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Morphological correlates with diet of fish assemblages in brush park fisheries of tropical estuaries

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Abstract Brush park fishery in Negombo estuary, Sri Lanka is a traditional fishing practice which relies on fishes attracted to artificial woody fish aggregation devices. This study investigates whether constituent species in these brush parks exhibit morphological variations in relation to their dietary habits. Fishes caught in brush parks were sampled from April 2014 to April 2016 covering rainy, intermediate and dry seasons. There were 817 specimens of 46 species belonging to 24 families. From each specimen, 17 morphological attributes were determined and diet composition of each species was analyzed in terms of relative biovolume. Trophic index of each species estimated from the proportions of dietary items and their possible trophic level in the community was significantly related to two body proportions (Maximum body height/Maximum body width and Total length/ Maximum body height) which described shape of fish. Principal component analysis of morphometric attributes and dietary habits indicated that the species in the higher trophic levels are characterized by slender, long-body shapes and those occupy lower trophic levels are predominantly laterally compressed with deep body shapes. As such, structure of coexisting species in brush parks of Negombo estuary is predominantly along the trophic dimension and is related to morphological traits of constituent species. The predictive power of ecomorphological correlates with diets of fish species other than mugilids which are attracted to brush parks, can therefore be considered as a useful tool for conducting rapid ecological assessment.

Keywords Dietary habits · Ecomorphology · FADs · Feeding ecology · Fish shelters · Trophic level

Introduction

The concept of ecomorphology, suggesting that the functional designs of animals are related to the environment they inhabit, is gaining momentum in studies on fish community ecology. In fish communities, habitat use (Pease et al. 2012; Sampaio et al. 2013; Soares et al. 2013; Bower and Piller 2015; Pessanha et al. 2015; Brandl et al. 2015), locomotion (Wainwright et al. 2002), and feeding strategies (Wainwright and Richard 1995; Hulsey and García De-León 2005; Wagner et al. 2009; Ramírez et al. 2015) are shown to be related to the morphological characters of fish. The environment where animals inhabit exposes them to various physical forces that can impose a wide range of functional demands (Wainwright and Reilly 1994). The morphological and physiological traits of species help to meet those

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demands. High predictive power of ecomorphological approaches is a useful tool when conducting rapid ecological assessments (Hugueny and Pouilly 1999).

Many studies are reported on the feeding ecology in relation to morphological attributes of fish communities such as those in coral reefs (Wainwright and Bellwood 2002; Elliott and Bellwood 2003; Price et al. 2011), sea grass beds (Motta et al. 1995), tropical estuaries (Pessanha et al. 2015), demersal marine habitats (Bohorquez-Herrera et al. 2015), floodplain lakes (Oliveira et al. 2010) and many freshwater habitats in temperate (Xie et al. 2001), tropical (Adite and Winemiller 1997; Hugueny and Pouilly 1999; Bhat 2005), and neo-tropical regions (Casatti and Castro 2006; Ibañez et al. 2007; López-Fernández et al. 2012; Ramírez et al. 2015). However, no information is reported about ecomorphological correlates of fish communities with their functional attributes in natural and artificial fish aggregation devices.

Attraction of fish to the shelters is purported to bring positive and negative effects. Provision of more habitats resulting in biomass increase and facilitating recruitment to the area are some of the positive impacts (Kingsford 1999). Whereas their impacts hypothesized to be negative when the fishes attracted to shelters are disadvantageous due to limited food supply compared to their free-ranging counterparts and are labelled as 'ecological traps' (Robertson and Hutto 2006).

Brush park fishery in Negombo estuary of Sri Lanka is a traditional fishing practice which relies on fishes attracted to artificial woody fish aggregation devices constructed by placing dense masses of mangrove twigs and branches in shallow regions of the estuary (Edirisinghe and Wijeyaratne 1986; Costa and Wijeyaratne 1995; Amarasinghe et al. 2002; Fig. 1). As the intrinsic nature of attraction to shelters in different fish species may vary from species to species, the structure of brush park fish communities may not be similar to that of open water regions of the estuary. In the process of acquiring resources, fish species interact with each other so that it can be hypothesized that morphological specializations in fish exists to match with the pattern of resource use in the brush park fish communities. This study investigates whether constituent species in brush parks exhibit morphological variations in relation to their diet, which can eventually be useful to understand the driving forces of co-existence of constituent species in the community, providing major fisheries management implications.

Material and methods

Sampling location

Negombo estuary, where the study was conducted is located between latitude 7°6′-7°12′ N and longitude 79°40′-79°53′ E on the west coast of Sri Lanka (Fig. 1). This shallow estuary covers an area of about 3164 ha and is connected to the sea year round at the northern end by a single narrow opening (Goonethilake et al. 2005). The estuary extends approximately 12.5 km in length, its width varies from 0.6 km to 3.6 km and has a shoreline of 24 km. Its mean depth is 0.65 m. The salinity of the estuary is strongly related to the freshwater influx from the river draining into the estuary during the inter-monsoonal seasons and tidal fluxes (Goonethilake et al. 2005), and ranges spatially from 0 ppt to 25 ppt (Gammanpila 2010).

Fishing activities of the Negombo estuary are dominated by five major types of fishing gear: trammel nets, drag nets, brush parks, cast nets and stake nets (Jayakody 1996). Brush parks are a traditional form of fishing method which are installed in shallow areas of the estuary piling dense masses of mangrove twigs to attract fish to the shelter. Fishers allow each brush park to soak for 3–97 days and at the time of harvesting, it is encircled with a net screen of mesh size 1.25–2.0 cm. The mangrove twigs are then removed from the enclosure and the fishes are harvested (Edirisinghe and Wijeyaratne 1986).

Fish sampling

Fishes were collected monthly in three major brush park fishing areas, Munnakkaraya, Katunayaka and Talahena (Fig. 1) in the estuary over a period of two years from April 2014 to April 2016, covering the rainy, intermediate and dry seasons. For ethical clearance, permission for conducting research was obtained from the University of Kelaniya, Sri Lanka. On each sampling visit, one brush park was sampled. Accordingly, 64 brush parks were sampled during the study period. From each brush park sampled, a representative sample caught was obtained and fish specimens were fixed injecting 10% buffered formalin into body cavity and were transferred to the laboratory for the analysis of morphometric data and diet. Fish were identified based on the fish identification guides for Sri Lankan waters (Munro 1955; De Bruin et al. 1995).

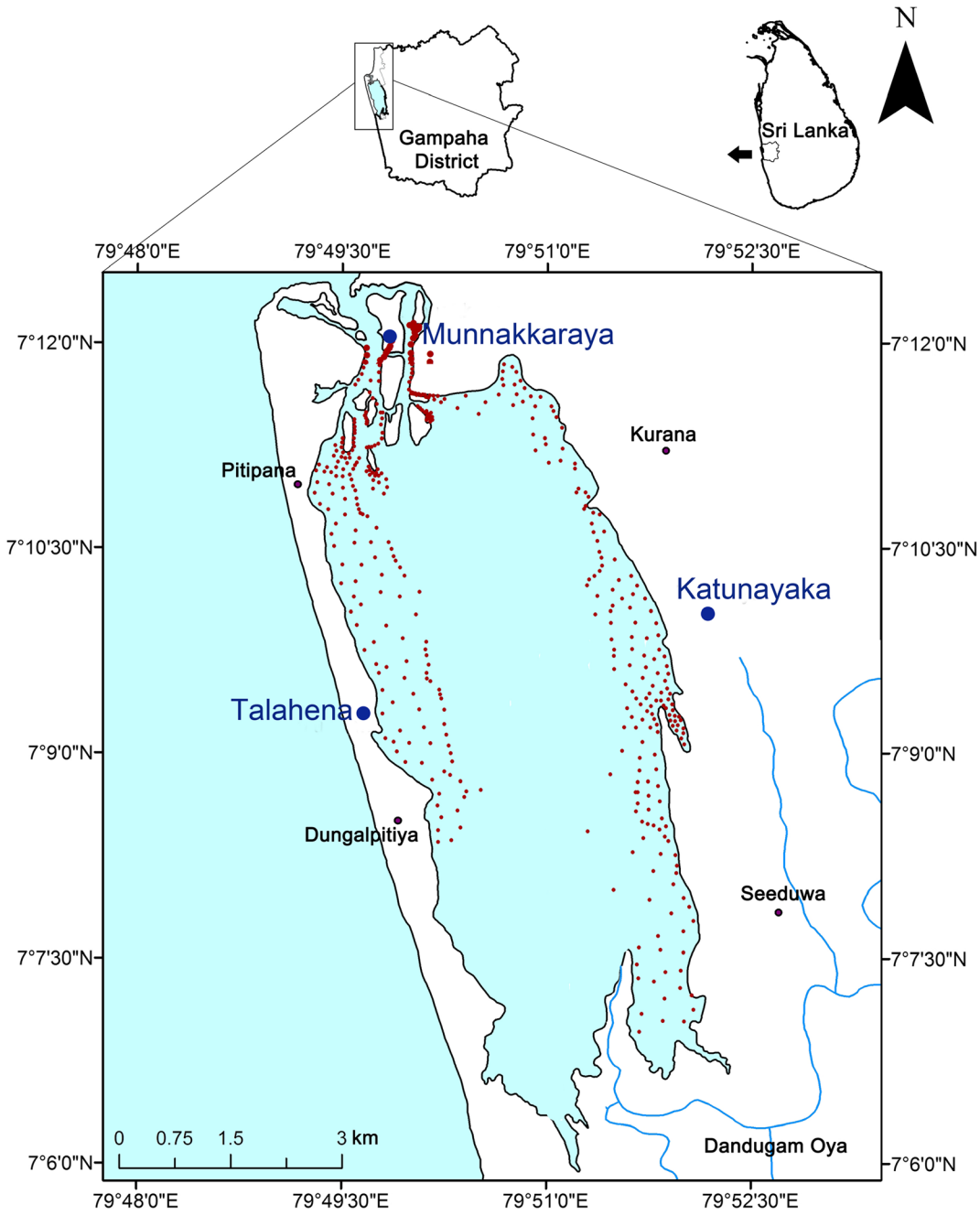

Fig. 1 Map of Negombo estuary illustrating distribution of brush parks (red dots), fishing villages and inflowing river (Dandugam Oya)

Morphological measurements

In each specimen, five coded variables and twelve linear measurements (Table 1) were determined based on the observed associations between morphological features and ecological parameters from studies elsewhere (Winemiller 1991; Adite and Winemiller 1997; Pessanha et al. 2015). Linear morphometric measurements were transformed into ratios in order to reduce the allometric (size dependency) effect and to have a functional interpretation (Faye et al. 2012). Accordingly, relative measurements of maximum body width, maximum body height, gut length, head length and head height were calculated using the standard length as the

Table 1 Coded and mensural morphometric variables determined, abbreviations (Abv) used for the variables and the description of the variables

Morphological characters	Abv	Description
Coded variables		
Shape of the caudal fin	CDF	Rounded = 1; truncate = 2; emarginated = 3; lunate = 4; forked = 5; Pointed = 6
Shape of the pectoral fin	PEC	Rounded = 1; intermediate = 2; pointed = 3
Position of the eye	EP	Lateral = 1; dorso lateral = 2; bulging on top of head = 3
Orientation of the mouth	MTH	Dorsal = 1; supra-terminal = 2; terminal = 3; sub-terminal = 4; inferior = 5; ventral = 6
Number of pairs of barbels	BB	0 = 1; *I* = 2; II = 3; III = 4; IV = 5
Mensural variables		
Total length	TL	Distance from the tip of closed mouth to end of the caudal fin
Standard length	SL	Straight line distance from tip of closed mouth to the terminus of the vertebral column
Maximum body height	MHB	Maximum vertical distance perpendicular to body axis
Maximum body width	MWB	Width at the widest part of the body
Gut length	GL	Distance from esophagus to anus without stretching
Head length	HL	Straight line distance from the anterior tip of closed mouth to posterior edge of opercular membrane
Head height	HH	Distance between the upper and lower edges of the head
Eye diameter	DE	Diameter between fleshly orbit along the anterior/posterior axis
Eye distance	ED	Distance between the fleshly orbit of right and left eye
Height of mouth	HM	Vertical distance between the highest part of the mouth when it is fully open
Width of mouth	WM	Width at the widest part of the mouth when it is fully open
Snout length	SNL	Straight line distance from the pupil of the eye at its midpoint to the anterior margin of the upper jaw

denominator. Head length was used as the denominator for relative measurements of width of mouth, height of mouth, eye diameter, eye distance and snout length. Morphological variables were determined using a vernier caliper and a ruler. Mean value for each variable for each species was then determined.

Dietary analysis

All fish specimens used for measuring morphological characteristics were used in the dietary analyses. Each preserved fish specimen was dissected and the total length of gut was measured. In each specimen, the stomach contents were extracted to prepare a suspension of 10 ml by adding 10% buffered formalin. For fish, which do not have well-developed conspicuous stomach, contents in the first one-third of the intestine were considered as the recently ingested food and were used for making suspension. From each suspension, three sub samples of one ml each were examined under microscope (10 × 10 magnification) using a Sedgwick-rafter counting chamber for qualitative and quantitative determination of stomach/gut contents. Since the stomach contents consisted of numerous genera and species, they were assigned to 11 broader groups (Table 2). Empty stomachs and stomachs with almost fully digested food were excluded. Since small food items were prevalent in the stomach contents, indirect volumetric analysis was employed by comparing food items with unit of known volume. Biovolume 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). Relative volume of each food category in stomach/gut content of individual fish was summed across all samples to estimate the dietary volumetric proportion (%) of each food category in each species for the final analysis.

Trophic index

Trophic index was calculated for each species to determine the relative position in the food web. For a consumer species i, trophic index is defined as:

Table 2 Food categories, their trophic classes and main components of each food category

Food category	Abbreviation	Trophic class	Food Items
Phytoplankton	PP	0	Diatom, blue green algae, green algae, filamentous algae
Macrophytes	MP	0	Terrestrial and aquatic macrophyte plant material
Detritus	DE	0	Decayed plant and animal matter
Mollusks	ML	1	Bivalves and gastropods
Macrobenthos	MB	1.5	Annelids, Nematodes, *Caridina*
Small zooplankton	SZ	1.5	Rotifers (*Brachionus, Trichocerca, Keratella*,) and dinoflagellates
Cladocerans	CD	1.5	*Daphnia, Moina, Diaphanasoma*
Copepods	CP	1.5	Calanoids, Cyclopoids, Harpactocoids
Ostracods	OC	1.5	*Chydorus, Macrothrix, Cypridopsis*
Insects	IN	1.5	Terrestrial and aquatic insects
Fish	FH	2	Fish scales, fish eggs, juvenile fish, fish skeletons

$$Troph_i = 1 + \sum_{j=1}^{n} Troph_j \left(p_{ij}\right) \quad (1)$$

where $Troph_j$ is the trophic level of prey item j, and p_{ij} represents the fraction of food (proportion by volume) consumed by species i consisting of prey item j in the diet (Winemiller 1990).

Data analysis

The following two body proportions (P1 and P2) which were reported to be related to diet of fish (Catella and Petrere 1998; Weliange and Amarasinghe 2007) were determined for each species.

$$P1 = \frac{MHB}{MWB} \quad (2)$$

$$P2 = \frac{TL}{MHB} \quad (3)$$

where, MHB = Maximum body height, MWB = Maximum body width and TL = Total length. These body shapes are such that laterally compressed species are characterized with high P1 and dorso-ventrally flattened species have low P1 values. Species with high P2 are elongated fish and those with low P2 are deep-bodied fish.

For preliminary investigation of the relationship of body shape to dietary habits, these body proportions were related to $Troph_i$ estimated from eq. 1 above. The data sets of 10 relative measurements of 12 morphological parameters, 5 coded variables. (Table 1) and dietary data assigned to 11 taxonomic groups (Table 2) were then used for multivariate statistical analyses. Morphometric and dietary data were fourth root transformed to reduce non-normality as this approach is effective for datasets with many very low values and a few large values (Quinn and Keough 2002). A principal component analysis (PCA) was used to highlight the underlying species segregation patterns of multivariate data sets of morphological and dietary parameters. PC scores based on 15 morphological parameters and the PC scores of 11 dietary categories were related to examine whether there was a significant correlation between morphology and diet as PC1 and between PC scores of morphology and $Troph_i$. Multivariate statistical analyses (PCA) were performed using Minitab (Version 16) software package.

Results

During the study period, 817 specimens were obtained from the harvests of brush parks. There were 46 species belonging to 24 families. Number of specimens per species used for the analysis of morphometric variables and dietary habits varied from 1 to 107 (Table 3). Coded and mensural morphometric variables are given in supplementary Tables S1 and S2 respectively. Volumetric proportions of diets in the stomach/gut contents of individual species are given in supplementary Table S3.

Table 3 Fish species examined, their abbreviations (Abv), size ranges (cm) and trophic indices

Family	Scientific name	Abv	N	Size range (cm)	Trophic Index
Acanthuridae	*Acanthurus gahhm*	Aga	21	6.2–17.4	1.23
Ambassidae	*Ambassis gymnocephalus*	Ag	13	8.1–17.4	2.45
Anguillidae	*Anguilla bicolor bicolor*	Abb	1	60.3	2.90
Apogonidae	*Apogon hyalosoma*	Ah	3	8.9–13.2	2.58
Ariidae	*Arius jella*	Aj	24	14.6–30.5	2.66
	Arius maculatus	Am	9	10.6–28.7	2.93
Carangidae	*Caranx sexfasciatus*	Cs	23	9.2–17.3	2.68
	Carangoides talamparoides	Ct	2	12.4–17.7	2.65
Centropomidae	*Lates calcarifer*	Lc	34	18.1–48.3	2.92
Cichlidae	*Etroplus suratensis*	Es	96	5.5–23.5	1.11
	Oreochromis mossambicus	Om	2	25.3–29.5	1.22
	Oreochromis niloticus	On	3	21.4–22.3	1.18
Eleotridae	*Ophiocara porocephala*	Op	5	14.2–20.7	2.36
Gerreidae	*Gerres abbreviatus*	Ga	16	7.5–14.4	2.35
	Gerres filamentosus	Gf	1	8.6	2.25
	Gerres oyena	Goy	9	9.9–13.5	1.57
	Gerres oblongus	Go	6	9.1–15.2	1.94
Haemulidae	*Plectorhinshus gibbosus*	Pg	12	7.1–22.1	2.43
Leiognathidae	*Leiognathus equulus*	Le	1	7.7	2.62
	Leiognathus fasciatus	Lfa	1	9.1	2.43
Lethrinidae	*Lethrinus rubrioperlulatus*	Lr	1	9.0	2.57
Lutjanidae	*Lutjanus argentimaculatus*	La	66	14.3–33.0	2.74
	Lutjanus fulviflamma	Lf	19	10.4–15.7	2.76
	Lutjanus kasmira	Lk	4	10.6–15.9	2.80
	Lutjanus russelli	Lru	41	8.0–26.9	2.65
Monodactylidae	*Monodactylus argenteus*	Ma	12	6.9–9.2	1.70
Mugilidae	*Liza macrolepis*	Lm	24	17.1–50.0	1.16
	Liza melinoptera	Lme	32	11.3–45.2	1.15
	Liza parsia	Lp	7	13.6–27.3	1.18
	Liza sascasia	Lsa	2	21.8–23.4	1.02
	Liza subviridis	Ls	25	15.2–49.2	1.13
	Mugil cephalus	Mc	12	18.2–54.4	1.10
	Valamugil buchanani	Vb	5	12.2–50.3	1.00
	Valamugil seheli	Vs	24	12.6–28.5	1.11
Plotosidae	*Plotosus canius*	Pc	7	34.4–59.0	2.50
Scatophagidae	*Scatophagus argus*	Sa	37	7.2–22.7	1.10
Serranidae	*Epinephelus malabaricus*	Em	41	13.8–40.1	2.75
	Epinephelus coioides	Ec	9	10.1–31.5	2.80
	Epinephelus tauvina	Et	1	35.7	2.78
Sparidae	*Acanthophagus berda*	Ab	31	9.2–33.5	2.45
Sphyraenidae	*Sphyraena jello*	Sje	1	30.8	3.00
Sillaginidae	*Sillago sihama*	Ss	10	12.5–32.7	2.20
Siganidae	*Siganus jarvus*	Sj	107	8.8–22.9	1.17
	Siganus lineatus	Sl	10	10.9–23.2	1.01
	Siganus vermiculatus	Sv	6	11.7–20.3	1.13
Terapontidae	*Terapon puta*	Tp	1	10.9	3.00

Body proportions verses diet

Fish species with high P1 were laterally compressed with deep bodies (*Monodactylus argenteus*, *Leiognathus equulus*, *Scatophagus argus* and *Acanthurus gahhm*) and species with high P2 were slender with long-bodies (*Anguilla bicolor bicolor, Plotosus canius, Sillago sihama* and *Sphyraena jello*). There were weak correlations between the relationships between P1 and $Troph_i$ ($r = -0.118$) and P2 and $Troph_i$ ($r = 0.176$). However, these two morphological variables were significantly related to $Troph_i$ (Fig. 2a and b) when data points pertaining to fish species of family Mugilidae were disregarded indicating that body shapes can be used as predictors of dietary habits.

Principal component analysis

As the relationships of body proportions and trophic indices (Fig. 2a and b) were stronger without mugilids, PCAs of morphological variables and diets were performed separately with and without mugilids.

Morphological analyses of all species

The first three PC axes of morphological variables, which had eigenvalues >1, explained 62.6% of the cumulative variance (Table 4). The first principal component (PC1) accounted for 28.4% of cumulative variance and was most influenced positively by higher DE, MHB, HH, SNL and PEC and negatively by higher EP, WM, HM and BB. Species which occupied the positive PC scores on this axis such as *Monodactylus argenteus, Gerres abbreviates, Acanthurus gahhm, Leiognathus equulus, G. oblongus, Etroplus suratensis, Scatophagus argus,* possessed deeper bodies, larger eyes and long snouts. Species such as *Anguilla bicolor bicolor* and *Plotosus canius* which occupied negative scores of the PC1 axis possessed slightly dorso-lateral eyes, wide mouths and barbels (Fig. 3a, upper panel).

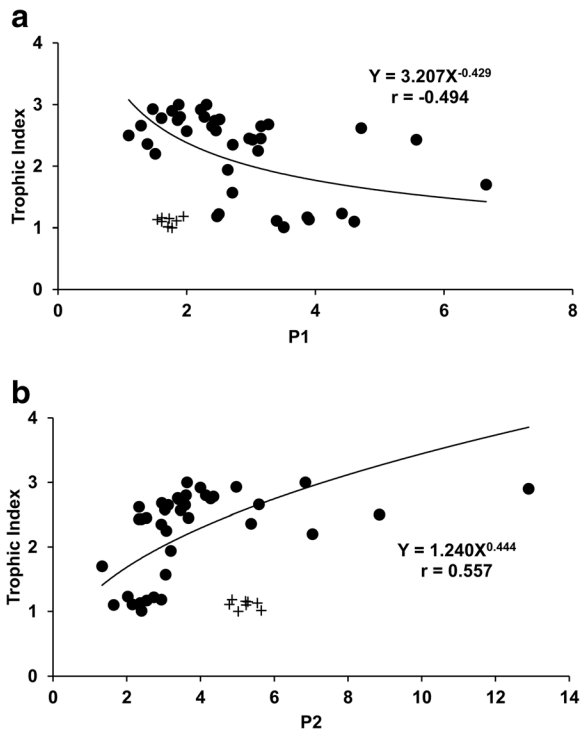

Fig. 2 Relationships of (**a**) P1 (Maximum body height/Maximum body width) verses trophic index; and (**b**) P2 (Total length/ Maximum body height) verses trophic index ($Troph_i$). Here, species belong to family Mugilidae (crosses) were excluded from the analysis. Both relationships are significant at 0.01 probability level ($p < 0.01$)

Table 4 PCA score on the 15 morphological variables of all fish species

	PC1	PC2	PC3
Eigen value	4.255	3.136	1.996
Proportion	0.284	0.209	0.133
Cumulative variance	0.284	0.493	0.626
Coded variables			
CDF	0.106	***−0.377***	0.085
PEC	**0.294**	−0.115	**0.215**
EP	***−0.390***	−0.093	0.176
MTH	0.151	***−0.402***	0.176
BB	***−0.181***	***−0.192***	**0.432**
Mensural variables			
MHB	**0.394**	0.130	0.005
MWB	0.159	0.122	**0.535**
GL	0.082	−0.166	**0.216**
HL	0.154	**0.448**	**0.208**
HH	**0.330**	**0.315**	0.153
DE	**0.402**	−0.022	***−0.103***
ED	0.153	***−0.401***	**0.204**
HM	***−0.182***	**0.291**	0.179
WM	***−0.212***	0.178	**0.463**
SNL	**0.333**	−0.018	0.005

Bold – positive loading; Bold italics – negative loading. Abbreviations of morphometric variables are as given in Table 1

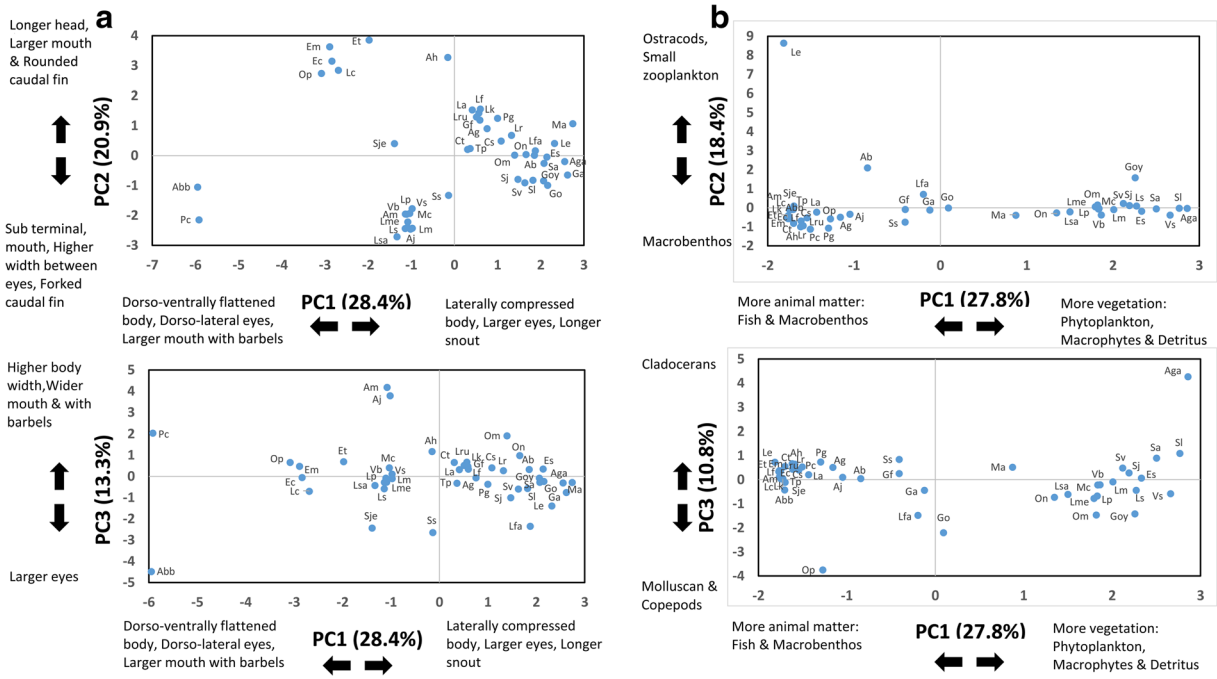

Fig. 3 Two-dimensional plots of PC scores of the first three PC axes (**a**) = based on morphological data of all species (upper panel: PC1 verses PC2; lower panel: PC1 verses PC3); and (**b**) = based on dietary data of all species (upper panel: PC1 verses PC2; lower panel: PC1 verses PC3)

The second PC axis (PC2) which explained 20.9% of the variance, was influenced positively by higher HL, HH and HM. Species such as *Epinephelus tauvina, E. malabaricus, E. coioides, Apogon hyalosoma, Lates calcarifer* and *Ophiocera porocephala* having higher head length, larger mouth and rounded caudal fin had positive scores of the PC2 axis. Fishes of family Mugilidae (*Liza sascasia, L. subviridis, L. macrolepis, L. melinoptera*) and *Arius jella, A. maculatus* had high negative scores for PC2 and possessed higher width between eyes, terminal or sub terminal mouth and forked caudal fins (Fig. 3a, upper panel).

The third PC axis (PC3) explained 13.3% of the variance and was influenced positively by higher MWB, higher WM, higher ED and presence of barbels and negatively by higher DE (Table 4). *Arius maculatus, A. jella* and *Plotosus canius* occupied positive scores on this axis, which possessed wider bodies, larger mouth and barbels (Fig. 3a, lower panel). *Anguilla bicolor bicolor, Sillago sihama* and *Sphyraena jello* had high negative scores for PC3 and had larger eyes.

Dietary analyses of all species

Volumetric proportions of 11 diet categories in the 46 fish species studied are given in supplementary Table S2. Results of PCA of dietary data (Table 5) indicate that the first three PCs explained 57.0% total variance. The first PC axis (PC1; variance explained = 27.8%) was positively influenced by consumption of more plant matter such as phytoplankton, macrophytes and detritus, and negatively by more animal matter, mainly fish and macrobenthos with dominance of microcrustaceans (Fig. 3b, upper panel). *Acanthurus gahhm, Siganus lineatus, Valamugil seheli, Scatophagus argus, Etroplus suratensis, Liza subviridis, Gerres oyena, S. javus* had higher positive scores on first PC axis and fed on mostly phytoplankton, macrophytes and detritus. *Leiognathus equulus, Epinephelus tauvina, E. coioides, Lutjanus kasmira, L. fulviflamma, E. malabaricus, Arius maculatus, Lates calcarifer, Anguilla bicolor bicolor, Carangoides talamparoides, Sphyraena jello, Terapon puta* and *Apogon hyalosoma*, which were predominantly carnivorous

Table 5 PCA on 11 dietary variables of all fish species

	PC1	PC2	PC3
Eigenvalue	3.05	2.025	1.1900
Proportion	0.278	0.184	0.108
Cumulative variance	0.278	0.462	0.570
Coefficients			
PP	**0.458**	0.122	0.162
MP DE ML	**0.448**	−0.017	**0.209**
DE MB	**0.421**	−0.031	***−0.214***
ML SZ	−0.034	−0.030	***−0.625***
MB SZCD	***−0.358***	***−0.275***	**0.255**
SZ	−0.088	**0.641**	0.096
CD	0.134	−0.006	**0.539**
CP	0.178	**0.253**	***−0.338***
OC	−0.096	**0.645**	0.086
IN	0.138	−0.036	−0.079
FH	**−0.443**	0.125	−0.019

Bold – positive loading; Bold italics – negative loading. Abbreviations of food items as given in Table 2

(fed on animal matter, fish and macrobenthos) had high negative values on PC1 axis.

The second PC axis (PC2; variance explained = 18.4%) was positively associated with consumption of ostracods and small zooplankton and negatively with feeding on more macrobenthos. Species such as *Leiognathus equvulus* had high positive scores on PC2 and *Plotosus canius, Plectorhinshus gibbosus* and *Apogon hyalosoma* occupied the region of negative scores on PC2 axis (Fig. 3b, upper panel).

The loading of third principal component axis (PC3), which explained 10.8% of the variance, was most positively influenced by consumption of cladocerans and negatively influenced by consumption of mollusks and copepods. Fish species such as *Acanthurus gahhm* had positive PC scores on this axis and *Ophiocara porocephala, Gerres oblongus, Lutjanus fulviflamma, Oreochromis mossambicus* and *G.oyena* had high negative scores on the this axis (Fig. 3b, lower panel).

Morphological analyses without Mugilidae

In the PCA performed for the morphological variables without the members of Mugilidae, the first three PC axes explained 64.2% of the cumulative variance (Table 6). The first principal component (PC1) explained 31.8% of the variance and was most influenced

Table 6 PCA on the 15 morphological variables without mugilids (WoM)

	PC1	PC2	PC3
Eigenvalue	4.767	2.713	2.1448
Proportion	0.318	0.181	0.143
Cumulative variance	0.318	0.499	0.642
Coded variables			
CDF	0.193	***−0.364***	−0.067
PEC	**0.281**	−0.123	−0.173
EP	***−0.370***	−0.028	***−0.232***
MTH	0.209	***−0.398***	−0.162
BB	***−0.147***	***−0.388***	***−0.413***
Mensural variables			
MHB	**0.355**	0.178	0.007
MWB	0.134	**0.247**	***−0.532***
GL	0.138	0.065	***−0.273***
HL	0.051	**0.473**	-0.218
HH	0.261	**0.390**	−0.147
DE	**0.372**	0.058	**0.128**
ED	**0.297**	*−0.197*	***−0.276***
HM	***−0.254***	0.064	−0.135
WM	***−0.229***	0.043	**−0.421**
SNL	**0.322**	−0.149	0.025

Bold – positive loading; Bold italics – negative loading. Abbreviations of morphometric variables are as given in Table 1

positively by DE, MHB, SNL, ED and PEC and negatively by EP, HM. WM and BB. Species with positive cores on this axis such as *Acanthurus gahhm, Gerres abbreviates, Monodactylus argenteus, G. oblongus, Etroplus suratensis, Scatophagus argus* were characterized with larger eyes, taller bodies, higher distance between eyes, longer snouts and intermediate shape of the pectoral fins. Species such as *Anguilla bicolor bicolor and Plotosus canius,* which had negative scores of the PC1 axis possessed dorso-lateral eyes, larger mouths and barbels (Fig. 4a, upper panel).

The second PC axis (PC2), which explained 18.1% of the variance, was influenced positively by HL, HH and MWB and the species contributed were *Apogon hyalosoma, Epinephelus tauvina, E. malabaricus, E. coioides.* Species such as *Plotosus canius, Arius jella, A. maculatus* and *Anguilla bicolor bicolor* had high negative scores for second PC axis and these species possessed terminal and sub terminal mouth with barbels and pointed and forked caudal fin (Fig. 4a, upper panel).

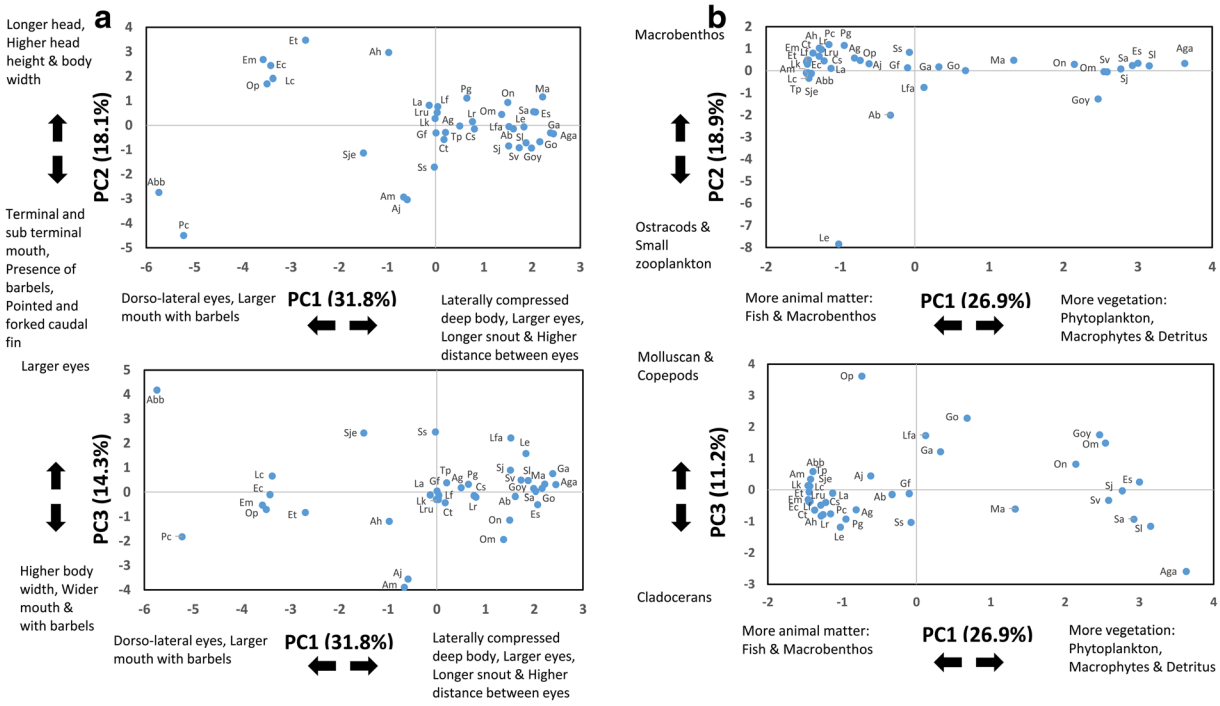

Fig. 4 Two-dimensional plots of PC scores of the first three PC axes (**a**) = based on morphological data of fish species without Mugilidae (upper panel: PC1 verses PC2; lower panel: PC1 verses PC3); and (**b**) = based on dietary data of fish species without Mugilidae (upper panel: PC1 verses PC2; lower panel: PC1 verses PC3)

The third PC axis (PC3) explained 14.3% of the variance and was influenced positively by higher DE and negatively by higher MWB, WM, ED and GL and presence of barbels (Table 6). *Anguilla bicolor bicolor* occupied positive scores and *Arius jella* and *A. maculatus* had negative scores on this axis (Fig. 4a, lower panel).

Dietary analyses without Mugilidae

Results of PCA of dietary data in the fish species without members of family Mugilidae are given in Table 7. The first three PCs explained 57.0% total variance of the data set. The first PC axis (PC1) explained 26.9% of the variance and was positively influenced by those which consume plant matter such as phytoplankton, macrophytes and detritus and negatively by those which feed on fish and macrobenthos with dominance of small crustaceans (Fig. 4b, upper panel). *Acanthurus gahhm, Siganus lineatus, Etroplus suratensis, Scatophagus argus, S. javus, S. vermiculatus and Oreochromis mossambicus*, which fed mostly on phytoplankton, macrophytes and detritus had higher positive scores in the PC1 axis, and those which were predominantly carnivorous had high negative values.

Table 7 PCA on 11 dietary variables without mugilids

	PC1	PC2	PC3
Eigenvalue	2.964	2.079	1.237
Proportion	0.269	0.189	0.112
Cumulative variance	0.269	0.458	0.570
Food items			
PP	**0.513**	−0.082	−0.075
MP DE ML	**0.457**	0.046	*−0.274*
DE MB	**0.405**	0.029	0.169
ML SZ	0.012	0.025	**0.665**
MB SZCD	***−0.322***	**0.317**	*−0.309*
SZ	−0.054	***−0.626***	−0.164
CD	0.199	0.029	***−0.341***
CP	0.178	*−0.239*	**0.380**
OC	−0.055	***−0.636***	−0.152
IN	0.106	0.034	0.171
FH	***−0.413***	−0.183	0.114

Bold – positive loading; Bold italics – negative loading. Abbreviations of food items as given in Table 2

The second PC axis (PC2) explained 18.9% of the variance and was positively loaded by macrobenthos feeders. Species such as *Plotosus canius Plectorhinshus gibbosus* and *Apogon hyalosoma* had high positive scores in PC2 axis and species such as *Leiognathus equvlus*, which consumed small zooplankton and ostracods represented negative scores on PC axis 2 (Fig. 4b, upper panel).

The third principal component axis (PC3), which explained 11.2% of the variance, was most positively influenced by species which consumed mollusks and copepods and negatively by those which consumed cladocerans. Fish species such as *Ophiocara porocephala* and *Gerres oblongus* were positively loaded on this axis and *Acanthurus gahhm, Leiognathus equvlus* and *Siganus lineatus* had high negative scores on this axis (Fig. 4b, lower panel).

Relationship between morphology and diet

When all species were considered, there was a significant correlation between PC1 morpho and PC1 diet (Fig. 5a) but PC1 (morpho) was not significantly correlated with $Troph_i$ (Fig. 5b).

However, when the members of the family Mugilidae were removed from the multivariate data sets, there was a stronger positively significant correlation ($p < 0.001$) between the scores of first PCs of morphological and dietary data (Fig. 6a). This was further confirmed by the negatively significant ($p < 0.001$) relationship of trophic index ($Troph_i$) and PC1 (Morpho) (Fig. 6b), where high trophic level species were with low negative scores of PC1 (Morpho), and positive PC1 (Morpho) scores were with low trophic level species. Despite low variance explained by PC1 (Morpho) and PC1 (Diet) of fish species without mugilids, which were 31.8% and 26.9% respectively (Fig. 4), their significant correlations provide evidence for the concept of ecomorphology in food resource utilization in the fish assemblage.

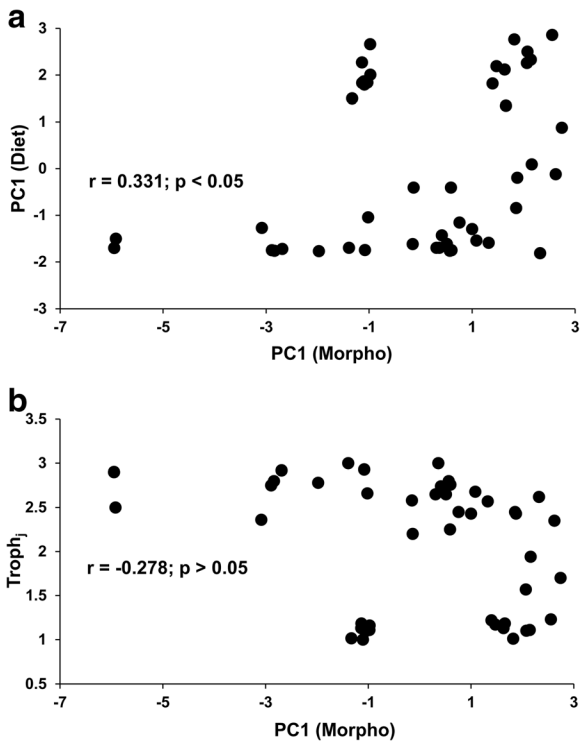

Fig. 5 **a** Scatter plot of PC1 scores based on morphological data (morpho) against those based on dietary data (diet) of all species; (**b**) Scatter plot of PC1scores based on morphological data (morpho) against trophic index ($Troph_j$) of all species

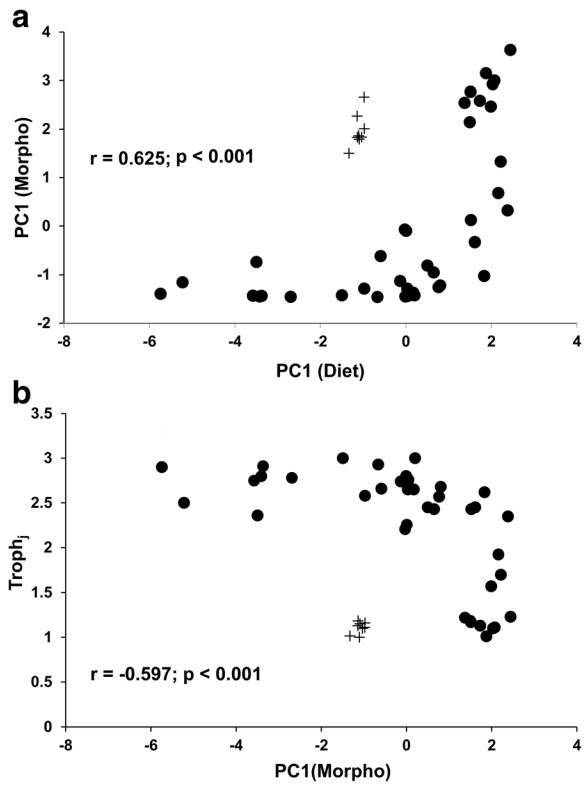

Fig. 6 **a** Scatter plot of PC1 scores based on morphological data (morpho) against those based on dietary data (diet) of fish species excluding mugilids; (**b**) Scatter plot of PC1 scores based on morphological data (morpho) against trophic index ($Troph_j$) of fish species excluding mugilids. Crosses indicate values corresponding to mugilids

Discussion

Brush park fisheries are found in shallow waters of rivers and estuaries in many parts of the world as kinds of fish aggregation devices which generally produce higher yields per unit area than in open-water capture fisheries (Welcomme 2002). In some regions such as West Africa, brush parks are placed for longer periods (>12 months; Niyonkuru and Laleye 2010) and as such, they provide spawning areas for many fish species (Welcomme 2002, 2005). However, brush parks in Negombo estuary are placed for attraction of fish for much less time period (3–97 days), so that it is unlikely that they serve as spawning grounds for fish. Fish species that are attracted to these brush parks in search of food and shelter are therefore essentially temporary visitors. Ward and Samarakoon (1981) who studied reproductive tactics of two indigenous cichlid species in Negombo estuary, *Etroplus maculatus* and *E. suratensis* have shown that nest site selection by two species were not uniform. *E. maculatus* was reported to select dense vegetation where nests were camouflaged whereas *E. suratensis* selected sparse vegetation for nesting Ward and Samarakoon (1981). Of these two species, only *E. suratensis* was reported from the fish landings of brush parks during the present study, and *E. maculatus* was extremely rare in Negombo estuary. Although both these cichlid species are known to attract to brush shelter, short duration of placing brush parks might not favour their reproductive behaviour.

In many fish species, different patterns of resource exploitation are known to be reflected by substantial differentiation of morphological characters which permits prediction of resource exploitation patterns from morphological attributes (RÜber and Adams 2001; Bohorquez-Herrera et al. 2015; Pessanha et al. 2015). From the present analysis, it is evident that the body shapes of the members of fish assemblages attracted to the brush parks are related to their trophic indices as reported from a flood-plain lake in Brazil (Catella and Petrere 1998) and from Sri Lankan reservoir fish communities (Weliange and Amarasinghe 2007). The deviation of mugilids from this trend may be due to specialized feeding habits of these species. Members of the family Mugilidae are known to ingest sand particles to grind phytoplankton in their gizzard (Thompson 1966; Wijeyaratne and Costa 1987, 1988).

Present analysis has given evidence that morphological attributes of fish assemblages in the brush parks in Negombo estuary are significantly correlated to their diet. Winemiller et al. (1995) observed that fish species with larger eyes positioned laterally on the head, terminal or sub-terminal mouth and short body fed on algae and detritus. A study on dietary habits of fish species in three Sri Lankan reservoirs by Weliange and Amarasinghe (2007) also found that laterally compressed, deep bodies fish species feed on phytoplankton, higher plants and detritus, which represent lower trophic levels in the food web. Such ecomorphological correlates with diet were evident in the present study and laterally compressed species such as *Acanthurus gahhm*, *Etroplus suratensis, Siganus* sp., and *Scatophagus argus*, fed on periphyton attached to the mangrove twigs of brush parks, macrophytes and detritus. It was also evident from the results that body shapes of carnivorous species that occupied higher trophic levels were characterized by slender bodies.

Ecomorphological studies in fish provided robust evidence of morphological correlates with diet. For example, shape of fish mouth is related to the differentiated mechanical action to capture various types of available food resources (Motta et al. 1995). The possession of a relatively large mouth in predators was shown to be positively correlated with prey size (Gatz 1979; Wainwright and Richard 1995; Piet 1998; Soares et al. 2013). Xie et al. (2001) have shown that significant dietary-morphological correlation in fish assemblages in a Chinese lake was associated with mouth gape. Results of this study also provided evidence for this effect and fish species having relatively large mouth size and longer body (*Arius* sp., *Anguilla bicolor bicolor* and *Lates calcarifer*) consumed greater amount of fish in their diet. According to Bhat (2005), Soares et al. (2013) and Pessanha et al. (2015), bottom feeding fish species were characterized by wider bodies and lower body depths (compressed or flattened bodies). The structural or anatomical adaptations of more compressed, flattened bodies of bottom-dwelling fishes support greater contact with the substrate and greater stability (Oliveira et al. 2010; Pagotto et al. 2011), and capture distinct types of prey (Bohorquez-Herrera et al. 2015). The presence of barbels and a ventrally oriented mouth are related to benthic feeding habit of fishes (Gatz 1979; Piet 1998), and head length and mouth position are significantly correlated with phylogeny (López-Fernández et al. 2012). Dorsally located smaller eyes are possessed by benthic predators, as barbels could facilitate to mechanically detect their prey in muddy bottoms

(Wikramanayake 1990; Casatti and Castro 2006). This set of attributes confirmed by the present study, where the large proportion of benthic food items, particularly macro crustaceans were recorded in the diets of the *Plotosus canius* and *Plectorhinshus gibbosus*, which were characterized by the possession of small up-positioned eyes, longer head, ventrally oriented wider mouth and barbels.

Fish assemblages in brush parks are shade-philic species or those which are attracted to shelter in search of prey organisms (Welcomme 2002). Present analysis has shown that there are morphological similarities of the fishes which utilize similar food resources. According to the hypothesis of ecomorphology in fishes, those with similar morphological characters should use similar resources (Gatz 1979; Winemiller 1990).

There were studies which reported weak correlation between morphological traits and diet (Douglas and Matthews 1992; Motta et al. 1995; Labropoulou and Markakis 1998; Barnett et al. 2006; Cochran-Biederman and Winemiller 2010; Soares et al. 2013; Silva-Camacho et al. 2014; Brandl et al. 2015). It is also known that according to the concept of ecomorphology, apart from food resource utilization, there are many ecomorphological correlates among fishes with regard to locomotion (Pease et al. 2012), habitat occupancy including microhabitat utilization (Motta et al. 1995; Sampaio et al. 2013; Soares et al. 2013) etc. Cochran-Biederman and Winemiller (2010) also stated that absence of close relationship between morphology and dietary habits of fish may be due to the fact that morphological traits are related to multitude of functions associated with reproduction, locomotion and defense, in addition to feeding.

Attraction to shelter is an inherent characteristic of some fish species, and in some situations, fish aggregation devices in sheltered habitats are disadvantageous due to limited supply of food resources compared to open waters, a process that paved way to consider fish shelters as 'ecological traps' (Robertson and Hutto 2006). Although abundance of some food organisms such as microcrustaceans and shrimp juveniles, which are prey organisms for some opportunistic feeders may vary temporally, food limitations to fish species in brush parks would be unlikely as these fish feed on variety of food items. Hugueny and Pouilly (1999) also indicated that food availability would be more important than morphological adaptations of fish. Opportunistic feeders generally feed on several food types depending on the availability during particular periods of the year, but their morphological specializations may be for particular food items (Ramirez et al. 2015).

Present study has shown that community structure of coexisting species in brush parks of Negombo estuary is predominantly along the trophic dimension and is related to morphological traits of constituent species. As such, there is a certain degree of predictability of fish species which are attracted to brush parks. Brush parks are known to be fish aggregating devices which produce higher fish yields per unit area, and therefore as suggested by Welcomme (2002), with proper management these structures can be changed from simple fish attracting devices to a form of extensive aquaculture for achieving even higher fish yields. Also as mentioned by Hugueny and Pouilly (1999), due to high predictive power of ecomorphological correlate with the diets of fish assemblages in the brush parks of Negombo estuary, this approach is a useful tool when conducting rapid ecological assessments.

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