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[†]Trophic level of fishes occurring along the Indian coast

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Abstract

Data on the trophic level (TrL) of 707 species of exploited finfishes, crustaceans and cephalopods along the Indian coast were collected from different sources. The TrL ranges from 2.0 to 4.7 and the mean TrL is 3.5. The mean TrL of pelagic finfishes is 3.68, and the TrL decreased towards demersal habitat (3.44). A strong positive correlation exists between maximum body length of finfishes and TrL. The mean TrL of exploitation was 3.25. The complexities of assigning TrL values are discussed.

Keywords: Trophic level, fisheries, body size, habitat, Indian seas

Introduction

There are extensive studies on the stomach content of marine fishes, crustaceans and cephalopods occurring along the Indian coasts, where hundreds of individuals of more than 330 species have been sampled over several decades. However, multispecies prey-predator models or only two food webs have been constructed so far since the functional position within the food web has been determined for a very few species, (Vivekanandan *et al.,* 2003; Mohamed *et al*., 2008). To consolidate the available information on the trophic level of fishes, we have taken advantage of the available trophic level values for finfish species and supplemented them with published records on the stomach contents of finfishes, crustaceans and cephalopods occurring along the Indian coasts. These values are expected to form the basis (i) for construction of food webs, (ii) understanding the trophic interactions within the commercially exploited fish stocks, (iii) for identifying the mean trophic level at which the fish stocks are exploited (Vivekanandan *et al*., 2005; Bhathal and Pauly, 2008) and (iv) to evolve the much needed ecosystem-based fisheries management approach.

Material and Methods

The list of species occurring along the Indian coast was taken from the species catalogue published by the Central Marine Fisheries Research Institute (CMFRI, 2000). FishBase (*www.fishbase.org*) provides trophic level of thousands of species of finfishes occurring in the world oceans. From this database, values for 581 finfish species occurring in the Indian seas were selected. In addition to this, information published in the *Indian Journal of Fisheries, Journal Marine Biological Association of India* during 1958-2007 and Mohamed *et al.* (2008) on the diet composition were gathered for 263 species of finfishes, 52 species of crustaceans and 18 species of cephalopods occurring in the Indian seas.

Data on trophic levels given in FishBase are based on the estimations on diet composition data by using the following equation (Christensen and Pauly, 1992):

$$TL_i = 1 + \Sigma(DC_{ij}.TL_j)$$

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where TL_i is the trophic level of species *i*, DC_{ij} is the proportion of prey species *j* in the diet of species *i* and TL_j is the trophic level of prey species *j*. The primary producers (i.e., plants) and detritus are assigned a definitional TL of 1.

These data sources provided trophic level values for 707 species, which included 637 species of finfishes, 52 species of crustaceans and 18 species of cephalopods. All the 707 species were categorized into 53 commercially important subgroups/species, following CMFRI (2000), by taking into account (i) the taxonomic groups to which they belong to, and (ii) their quantitative contribution to the catches. Each group, thus categorized, consisted of one species (for e.g., the oil sardine *Sardinella longiceps*) to 114 species (other perches). The family name(s) for each species/group is given in Table 1. By considering the feeding habit, the subgroups/species were assigned names as herbivores & detritivores (TrL: 2.00 to 2.50), omnivores (TrL: 2.51 to 3.00), midlevel carnivores (TrL: 3.01 to 3.50), high level carnivores (TrL: 3.51 to 4.00) and top predators (TrL: > 4.01) (Table 1). The species names mentioned in this paper are the accepted names found in FishBase (*www.fishbase.org*).

Information on the habitat of all the species and the maximum (total) length of all finfishes were collected from FishBase (*www.fishbase.org*), Fischer and Whitehead (1974), Fischer and Bianchi (1984) and CMFRI (2000). To determine the mean TrL at which the fish stocks are exploited, the data on the annual average landings for each of the 53 groups were obtained for the years 2006 and 2007 (CMFRI, 2007, 2008). The mean TrL of exploitation was estimated by multiplying the annual average landings by the TrL of individual groups, and then taking a weighted mean (Pauly *et al*., 1998; Vivekanandan *et al*., 2005).

Results and Discussion

***Complexity of assigning TrL values*: **The approach to assign numeric TrL value to each species is, due to the following reasons, an over-simplification:

Table 1. Trophic level (TrL) of commercially important fish groups/species along the Indian coast

Group/Species	Family	Species* (Number)	TrL	SE	CV(%)
GROUP I. PLANTS & DETRITUS** (TrL: 1.00)					
GROUP II. HERBIVORES & DETRITIVORES (TrL: 2.00 TO 2.50)					
Tenualosa ilisha	Clupeidae	1	2.00	0.000	0.0
Mullets	Mugilidae	11	2.42	0.157	6.5
Sardinella longiceps	Clupeidae	1	2.50	0.000	0.0
GROUP III. OMNIVORES (TrL: 2.51 TO 3.00)					
Penaeid prawns	Penaeidae,Solenoceridae	29	2.51	0.011	0.4
Nonpenaeid prawns	Hippolytidae, Palaemonidae, Sergestidae	3	2.51	0.036	1.4
Crabs	Portunidae	9	2.70	0.050	1.9
Other shads	Clupeidae	11	2.98	0.059	2.0
Stomatopods	Squillidae	5	3.00	0.025	0.8
GROUP IV. MIDLEVEL CARNIVORES (TrL: 3.01 to 3.50)					
Lesser sardines	Clupeidae	11	3.15	0.087	2.8
Silverbellies	Leiognathidae	12	3.17	0.163	5.1
Whitebaits	Clupeidae	8	3.20	0.111	3.5
Lactarius lactarius	Lactariidae	1	3.20	0.000	0.0
Flying fishes	Exocoetidae	2	3.20	0.000	0.0
Pomfrets	Stromateidae	2	3.20	0.000	0.0
Other perches	Acanthuridae, Ambassidae, Apogonidae, Blennidae, Caesionidae, Centropomidae, Coryphaenidae, Drepanidae, Echeneidae, Gerreidae,Gobiidae Haemulidae, Menidae, Pomacentridae, Priacanthidae,	114	3.20	0.043	1.3

	Rachycentridae, Scaridae, Sparidae, Terapontidae				
Lobsters	Palinuridae, Scyllaridae	6	3.20	0.021	0.7
Other clupeids	Pristigasteridae	6	3.27	0.094	2.9
Setipinna	Engraulidae	2	3.30	0.420	12.7
Bregmaceros mccllelandi	Bregmacerotidae	1	3.30	0.000	0.0
Octopus	Octopodidae	6	3.30	0.046	1.4
Miscellaneous	Balistidae, Chanidae, Elopidae, Fistulariidae, Macrouridae, Megalopidae, Molidae, Platycephalidae, Triacanthidae	73	3.33	0.060	1.8
Coilia	Engraulidae	4	3.35	0.099	3.0
Flatfishes	Cynoglossidae, Soleidae	18	3.39	0.039	1.2
Thryssa	Engraulidae	11	3.40	0.125	3.7
Indian mackerels	Scombridae	2	3.40	0.000	0.0
Flounders	Bothidae	10	3.42	0.050	1.5
Catfishes	Ariidae, Plotosidae	14	3.44	0.085	2.5
Sciaenids	Sciaenidae	32	3.50	0.086	2.5
Cuttlefishes	Sepiidae	6	3.50	0.046	1.3
GROUP V. HIGH LEVEL CARNIVORES (TrL: 3.51 to 4.00)					
Threadfin breams	Nemipteridae	14	3.53	0.008	0.2
Goatfishes	Mullidae	5	3.54	0.150	4.2
Threadfins	Polynemidae	7	3.55	0.163	4.6
Rays	Dasyatidae, Mobulidae, Myliobatididae, Pristidae, Rhinobatidae, Rhinopteridae	28	3.58	0.102	2.8
Halfbeak & Fullbeaks	Belonidae, Hemiramphidae	6	3.60	0.314	8.7
Emperors	Lethrinidae	14	3.61	0.089	2.5
Harpadon nehereus	Harpadontidae	1	3.70	0.000	0.0
Squids	Loliginidae	6	3.70	0.046	1.2
Scads	Carangidae	9	3.76	0.127	3.4
Eels	Anguillidae, Congridae, Muraenesocidae, Muraenidae	9	3.84	0.140	3.6
Snappers	Lutjanidae	60	3.88	0.055	1.4
Rockcods	Serranidae	18	3.90	0.083	2.1
Sharks	Alopiidae, Carcharhinidae, Hemigaleidae, Hemiscyliidae, Lamnidae, Rhiniodontidae, Scyliorhinidae, Sphyrnidae, Stegostomatidae	42	4.00	0.066	1.7
GROUP VI. TOP PREDATORS (TrL: >4.01)					
Other carangids	Carangidae	35	4.07	0.072	1.8
Leatherjackets	Carangidae	4	4.15	0.231	5.6
Ribbonfishes	Trichiuridae	6	4.20	0.287	6.8
Lizardfishes	Synodontidae	4	4.30	0.196	4.6
Wolf herrings	Chirocentridae	2	4.35	0.210	4.8
Megalaspis cordyla	Carangidae	1	4.40	0.000	0.0
Psettodes erumei	Psettodidae	1	4.40	0.000	0.0
Barracudas	Sphyraenidae	4	4.40	0.127	2.9
Seerfishes	Scombridae	5	4.40	0.105	2.4
Tunas	Scombridae	9	4.40	0.025	0.6
Billfishes	Istiophoridae	6	4.52	0.019	0.4

* Number of species for which information on diet and/or trophic level estimates are available

** No commercial exploitation

SE=Standard Error (Standard Deviation/$\sqrt{n}$)

CV=Coefficient of Variation ((SE/Mean TrL)*100)

(i) The TrL changes during ontogeny of fishes. Fish larvae, which usually feed on herbivorous zooplankton (TrL: 2.0), have a TrL > 2.0, whereas adult fishes like the Indian oil sardine continue to feed on plankton. The juveniles and adults of several other fishes consume small fishes (TrL: 3.0), thereby moving up in the TrL (> 3.0). In piscivorous large fishes such as the tunas, the TrL values culminate at around 4.5. Thus, the larval stages of planktivores as well as the apex predators usually start at similar positions in the TrL, but the predators move to higher TrL in ontogeny. The juveniles of the threadfin bream *Nemipterus japonicus* prefer shrimp-dominated crustacean (TrL: 2.5 to 2.7) diet, whereas the adults predate mostly on fishes (TrL: 3.1 to 3.4), which are larger in size compared to the shrimps (Vivekanandan, 2001). Hence, the TrL of juveniles of *N. japonicus* is 2.8 whereas that of the adults is 3.5. On the other hand, there are a few species for which the TrL of the adults is lower than that of the juveniles. For instance, the spacing of gill rakers determines the size of food organism that could be sieved by the filter feeders. During ontogeny, the number of gill rakers increase in the oil sardine *S. longiceps*; the juveniles have only 145 gill rakers and the adults have 258. Consequently, the juveniles feed on zooplankton (TrL: 2.0), and the adults are able to feed on minute organisms such as diatoms and dinoflagellates (TrL: 1.0) (Devaraj *et al*., 1997).

(ii) Most species, to a certain degree, are opportunistic feeders, and switch between food items depending upon seasonal availability and abundance of prey. For instance, the Indian mackerel *Rastrelliger kanagurta* feed on phytoplankton (TrL: 2.0) during June-August and on zooplankton (TrL: 3.0) during the other months off Cochin (Noble, 1974). The Indian white prawn *Penaeus indicus* feed on algae (TrL: 2.0) during the monsoon season and on small molluscs (TrL: 2.4) during the postmonsoon months (Kuttiyamma, 1973).

Several fishes, especially the predators, are opportunistic feeders and feed on a wide spectrum of organisms. For instance, the diet of the spadenose shark *Scoliodon laticaudus* consists of at least 20 families of finfishes (TrL: 3.2 to 3.7) in addition to crustaceans such as penaeid and nonpenaeid prawns (TrL: 2.5), squilla (TrL: 3.0), crabs (TrL: 2.7), and molluscs such as cuttlefishes (TrL: 3.5), squids (TrL: 3.7) and gastropods (TrL: 2.5) (Mathew, 1992).

Range of TrL among the exploited stocks: The TrL of 707 species of commercially exploited major fish, crustaceans and cephalopods ranges from 2.0 (the shad, *Tenualosa ilisha*) to 4.7 (the ribbonfish *Eupleurogrammus muticus*). As a group, the mean trophic level of billfishes (Family: Istiophoridae) was the maximum (4.52 ± 0.019; Table 1). Based on the TrL, the exploited groups could be classified as (i) herbivores & detritivores (TrL: 2.00 to 2.50), (ii) omnivores (TrL: 2.51 to 3.00), (iii) midlevel carnivores (TrL: 3.01 to 3.50), (iv) high level carnivores (TrL: 3.51 – 4.00) and (v) top predators (TrL: > 4.00). Maximum number of species (341) are midlevel carnivores and feed at the TrL of 3.01-3.50 (Fig. 1). The mean TrL for the 707 species is 3.50 ± 0.121. The standard error in the TrL of a few groups such as penaeid prawns, tunas and billfishes is very low (coefficient of variation, CV: <1.0%), whereas for six groups, the SE was high (CV: >5.0%). The SE does not indicate the uncertainty about the TrL but reflects the wide differences in the feeding habit between the species in those groups. For instance, the feeding habit of 12 species of silverbellies (CV: 5.1%) is governed by the nature of their mouth. The mouths of *Secutor insidiator* and *S. ruconius* (TrL: 2.5) are protrusible upwards and they feed mainly on plankton. The mouths of 9 species of *Leiognathus* (TrL: 2.4 to 3.6) are protrusible both forward or upward, and hence, benthic organisms like the polychaetes, crustaceans,

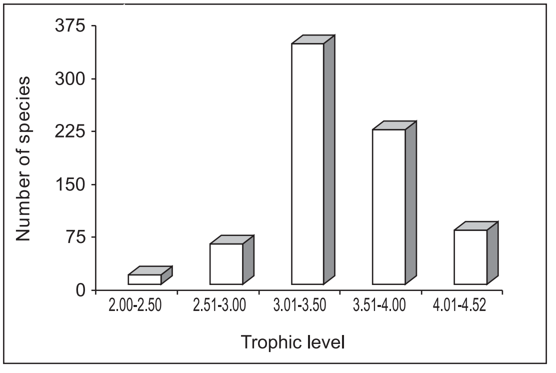

Fig. 1. Frequency distribution of fish species in trophic level groupings

Table 2. Distribution of commercially important fish groups/species in each major habitat along the Indian coast; the figures represent the number of species for which trophic level values are available

Group/Species	Pelagic	Bentho- pelagic	Demersal	Reef associated	Total
Tenualosa ilisha	1	0	0	0	1
Mullets	1	1	8	1	11
Sardinella longiceps	1	0	0	0	1
Penaeid prawns	0	0	29	0	29
Non-penaeid prawns	0	0	3	0	3
Crabs	4	0	3	2	9
Other shads	11	0	0	0	11
Stomatopods	0	0	5	0	5
Lesser sardines	11	0	0	0	11
Silverbellies	0	1	11	0	12
Whitebaits	8	0	0	0	8
Lactarius lactarius	0	0	1	0	1
Flying fishes	2	0	0	0	2
Pomfrets	0	2	0	0	2
Other perches	7	4	49	54	114
Lobsters	0	0	0	6	6
Other clupeids	5	0	0	1	6
Setipinna	2	0	0	0	2
Bregmaceros mccllelandi	1	0	0	0	1
Octopus	0	0	6	0	6
Miscellaneous	12	8	39	14	73
Coilia	4	0	0	0	4
Flatfishes	0	1	16	1	18
Thryssa	11	0	0	0	11
Indian mackerel	0	2	0	0	2
Flounders	0	0	9	1	10
Catfishes	0	0	13	1	14
Sciaenids	0	14	18	0	32
Cuttlefishes	0	0	6	0	6
Threadfin breams	0	0	10	4	14
Goatfishes	0	0	2	3	5
Threadfins	0	0	7	0	7
Rays	3	7	14	4	28
Halfbeaks & Fullbeaks	6	0	0	0	6
Emperors	0	0	6	8	14
Harpadon nehereus	0	1	0	0	1
Squids	0	6	0	0	6
Scads	7	0	1	1	9
Eels	0	0	8	1	9
Snappers	1	2	9	48	60
Rock cods	0	0	7	11	18
Sharks	11	7	18	6	42
Other carangids	13	3	3	16	35
Leather jackets	4	0	0	0	4
Ribbonfishes	0	6	0	0	6
Lizardfishes	0	0	2	2	4
Wolf herring	2	0	0	0	2
Megalaspis cordyla	1	0	0	0	1
Psettodes erumei	0	0	1	0	1
Barracudas	0	0	0	4	4
Seerfishes	5	0	0	0	5
Tunas	9	0	0	0	9
Billfishes	6	0	0	0	6
Total	149	65	304	189	707

gastropods and bivalves form the major food. *Gazza minuta*, by virtue of the presence of canine teeth, feed on crustaceans and small fishes and is comparatively higher in the trophic level (4.4).

Habitat and TrL: The commercially exploited species along the Indian coast were categorized into four major habitats: 149 species are pelagic, 65 benthopelagic, 304 demersal and 189 reef-associated (Table 2). Sharks, rays, other perches, carangids and mullets are distributed in all the four habitats, whereas clupeids, Indian mackerel and scombroids are restricted to pelagic life. The major and minor perches and flatfishes are restricted either to demersal or reef-associated habitat. The mean trophic level of the pelagics (n=149) is 3.68 and the TrL decreases towards demersal habitat; the TrL of the demersals (n=304) is 3.44 (Fig. 2). The number of pelagic species with low TrL (2.00 to 3.50) is less (65 species; for e.g., clupeids) compared to the number of demersals (180 species; for e.g., penaeid and nonpenaeid prawns, crabs, stomatopods) with low TrL (2.51 to 3.50). Moreover, the pelagic habitat supports as high as 48 top predatory species (for e.g., wolf herring, seerfishes, tunas, billfishes) compared to only 28 species of top predatory demersals (for e.g., lizardfishes, halibut).

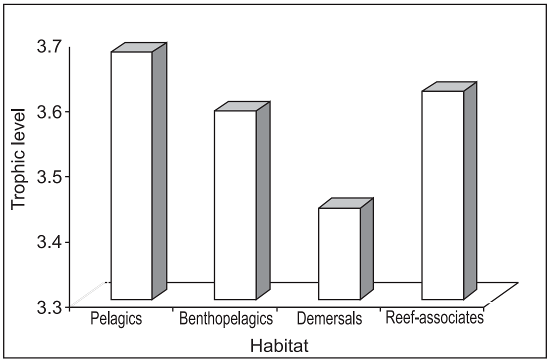

Fig 2. Mean trophic level of fish species distributed in different habitats

Maximum body length and TrL: The maximum body length of finfishes (n=637 species) occurring along the Indian coast ranged from 4 cm (the sleeperfish, *Eleotris lutea*) to 2000 cm (the whale shark, *Rhiniodon typus*). The whale shark is by far the largest fish, and the next largest fish considered in the present study is the sawfish, *Pristis pectinata* (760 cm). However, the maximum body length of 341 species is below 40 cm.

The frequency distribution of small fish species is high at low TrL (< 3.5). For instance, the TrL of 138 species (92.7%) in 4-20 cm length is <3.5 (Table 3). On the other hand, the trophic level of 84% of

Table 3. Distribution of finfishes of different maximum length in the trophic level categories; the values represent number of finfish species

Length group	Trophic level						
(cm)	2.00-2.50	2.51-3.00	3.01-3.50	3.51-4.00	4.01-4.50	4.51-4.70	Total
Length group: 4 to 100 cm							
4-20	8	49	81	11	0	0	149
21-40	4	17	106	46	16	2	191
41-60	3	5	34	23	13	0	78
61-80	3	2	13	20	14	2	54
81-100	0	0	6	14	18	1	39
Length group: 4 to 2000 cm							
4-100	18	73	240	114	61	5	511
101-200	1	1	18	16	41	0	77
201-300	1	0	4	3	16	0	24
301-400	0	0	4	0	12	0	13
401-500	0	0	0	0	4	1	5
501-600	0	0	0	0	2	0	2
601-700	0	0	0	0	1	0	1
700-800	0	0	0	0	4	0	4
801-2000	0	0	0	1	0	0	1
Total	20	74	263	132	144	5	638

50 large species (length: >200 cm) is > 4.0. However, an attempt to regress the maximum body length of finfishes against the respective TrL yielded a poor correlation ($r^2 = 0.2$). This is due to wide variations in the feeding habits especially among fishes below 300 cm length (Fig. 3). For instance, the maximum body length of the blennid *Istiblennius edentulus* and the shark *Eridacnis radcliffei* is almost equal (20 cm) but they have wide difference in the trophic level, i.e., 2.4 and 4.2, respectively. Comparatively, the TrL of large fishes (>300 cm) does not vary considerably and is, almost exclusively above 3.5. It appears that (i) small fishes (21-100 cm) are adapted to feed at all TrL (2.0 to 4.6); but (ii) most large fishes (>400 cm) are adapted only for predation

Fig 3. Trophic level of finfishes as a function of maximum body length

and could not feed at TrL lower than 4.0, i.e., the large predators predate on other predators. Hence, the large predators, which are the target for many fisheries, operate within a narrow range of TrL and are most vulnerable to depletion of their preferred prey and overexploitation.

Categorization of length into 20 cm (between 4 and 100 cm) and 100 cm (between 4 and 800 cm) length groups revealed a clearly increasing trend in the TrL with increasing length. The TrL increased from 3.15 ± 0.028 (SE) for the 4-20 cm length group to 4.44 ± 0.098 for the 401-500 cm length group but there was no further increase in the TrL for fishes larger than the 401-500 cm length group (Fig. 4). A strong correlation between the body length and TrL has already been demonstrated by Christensen and Pauly (1993).

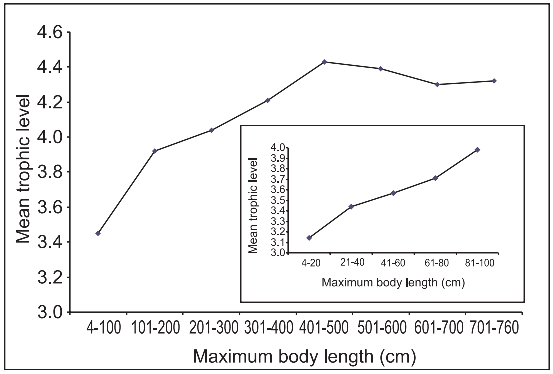

Fig. 4. Relationship between maximum body length and mean trophic level of finfishes

Exploitation: The annual average fish landings were 2,796,162 tonnes along the Indian coast during 2006 and 2007 (CMFRI, 2007, 2008). Based on the TrL values determined for different species/groups, it is estimated that the maximum exploitation was at the TrL of 3.01-3.50 (midlevel carnivores: 1,202,350 t; 43.0% of the total landings; Fig. 5) during 2006-2007; 27.3% of biomass exploited consisted of herbivores, detritivores and omnivores (TrL: 2.00-3.00) and 29.7% consisted of high level carnivores and top predators (TrL: 3.51-4.52). The mean TrL of exploitation was 3.25. The oil sardine (4,45,931 t), the lesser sardines (91,934 t), the penaeid (1,87,257 t) and nonpenaeid prawns (1,54,920 t), whitebaits (46,657 t) and silverbellies (67,241 t), which are low in the food web, contribute 35.5% to the total landings as well as to the major food requirements of several fish groups up in the food web. Overfishing at the bottom of the food web would lead to shortage of food up in the food web.

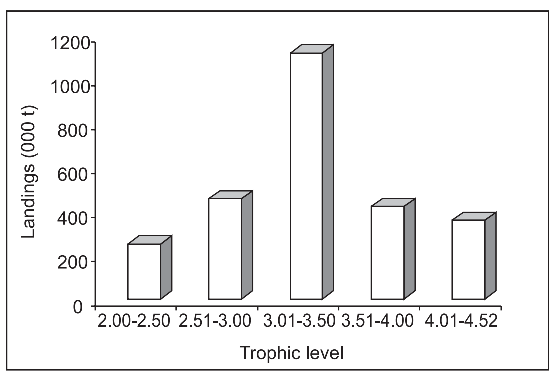

Fig. 5. Annual average landings of fishes in different trophic levels during 2006 and 2007

On the other hand, overfishing at the top of the food web, which is demonstrated to occur in almost all fished areas around the globe (Pauly *et al.*, 1998; Vivekanandan *et al*., 2005), would lead to increase in the biomass of fish groups lower in the food web thereby resulting in severe competition for food.

In this paper, the TrL values have been assigned by considering the entire Indian coast as one homogeneous ecosystem. However, there may be temporal and spatial differences in the TrL depending up on the type of prey available to the fish during different seasons and in different areas along the coast. Hence, the TrL analysis should be extended to include temporal and spatial information to verify the web structure.

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