Dietary Guild Structure in Fish Assemblages and Trophic Position of Constituent Species in Brush Parks of a Tropical Estuary

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Abstract

Trophic guild structure and dietary niche breadth in tropical fish communities are important to identify functional groups and to understand how trophic positions of constituent species help coexistence. Objective of the present study was to investigate whether the constituent species of fish assemblages in brush parks could be grouped into trophic guilds and how these species contribute to structure the fish community along trophic dimensions. Diets of 46 fish species caught in brush parks were analysed and the food items were categorised into 11 broad groups. Based on the composition of diets, fish were grouped into 8 trophic guilds. Levin's index of niche breadth indicated that the constituent species in the trophic guilds for which food was abundant, were generalists, whereas the trophic guilds of higher trophic levels were specialists. Within each trophic guild, constituent species showed different trophic indices indicating low inter-specific competition resulting in optimum food resource utilisation.

Keywords: artificial fish shelters; dietary habits; fish aggregation devices; fish community structure; trophic index

Introduction

Following the original definition of environmental guild (Root 1967), a trophic guild of biological communities can be defined as a group of species that exploit the same category of food resources in a similar way. Hence grouping of constituent species in a fish community is possible based on their functional role rather than taxonomy (Garrison and Link 2000; Ramirez-Luna et al. 2008). This is of particular importance because the members of any particular guild play more or less similar functional roles providing vital information on the flow of energy and biomass within food webs (Hawkins and MacMahon 1989) as well as on species interactions. Many tropical fish communities such as those inhabiting coral reefs (Longo et al. 2014; Palacios and Zapata 2014; Boaden and Kingsford 2015), seagrass beds (Livingston 1982) and floodplains (Jepsen et al. 1997; Whitley and Bollens 2014), and those that are attracted to artificial fish aggregation devices (FADs) (Deudero 2001) exhibit complex species interactions. Hence, simplification of these complex interactions based on the guild structure is recognized as an important approach for studying ecology of fish communities (Garrison and Link.2000; Coll et al. 2006).

Fish aggregating devices (FADs) are mostly artificial fish shelters to which many fish species are attracted and thereby supporting productive fisheries in many parts of the world (Dempster and Taquet 2004). Well documented FADs established as traditional fishing devices are brush parks in Negombo estuary, Sri Lanka (Amarasinghe et al. 2002), Acadjas in Benin, West Africa (Lalèyè 2000; Niyonkuru and Lalèyè 2010), Katha in Bangladesh (Uddin et al. 2015) and Samrah in Great Lake in Cambodia (Ho 1999; Lamberts 2001; Baran 2005; Mekong River Commission 2015). FADs produce higher fish yields per unit area compared to open water fisheries (Welcomme 2002). Fish assemblages in brush parks consist of species that are attracted to shelter or to feed on periphytic food materials (Van Dam et al. 2002). In addition, opportunistic predators are also attracted to brush parks (Malone et al. 2011). These fish assemblages are structured in trophic dimensions for efficient utilization of food resources. Gammanpila et al. (2017) have shown that ecomorphology of the fish species in the brush parks of a tropical estuary correlates with diet. Knowledge on feeding ecology of the fish species in an assemblage provides insight into trophic interactions, which are of immense importance to fisheries managers opt for ecosystem-based management (Pikitch et al. 2004).

In the present study, the trophic guilds of the fish assemblages in brush parks in Negombo estuary, Sri Lanka were identified. In addition, the contribution of the individual fish species to the structure of the fish communities along trophic dimensions was investigated.

Materials and Methods

Study area

Negombo estuary in Sri Lanka, which is located between latitudes 7°6'–7°12'N and longitudes 79°40'–79°53' E is a shallow estuary with a mean depth of 0.65 m. It covers an area of 3,164 ha (Goonethilake et al. 2005) with a maximum length of 12.5 km and maximum width of 3.6 km. It has a shoreline of 24 km and about 10 % of the estuary has a depth < 0.5 m (Jayakody 1996).

Brush parks are traditional forms of fish aggregation devices installed in shallow areas of the estuaries, rivers and reservoirs using dense masses of brushwood (Welcomme 2002). About 2,200 brush parks with a mean surface area of 51.8 m2, covering 11.3 ha and yielding 12.46 t ha^{-1} yr^{-1} were reported in this estuary in 1998 (Amarasinghe et al. 2002).

Sampling of fish

Fish sampling was carried out once a month from three major brush park fishing areas (Munnakkaraya, Katunayaka and Talahena; Fig. 1) in the estuary from April 2014 to April 2016. For ethical clearance, permission for conducting research was obtained from the University of Kelaniya, Sri Lanka. Fish that were harvested by surrounding brush parks with an encircling net were chosen for dietary analysis. Accordingly, 64 brush parks were sampled during the study period, encompassing the wet (May to September), intermediate (October-November and March-April) and dry (December to February) seasons of the year. Fish specimens were fixed by injecting 10 % buffered formalin into body cavity, packed in 10 % formalin solution and were transported to the laboratory for dietary analysis. Fish were identified based on the fish identification guides for Sri Lankan waters (Munro 1955; De Bruin et al. 1995).

Dietary analyses

Stomach contents of each specimen were extracted and a suspension of 10 mL was prepared by adding 10 % buffered formalin. For fish species that did not have a well-developed stomach, contents in the first one-third of the intestine, which were considered as the recently ingested food, were used. From each suspension, three subsamples of one mL each were examined under a microscope (10 × 10 magnification) using a Sedgwick-rafter counting chamber for qualitative and quantitative analysis of stomach/gut contents (Wijeyaratne and Costa 1986; Weliange and Amarasinghe 2003). Empty stomachs or stomach with almost fully digested food were excluded. Bio-volume of each individual food categories was determined using a cell of *Pinnularia*, a predominant alga belonging to Class Bacillariophyceae, as the standard and expressed as volumetric percentage of the total food items in the stomach/gut content (Hynes 1950; Hyslop 1980; Wijeyaratne and Costa 1986). Relative bio-volume of each food category in stomach/gut contents of individual fish was summed across all samples and the percentage volumetric proportion of diet in each species was determined.

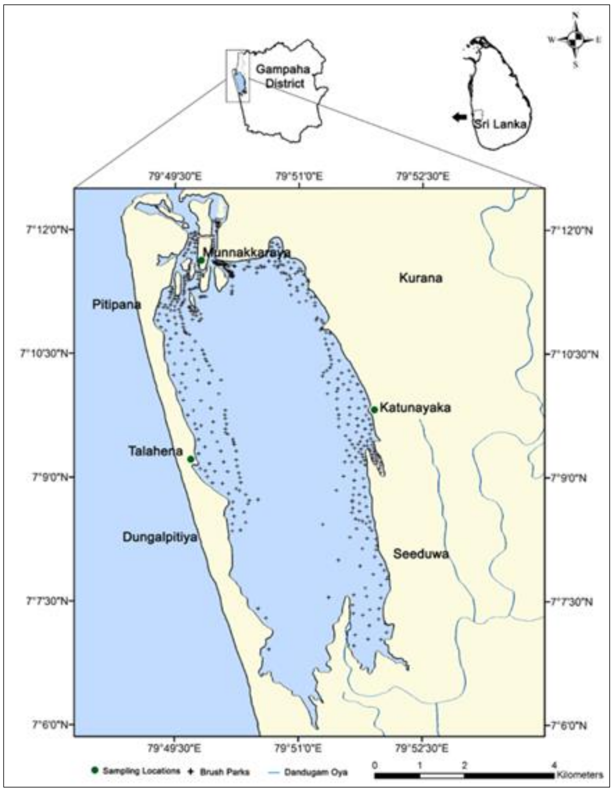

Fig. 1. Map of Negombo estuary showing locations of brush parks (crosses). The inflowing river (Dandugam Oya) into the estuary is also shown here. Maps of Sri Lanka and Gampaha district indicate geographical location of Negombo estuary.

Trophic classification

For the analysis of trophic pattern, the stomach/gut contents were assigned to eleven broader categories: phytoplankton, macrophytes, detritus, molluscs, soft-bodied macrobenthos, small zooplankton, cladocerans, copepods, ostracods, insects and fish. The food items consumed were classified into different trophic levels (Table 1; Winemiller 1990).

Table 1. Eleven food categories, their trophic classes and main components of each food category (Modified from Winemiller 1990).

Food category	Abbreviation	Trophic class	Food items
Phytoplankton	PP	0	Diatom, blue green algae, green algae, filamentous algae
Macrophytes	MP	0	Aquatic plants
Detritus	DE	0	Fine organic material
Mollusks	ML	1	Bivalves and gastropods
Soft-bodied Macrobenthos	MB	1.5	Annelids, Nematodes, *Caridina*
Small zooplankton	SZ	1.5	*Brachionus*, *Trichocerca*, *Keratella*, dinoflagellates
Cladocerans	CD	1.5	*Daphnia*, *Moina*, *Diaphanasoma*, *Chydoris*, *Macrothrix*
Copepods	CP	1.5	Calanoids, Cyclopoids, Harpectocoids
Ostracods	OC	1.5	*Cypridopsis*
Insects	IN	1.5	Predominantly aquatic insects
Fish	FH	2	Fish scales, fish eggs, small/juvenile fish, fish skeletons

The plant materials (primary producers) were included in trophic class 0 (T = 0.00), invertebrates in the trophic class 1.5 (T = 1.5) as they were omnivores, predatory fish in trophic class 2 (T = 2.0). Trophic index for each species (T_i) was computed using the following equation (Adams et al. 1983; Winemiller 1990).

$$T_i \ = \ 1.0 \ + \ \sum_{j=1}^{n} T_j \, (p_{ij}) \qquad (1)$$

where T_j was the trophic class of prey item j (as defined in Table 1 above), and p_{ij} was the fraction of food (proportion by volume) consumed by species i consisting of prey item j in the diet (Winemiller 1990). This index represents the trophic position of each species in the fish assemblage in a trophic continuum, which represents the ecological pyramids more accurately than by discrete levels (Adams et al. 1983: Cousins 1987).

Trophic guilds

Mean proportions of food item consumed by each of the 46 species were double square root transformed to reduce heteroscedasticity as this approach is effective for datasets with many very low values and a few large values (Quinn and Keough 2002). A similarity matrix, constructed based on Euclidean distances of the degree of dietary similarities between species (McQuitty 1966), was used to ordinate the 46 fish species studied from non-metric multi-dimensional scaling (n*MDS*) and the trophic guilds of fish species were identified. Similarity analysis and n*MDS* were performed by PRIMER 5 statistical package (Clarke and Warwick 2001). These trophic guilds were named based on the food item that contributed most to the diet. In most trophic guilds, the prominent food items contributed over 50 % of the diets. Here, consistency of labelling a trophic guild was not based on proportion of taxonomic group of any particular food items. For example, molluscivore and invertivore were two trophic guilds in the present analysis although members of both guilds fed on invertebrates. Adite and Winemiller (1997) and Garrison and Link (2000) have also adopted a similar criterion for naming trophic guilds.

Dietary niche breadth

Dietary niche breadth was calculated to determine the relative level of diet specialisation of fish in the brush park assemblages. Levin's niche breadth index was calculated using the following equation (Levins 1968).

$$B \ = \ 1 \, / \, \sum^{n} P_i^2 \qquad (2)$$

where B is the dietary niche breadth, P_i is the volumetric proportion of food item i in the diet and n is the total number of food items in the diet. B ranges from 1, when only single resource is used (specialist), to n, when all different type of resources are used in equal proportion (generalist). In the present study, species were categorised as highly specialists (range of B: 1.0–1.25), specialists (range of B: 1.25–1.50), and generalists ($B > 1.5$).

Relative abundance

Relative abundance of a particular fish species was calculated as the number of individuals of that species divided by the total number of fishes collected from brush parks during the study period.

Relationship between trophic index and dietary niche breadth

For each trophic guild, the relationships between the trophic index and dietary niche breadth of constituent species were determined using linear and second order regression analyses to illustrate whether there were divergences of dietary habits among constituent species in each guild. As these possible relationships would indicate that each species occupy different trophic levels irrespective of dietary niche breadth, they were used to show that dietary overlaps were unlikely among constituent species within a trophic guild. Regression analyses were performed using Minitab (Version 16) software package.

Results

Trophic guilds

Total number of 817 specimens belonging to 46 fish species of 24 families were used for the dietary analysis (Table 2). Number of specimens in each species used for this analysis varied from 1 to 107. Relative proportions by volume of each of the food categories in 46 species are given in Table 3.

The n*MDS* plot (Fig. 2) resulted six major trophic guilds and two minor guilds. The major trophic guilds were labelled as piscivore (guild i), having eight species with more than 50 % fish in their diet. The fish species that consumed both invertebrates and fish (guild ii) were represented by ten species. The invertivore guild (guild iii) was represented by eight species and they had more than 60 % invertebrates in their diet. Fishes of omnivore guild (guild v) consumed food items from different origins (plant and animal) and were

Table 2. Fish species examined, their abbreviations (Abv), number of analysed stomachs (N) and size (total length) ranges of fish species in the assemblages of brush parks in Negombo estuary.

Family	Scientific name	Abv	N	Size range (cm)
Acanthuridae	*Acanthurus gahhm* (Forsskål, 1775)	Ac	21	6.2-17.4
Ambassidae	*Ambassis gymnocephalus* (Lacepède, 1802)	Ag	13	8.1-17.4
Anguillidae	*Anguilla bicolor bicolor* McClelland, 1844	An	1	60.3
Apogonidae	*Apogon hyalosoma* Bleeker, 1852	Ah	3	8.9-13.2
Ariidae	*Arius jella* Day, 1877	Aj	24	14.6-30.5
	Arius maculatus (Thunberg, 1792)	Am	9	10.6-28.7
Carangidae	*Caranx sexfasciatus* Quoy & Gaimard, 1825	Cs	23	9.2-17.3
	Carangoides talamparoides Bleeker, 1852	Ct	2	12.4-17.7
Centropomidae	*Lates calcarifer* (Bloch, 1790)	Lc	34	18.1-48.3
Cichlidae	*Etroplus suratensis* (Bloch, 1790)	Es	96	5.5-23.5
	Oreochromis mossambicus (Peters, 1852)	Om	2	25.3-29.5
	Oreochromis niloticus (Linnaeus, 1758)	On	3	21.4-22.3
Eleotridae	*Ophiocara porocephala* (Valenciennes, 1837)	Op	5	14.2-20.7
Gerreidae	*Gerres abbreviates* Bleeker, 1850	Ga	16	7.5-14.4
	Gerres filamentosus Cuvier, 1829	Gf	1	8.6
	Gerres oyena (Forsskål, 1775)	Gy	9	9.9-13.5
	Gerres oblongus Cuvier, 1830	Go	6	9.1-15.2
Haemulidae	*Plectorhinshus gibbosus* (Lacepède, 1802)	Pg	12	7.1-22.1
Leiognathidae	*Leiognathus equulus* (Forsskål, 1775)	Le	1	7.7
	Leiognathus fasciatus (Lacepède, 1803)	Lg	1	9.1
Lethrinidae	*Lethrinus rubrioperculatus* Sato, 1978	Lh	1	9.0
Lutjanidae	*Lutjanus argentimaculatus* (Forsskål, 1775)	La	66	14.3-33.0
	Lutjanus fulviflamma (Forsskål, 1775)	Lf	19	10.4-15.7
	Lutjanus kasmira (Forsskål, 1775)	Lk	4	10.6-15.9
	Lutjanus russelli (Bleeker, 1849)	Lr	41	8.0-26.9
Monodactylidae	*Monodactylus argenteus* (Linnaeus, 1758)	Ma	12	6.9-9.2
Mugilidae	*Liza macrolepis* (Smith, 1846)	Lm	24	17.1-50.0
	Liza melinoptera (Valenciennes, 1836)	Lt	32	11.3-45.2
	Liza parsia (Hamilton, 1822)	Lp	7	13.6-27.3
	Cicamugil cascasia (Hamilton, 1822)	Lz	2	21.8-23.4
	Liza subviridis (Valenciennes, 1836)	Ls	25	15.2-49.2
	Mugil cephalus Linnaeus, 1758	Mc	12	18.2-54.4
	Valamugil buchanani (Bleeker, 1853)	Vb	5	12.2-50.3
	Valamugil seheli (Forsskål, 1775)	Vs	24	12.6-28.5
Plotosidae	*Plotosus canius* Hamilton, 1822	Pc	7	34.4-59.0
Scatophagidae	*Scatophagus argus* (Linnaeus, 1766)	Sa	37	7.2-22.7
Serranidae	*Epinephelus malabaricus* (Bloch & Schneider, 1801)	Em	41	13.8-40.1
	Epinephelus coioides (Hamilton, 1822)	Ec	9	10.1-31.5
	Epinephelus tauvina (Forsskål, 1775)	Et	1	35.7
Sparidae	*Acanthopagrus berda* (Forsskål, 1775)	Ab	31	9.2-33.5
Sphyraenidae	*Sphyraena jello* Cuvier, 1829	Sp	1	30.8
Sillaginidae	*Sillago sihama* (Forsskål, 1775)	Ss	10	12.5-32.7
Siganidae	*Siganus javus* (Linnaeus, 1766)	Sj	107	8.8-22.9
	Siganus lineatus (Valenciennes, 1835)	Sl	10	10.9-23.2
	Siganus vermiculatus (Valenciennes, 1835)	Sv	6	11.7-20.3
Terapontidae	*Terapon puta* Cuvier, 1829	Tp	1	10.9

Table 3. Volumetric proportions of different food categories and trophic index of each fish species assemblage in brush parks in Negombo estuary (PP = Phytoplankton, MP = Macrophytes, DE = Detritus, ML = Mollusks, MB = Macrobenthos, SZ = Small zooplankton, CD = Cladocerans, CP = Copepods, OS = Ostracods, IN = Predominantly aquatic insects and FH = Fish). Abbreviations (Abv) of the names of fish species are as given in Table 2. In each row, the major food items are indicated in bold.

Abv	Food items (proportions)											Trophic index
	PP	MP	DE	ML	MB	SZ	CD	CP	OS	IN	FH	
Ac	**0.53**	0.18	0.17	0.00	0.06	0.00	0.02	0.01	0.00	0.00	0.04	1.23
Ag	0.06	0.02	0.01	0.00	**0.72**	0.00	0.00	0.03	0.00	0.00	0.16	2.45
An	0.00	0.00	0.00	0.05	0.10	0.00	0.00	0.00	0.00	0.00	**0.85**	2.90
Ah	0.00	0.00	0.00	0.00	**0.85**	0.00	0.00	0.00	0.00	0.00	0.15	2.58
Aj	0.03	0.01	0.02	0.04	0.36	0.00	0.00	0.03	0.00	0.01	**0.51**	2.66
Am	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	**0.87**	2.93
Cs	0.02	0.02	0.01	0.00	0.45	0.00	0.00	0.00	0.00	0.00	**0.50**	2.68
Ct	0.00	0.00	0.00	0.00	**0.70**	0.00	0.00	0.00	0.00	0.00	0.30	2.65
Lc	0.00	0.00	0.00	0.00	0.14	0.00	0.00	0.00	0.00	0.00	**0.86**	2.92
Es	0.30	0.24	**0.39**	0.02	0.02	0.00	0.00	0.01	0.00	0.01	0.02	1.11
Om	0.11	0.13	**0.58**	0.08	0.00	0.00	0.00	0.10	0.00	0.00	0.00	1.22
On	0.12	0.08	**0.68**	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.07	1.18
Op	0.00	0.00	0.00	**0.53**	0.21	0.00	0.00	0.00	0.00	0.00	0.26	2.36
Ga	0.21	0.01	0.01	0.03	0.26	0.00	0.00	0.05	0.00	0.01	**0.42**	2.35
Gf	0.27	0.00	0.00	0.00	**0.36**	0.00	0.00	0.05	0.00	0.00	0.32	2.25
Gy	**0.62**	0.00	0.00	0.00	0.05	0.00	0.00	0.33	0.00	0.00	0.00	1.57
Go	0.12	0.00	**0.25**	0.21	0.12	0.00	0.00	0.07	0.00	0.00	0.22	1.94
Pg	0.04	0.00	0.01	0.00	**0.93**	0.00	0.00	0.00	0.00	0.00	0.02	2.43
Le	0.12	0.00	0.00	0.00	0.01	0.01	0.00	0.08	0.16	0.00	**0.61**	2.62
Lg	0.18	0.00	0.03	0.08	0.00	0.00	0.00	0.14	0.00	0.00	**0.57**	2.43
Lh	0.01	0.00	0.00	0.00	**0.81**	0.00	0.00	0.00	0.00	0.00	0.18	2.57
La	0.04	0.03	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	**0.68**	2.74
Lf	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	**0.53**	2.76
Lk	0.00	0.00	0.00	0.02	0.37	0.00	0.00	0.00	0.00	0.00	**0.62**	2.80
Lr	0.02	0.00	0.00	0.00	**0.61**	0.00	0.00	0.00	0.00	0.00	0.36	2.65
Ma	0.18	**0.25**	0.15	0.02	0.24	0.00	0.00	0.00	0.00	0.00	0.16	1.70
Lm	0.21	0.23	**0.46**	0.01	0.05	0.00	0.00	0.04	0.00	0.00	0.01	1.16
Lt	0.16	0.10	**0.64**	0.02	0.01	0.00	0.00	0.07	0.00	0.00	0.01	1.15
Lp	0.06	0.21	**0.62**	0.02	0.00	0.00	0.00	0.06	0.00	0.00	0.04	1.18
Lz	0.15	0.01	**0.83**	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	1.02
Ls	0.21	0.25	**0.45**	0.03	0.00	0.00	0.00	0.07	0.00	0.00	0.00	1.13
Mc	0.31	0.08	**0.55**	0.00	0.04	0.00	0.00	0.03	0.00	0.00	0.00	1.10
Vb	0.04	0.22	**0.75**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Vs	0.21	0.15	**0.58**	0.00	0.02	0.00	0.00	0.01	0.00	0.03	0.01	1.11
Pc	0.00	0.00	0.00	0.02	**0.93**	0.00	0.00	0.00	0.00	0.00	0.04	2.50
Sa	**0.43**	0.37	0.13	0.00	0.05	0.00	0.00	0.01	0.00	0.00	0.01	1.10
Em	0.00	0.00	0.00	0.00	**0.50**	0.00	0.00	0.00	0.00	0.00	**0.50**	2.75
Ec	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.00	0.00	0.00	**0.51**	2.80
Et	0.00	0.00	0.00	0.00	0.44	0.00	0.00	0.00	0.00	0.00	**0.56**	2.78
Ab	0.03	0.12	0.07	0.04	0.01	0.00	0.09	0.00	0.00	0.00	**0.62**	2.45
Sp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	3.00
Ss	0.07	0.17	0.00	0.00	**0.61**	0.00	0.00	0.01	0.00	0.00	0.14	2.20
Sj	**0.40**	0.21	0.28	0.01	0.07	0.00	0.00	0.02	0.00	0.00	0.01	1.17
Sl	**0.47**	0.44	0.08	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	1.01
Sv	**0.58**	0.17	0.16	0.02	0.01	0.00	0.00	0.00	0.01	0.00	0.04	1.13
Tp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**1.00**	3.00

represented by two species, whereas herbivore guild (guild vi) was represented by five species having more than 60 % plant material (phytoplankton and macrophytes) in their diet. The detritivore guild (guild vii) consisting of fish that had more than 40 % detritus in their diet was composed of eleven species. The other two minor guilds were represented by one species each. The diet of *Ophiocara porocephala* (Valenciennes, 1837) which contained 53 % molluscs was labelled as molluscivore (guild iv) and that of *Gerres oyena* (Forsskål, 1775) which contained 62 %

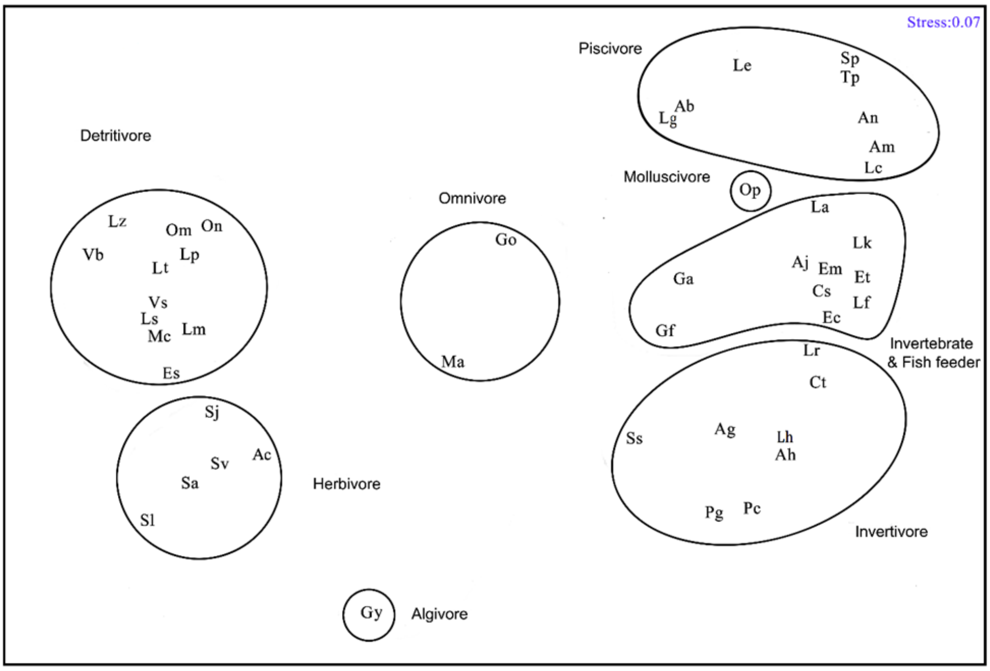

Fig. 2. Non-metric multi-dimensional scaling (n*MDS*) ordination based on dietary habits of 46 fish species in the brush parks of the Negombo estuary. Stress value of 0.07 indicates that two dimensional n*MDS* plot is sufficient to ordinate the fish species. The eight clusters represent trophic guilds. The abbreviations of species names belonging to individual trophic guilds are as given in Table 2.

algae, was labelled as algivore (guild viii). It must be noted that this classification of trophic guilds was not strictly based on taxonomic groups. Adite and Winemiller (1997) also categorised fish species feeding on various taxonomic groups of invertebrates into several trophic guilds such as invertebrate feeders, worm feeders, insectivores and molluscivores.

Trophic index, dietary niche breadth and relative abundance

Trophic indices estimated on the basis of dietary composition using equation 1 above, that ranges from 1 to 3 are given in Table 3. The lowest trophic indices (1.00–1.25) were recorded in the detritivore and herbivore guilds while the highest indices (2.5–3.0) were recorded in the piscivore guild. The algivore guild had a trophic index of 1.57 while that of omnivore guild ranged from 1.5 to 2.00. The trophic index of molluscivore guild was 2.36 and that of invertivore guild ranged from 2.2 to 2.65. Broad ranges of trophic indices (Fig. 3A) indicated that fish species in each trophic guild fed on a variety of food items.

Levin's index for dietary niche breadth (*B*) ranged from 1 in piscivore guild to 5.16 in omnivore guild (Fig. 3B). The narrow ranges for dietary niche breadth were recorded for the herbivore and invertivore trophic guilds. *B* value of 1 indicates that the fish species feeds only on a single prey type (high specialists) and *B* value of > 1.5 indicates that the fish species ingests a diverse range of food types (generalists). Accordingly, *Sphyraena jello* Cuvier, 1829 and *Terapon puta* Cuvier, 1829 in piscivores trophic guild were high specialists, *Arius maculatus* (Thunberg, 1792), *Lates calcarifer* (Bloch, 1790) and *Anguilla bicolor bicolor* McClelland, 1844 were specialists, whereas *Leiognathus fasciatus* (Lacepède, 1803), *Acanthopagrus berda* (Forsskål, 1775) and *Leiognathus equvlus* (Forsskål, 1775) in the same trophic guild were moderate generalists. In invertivore guild, *Plotosus canius* Hamilton, 1822 and *Plectorhinshus gibbosus* (Lacepède 1802) were high specialists, *Apogon hyalosoma* (Bleeker, 1852) and *Lethrinus rubrioperculatus* Sato, 1978 were specialists. Only fish species, *Cicamugil cascasia* in detritivore guild showed specialist dietary habits. In herbivore (guild vi), omnivore (guild v) and invertebrate and fish (guild ii) trophic guilds, all species were generalists (Fig. 3B). As the molluscivore and algivore guilds had only one species each, they were not treated as specialists.

Relative abundance of fish species in piscivore and invertivore guilds was low while that of some species in herbivore, omnivore and detritivore guilds were high (Fig. 3C). The herbivore guild was dominated by *Siganus javus* (20.4 %) and *Scatophagus argus* (Linnaeus, 1766) (9.5 %). The omnivore guild was dominated by *Monodactylus argenteus* (Linnaeus, 1758) (17.5 %) and in detritivore guild, *E. suratensis* was the most abundant having 11.5 % of total number of fish in the assemblage. In piscivore guild, only *Arius maculatus* (6.4 %) registered over 5 % of abundance. None of the species in invertivore and invertebrate and fish feeding guilds had a relative abundance greater than 5 % (Fig. 3C).

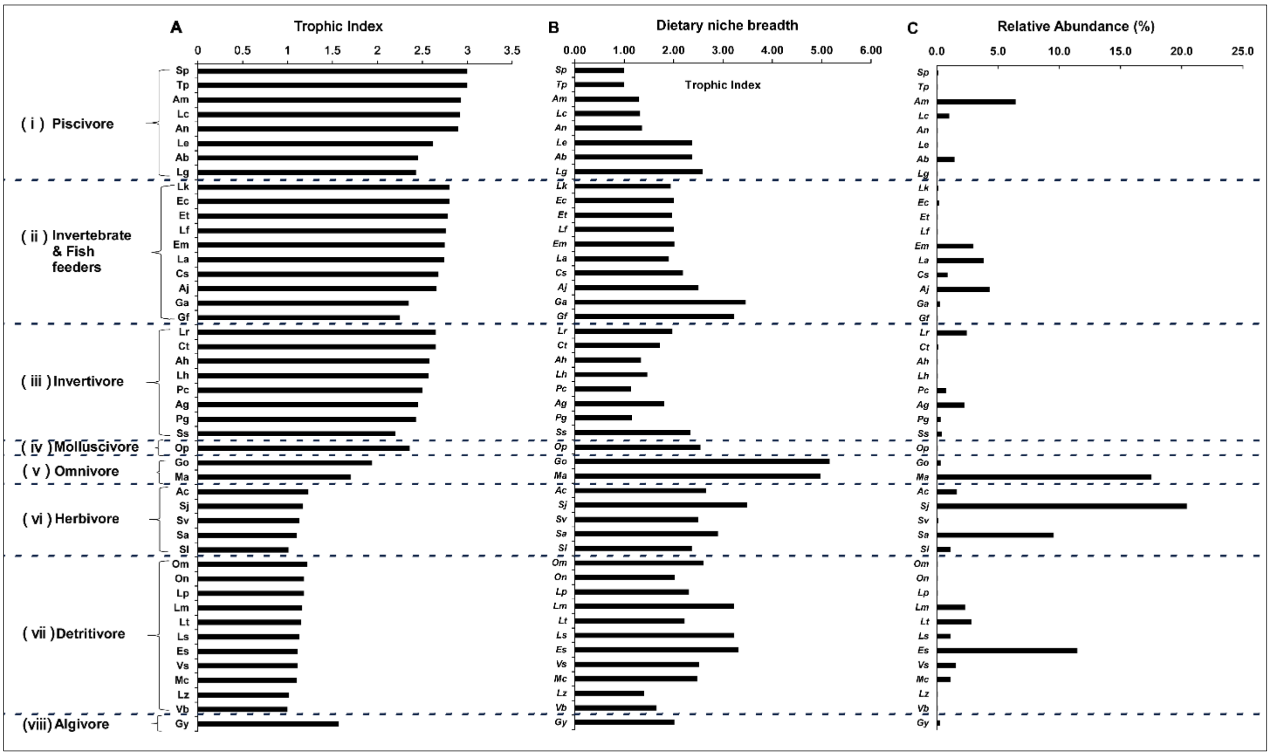

Fig. 3. Trophic indices (A), Levin's dietary niche breadths (B) and relative abundance (C) of the 46 fish species collected from the brush parks of the Negombo estuary. Abbreviations of species names are as given in Table 2.

These indicate that the species occupying lower trophic levels in the food web (i.e., herbivore, omnivore and detritivore guilds) were more abundant whereas those occupying higher trophic levels were less abundant.

Trophic continuum and dietary niche breadth

The significant negative linear and negative second order relationships ($P < 0.05$) were observed respectively between T_i and dietary niche breadth (B) in the piscivore guild and fish consumed invertebrates and fish guild (Figs. 4A and 4B). These indicate that fish species in both guilds which fed on several types of prey occupied wide ranges of trophic indices (T_i) in the upper trophic levels. These also show that the species in higher trophic levels were specialists having narrow dietary niche breadths. On the other hand, species with lower T_i, fed different food items, mainly on soft-bodied macrobenthos and fish (Table 3). In the invertivore guild, a significant negative second order relationship ($P < 0.05$) was observed between T_i and dietary niche breadth (Fig. 4C). This indicated that individual species in this trophic guild also occupied different levels in the trophic continuum. They were also either specialists or generalists. Among the invertivores, the species with the highest dietary niche breadth (*Sillago sihama* (Forsskål, 1775)) had a relatively low T_i while some others with high dietary niche breadth also had relatively high T_i values. Four species which can be considered as specialists also had intermediate T_i values. As there were only two species in the omnivore trophic guilds (Figs. 2 and 3) species in omnivore and herbivore guilds were combined to determine the relationship between T_i and B and a significant positive second-order relationship ($P < 0.05$) was found between T_i and B (Fig. 4D). This indicates that the constituent species of this trophic guild show opposite of those in the piscivore guild. In this guild, there were no specialists and the species which occupied higher trophic levels in the trophic continuum had wider dietary niche breadths as they fed on both plant matter and animal matter (Table 3). In the detritivore trophic guild, a significant parabolic relationship ($P < 0.05$) was observed between T_i and dietary niche breadth (Fig. 4E). In this trophic guild, there were only one species which had lower (< 1.5) dietary niche breadth, which could be treated as specialists while rest of the species were generalists having higher B values. Presumably, there was no food limitation for constituent species in this trophic guild.

Discussion

The structure of fish communities aggregated in fish shelters is not expected to be similar to those in natural habitats because the species that are attracted to such structures are mostly "shade-philic" species and perhaps predators in search of prey organisms. The trophic guild structure of fish communities associated with natural reefs and artificial reefs such as shipwrecks was also found to

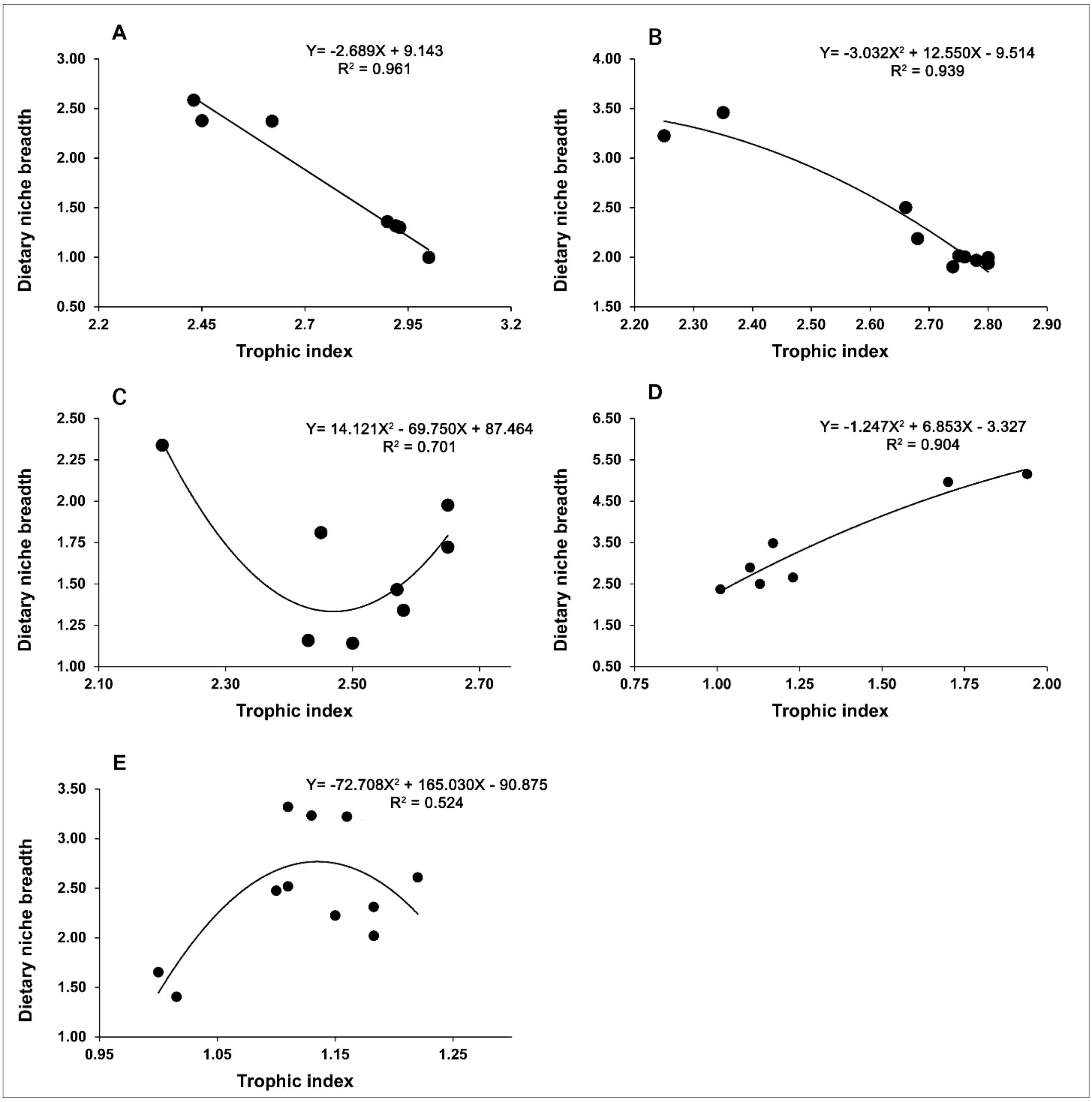

Fig. 4. The relationships between trophic index and dietary niche breadth in the five trophic guilds. (A): Piscivore, (B): Invertebrates and fish feeders, (C): Invertivore, (D): Herbivore and omnivore and (E) Detritivore. Here, species in trophic guilds, herbivore and omnivore were pooled due to less number of species in each guild.

be different from each other (Arena et al. 2007; Simon et al. 2013), and therefore, the energy flow in the two fish shelters may not be the same. Fish communities in shelters such as brush parks might be structured in such a way that the constituent species would find refuge from predators and enhance schooling behaviour (Dempster and Taquet 2004). In some regions such as West Africa, where brush parks are placed for longer periods of > 12 months (Niyonkuru and Lalèyè 2010), community structure of fish assemblages can be expected to be somewhat stabilized. However, brush parks in Negombo estuary are maintained for much less time period (3–97 days), and as such, fish species that are attracted to these brush parks in search of food and shelter are temporary visitors (Amarasinghe et al. 2002; Gammanpila et al. 2017).

Results of the present study revealed that, despite their relatively short stay in the brush parks, the fish assemblages associated with the brush parks are composed of eight distinct trophic guilds. Knowledge on trophic guilds are particularly useful to simplify the structure and dynamics of complex tropical aquatic ecosystems (Garrison and Link 2000). As the members of each trophic guild play somewhat similar roles, understanding the guild structure is useful to postulate how fisheries exploitation regimes impact on trophic dynamics. One of the limitations of the present study was the small sample size of some species. However, it may not have a significant impact because of the low variability of dietary composition of individual fish species. Earlier studies on food and feeding habits of *Sphyraena jello* (Bachok et al. 2004; Mohanraj and Prabhu 2012), *Anguilla bicolor* (Rupasinghe and Ettygalle 2006), *Epinephelus* sp., *Leiognathus equulus* (Forsskål, 1775) and *L. fasciatus* (Hajisamae and Ibrahim 2008) also indicated that these species belong to the similar trophic guilds as found in the present study.

Coexistence of constituent species with more or less similar dietary habits in a fish community is generally possible when there is a niche segregation along temporal, spatial and trophic dimensions (Edirisinghe and Wijeyaratne 1986; Piet et al. 1999). A trophic guild consists of species that exploit similar food resources in a similar way (Root 1967; Garrison and Link 2000) and as such, one can expect that dietary overlaps among species of a trophic guild may lead to inter-specific competition. However, in fish communities with complex interactions, ecological strategies appear to exist for relaxing inter- and intra-specific competition (Carr et al. 2002; Boaden and Kingsford 2015). Although each trophic guild is represented by species with similar dietary habits (Root 1967), results of the present study suggests that even within a trophic guild, constituent species occupy different trophic positions relaxing competition for food resources when a trophic continuum is considered. This is particularly so for fish species occupying higher trophic levels where competition for food resources might be keen as opposed to those occupy in lower trophic levels with abundant food resources.

In many oceans including the Mediterranean sea (Riera et al. 1999; Massuti et al. 1999), Indian Ocean (Ariyarathna and Amarasinghe 2012) and Central America (Hunter and Mitchell 1967), flotsam associated fisheries are established. Despite the relatively short duration of fish assemblages in these artificial shelters, coexistence of constituent species might conform to divergence of resource exploitation especially the food. Trophic guild structure broadly indicates dietary niche divergence of coexisting species along the trophic dimension. It is also suggested that in artificial fish shelters such as FADs, flotsam, floating fish cages, petroleum drilling platforms and brush parks, availability of food resource is limited and therefore these shelters can be considered as 'ecological traps' (Marsac et al. 2000; Menard et al. 2000; Hallier and Gaertner 2008). Nevertheless, the concept of 'ecological trap' is shown not to be always true when fish assemblages attracted to fish shelters are considered (Schaefer and Fuller 2002). Similarly, it can be argued that similar dietary habits of the constituent species in a trophic guild may increase inter-specific competition for food. Present analysis however, has shown that within a trophic guild, component species occupy slightly different trophic levels, which are defined by trophic indices (Fig. 3A). Here trophic index (T_i) was defined as a continuum rather than a discrete trophic level in conventional food web studies (Winemiller 1990).

Results of the present study also showed that the constituent species of trophic guilds exhibit broad dietary niche breadth. Trophic generalists are characterised by high dietary overlap whereas trophic specialists often require trophic divergence for their co-existence (Weliange and Amarasinghe 2003). It can therefore be stated that although the fish assemblages aggregated in artificial fish shelters such as brush parks consist of trophic guilds, they are structured through trophic divergence. In animal communities, trophic divergence is known to be an important process that generates diversity (Grant and Grant 2006), and it also has important implications in ecological dynamics by reducing inter-specific competition for food (Post et al. 2008). Divergence in the use of food resources that results less exploitative competition appears to exist in brush parks too. This is of particular importance because management of tropical fish stocks and the aquatic ecosystems that support them will require a good knowledge of food web ecology (Winemiller and Jepsen 1998). Ecologically, food and feeding not only affect the energy transfer and subsequent growth and survival of prey and predators, but also the distribution, abundance and demographics of fishes (Brodeue et al. 2017).

Findings of the present study therefore have significant implications in fisheries management because fisheries associated with natural and artificial fish shelters contribute significantly to enhance fisheries production in many parts of the world (Dempster and Taquet 2004). Furthermore, trophic guild structure in fish assemblages have a potential utility value as a rapid appraisal method to assess the impact on the ecosystems. For example, Welcomme et al. (2006) have shown that environmental guilds of fish assemblages can be used as a tool to assess the impacts on fluvial ecosystems and that they can assist in predicting responses of river fish biota to anthropogenic changes such as river damming and water diversion. Also, knowledge about community-wide interactions that regulate the dynamics of exploited fishery resources is recognized to be important for fisheries management (Jennings and Kaiser 1998). As such, findings of the present study can be used as a baseline for future assessment of environmental impacts, which would be useful in ecosystem-based management of brush park fisheries.

Conclusion

Trophic guild, by definition is represented by species with similar dietary habits. In the present study, it was revealed that fish species attracted to brush parks in a Sri Lankan estuary were organized in different trophic guilds and the constituent species of a particular trophic guild show broad dietary niche breadth. When a trophic continuum is considered, it was evident that within a trophic guild, constituent species occupy different trophic positions relaxing competition for food resources. The species in lower trophic levels were mostly generalists while those in higher trophic guilds were specialists. Trophic generalists in the lower trophic levels without having food resource limitations were evidently characterized by high dietary overlap whereas trophic specialists with food limitation at higher trophic levels exhibited greater trophic divergence for relaxing inter-specific competition. These findings can be used as a baseline for future assessment of environmental impacts, which would be useful in ecosystem-based management of brush park fisheries.

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