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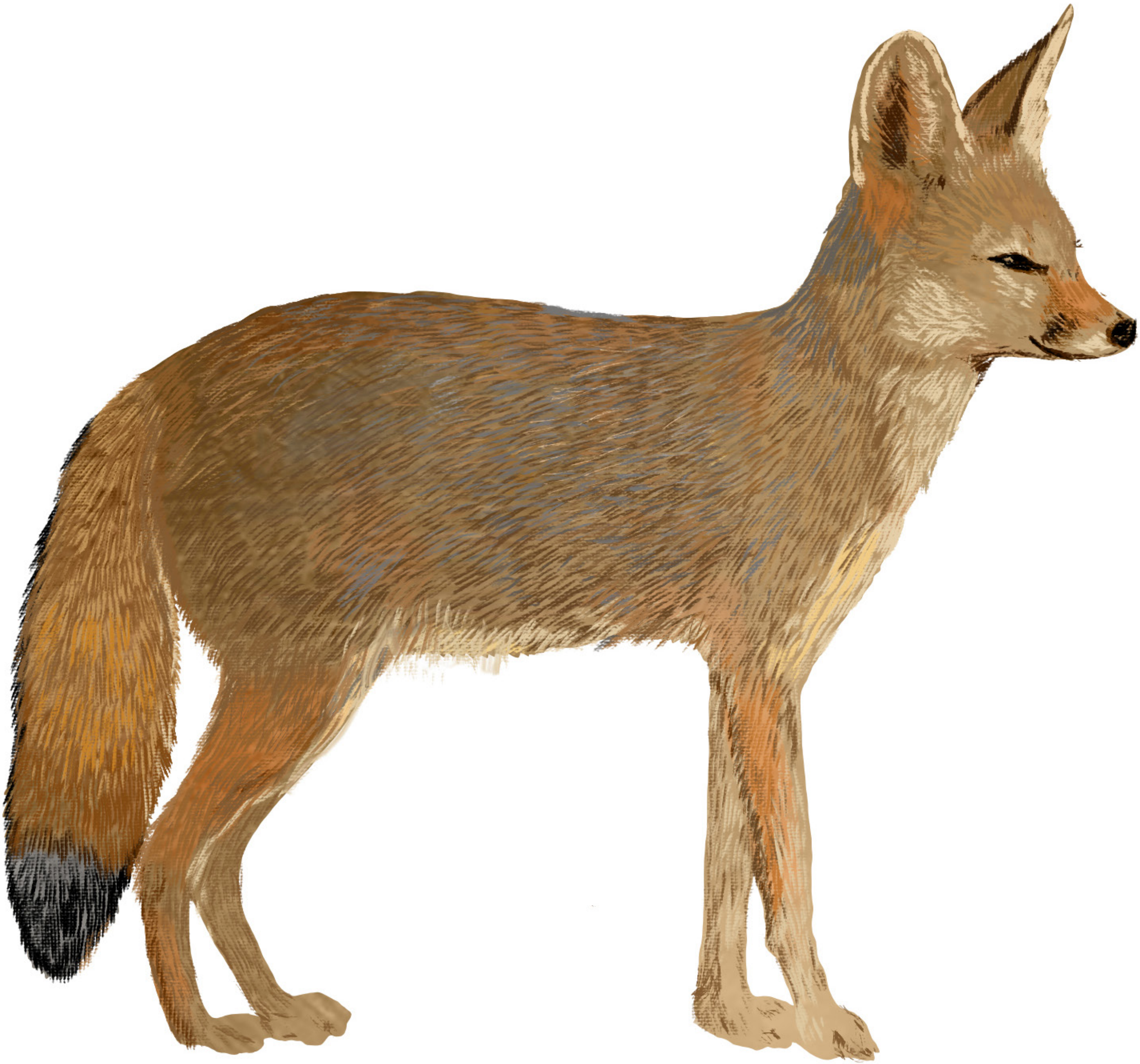

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Cover: Bengal Fox *Vulpes bengalensis*—digital illustration. © Alagu Raj.

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ARTICLE

Habitat heterogeneity and taxonomic diversity of fish fauna in estuaries: a study from southern Sri Lanka

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Abstract: A survey was conducted to identify fish fauna related to the dominant habitats, viz., (i) Honduwa Lake (stagnate water), (ii) estuarine area with mangroves, (iii) freshwater marshy area with floating aquatic vegetation, (iv) canals, and (v) river, in the Dedduwa estuary of southern Sri Lanka. Thirty-nine species of fish including two endemics (to the island) were identified, including members of major migratory families such as Anguillidae and Megalopidae. Based on the abundance of species, the Bray-Curtis similarity index indicated a clear separation of the canal and freshwater marsh, with other studied areas. Similarly, the taxonomic diversity of the canal and freshwater marsh was high, indicating high variation and diversity of the species and genera. Protection of mangroves and related habitats is important to maintain the stability and long-term existence of fish fauna in the estuary. Effective monitoring is proposed for detecting and eliminating illegal encroachments, mangrove clearance, and illegal fishing activities. Moreover, improving the knowledge and awareness among members of the local community, politicians, and environment officers about the importance of the region's biodiversity implementing strong policies, and creating a strong responsible stakeholder bond are required to ensure the long-term sustainability of the estuary.

Keywords: Brackishwater, catadromy, conservation, fish diversity, fish migration, mangroves, taxonomic distinctness.

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INTRODUCTION

Estuaries are considered one of the most productive coastal ecosystems in the tropics (Whittaker & Likens 1975; Whitfield & Elliott 2011; Sreekanth et al. 2017). Ecologically, estuaries are highly significant as they provide critical ecosystem services including coastal protection (Barbier 2020), carbon sequestration (Douglas et al. 2022; Das et al. 2023), sediment filtration (Schubel & Carter 1984; Teuchies et al. 2013), and habitat enrichment (Cardoso 2021; Denis et al. 2022). These ecosystem services are essential in sustaining the coastal biodiversity and well-being of aquatic taxa (Cardoso 2021). Among the various ecological services, the most significant is habitat provisioning and maintaining ecosystem integrity in coastal environments (Blaber et al. 1989; Sreekanth et al. 2020). Estuaries form a transition zone between river and maritime environments and are hence always influenced by tidal fluctuation and freshwater fluxes (Potter et al. 2010). These heterogenous physico-chemical changes featured unique and variable habitat formations such as mangroves, shallow open waters, freshwater and saltwater marshes, swamps, sandy beaches, mud and sand flats, rocky shores, river deltas, tidal pools, and seagrass beds enhancing the habitat complexity and species composition in estuaries (Hagan & Able 2003). The diversified habitats in the estuaries are known to provide nurseries and feeding grounds for fish essentially for larval stages (Potter et al., 2013; Guerreiro et al. 2021). Therefore, estuaries provide refuges for a wide variety of fishes including both marine and freshwater species to complete their life cycles (Blaber et al. 1989; Whitfield & Elliott 2002; Elliott et al. 2007).

Distribution of fishes in an estuary is fundamentally determined by habitat heterogeneity, prey predator relationship, and water chemistry (Jackson et al. 2001; Maes et al. 2005; Kadye et al. 2008; Sreekanth et al. 2020). The productivity of the habitats is equally important to determine the dietary compositions of fishes (Hagan & Able 2003). The climatic fluctuations and changes in precipitation determine the level of productivity (e.g., accumulation of autochthonous and allochthonous nutrients) and trophic relationship among fishes (Gillanders et al. 2011; Sreekanth et al. 2019). The lowland reaches of rivers are characterized by high levels of suspended solids inducing high turbidity (Cyrus & Blaber 1987). Hence, productivity is largely determined by the nutrient loads from the upper reaches of the river. In the freshwater–seawater transition zone, these particles are effectively 'trapped' due to flocculation and converging suspended sediment fluxes (Kranck 1981). River mouths, estuaries, or transitional waters represent the transition between freshwater and marine environments and are influenced by both aquatic realms (Robinson et al. 1999). This makes estuaries unique ecosystems with a range of salinity gradients, from freshwater to seawater in addition to lentic and lotic habitats (Ruhl 2013). Fish species with the ability to tolerate huge salinity gradients can be identified in these various habitats and microhabitats (Barletta et al. 2005; Breine et al. 2011). Hence, species richness in estuaries is commonly dominated by marine species (Whitfield 1999; Franco et al. 2008). Moreover, fishes show migration between estuaries and other ecosystems and are also benefited by the estuaries markedly in larval development and predator avoidance (Dando 1984; Leggett 1984).

Estuaries in Sri Lanka are highly characterized by the variability in size, shape, configuration, ecohydrology, and tidal fluxes (Miththapala 2013). These wetlands cover approximately 93,075 ha in Sri Lanka's coastal zone (Department of Coast Conservation and Coastal Resource Management 2018). Though these ecosystems provide important habitats for fish taxa, proper ecological studies are scarce to determine the pattern of fish assemblages associated with the various habitats. Ministry of Forestry and Environment (1999) reported 53 fish species in mangrove ecosystems in Sri Lanka. Estuaries a highly dynamic ecosystems, and these facts provide essential evidence to determine conservation priorities in coastal environment management. These mangrove and estuarine areas are increasingly subjected to degradation due to anthropic interventions including tourism, sewage disposal, the introduction of exotic species, and river diversions (Samarakoon & Samarawickrama 2012; Miththapala 2013). Therefore, these ecosystems are particularly important for integrating sound ecological management with sustainable economics (Meire et al. 2005). Hence, the current study was conducted to understand the common characteristics of habitat heterogeneity and fish faunal assemblages associated with estuarine ecosystems.

MATERIALS AND METHODS

Study area

Dedduwa estuary is fed by the Bentota River and is situated in the southwestern part of Sri Lanka. Ecologically, the Dedduwa estuary is remarkably important as it comprises diversified mangroves and related estuarine habitats, which provide essential living environments for assemblages of fauna and flora. The study area is approximately 8 km^2 (Figure 1) and consists of five different types of habitats, viz.: (i) 'Honduwa' Lake (lentic), (ii) marshy area with associate aquatic vegetation, (iii) mangroves, (iv) canals, and (v) river. The Honduwa area is characterized by stagnant saline water (approximately 0.95 km^2). There are two major canals connected to Honduwa; one runs through the inland and connects to the estuary and the other is from the estuary to the sea. Therefore, the Honduwa Lake often experiences the gradients of salinity fluctuation. The maximum depth is approximately 2.1 m. *Sonneratia caseolaris* and *Rhizophora apiculata* are the most dominant mangroves in the area with other associates such as *Dillenia suffruticosa*, *Derris trifoliate*, and *Acrostichum aureum*. The marshy area is approximately 0.1 km^2. This area contains open water with floating aquatic vegetation. Most of the open water area is covered by aquatic vegetation such as *Aponogeton crispus, Pistia stratiotes*, *Ceratophyllum demersum*, *Ipomoea aquatica*, *Hydrilla verticillata*,

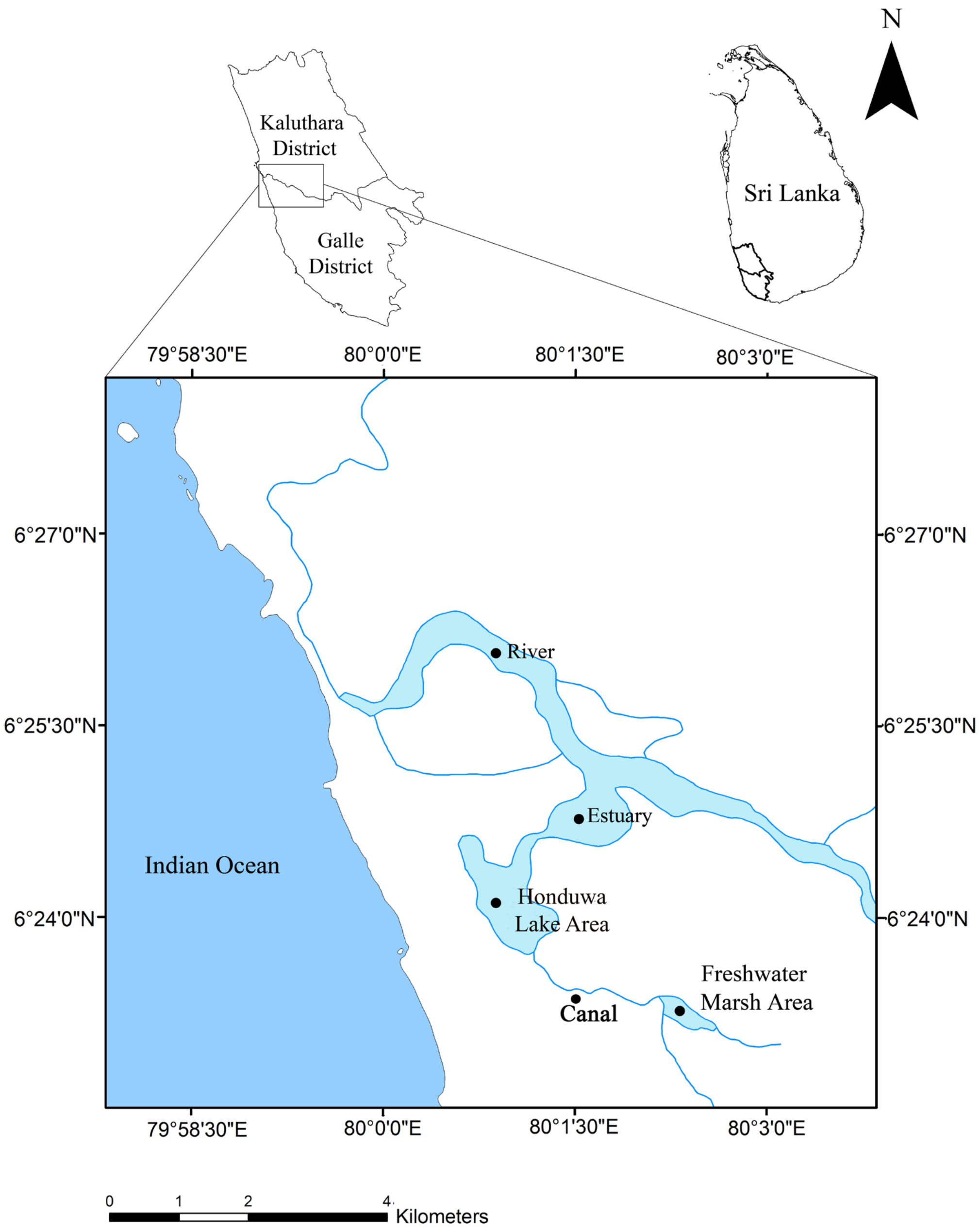

Figure 1. Location of Dedduwa estuary, Sri Lanka. The different sites surveyed for the fish fauna are also marked.

Utricularia aurea, *Nympoides* spp., *Nymphaea* spp., *Eichhornia crassipes*, and *Salvinia molesta*. The floating and marginal vegetation provide vital refugees for aquatic invertebrates. Hence, this marshy area is rich with wetland ichthyofauna. Some areas are entirely infested with invasive aquatic plants like *Salvinia molesta* and submerged during the rainy period. Therefore, the abundance of aquatic fauna possibly shows great fluctuations year-round. Water pools with aquatic weeds provide good nursery grounds for small fishes. This area is highly influenced by human alterations. Hence, associated vegetation has been invaded by invasive plants such as *Annona glabra* and *Typha angustifolia*. The marsh located next to Honduwa Lake (see Figure 1) is approximately 0.86 km^2 in extent. This area contains mixed vegetation of mangroves and freshwater aquatic plants. Most of the area has open water and is probably ideal for euryhaline fish species. Much of the riparian vegetation is densely covered by alien *D. suffriticosa* which provides a shady environment for aquatic fauna. A patchy distribution of mangroves can be seen in the marginal areas and provide nursery grounds for various fish species. The canal contains slow-moving water. Due to less salinity compared to the estuary or river mouth and high turbulence, this water may provide proper living environments for rheophilic freshwater species and anadromous fishes. The canal extends for 2.19 km and most of the area is covered by mangroves. This is an important migratory pathway for both marine and brackish water fish species and is highly influenced by tidal fluctuations. Mixed vegetation with several species of mangrove (e.g., the considerable distribution of *Nypa fruticans*) and mangrove associates can be seen in the area.

Data collection

Fish samples were collected from September to October 2019 in each of the five sites using a dragnet of the dimension of 1.5 x 1.5 m with a 2 mm mesh size. Although some other sampling methods such as gillnets cast nets and traps were also used, the data collected from those sampling methods were excluded from analysis due to the inconsistency of the samplings. Every accessible location with different biological (e.g., different vegetation types) and physical characteristics (e.g., in different water depths and flow rates) was surveyed, and data were collected for the analysis. Altogether 117 samples were collected for the analysis covering all the habitat types (Table 1). The number of individuals of different species caught in every sampling effort was recorded separately. The anthropogenic activities that were carried out at each sampling site were observed such as disposal of sewage and fishing activities. Also, the abundance of microhabitat types was noted in different segments of the river and estuary (see Table 5 in the results section).

Diversity indices

The diversity of fish in each site was estimated using the following different methods in Primer V.5.2.2 software (Clark & Warwick 2001).

i. Shannon-Wiener index (H') (Shannon 1948)

$$H = -\sum pi. \ln pi$$

where p_i = the proportion of species *i* relative to the total number of species

ii. Margalef diversity index (*d*) (Margalef 1958)

$$d = \frac{S-1}{\ln N}$$

where S is the number of species, and N is the total number of individuals in the sample.

iii. Brillouin index (Brillouin 1956), *HB*, was calculated using:

$$HB = \frac{\ln Ni - \sum_{i=1}^{s} \ln ni}{N}$$

where *N* is the total number of individuals in the sample, *ni* is the number of individuals belonging to the i^{th} species, and *s* is the species number. The Brillouin index measures the diversity of a collection, as opposed to the Shannon index which measures a sample.

iv. Fisher's alpha, *S* (Fisher et al. 1943)

This is a parametric index of diversity given below assumes that the abundance of species follows the ln series distribution:

$$\frac{S}{N} = \frac{(1-x)}{x[-\ln(1-x)]}$$

where *S* is the number of taxa, *N* is the number of individuals

$$\alpha = \frac{N(1-x)}{x}$$

where α the diversity index

v. Simpson index, *D* (Simpson 1949)

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)}$$

where N is the total number of individuals in the sample, and n is the number of individuals belonging to a certain species. It measures the 'evenness' of the community ranging from 0 to 1.

vi. Pielou's evenness index (J) (Pielou 1969, 1975)

$$J = H/\log(S)$$

If H is the observed Shannon-Wiener index, the maximum value this could take is log(S), where S is the total number of species in the habitat.

Table 1. Summary of the sampling efforts of five different aquatic habitats in the Dedduwa estuary, Sri Lanka.

Habitat	Total number of samples
Honduwa Lake area	27
Estuarine area	24
Canal area	32
Rivermouth	15
Mashy area with floating aquatic vegetation	19

Taxonomic distinctness tests

To determine the taxonomic distance the following approach was adopted. Species were classified to all major taxonomic levels in a Linnean classification following the taxonomy of the fauna (Beesley et al. 1998). A constant path length (ω = 1) between levels was used to calculate the taxonomic distance between species pairs (Warwick & Clarke 1995). Average Taxonomic Distance (AvTD) was calculated using presence/absence data from each site. Using each separate dataset, taxonomic distinctness was quantified using the TAXDTEST procedure in the PRIMER-V.5.2.2 software package (Clarke & Warwick 2001). The 'variation in taxonomic distinctness' [VarTD, Lambda (+)] between every pair of species recorded in a study. It matches the previously defined 'average taxonomic distinctness' [AvTD, Delta (+)], which is the mean path length through the taxonomic tree connecting every pair of species in the list. VarTD is simply the variance of these pairwise path lengths and reflects the unevenness of the taxonomic tree. Samples from the master list were used to generate an expected distribution of values, including a mean and 95% confidence interval. The expected distribution was represented visually as a funnel plot, showing values for different numbers of species, and the observed values were overlaid on the plot. This was used to test the null hypothesis that each observed value had the same value as one predicted using the master list, rejected at the 5% significance level (Clarke & Warwick 2001; Smith & Rule 2002), i.e., sites falling outside the 95% confidence limits were interpreted as having an AvTD value significantly lower (or higher) than expected.

Comparative analysis of ichthyofaunal diversity and abundance

To compare the diversity and abundance of fish in each habitat type, the mean abundance data of each species were used. The similarities of fish communities among sampling sites were determined by the Bray-Curtis similarity coefficient (Bray & Curtis 1957). The ln (x+1) transformation was used before analysis due to the presence of zero values. The ordination of non-metric Multidimensional Scaling (MDS) of sampling sites was determined based on the Bray-Curtis similarity matrix (Clarke & Warwick 2001) using the PRIMER-5 software package (Version 5.2.2). Bray-Curtis similarity analysis was done by using two different approaches. One approach was the analysis performed by separating abundance data for the different species into the five habitat types identified (Table 1) and the second approach was considering all the sampling locations as a single data set and freely clustered it according to the similarity of species composition in each location.

RESULTS

Altogether 41 species of fish were identified including marine, true estuarine, and freshwater species (Table 2). A higher number of species was recorded at the Honduwa Lake and the estuary (18 species in each habitat) while the lowest (12 species) was recorded associated with the river (Table 4). Of these, *Clarias brachysoma* and *Horadandia atukorali* were the endemic freshwater species identified. Species namely *Oryzias dancena, Etroplus suratensis, Ambassis ambassis, Butis butis,* and *Bhava vittatus* were identified in all five different habitat types (Table 2). The results of the present study did not show any dominant group in the assemblage. In Honduwa Lake, estuary, and river the most dominant species were *Ambassis ambassis, Butis butis, O. dancena,* and *Etroplus suratensis* contributing 88.4%, 77.9%, and 74.5 % in abundance respectively (Figure 2). The most abundant species in freshwater marsh habitats were *Horadandia atukorali* (42.3%) and in the canal area was *Ehirava fluviatilis* (29%) (Figure 2). The occurrence of dominant species in saline waters (e.g., estuarine area and Honduwa Lake) showed approximately a similar pattern in abundance. Comparing saline habitats with freshwater habitats (e.g. marsh with aquatic vegetation) a remarkable difference in patterns of species dominance was observed (Figure 2).

When the Bray-Curtis similarity index based on the abundance of fish species is considered, the freshwater marshy habitat was separated from other sampling sites at about the 28.9% level of similarity (Figure 3). The similarity level of fish abundance in the canal area with Honduwa Lake is approximately 51.2% (Figure 3). Also, the canal area with Honduwa Lake further separated from the rest of the sampling sites in the MDS ordination

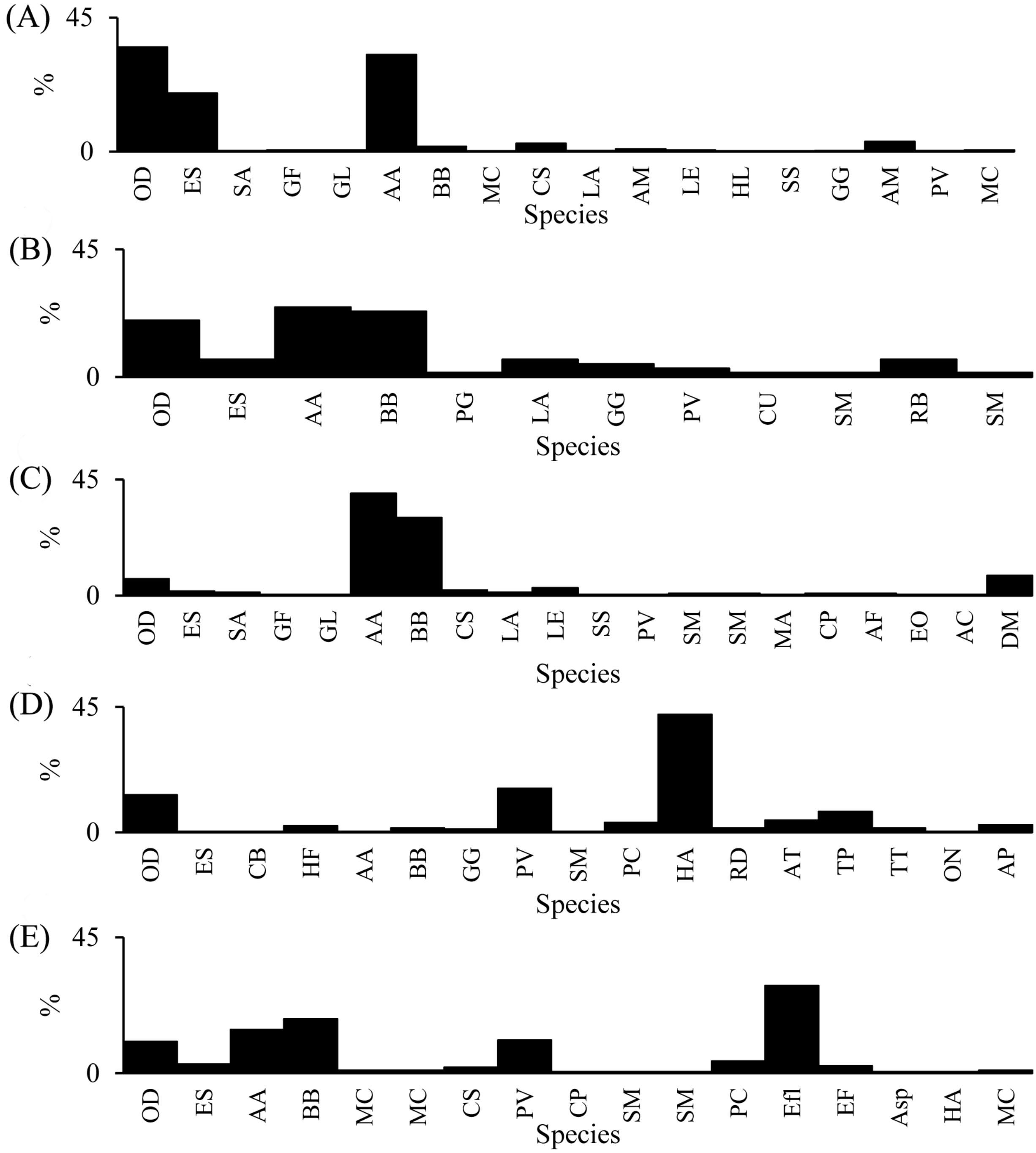

Figure 2. Relative abundance of identified fish species in five habitats studied in the Dedduwa Estuary, Sri Lanka: A—Honduwa Lake | B—River | C—Estuarine area | D—Freshwater Marshy habitat | E—Canal. Abbreviations of the species are given in Table 2.

(Figure 4). The diversity indices Shanon, Brillouin, and Simpson showed the highest diversity in river and canal habitats. Margelef index showed the highest species richness in estuarine habitats. The evenness of the species is approximately high in estuary and canal (Table 3).

The Bray Curtis similarity analysis for the species abundance of different habitats indicated five distinct clusters in a 25% similarity level (Figure 5). It differentiates the freshwater marsh and the canal into a single cluster (I) possibly due to the similarity of habitat choices of freshwater fishes associated with the two areas (e.g., low salinity). Honduwa Lake, canal, estuary, and some sampling locations in the river are grouped into a single cluster at 20% similarity level. As majority of the species in these four habitats are common except a

Table 2. Checklist of ichthyofauna recorded from the different habitats in the Dedduwa estuary, Sri Lanka. Endemic species are mentioned in bold letters. The migratory habit of relevant fishes is also mentioned as superscripted abbreviations after the scientific name. All the abbreviations are explained after the table.

	Family	Scientific name (abbreviation)	Common name	Conservation status		Habitats					Salinity range	Source
				NCS	GCS	HLH	ES	RI	FWM	CN		
1.	Adrianichthyidae	*Oryzias dancena* (OD)	Rice fish	NE	LC	+	+	+	+	+	Polyhaline	Roberts 1998
2.	Ambassidae	*Ambassis ambassis* $^{\text{Oce.}}$ (AA)	Commerson's glassy	NE	LC	+	+	+	+	+	Polyhaline	Fricke 1999
3.	Anabantidae	*Anabas testudineus* $^{\text{Pot.}}$ (AT)	Climbing perch	LC	LC				+		Mesohaline	Talwar and Jhingran 1991
4.	Anguillidae	*Anguilla* spp.$^{\text{Cat.}}$ (AS)	Eel							+	Polyhaline	Kottelat 2013
5.	Aplocheilidae	*Aplocheilus parvus* (AP)	Dwarf panchax	LC	LC				+		Mesohaline	Seegers 1997
6.	Ariidae	*Arius maculatus* $^{\text{Pot.}}$ (AM)	Spotted catfish	NE	NE	+					Polyhaline	Kailola 1999
7.	Carangidae	*Caranx sexfasciatus* $^{\text{Amp.}}$ (CS)	Bigeye trevally	NE	LC	+	+	+		+	Polyhaline	Paxton 1989
8.	Channidae	*Channa punctata* $^{\text{Pot.}}$ (CP)	Spotted snakehead	LC	LC				+		Mesohaline	Pethiyagoda 1991
9.	Channidae	Channa *striata* $^{\text{Pot.}}$ (CS)	Striped snakehead	LC	LC				+	+	Mesohaline	Pethiyagoda 1991
10.	Cichlidae	*Etroplus suratensis* (ES)	Pearl spot	LC	LC	+	+	+	+	+	Mesohaline	Pethiyagoda 1991
11.	Cichlidae	*Oreochromis niloticus* $^{\text{Pot.}}$ (ON)	Nile tilapia	EX	LC			+			Mesohaline	Trewavas 1983
12.	**Clariidae**	***Clarias brachysoma** ** **(**CB)	**Walking catfish**	**VU**	**NE**				**+**		Oligohaline	Pethiyagoda 1991
13.	Clupeidae	*Anodontostoma chacunda* $^{\text{Ana.}}$ (AC)	Chacunda gizzard shad	NE	LC		+				Polyhaline	Whitehead 1985
14.	Clupeidae	*Dayella malabarica* $^{\text{Amp.}}$ (DM)	Day's round herring	NE	LC		+				Polyhaline	Whitehead 1985
15.	Clupeidae	*Ehirava fluviatilis* $^{\text{Amp.}}$ (EF)	Malabar sprat	NE	LC					+	Polyhaline	Whitehead 1985
16.	Cyprinidae	*Plesiopuntius bimaculatus* (PB)	Redside barb	LC	LC				+		Oligohaline	Pethiyagoda 1991
17.	Cyprinidae	*Bhava vittatus* (PV)	Silver barb	LC	LC	+	+	+	+	+	Mesohaline	Pethiyagoda 1991
18.	Cyprinidae	*Rasbora dandia* (RD)	Broadline striped rasbora	LC	LC				+		Oligohaline	Silva et al. 2010
19.	Cyprinidae	***Horadandia atukorali**** (HA)	**Green carplet**	**VU**					+	+	Mesohaline	Pethiyagoda 1991
20.	Eleotridae	*Butis butis* $^{\text{Amp.}}$ (BB)	Duckbill sleeper	NE	LC	+	+	+	+	+	Polyhaline	Hoese 1986
21.	Eleotridae	*Eleotris fusca* $^{\text{Amp.}}$ (EF)	Dusky sleeper	NE	LC					+	Polyhaline	Maugé 1986a
22.	Gerreidae	*Gerres filamentosus* $^{\text{Amp.}}$ (GF)	Whipfin silver-biddy	NE	LC	+	+				Polyhaline	Woodland 1984
23.	Gerreidae	*Gerres limbatus* $^{\text{Amp.}}$ (GL)	Saddleback silver-biddy	NE	LC	+	+				Polyhaline	Iwatsuki et al. 2001
24.	Gobiidae	*Glossogobius giuris* $^{\text{Amp.}}$ (GG)	Tank goby	LC	LC	+		+	+		Polyhaline	Maugé 1986b
25.	Gobiidae	*Caragobius urolepis* $^{\text{Amp.}}$ (CU)	Scaleless worm goby	NE	LC			+			Mesohaline	Kottelat et al. 1993
26.	Gobiidae	*Oligolepis* cf. *acutipennis* $^{\text{Amp.}}$ (OA)	Sharptail goby	NE	LC			+			Polyhaline	Maugé 1986b
27.	Gobiidae	*Gobius malabaricus* $^{\text{Amp.}}$ (GM)	Malabar goby	NE	LC		+	+			Polyhaline	Maugé 1986b
28.	Hemiramphidae	*Hyporhamphus limbatus* $^{\text{Pot.}}$ (HL)	Congaturi halfbeak	NE	LC	+					Polyhaline	Collette and Su 1986
29.	Heteropneustidae	*Heteropneustes fossilis* (HF)	Asian stinging catfish	LC	LC				+		Mesohaline	Rainboth 1994

	Family	Scientific name (abbreviation)	Common name	Conservation status		Habitats					Salinity range	Source
				NCS	GCS	HLH	ES	RI	FWM	CN		
30.	Leiognathidae	*Leiognathus equulus* [Amp.] (LE)	Common ponyfish	NE	LC	+	+				Polyhaline	James 1984
31.	Lutjanidae	*Lutjanus argentimaculatus* [Oce.] (LA)	Mangrove red snapper	NE	LC	+	+	+			Polyhaline	Allen 1985
32.	Megalopidae	*Megalops cyprinoides* [Amp.] (MC)	Indo-Pacific tarpon	NE	DD	+				+	Polyhaline	Whitehead 1984
33.	Monodactylidae	*Monodactylus argenteus* (MA)	Silver moony	NE	LC		+				Polyhaline	Heemstra 1984
34.	Mugilidae	*Mugil cephalus* [Cat.] (MC)	Flathead grey mullet	NE	LC	+				+	Polyhaline	Harrison 1995
35.	Osphronemidae	*Pseudosphromenus cupanus* (PC)	Spiketail paradisefish	LC	LC				+	+	Mesohaline	Pethiyagoda 1991
36.	Osphronemidae	*Trichopodus trichopterus* (TT)	Three spot gourami	EX	LC				+		Oligohaline	Rainboth 1996
37.	Osphronemidae	*Trichopodus pectoralis* (TP)	Snakeskin gourami	EX	LC				+		Oligohaline	Rainboth 1996
38.	Scatophagidae	*Scatophagus argus* [Amp.] (SA)	Spotted scat	NE	LC	+					Polyhaline	Schofield 2021
39.	Sillaginidae	*Sillago sihama* [Amp.] (SS)	Silver sillago	NE	LC	+	+				Polyhaline	McKay 1992
40.	Soleidae	*Brachirus orientalis* [Ana.] (BO)	Oriental sole	NE	NE		+				Polyhaline	Munroe 2001
41.	Tetraodontidae	*Chelonodon patoca* [Ana.] (CP)	Milk spotted puffer	NE	LC		+			+	Polyhaline	Kottelat et al 1993

Amp.—Amphidromous | Ana.—Anadromous | Cat.—Catadromous | CN—Canal | DD—Data deficiency | E—English | ES—Estuary | EX—Exotics | FWM—Freshwater marshy area | GCS—Global conservation standards | HLH—Honduwa Lake habitat | LC—Least concern | NCS—National conservation standards | Oce.—Oceanodromous | Pot—Potamodromous | RI—River | S—Sinhala | VU—Vulnerable; ***/bold**—Endemic

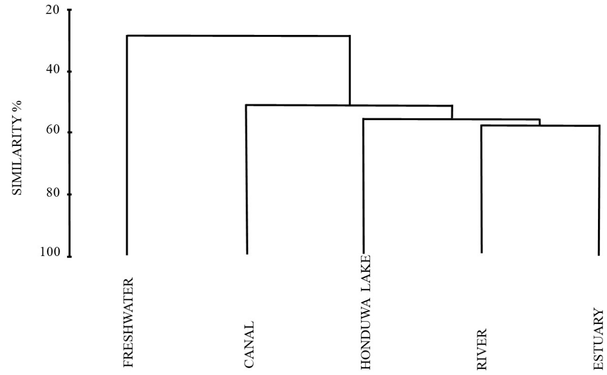

Figure 3. Bray-Curtis similarity of the sampling sites of Dedduwa Estuary, Sri Lanka based on the relative abundance of fish species.

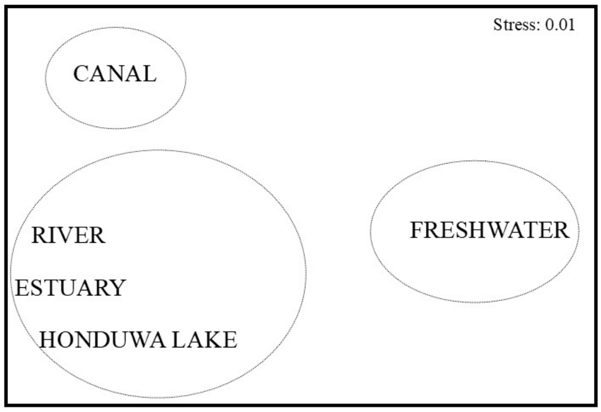

Figure 4. Two-dimensional MDS ordination of sampling sites of Dedduwa Estuary, Sri Lanka according to the relative abundance of fish species.

few species such as *Megalops cyprinoides, Scatophargus argus, Monodactylus argentius*. These four habitats were somewhat similar due to the presence of mangroves. *B. butis* and *A. Ambassis*, are almost equally distributed among canal, estuary, river, and Honduwa Lake, indicating approximately a similar species composition among sites. At the 25% similarity level, this cluster split into two distinct clusters, possibly due to the higher number of *A. ambassis* and *B. butis* caught in cluster V compared to cluster IV. Cluster II and III contained different species whereas Cluster III contained *O. dancena* and *E. suratensis* which were not observed in Cluster II. The Margelef species richness index was higher in clusters I and IV which were associated with freshwater/canal habitat and a combination of canal, estuary, Honduwa Lake, and river respectively. Simpson index was high in clusters I, II, and V (Table 4). The values of Fisher and Pielou's indices are comparatively higher in clusters I, II and V. Similarly, Shannon and Brillouin

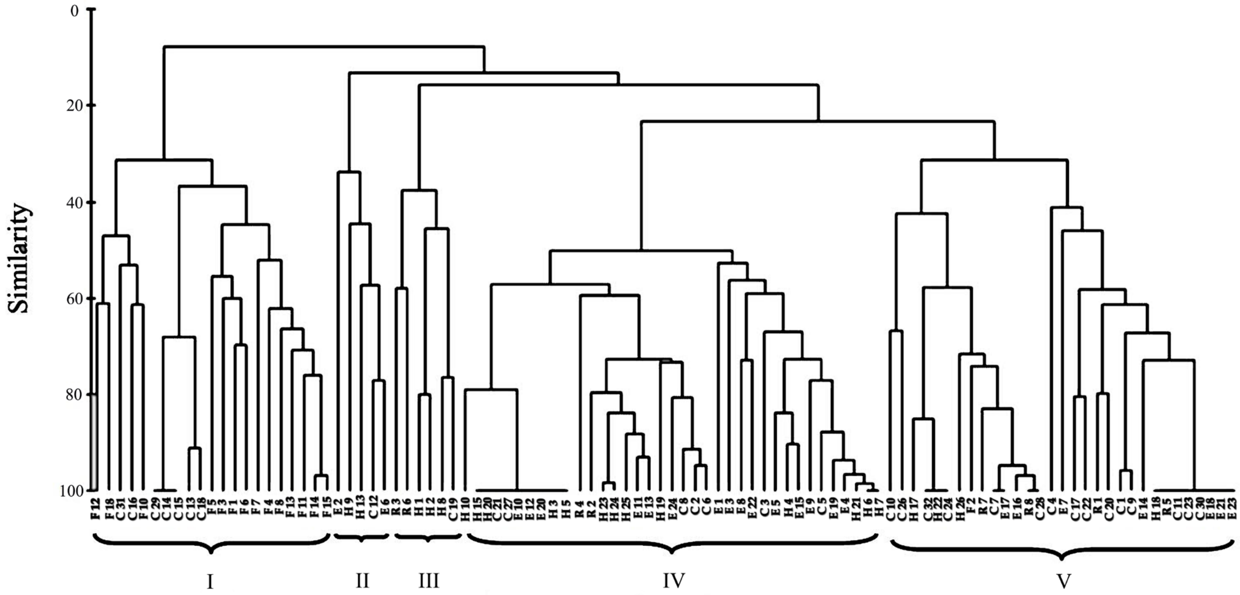

Figure 5. Bray-Curtis similarity of the sampling sites of Dedduwa Estuary, Sri Lanka based on the relative abundance of fish species in different sampling efforts. Five different clusters with a 25% similarity level are marked separately. C—Canal | E—Estuarine area | F—Freshwater marsh | H—Honduwa Lake | R—River.

indices indicate high species richness and evenness in clusters I, II, and V (Table 4).

The taxonomic diversity of the area is within the expected diversity (see Figure 6A). The taxonomic diversity is expressed as observed average taxonomic distinctions (Figure 6A) and variation of taxonomic distinctions (Figure 6B). Honduwa Lake and the estuary are occupied by nearly similar species. Therefore, taxonomic diversity shows an approximately similar variation (Figure 6A). The canal includes species in different genera such as *Anguilla, Eleotris,* and *Channa* and therefore, the canal is different from the other four habitats with taxonomic diversity (Figure 6A). Freshwater habitat was occupied by distinctive genera such as *Rasbora, Anabas, Horadandia, Channa, Clarias, Heteropneustes,* and *Puntius*. Therefore, freshwater habitats also showed high and distinctive taxonomic diversity beyond the expected taxonomic variation compared to other habitats (Figure 6B). The overall taxonomic diversity is shown in Fig. 7 indicating probability contours (back-transformed ellipses) between AvTD and VarTD with a range of sublist sizes.

The fish fauna seems influenced by the various fishing activities of the fishers. Though commercial fishing activities are uncommon, artisanal fishers operate their vessels in every accessible area. Brush piles were found in Honduwa Lake in the northern part of the estuary. Encircling nets were operated in the river, Honduwa Lake, and the estuarine area. No operation of encircling nets was observed in the canal segment (Table 5).

DISCUSSION

The fish fauna of estuarine systems has long been regarded as dominated by estuarine-dependent or estuarine-opportunistic marine species, with the movement of fishes among different salinity gradients being largely determined by the distribution of various habitats and tidal influences (Vieira & Musick 1994). The current finding of 41 fish species from the estuary and related habitats provides insight into the importance of habitat assessment and biodiversity conservation. The fish assemblage in the area is highly vulnerable to being threatened due to the proposed future development activities. Some species have a wide distribution and are found in several habitats while others show a more confined distribution restricted to specialized habitats (see Figure 2). The current study reveals that the distribution of fish species in Honduwa Lake, the Dedduwa Estuary, and the river shows a closely similar pattern. The distribution of species in the canal and freshwater marsh area is different from Honduwa Lake, estuarine area, and river (Figure 4). The variation of salinity could be the major limiting factor for the species distribution among these habitats. The major difference among the three systems is that the Honduwa and the estuarine area act as a lentic ecosystem while the

Table 3. Different diversity indices and related diversity values were calculated to represent the fish diversity of studied habitats in the Dedduwa Estuary, Sri Lanka.

	S	N	Margelef index	Pielou's evenness	Fisher evenness	Brillouin	Shanon	Simpson index
Honduwa	18	576	2.67	0.55	3.52	1.54	1.59	0.74
River	12	213	2.04	0.81	2.72	1.90	2.03	0.84
Estuary	18	164	3.06	0.59	4.41	1.60	1.72	0.74
Canal	15	377	2.74	0.74	4.01	1.89	2.02	0.84
Freshwater	16	253	2.52	0.68	3.38	1.79	1.90	0.77

S—Total number of species or species richness | N—Number of individuals tested for the analysis.

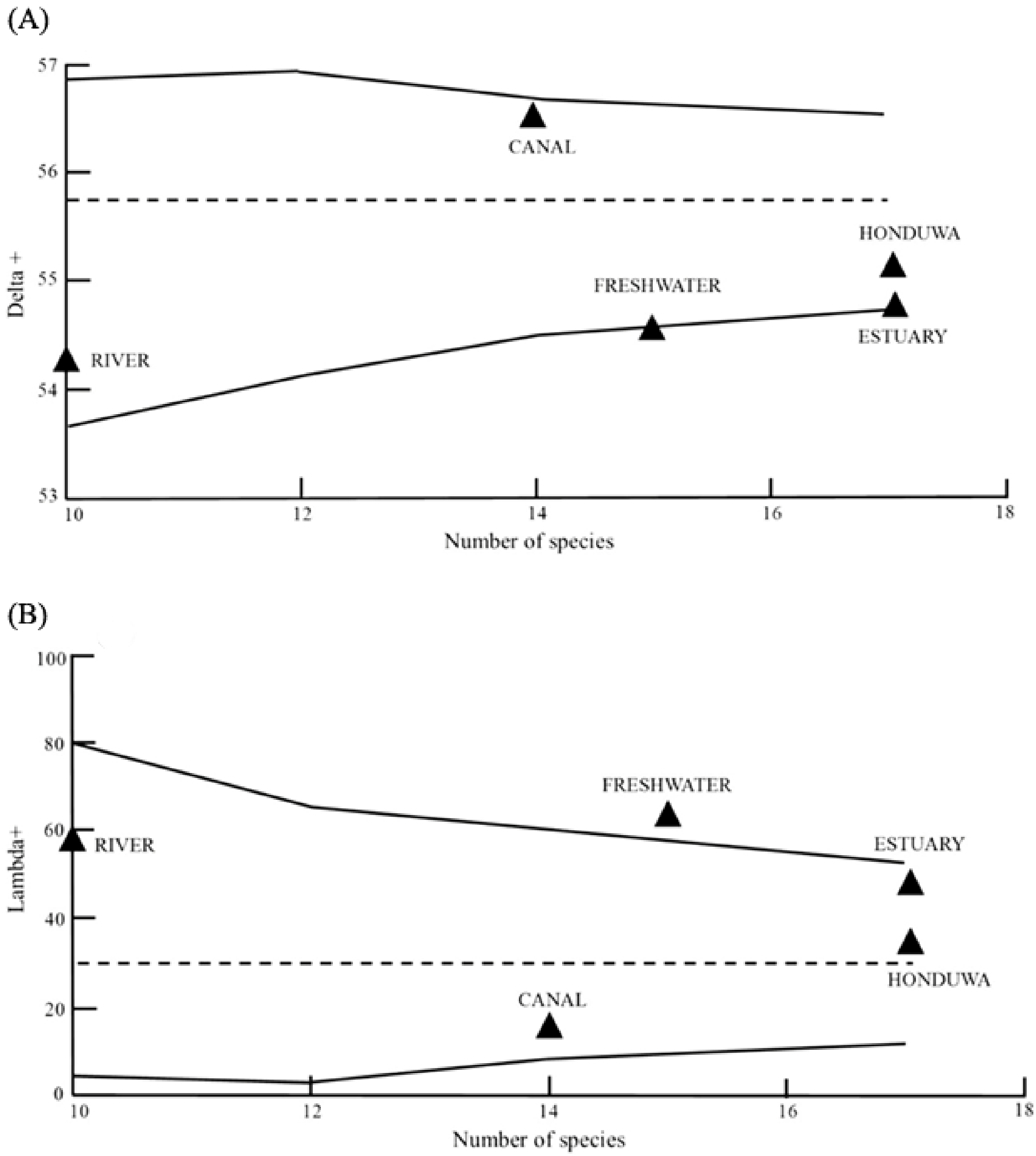

Figure 6. Confidence funnels showing values of (A) observed average taxonomic distinctness (AvTD, Δ+) and (B) variation in taxonomic distinctness (VarTD, Λ+) of fish diversity of Dedduwa estuary, Sri Lanka overlaid on the predicted mean and its 95% confidence interval related.

Table 4. Different diversity indices and related diversity values were calculated to represent the fish diversity of the Dedduwa Estuary, Sri Lanka, for different given clusters in Bray-Curtis similarity analysis in Figure 6.

Cluster	S	N	Margelef index	Pielou's evenness	Fisher evenness	Brillouin	Shanon	Simpson index
I	18	346	2.91	0.67	4.03	1.86	1.94	0.78
II	13	403	2.00	0.78	2.56	1.96	2.02	0.79
III	11	747	1.51	0.46	1.82	1.07	1.09	0.51
IV	18	406	2.83	0.51	3.85	1.40	1.47	0.68
V	14	227	2.40	0.80	3.29	1.80	1.91	0.81

S—Total number of species or species richness | N—Number of individuals tested for the analysis.

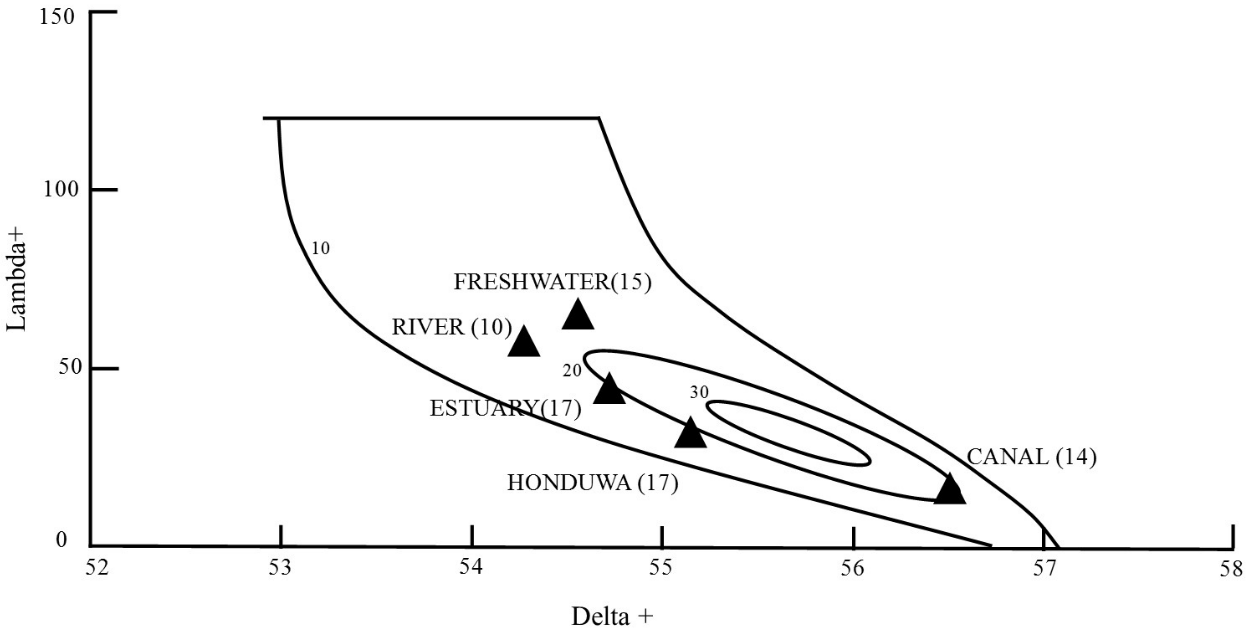

Figure 7. Probability contours (back-transformed ellipses) between AvTD and VarTD with a range of sublist sizes: m = 10, 20, and 30; Plot is based on 1,000 simulations. Simulated fish assemblages were generated from a total species list representing all fishes collected over all surveys.

river is a lotic ecosystem. This difference may have also brought about differences in ichthyofaunal diversity and distribution among habitats.

According to the results presented in this study, the species distribution in the two different salinity gradients in freshwater and brackish water habitats is comparatively different (Figure 3). The species with a wide range of distribution probably are euryhaline (Bulger et al. 1993). Majority of the species recognized as the juvenile stage which denoted mangroves of the riparian habitat provide proper feeding and nursery ground for juvenile stages. The glass eels of *Anguilla* spp. found from the canal area provides evidence of the breeding migration of the catadromous species (Table 2). IUCN (2011), describes the breeding migration of *Anguilla bicolor* (Level fin eel) in the Kala Oya River basin of Sri Lanka and further explains the importance of seagrass beds as refuges of the glass eels. The current finding of glass eels associated with canals and estuaries is particularly important because it explains the eel migration and probably a good indicator of future conservation actions. Nevertheless, the presence of fishes with different migration types such as Amphidromous, Anadromous, Potadromous, and Oceanodromous highlights the importance of the estuary for stabilizing the community structure of fishes (Table 2).

The results show the freshwater habitats (e.g. canal and marsh) are clearly distinguished from brackish water habitats according to the species composition (Figure 6). These canals in more inland areas are connected with freshwater habitats and provide perfect habitats

Table 5. The presence of aquatic vegetation and related anthropogenic activities at the five sampling sites of the Dedduwa Estuary, Sri Lanka.

	Presence of aquatic vegetation		Anthropogenic activities		
	Presence of mangroves	Presence of aquatic weeds	Encircling nets	Disposal of waste	Brush park
Honduwa Lake habitat	H	-	+	-	+
Estuary	H	-	+	-	-
River	H	-	+	+	-
Canal	L	+	-	-	-
Freshwater marsh	-	+	-	+	-
H—high | L—Low | +/-—Presence/Absence.					

for Polyhaline (conditions ranging from a salinity of 18 –30 ppt), Mesohaline (waters with a salinity between 5 and 18 ppt), and Oligohaline (waters with salinity from 0.5–5 ppt) species (Karleskint 1998) because with high salinity influx, those species probably migrate towards the headwaters of the canal and streams probing for fewer salinity areas (Table 2).

In this analysis, different indices were used to describe the diversity of fish fauna in different habitats in the estuarine area. Because different diversity indices give results in different integrity. The Shannon index is based on percentage composition by species (Magurran 1988). When the randomness of the sampling cannot be guaranteed, the Brillouin index was used to calculate the heterogeneity (Southwood & Henderson 2000). This is because several sampling locations were inaccessible, due to the abundance of crocodiles, snags, and high water depth. Shannon index gives similar results where proportional abundance and number of species in the sample remain constant (Magurran 1988). The Brillouin index measures diversity as opposed to the sample. Both Shanon and Brillouin indices have given approximately similar results as indicated by Magurran (2004). Simpson index is more biased towards the most abundant species rather than species richness (May 1975). Pielou's evenness is an index that measures diversity along with species richness. Compared with indices such as Simpson's index or Shannon's index, a more thorough description of a community structure can be interpreted using Pielou's evenness (Heip & Herman 2001). Margalef's diversity index is a species richness index (Gamito 2010). Many species richness measures suffer from the problem that they are strongly dependent on sampling effort. The greater the sampling effort potentially the higher the index value. Thus, comparing metrics from samples collected with differing levels of sampling effort can be difficult and possibly misleading (Gamito 2010). As mentioned above (see methodology section) data generated from the alternative sampling efforts were excluded from the analysis, and the analysis may have been affected due to insufficient representation of fish species in the samples. Further considering the diversity measurements, Fisher's Alpha (α) is widely used as a diversity index to compare communities varying in the number of individuals (N), because theoretically independent of sample size. This is highly dependent on the sample size and the total number of species (Magurran 1988). Hence, Honduwa Lake habitat and estuarine area (Table 3) and Cluster I and IV (Table 4) show higher Fisher's alpha indices.

The average taxonomic distinctness index (AvTD, Δ+) measures the average taxonomic distance between species at a site, or the average path length joining every pair of individuals in a sample, using a standard Linnean classification, i.e. species, genus, family, order, class etc. (Warwick & Clarke 1995). The variation in taxonomic distinctness index (VarTD, Λ+) measures the variation in the average distance between species pairs (Clarke & Warwick 2001). The taxonomic diversity of the fish fauna observed in the area is within the expected range (Figure 6) confirming the high accuracy of the sampling. Except for migratory species, the distribution of the fish fauna in the estuarine areas is location-specific (Bruno et al. 2013). This specifies the ecological significance and conservation needs of the different types of habitats to conserve different species. Results show the freshwater habitats are unique to several endemic species, especially around marshes including *Horadandia atukorali* and *Clarias brachysoma*. These two species are highly localized for aquatic habitats with submerged vegetation (Pethiyagoda 1991).

The area is extremely popular for the tourism industry. The high visitor pressure and pollution of the freshwater systems seem to be a major threat to the freshwater fish fauna. The loss of riparian habitats was also observed during the field observations. Freshwater species abundance was higher in inland marshes and canals where there is less tidal effect. Though, mesohaline freshwater species like *Channa* spp. and *Puntius* spp. (Table 2) were observed in these freshwater segments, those species were not detected in the brackish water areas. The abundance and distribution of freshwater species increased notably with rainfall. These abiotic factors are important to explain the range expansion of the freshwater species in estuarine systems (Drinkwater & Frank 1994).

CONCLUSIONS

Fish fauna in the Dedduwa estuary provides insight into habitat preference and fish assemblages. The mutualistic relationship between fishes and habitats promotes the stability and functionality of this wetland habitat. The presence of the two endemic and vulnerable species—*Horadandia atukorali* and *Clarias brachysoma*—in marshy freshwater habitat and catadromous migration of *Anguilla* spp. highlights the conservation importance. In the current study freshwater systems are associated with canals where water quality is often vulnerable due to anthropogenic inputs such as sewage and solid waste and are likely to have noticeable impacts on the freshwater and amphidromous fishes. Though the species richness in the studied habitat was approximately similar, higher variations were observed in the abundance of different species. This demonstrates the habitat-orientated species distribution and ontogenetic habitat shifting of different species in the study area. The presence of fish species with different migratory habits denoted the importance of the estuary as a refuge and feeding ground for juvenile fish during their critical development stages. Therefore, current habitat alterations and pollution loads from different sources would affect the movement of the fishes and must be kept to be minimum.

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