | 61.0 | 4.2 | 9.3 | 2.6 |
| Penaeid shrimps | 2.0 | 1.2 | 5.7 | 8.5 | 8.0 | 5.2 | 0.0 | 0.0 | 0.0 | 0.4 | 17.6 | 16.8 | 0.1 | 2.5 | 0.0 |
| Benthic crabs | 0.0 | 0.0 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 19.6 | 1.1 | 0.0 | 0.2 |
| Crustacean larvae | 0.0 | 0.0 | 0.0 | 1.7 | 1.1 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 5.9 | 0.5 | 0.0 |
| *Oratosquilla nepa* | 0.0 | 50.0 | 50.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Acetes indicus* | 1.3 | 24.9 | 29.2 | 84.2 | 74.2 | 13.5 | 0.0 | 0.0 | 0.0 | 0.4 | 5.9 | 0.0 | 6.0 | 80.0 | 96.6 |
| Copepods | 37.4 | 3.5 | 6.5 | 1.8 | 0.5 | 3.8 | 24.3 | 24.6 | 19.7 | 0.0 | 0.0 | 0.0 | 4.8 | 0.2 | 0.0 |
| Crustacean zooplankton | 5.0 | 2.0 | 0.3 | 0.9 | 0.3 | 0.0 | 1.4 | 4.8 | 8.5 | 0.0 | 1.4 | 1.1 | 0.0 | 0.0 | 0.0 |
| Cephalopods | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.6 | 0.0 | 1.4 | 0.1 |
| Gastropods | 0.6 | 0.1 | 0.9 | 0.0 | 0.0 | 0.0 | 0.6 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Bivalves | 0.4 | 0.0 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Polychaete worms | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 1.3 | 4.4 | 3.1 | 0.0 | 1.0 | 0.9 | 18.8 | 0.1 | 0.0 |
| Nematodes | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Diatoms | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 3.1 | 6.4 | 7.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Sand | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Foraminiferans | 1.5 | 0.1 | 0.2 | 0.0 | 0.0 | 0.0 | 1.2 | 0.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Detritus | 29.9 | 3.1 | 1.4 | 0.0 | 0.2 | 0.3 | 58.8 | 51.5 | 58.8 | 0.0 | 0.0 | 0.0 | 59.1 | 6.0 | 0.6 |

| | *Lactarius lactarius* | | | *Pampus argenteus* | | | *Carcharhinus limbatus* | | | *Nemipterus japonicus* | | | *Nemipterus mesoprion* | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large |
| Teleosts | 0.9 | 69.5 | 98.6 | 1.7 | 1.9 | 2.8 | 96.6 | 63.2 | 88.6 | 28.3 | 19.8 | 20.7 | 7.5 | 8.6 | 13.7 |
| Penaeid shrimps | 0.0 | 0.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.2 | 9.9 | 32.8 | 33.4 | 65.4 | 23.1 | 18.1 |
| Benthic crabs | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 29.9 | 17.3 | 13.5 | 0.0 | 0.1 | 1.2 |
| Crustacean larvae | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Oratosquilla nepa* | 0.8 | 1.4 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.4 | 0.0 | 11.5 | 0.5 | 0.0 | 2.7 | 0.0 | 0.0 |
| *Acetes indicus* | 96.1 | 24.8 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 15.6 | 22.8 | 25.5 | 24.2 | 65.4 | 49.1 |
| Copepods | 0.0 | 0.0 | 0.0 | 39.9 | 42.8 | 45.3 | 0.0 | 0.0 | 0.0 | 1.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Crustacean zooplankton | 0.0 | 0.0 | 0.0 | 7.2 | 4.3 | 5.9 | 0.0 | 0.1 | 0.0 | 0.3 | 0.1 | 0.0 | 0.0 | 0.0 | 0.3 |
| Cephalopods | 0.0 | 0.1 | 0.3 | 0.0 | 0.0 | 0.0 | 3.2 | 36.0 | 11.2 | 2.5 | 6.6 | 6.9 | 0.1 | 2.8 | 17.6 |
| Gastropods | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 |
| Bivalves | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| Polychaete worms | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 |
| Nematodes | 0.0 | 0.0 | 0.0 | 0.2 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Diatoms | 0.0 | 0.0 | 0.0 | 2.3 | 2.8 | 4.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Sand | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Foraminiferans | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Detritus | 2.1 | 3.8 | 0.9 | 48.7 | 48.2 | 41.3 | 0.2 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

| | *Rhynchobatus djiddensis* | | | *Cynoglossus macrostomus* | | | *Grammoplites suppositus* | | | Spinycheek grouper | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large |
| Teleosts | 2.9 | 2.2 | 21.2 | 12.4 | 11.6 | 2.0 | 15.4 | 13.5 | 9.3 | 1.7 | 5.8 | 79.5 |
| Penaeid shrimps | 9.2 | 19.1 | 4.5 | 0.0 | 0.0 | 0.0 | 11.0 | 39.0 | 51.3 | 0.3 | 2.9 | 11.7 |
| Benthic crabs | 0.2 | 1.2 | 6.1 | 0.0 | 0.0 | 0.0 | 19.7 | 42.4 | 31.7 | 81.8 | 55.2 | 8.8 |
| Crustacean larvae | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Oratosquilla nepa* | 2.9 | 3.9 | 1.2 | 0.0 | 0.1 | 0.0 | 50.1 | 0.5 | 0.0 | 7.6 | 6.7 | 0.0 |
| *Acetes indicus* | 84.6 | 69.8 | 55.8 | 0.0 | 0.0 | 0.0 | 0.0 | 4.5 | 7.7 | 8.0 | 25.3 | 0.0 |
| Copepods | 0.0 | 0.0 | 0.0 | 1.1 | 3.1 | 2.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Crustacean zooplankton | 0.0 | 0.0 | 0.0 | 6.1 | 6.8 | 5.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Cephalopods | 0.0 | 3.8 | 11.2 | 0.0 | 0.0 | 0.0 | 1.2 | 0.0 | 0.0 | 0.0 | 2.2 | 0.0 |
| Gastropods | 0.0 | 0.0 | 0.0 | 12.0 | 3.8 | 8.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Bivalves | 0.0 | 0.0 | 0.0 | 2.9 | 6.6 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Polychaete worms | 0.0 | 0.0 | 0.0 | 15.9 | 14.4 | 47.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Nematodes | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Diatoms | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Sand | 0.0 | 0.0 | 0.0 | 3.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Foraminiferans | 0.0 | 0.0 | 0.0 | 17.9 | 9.9 | 2.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Detritus | 0.2 | 0.1 | 0.0 | 28.7 | 42.7 | 29.8 | 2.7 | 0.1 | 0.0 | 0.6 | 2.0 | 0.0 |

The mean trophic level of all guilds was $3.7 \pm 0.7$. Among the different trophic guilds, piscivores, which largely consume teleosts, had the highest mean trophic level ($4.3 \pm 0.2$), whereas true *Acetes* feeders consumed a broader range of prey items ($B = 4.5 \pm 1.5$). Among piscivores, the sub-guild 'fish and shrimp feeders' had both the highest mean trophic level and diet breadth ($4.4 \pm 0.2$ and $4.5 \pm 0.4$, respectively) followed by 'true piscivores' ($4.2 \pm 0.1$ and $3.6 \pm 1.4$, respectively) and 'fish and *Acetes* feeders' ($4.1 \pm 0.2$ and $2.2 \pm 0.3$, respectively). Detritus feeders, which consume largely detritus, had very low values of mean trophic level and diet breadth ($2.7 \pm 0.4$ and $2.7 \pm 1.0$ respectively). Among the detritus feeders, the sub-guild 'detritus and worm feeders' had the highest mean trophic level ($2.7 \pm 0.1$) and diet breadth ($3.8 \pm 0.8$), and among these, small *Johnieops sina* had the highest trophic level and diet breadth ($3.3 \pm 0.5$ and $3.7 \pm 1.4$, respectively).

### 3.4. Trophic guild attributes

#### 3.4.1. Detritus feeders

A large proportion of detritus and copepods, in the diet of *Carcharhinus limbatus*, *Pampus argenteus*, *Leiognathus bindus* and small *Priacanthus hamrur*, obviously formed a separate guild of

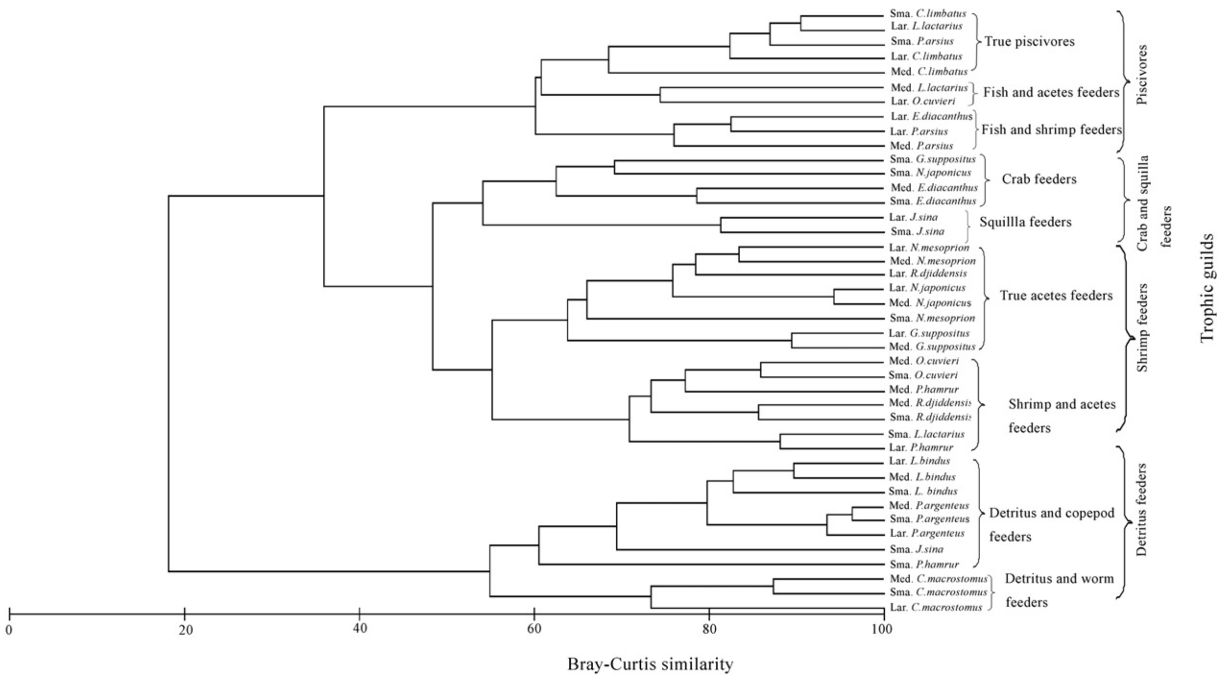


**Fig. 2.** Dendrogram showing the categorization of different trophic guilds within the demersal finfishes using group average clustering (Bray–Curtis similarity). Four major trophic guilds were formed at a similarity level of 50%. Predators grouped within a guild have significantly similar diet.

'detritus feeders'. SIMPER analysis showed an average group similarity of 62.8% (where 100% is complete similarity) with detritus contributing 60.9% and copepods contributing 21.2% to the similarities of the diet (Table 3). Based on their differential proportion of detritus and copepods, fishes of these guilds were again subdivided into 'detritus and worm feeders' and 'detritus and copepod feeders'. Significant differences were observed in similarity of diet between these sub-guilds (ANOSIM, Global $R$: 0.88, $P = 0.001$). *Cynoglossus macrostomus* consumed polychaete worms (21.9%) in addition to the large contribution of detritus (42.7%) to the diet and thus separated from the remaining detritus feeders as 'detritus and worm feeders' with an average similarity of 68.0%. However, the remaining eight detritus feeders, which included small *P. hamrur* and small *Johnieops sina* and all size groups of *P. argenteus* and *L. bindus*, formed a subcluster 'detritus and copepod feeders' with an average similarity of 76.1%. Fishes of these sub-guilds consumed large proportion of detritus (57.4%) and copepods (31.8%).

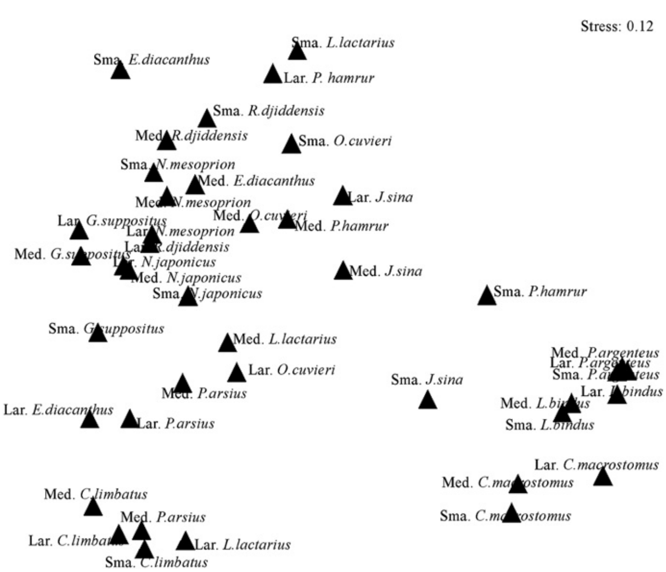


**Fig. 3.** Multi dimensional scaling (MDS) ordination of finfishes into guilds based on similarities. The low stress value (0.12) indicated a good separation among trophic guilds.

*3.4.2. Shrimp feeders*

This guild forms the largest demersal trophic group which were clustered together due to their greater feeding affinity to penaeid and non-penaeid shrimps. A total of fifteen size classes of predators were included in this group with an average diet similarity of 55.6% and the contribution to diet similarity was mainly from the non-penaeid shrimp, *Acetes indicus* (67.3%) and penaeid shrimps (17.6%) (Table 3). At a similarity level of 60%, this large cluster was again subdivided into 'true *Acetes* feeders' and 'shrimp and *Acetes* feeders'. While all size groups of *Nemipterus mesoprion*, medium and large *Nemipterus japonicus*, small and large *Grammoplites suppositus* and large *Rhynchobatus djiddensis* were together grouped as 'true *Acetes* feeders', the sub-guild 'shrimp and *Acetes* feeders' was constituted by small and medium *Otolithes cuvieri*, small and medium *R. djiddensis*, medium and large *Priacanthus hamrur* and small *Lactarius lactarius*. The SIMPER study showed an average similarity of 83.5% for 'true *Acetes* feeders' and they are nearly monophagous to this important prey, *A. indicus* which contributed 92.8% to total similarity of the prey of these predators. Penaeid shrimps (37.6%) and *A. indicus* (31.7%) were largely responsible for the observed total similarity of preys of these predators. Significant differences were observed between the similarity of 'true *Acetes* feeders' and 'shrimp and *Acetes* feeders' (ANOSIM, Global $R$: 0.67, $P = 0.001$).

*3.4.3. Crab and squilla feeders*

Benthic crabs and squilla dominated the diet of six predators and they formed a separate cluster 'crab and squilla feeders'. The SIMPER analysis showed that the squilla (mantis shrimp)

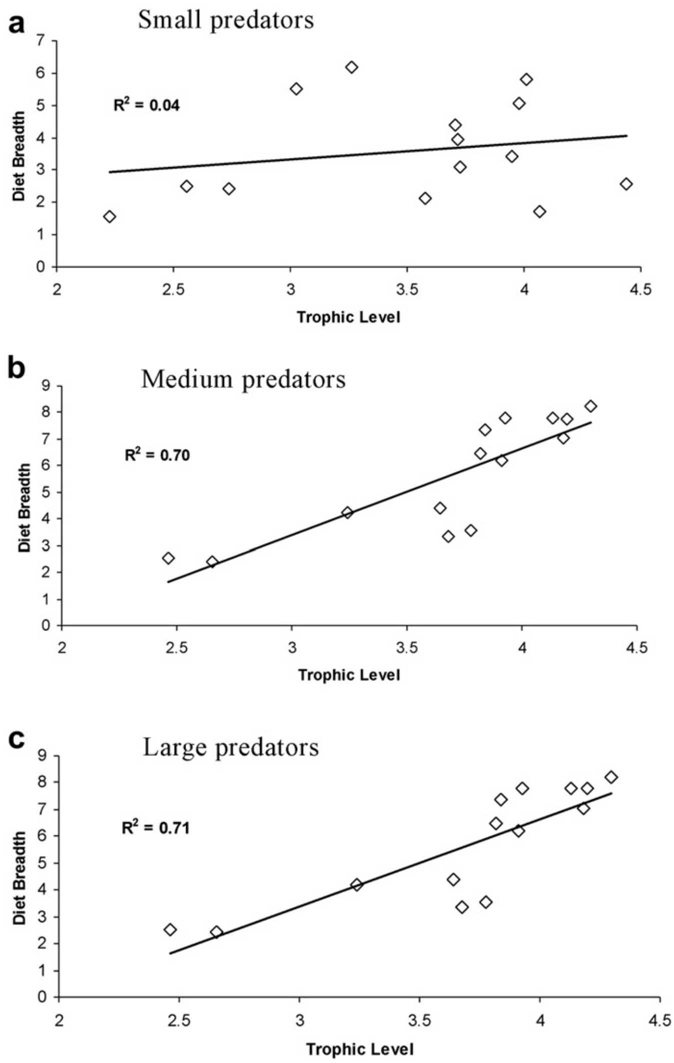


**Fig. 4.** Relationship between diet breadth and trophic level of a) small predator b) medium predators and c) large predators.

*Oratosquilla nepa* and benthic crabs contributed 34.3% and 24.4%, respectively to the observed average similarity of 48.3% (Table 3). Medium and large *Johnieops sina*, however, separated from the remaining groups and formed a sub-guild ‘squilla feeders’. This sub-guild had an average similarity of 85.3% and *O. nepa* contributed 58.6% to the similarity. The remaining four ‘crab and squilla feeders’, which include small *Epinephelus diacanthus*, small *Nemipterus japonicus* and small *Grammoplites suppositus* and medium *E. diacanthus*, clustered together and form a separate ‘crab feeders’ with an average similarity of 51.5%. Benthic crabs alone contributed 56.3% to the observed similarity.

#### 3.4.4. Piscivores

Teleost prey formed the most important diet of all size groups of *Carcharhinus limbatus*, medium and large sized fishes of *Pseudorhombus arsius*, *Otolithes cuvieri* and *Epinephelus diacanthus* and therefore formed a separate trophic guild. SIMPER analysis showed an average similarity of 74.7% with teleosts contributing to 96.3% of the similarities in the diet (Table 3). Piscivores could be subdivided into three sub-guilds based on the preference of other prey in addition to the most important teleost prey to the diet. The large preference for teleosts, most often >90% by IRI, by all size groups of *C. limbatus*, small *P. arsius* and large *Lactarius lactarius* clearly formed ‘true piscivores’ among piscivores. SIMPER showed an average similarity of 83.0% for true piscivores and teleosts alone contributed 97.7% of the similarity in diet. Medium and large *P. arsius* and large *E. diacanthus* together formed a cluster of ‘fish and shrimp feeders’. They had an average similarity of 82.4% in diet. Penaeid shrimps contributed 16.2% in addition to the major contribution of teleosts (79.32%) to the diet similarity of this sub-guild. The remaining piscivores, such as large *O. cuvieri* and medium *L. lactarius*, formed a sub-guild ‘fish and *Acetes* feeders’ with an average similarity of 83.8% and consumed *Acetes indicus* (16.1% by contribution) in addition to the large contribution of teleosts (82.9%) to diet. ANOSIM also revealed the existence of three sub-guilds among ‘piscivores’ (ANOSIM, Global $R$: 0.87; $P = 0.001$) and ‘true piscivores’ were apparently distinguished from ‘fish and shrimp feeders’ (ANOSIM, Global $R$: 0.99, $P = 0.001$).

**Table 3**
Relative similarities of different prey categories within major guilds based on SIMPER analysis. SD – standard deviation.

| Trophic guilds | Prey category | Average similarity | Sim/SD | % Contribution |
|---|---|---|---|---|
| Detritus feeders | | 62.8 | | |
| | Detritus | 45.2 | 3.9 | 60.9 |
| | Copepods | 23.2 | 1.1 | 21.2 |
| Shrimp feeders | | 55.6 | | |
| | *Acetes indicus* | 56.0 | 1.4 | 67.3 |
| | Penaeid shrimps | 20.9 | 0.8 | 17.6 |
| | Teleosts | 10.0 | 1.2 | 10.6 |
| Crab and squilla feeders | | 48.3 | | |
| | *Oratosquilla nepa* | 29.5 | 0.95 | 34.3 |
| | Benthic crabs | 31.2 | 0.71 | 24.4 |
| Piscivores | | 74.7 | | |
| | Teleosts | 80.6 | 6.88 | 96.3 |

### 3.5. Significant prey organisms

BVSTEP analysis provided the list of highly ranked prey organisms to various trophic guilds of the demersal fish community (Table 4). In each step, after a series of deletion of prey groups that did not influence the ordination process, the prey types which were observed to be highly influential for the predators were obtained. Among the five variable lists, *Acetes indicus*, penaeid shrimps, benthic crabs, teleosts and copepods were highly influential ($R^2 = 0.96$), whereas in the list with six variables, additional groups/species such as of cephalopods, diatoms, polychaete worms, *Oratosquilla nepa* and detritus were also highly influential. *Acetes indicus*, teleosts and penaeid shrimps were subjected to high predation by different demersal finfishes in the ecosystem.

**Table 4**
Significant prey groups in the benthic ecosystem in southeastern Arabian Sea based on BVSTEP analysis.

| No. of variables | $R^2$ | Prey groups with highest variability |
|---|---|---|
| 5 | 0.960 | Teleosts, penaeid shrimps, benthic crabs, *Acetes indicus*, copepods |
| 5 | 0.953 | Teleosts, penaeid shrimps, benthic crabs, *Acetes indicus*, cephalopods |
| 6 | 0.953 | Teleosts, benthic crabs, *Acetes indicus*, cephalopods, diatoms, detritus |
| 6 | 0.952 | Teleosts, penaeid shrimps, *Oratosquilla nepa*, *Acetes indicus*, polychaetes, detritus |

## 4. Discussion

The present study grouped the commercially exploited demersal finfish community of the southeastern Arabian Sea into four broad trophic guilds. Trophic guilds identified during the present study are based on the predator's feeding similarity in exploiting different prey resources in the ecosystem. Hierarchical clustering based on the Bray–Curtis similarity coefficient was used to group trophic guilds because it is often considered as a satisfactory coefficient for biological data (Clarke and Warwick, 1994). Though hierarchical clustering has the disadvantage of overemphasizing discontinuity, use of MDS proved to be a useful tool to exhibit individual predator relationships. According to a rough rule of thumb, for two-dimensional ordinations, stress value $<0.2$ gives good ordinations with no tendency towards misinterpretations (Clarke and Warwick, 1994).

Qasim (1972) attempted to group Indian marine fishes into nine broad trophic groups. He reported the dominance of carnivores over other groups. Most of the fish species during the present study are carnivores and the extent of carnivory increased with ontogeny. Many of the top predatory fishes which include large, medium and small size groups of *Carcharhinus limbatus*, *Otolithes cuvieri*, large *Pseudorhombus arsius*, and *Nemipterus mesoprion*, are piscivores and they become more piscivorous with size. Such ontogenic diet shifting is common in many fishes (Olson, 1996; Garrison and Link, 2000; Vivekanandan, 2001). Study of the diet of carnivorous fishes in relation to ontogeny showed that many fishes became more ichthyophagous with size and age (Renones et al., 2002; Manojkumar, 2003). Fishes with omnivorous feeding habits were grouped in 'detritus feeders'. Some species, specifically small *Cynoglossus macrostomus* and small *Pampus argenteus* during their young stages were omnivores and consumed mainly diatoms, copepods, other zooplankton and detritus; however, with increase in size, their diet shifted to mainly copepods, fish remains and detritus. Pati (1978) also observed a striking change in the diet of *P. argenteus* from the post larvae to adult. He reported that phytoplankters are the favourite diet of post larvae but as the length progressed they shifted to feeding on copepods and zooplankton. It is clear from the present study that carnivores when they are young, preferred crustaceans and other small invertebrates and the preference changed for teleost fishes and other carnivores as they grew in size and age. Similar ontogenic diet shifts with size were reported in *Epinephelus diacanthus* (Tessy, 1994), *Priacanthus hamrur* (Philip, 1998), *O. cuvieri* (Manojkumar, 2003), *Nemipterus japonicus* (Rao and Rao, 1991), *N. mesoprion* (Rao, 1989), *Lactarius lactarius* (Zacharia, 2003), *P. arsius* (Ramanathan and Natarajan, 1980) and *C. limbatus* (Heupel and Hueter, 2002).

There are many problems and uncertainties associated with diet analysis. Although 4716 fish guts belonging to fourteen fish species were analysed, the number of positively identified preys was 78. Unidentified and partly digested prey of many predators made the analysis difficult, in particular the analysis of *Carcharhinus limbatus* stomach contents, which were always in partly digested condition. The flesh of cephalopods, a large quantity of which was identified from *C. limbatus*, digests faster than fish flesh (Bigg and Fawcett, 1985) and their undigested beaks most often supported their indirect identification. Similarly, some prey items such as fish scales which get entangled in mucous or detritus are resistant to digestion and can stay for a long time in gut contents thereby creating analytical uncertainty in some fishes like *Leiognathus bindus* and *Pampus argenteus*. Unidentified fishes and digested animal matter, most often become a hindrance to precise identification of trophic guilds among fish communities due to their overall effect in increasing diet overlap and reducing separation between guilds (Garrison and Link, 2000). Regurgitation, most frequently observed in many groupers (Randall, 1967), produced an inaccurate picture of diet in *Epinephelus diacanthus*. Hence, specimens above 300 mm of the *E. diacanthus* and which were found to always have everted and empty stomachs in trawl catches, were discarded in the diet analysis.

Trophic guilds identified during the present study have similarity to other studies in other ecosystems. Garrison and Link (2000) analysed the dietary guild structure of the fish community in the northeastern United States based on ontogenic diet shift in six major trophic guilds. Piscivores, shrimp feeders and crab feeders, are common guilds in the northeastern United States and southeastern Arabian Sea. Similarly, based on seven years of multi-season trophic data, Livingston's (1982) grouped seagrass associated fishes in Apalachee Bay of Florida into three major trophic groups. Although this study cannot be directly compared with the present one, the methodology in grouping guilds based on prey contribution is quite similar to the present study. The similarity analysis which formed the basis of trophic guild determination, showed the pattern of prey resource use from small prey to large prey organisms by each predator in the guild. Generally, in marine systems, prey range from polychaetes to fish or small pelagic prey to benthic invertebrates, and such a prey pattern occurs in coastal marine ecosystems and coral reefs (Ross, 1986). In the present study, the highest trophic separation was observed between 'detritus feeders' and 'shrimp feeders' and between 'detritus feeders' and 'piscivores'. Due to ontogenic diet changes, many species were segregated into different guilds. Although there was no specific study on mouth parts and morphology for food and feeding in the present work, many authors attributed the changes in morphological features and habitat of fishes to food partitioning (Werner and Gilliam, 1984; Crowder, 1986; Liem, 1990). Vivekanandan (2001) reported crustaceans like penaeid prawns as the major food of *Nemipterus japonicus* (and that their body is morphologically adapted to predate such crustaceans) and hence they were grouped into 'shrimp feeders'. However, while all size groups of *Nemipterus mesoprion* preferred largely *Acetes* spp., only large and medium *N. japonicus* preferred *Acetes* spp. in their diet. Small *N. japonicus* were grouped in 'crab and squilla feeders'. This difference is primarily due to the differential depth distribution and habitat preference of the two species. While *N. japonicus* is a strict demersal and a more shallow-water species, *N. mesoprion* is a more deep-water denizen and able to ascend the column to feed on the mid-water swarming crustacean, *Acetes indicus*.

A trophic level of fishes varies with the prey composition and is usually high for large predators and carnivores (Vivekanandan et al., 2005). The positive correlation between trophic level and diet breadth in medium and large fishes shows that ontogeny has influenced the relationship between them. The high availability of most preferred prey is likely to be a factor in decreasing the relationship in small fishes. In juveniles, a low trophic level was recorded owing to the fact that the prey composition and diversity was much less and usually the trophic level increased during ontogeny, because larvae and juveniles are likely to feed at lower levels than conspecific adults (Pauly et al., 2001). Hence, there was a shift in trophic level in accordance with the ontogenic diet shift. This is in agreement with studies of Cortés (1999) on elasmobranchs. The lack of high diet breadth in some predators may be due to species foraging habits and/or predatory ability. Crowder and Cooper (1982) suggested that due to a high capture rate, diet breadth of a predator would be narrowest when food in a particular environment is abundant.

Members of various guilds, mainly shrimp feeders, showed strong impact on the sergestid shrimp, *Acetes indicus*. The BVSTEP analysis carried out in the present study also signals the role of *A. indicus* as a major link to sustain the trophic guilds especially 'shrimp feeders'. The sergestid shrimp, *A. indicus* is one of the low trophic level marine crustaceans (Vivekanandan et al., 2005). *Acetes* catches in India contribute to about 11.2% of world production and *A. indicus* is the most abundant species among the sergestid shrimps (Jaiswar and Chakraborty, 2005). It contributes 75% of the total non-penaeid shrimp landing in India and their exploitation is highest along the northeast Arabian Sea (Arvindandakshan and Karbhari, 1988). However, there is no information on the biomass of *A. indicus* in the southeastern Arabian Sea where exploitation of this species is also minimal. To ensure sustainable stocks of *Acetes* in the region covering the requirement of the fishery and the forage needs of predators, an appropriate management plan has to be evolved.

Members of the guild 'detritus feeders' such as *Cynoglossus macrostomus*, *Pampus argenteus* and *Leiognathus bindus* were observed to feed exclusively on detritus. Qasim (1972) concluded that detritus occurs at the bottom in coarsely particulate form and is perhaps the most readily available and universally abundant food material in shallow areas of the sea. Goswami (1996) estimated zooplankton biomass of the Indian EEZ and observed pockets of high zooplankton biomass along the southeastern Arabian Sea. Among the zooplankton, copepods are one of most dominant groups in the Arabian Sea (Madhupratap, 1999) and they formed a significant part of the diet in many fishes.

## 5. Conclusion

The present study brings out trophic groupings of fourteen demersal finfish species based on the predators feeding similarity. Demersal finfishes exploited from the southeastern Arabian Sea are benthic carnivores and are specialized feeders on benthic invertebrates and teleosts. As observed in most other predatory fishes, each predator in the present study changed its diet with size and this ontogenic feeding variation largely determined their further sub-grouping among them. The role of *Acetes indicus* as a major prey organism in the ecosystem which sustains many trophic guilds has been emphasized. Although diverse prey types were found, usually two or three prey types were dominant and shared between many predators and these prey types as a whole determined the trophic guild pattern.

## Acknowledgments

We are thankful to the Director, Central Marine Fisheries Research Institute, Cochin and Dr. C. Muthiah, Scientist-in-Charge of Mangalore Research Centre of CMFRI for providing facilities and encouragement. This work was funded by the Indian Council of Agricultural Research (ICAR), New Delhi through a cess fund scheme on trophic modelling (064/004). We are grateful to all staff of Mangalore Research Centre of CMFRI for their help in field work. We would also like to thank Dr. E. Vivekanandan and two anonymous reviewers for constructive criticism to improve the manuscript.

## References

Abdurahiman, K.P., Nayak, T.H., Zacharia, P.U., Mohamed, K.S., 2006. Diet and trophic ecology of silver pomfret, *Pampus argenteus* (Euphrasen, 1788) exploited from the Southeast Arabian Sea. Journal of the Marine Biological Association of India 48 (2), 206–212.

Abdurahiman, K.P., Nayak, T.H., Zacharia, P.U., Mohamed, K.S., 2007. Trophodynamics of spotfin flathead, *Grammoplites suppostius* (Troschel, 1840) from the Southeast Arabian Sea. Asian Fisheries Science 20, 125–143.

Alonso, K.M., Crespo, E.A., Pedraza, S.N., García, N.A., Coscarella, M., 2000. Food habits of the South American sea lion (*Otaria flavescens*) of Patagonia, Argentina. Fishery Bulletin 98, 250–263.

Arvindandakshan, M., Karbhari, J.P., 1988. *Acetes* shrimp fishery of Bombay coast. Marine Fisheries Information Service Technical & Extension Series 80, 28–29.

Bigg, M.A., Fawcett, I., 1985. Two biases in diet determination of northern fur seals (*Callorhinus ursinus*). In: Beddington, J.R. (Ed.), Marine Mammals and Fisheries. George Allen and Unwin Ltd., London, pp. 284–299.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27, 325–349.

Cartes, J.E., Abello, P., Lloris, D., Carbonell, A., Torres, P., Maynou, F., Desola, L.G., 2002. Feeding guilds of western Mediterranean demersal fish and crustaceans: an analysis based on a spring survey. Scientia Marina 66, 209–220.

Chambers, C.A., Dick, T.A., 2005. Trophic structure of one deep-sea benthic fish community in the eastern Canadian Arctic: application of food, parasites and multivariate analysis. Environmental Biology of Fishes 74, 365–378.

Christensen, V., Pauly, D., 1997. Placing fisheries resources in their ecosystem context. EC Fisheries Cooperation Bulletin 10, 9–11.

Clarke, K.R., Warwick, R.M., 1994. Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation. Natural Environment Research Council, Swindon, UK.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation, second ed. Primer-E Ltd, Plymouth.

Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 5, 726–738.

Cortés, E., 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science 56, 707–717.

Crowder, L.B., 1986. Ecological and morphological shifts in Lake Michigan fishes: glimpses of the ghost of competition past. Environmental Biology of Fishes 16, 147–157.

Crowder, L.B., Cooper, W.E., 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63, 1802–1813.

Devaraj, M., 1998. Food and feeding habits of the spotted seer, *Scomberomorus guttatus* (Bloch and Schneider), in the Gulf of Mannar and Palk Bay. Journal of the Marine Biological Association of India 40, 105–124.

Dhulked, M.H., 1962. Observations on the food and feeding habits of the Indian oil sardine *Sardinella longiceps* Val. Indian Journal of Fisheries 9, 37–47.

Ellis, J.K., Musick, J.A., 2006. Ontogenetic changes in the diet of sandbar shark, *Carcharhinus plumbeus*, in lower Chesapeake Bay and Virginia (USA) coastal waters. Environmental Biology of Fishes 80, 51–67.

Froese, R., Pauly, D., 2000. FishBase 2000: Concepts, Design and Data Sources. ICLARM, Los Banos, Laguna, Philippines, 344 pp.

Garrison, L.P., Link, J.S., 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202, 231–240.

Gerking, S.D., 1994. Feeding Ecology of Fish. Academic Press, San Diego, California.

Goswami, S.C., 1996. Zooplankton biomass and potential fishery resources of the EEZ of India. In: Qasim, S.Z. (Ed.), India's EEZ. Omega Scientific Publishers, New Delhi, p. 95.

Hajisamae, S., Chou, L.M., Ibrahim, S., 2003. Feeding habits and trophic organization of the fish community in shallow waters of an impacted tropical habitat. Estuarine Coastal and Shelf Science 58, 89–98.

Heupel, M.R., Hueter, R.E., 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery. Marine and Freshwater Research 53, 543–550.

Hynes, H.B., 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. Journal of Animal Ecology 19, 36–58.

Jaiswar, A.K., Chakraborty, S.K., 2005. Acetes, the preferred food of fishes along the northwest coast of India. Indian Journal of Fisheries 52, 215–219.

Kagwade, P.V., 1964. The food and feeding habits of the Indian oil sardine *Sardinella longiceps* Valenciennes. Indian Journal of Fisheries 11, 345–370.

Kim, G.W., DeVries, D.R., 2001. The influence of adult fish predation on freshwater, limnetic fish larvae: a mesocosm experiment. Transactions of the American Fisheries Society 130, 189–203.

Krebs, C.J., 1989. Ecological Methodology. Harper Collins, New York.

Larkin, P.A., Clark, C.W., Dann, N., Dutt, S., Hongskul, V., Levin, S.A., Newman, C.G., Pauly, D., Radach, D., Rosental, H.K., 1984. Strategies for multispecies management. In: May, R.M. (Ed.), Exploitation of Marine Communities. Springer-Verlag, Berlin, pp. 287–301.

Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, Princeton, 120 pp.

Liem, K.F., 1990. Aquatic versus terrestrial feeding modes: possible impacts on the trophic ecology of vertebrates. American Zoologist 30, 209–221.

Livingston, R.J., 1982. Trophic organization of fishes in a coastal seagrass system. Marine Ecology Progress Series 7, 1–12.

Longhurst, A.R., Pauly, D., 1987. Ecology of Tropical Oceans. Academic Press, San Diego, California, 389 pp.

Madhupratap, M., Nair, K.N.V., Gopalakrishnan, T.C., Haridas, P., Nair, K.K.C., Venugopal, P., Mangesh, G., 2001. Arabian Sea oceanography and fisheries of the west coast of India. Current Science 81, 355–361.

Madhupratap, M., 1999. Some special features of the trophic relationship in the Arabian Sea. In: Qasim, S.Z. (Ed.), India's EEZ. Omega Scientific Publishers, New Delhi, p. 87.

Manojkumar, P.P., 2003. Observations on the food and feeding habits of *Otolithes cuvieri* (Trewavas) off Veraval. Indian Journal of Fisheries 50, 379–385.

Mathews, C.P., Granados, J.L., Arvizu, J., 1973. Results of the exploratory cruises of the Alejandro de Humbolt in the Gulf of California. Reports of California Cooperative Oceanic Fisheries Investigations 17, 101–111.
Michael, P.A., John, A.M., Colvocoresses, J.A., 1996. Food and ontogenetic shifts in feeding of the goosefish, *Lophius americanus*. Journal of Northwest Atlantic Fishery Science 18, 99–103.
Odum, W.E., Heald, E.J., 1975. The detritus-based food web of an estuarine mangrove community. In: Cronin, L.E. (Ed.), Estuarine Research. Academic Press, New York, pp. 265–286.
Olson, M.H., 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77, 179–190.
Pati, S., 1978. The food and feeding habits of silver pomfret, *Pampus argenteus* (Euphrasen) with a note on its significance in fishery. In: Proceedings of 65th Indian Science Congress 3, pp. 230–231.
Pauly, D., 1998. Tropical fishes: patterns and propensities. Journal of Fish Biology 53, 1–17.
Pauly, D., Palomares, L., Froese, R., Sa-a, P., Vakily, M., Preikshot, D., Wallace, S., 2001. Fishing down Canadian aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences 58, 51–62.
Perez-Espana, H., Saucedo-Lozano, M., Raymundo-Huizar, A.R., 2005. Trophic ecology of demersal fishes from the Pacific shelf off central Mexico. Bulletin of Marine Science 77, 19–31.
Philip, K.P., 1998. Food and feeding habits of *Priacanthus hamrur* (Forsskål) from the upper east coast of India. Bulletin of Fisheries Survey of India 26, 12–25.
Pinkas, L.M., Oliphant, S., Iverson, I.L.K., 1971. Food habits of albacore, bluefin tuna and bonito in California waters. California Fish Game 52, 1–105.
Qasim, S.Z., 1972. The dynamics of food and feeding habits of some marine fishes. Indian Journal of Fisheries 19, 11–28.
Ramanathan, N., Natarajan, R., 1980. Food and feeding habits of *Psettodes erumei* (Bloch and Schn.) and *Pseudorhombus arsius* (Ham. Buch.). Matsya 6, 30–42.
Randall, J.E., 1967. Food habits of reef fishes in the West Indies. Studies in Tropical Oceanography 5, 655–847.
Rao, D.M., Rao, K.S., 1991. Food and feeding behaviour of *Nemipterus japonicus* (Bloch) populations off Visakhapatnam, South India. Journal of the Marine Biological Association of India 33, 335–345.
Rao, T.A., 1980. Food and feeding habits of *Pennahia macrophthalmus* Bleeker at Visakhapatnam. Indian Journal of Fisheries 27, 61–65.
Rao, T.A., 1989. Fishery of threadfinbreams at Waltair with notes on some aspects of biology of *Nemipterus mesoprion* (Bleeker). Journal of the Marine Biological Association of India 31, 103–109.
Renones, O., Polunin, N.V., Goni, R., 2002. Size related dietary shifts of *Epinephelus marginatus* in a western Mediterranean littoral ecosystem: an isotope and stomach content analysis. Journal of Fish Biology 61, 122–137.
Ross, E., 1980. Patterns of diet and forces of production: an economic and ecological history of the ascendancy of beef in the United States. In: Ross, E. (Ed.), Beyond the Myths of Culture: Essays in Cultural Materialism. Academic Press, pp. 181–225.
Root, R.B., 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43, 95–124.
Ross, S.T., 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia 2, 352–388.
Sivakami, S., 1995. Fishery and biology of the carangid fish *Megalaspis cordyla* (Linnaeus) off Cochin. Journal of the Marine Biological Association of India 37, 237–248.
Sokal, R.R., Rohlf, F.G., 1995. Biometry. W.H. Freeman & Co, New York.
Souter, D.W., Linden, O., 2000. The health and future of coral reef systems. Ocean and Coastal Management 43, 657–688.
Stergiou, K.I., Fourtouni, H., 2006. Food habits, ontogenetic diet shift and selectivity in *Zeus faber* Linnaeus, 1758. Journal of Fish Biology 39, 589–603.
Sutela, T., Huusko, A., 2000. Varying resistance of zooplankton prey to digestion: implications for quantifying larval fish diets. Transactions of the American Fisheries Society 129, 545–551.
Tessy, K.L., 1994. Studies on the Biology of Three Cultivable Species of Epinephelus from the South West Coast of India. Ph.D. thesis. Cochin University of Science and Technology, Cochin, pp. 1–219.
Vivekanandan, E., 2001. Predatory diversity of two demersal finfish species in the trawling grounds off Veraval. Indian Journal of Fisheries 48, 133–143.
Vivekanandan, E., Srinath, M., Pillai, V.N., Immanuel, S., Kurup, K.N., 2003. Marine fisheries along the southwest coast of India. In: Silvestre, G. (Ed.), Assessment, Management and Future Directions for Coastal Fisheries in Asian Countries, WorldFish Center Conference Proceedings, pp. 757–792.
Vivekanandan, E., Srinath, M., Kuriakose, S., 2005. Fishing the marine food web along the Indian coast. Fisheries Research 72, 241–252.
Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7, 139–172.
Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15, 393–425.
Yodzis, P., Winemiller, K.O., 1999. In search of operational trophospecies in a tropical aquatic food web. Oikos 87, 327–340.
Zacharia, P.U., 2003. Studies on the Fishery Biology and Population Dynamics of the White Fish *Lactarius lactarius* (Block & Schneider, 1801) Along the Karnataka Coast. Ph. D thesis. Mangalore University, Mangalore, pp. 1–188.
Zacharia, P.U., Mohamed, K.S., Purandahara, C., Mahadevaswami, H.S., Gupta, A.C., Nagaraja, D., Bhat, U.S., 1996. A bio-economic evaluation of the dual-fleet trawl fishery of Mangalore and Malpe. Marine Fisheries Information Service Technical & Extension Series 44, 1–12.