2.5 Reservoir food web with an emphasis on culture-based fisheries

Subodha U Silva
Department of Limnology and Water Technology, Faculty of Fisheries and Marine Sciences & Technology, University of Ruhuna, Sri Lanka

Asanka D Jayasinghe
Department of Limnology and Water Technology, Faculty of Fisheries and Marine Sciences & Technology, University of Ruhuna, Sri Lanka

KHM Ashoka Deepananda
Department of Fisheries and Aquaculture, Faculty of Fisheries and Marine Sciences & Technology, University of Ruhuna, Sri Lanka

Clive M Jones
Centre for Sustainable Tropical Fisheries and Aquaculture, James Cook University, Australia

Abstract

In Sri Lanka, reservoir ecosystems are abundant and significantly contribute to CBF, enhancing inland fish production, food security and economic benefits. Although, studies on reservoir food webs and species interactions are scarce and the influence of those interactions on CBF is still unclear. On top of that, there is no published information on using stable isotope (SI) analysis as a tool to assess trophic interactions in reservoir food webs in Sri Lanka. This study aimed to use SI analysis to examine the trophic relationships between species utilised in CBF and native species in reservoir ecosystems in Sri Lanka. Samples were collected from 6 reservoirs by visiting once every 3 months from May 2023 to June 2024 period. Samples included basal resources (plankton, detritus, aquatic plants) and consumers (culture-based fish species, macrobenthos and indigenous fish species). Tissue samples of all species were dried, powdered and sent to James Cook University, Australia, to determine $\delta^{13}C$ and $\delta^{15}N$ isotope ratios. Multivariate statistical analyses and Bayesian mixing models provided insights into species interactions supporting the development of a conceptual food web. The dietary proportions for CBF species, estimated using the SIMMR model, indicated that plankton (50.1%) was the dominant food source, emphasising the importance of pelagic nutrient pathways. Detritus (29.4%) served as the primary benthic resource. The trophic position analysis calculated using freshwater mollusks as baselines, revealed that *M. rosenbergii* (3.49), *Catla catla* (3.06), *Hypophthalmichthys molitrix* (3.08), and *Oreochromis niloticus* (2.88) occupied mid-to-high trophic levels. *Labeo rohita* (2.36) and *Cirrhinus mrigala* (2.00) were positioned at lower trophic levels, relying more on macrophytes and macrophytic detritus. Predators such as *Anguilla bicolor* (4.3) and *Channa* spp. (3.93) occupied the top trophic levels, with potential predation on highly valued GFP and other CBF species. These findings on trophic relationships provides a baseline for better management of CBF in reservoirs in Sri Lanka.

Keywords: *stable isotope analysis, culture-based fisheries, Macrobrachium rosenbergii, trophic position, reservoir food webs*

Introduction

Food webs illustrate complex feeding interactions within an ecosystem, describing how energy and nutrients move through different trophic levels (Garvey and Whiles 2016). Reservoirs are man-made environments synchronising with nature as time permits. With time, different species choose a reservoir environment as their habitat where species interactions and nutrient flows critically shape the structure of the reservoir food web. The majority of the agrarian reservoirs in Sri Lanka are several centuries, if not millennia, old and provide opportunities to study species interactions in quasi natural environments.

Perennial and seasonal reservoirs in Sri Lanka play a crucial role in sustaining aquatic biodiversity and supporting CBF. These reservoirs provide essential food resources and shelter for both indigenous and stocked fish species. Perennial reservoirs, which retain water throughout the year, create stable ecological conditions that support species such as *O. niloticus*, *L. rohita*, *C. mrigala*, *Hypophthalmichthys molitrix* and *C. catla*, which are commonly stocked under CBF programs in Sri Lanka (Jayasinghe et al. 2006). In contrast, seasonal reservoirs, which undergo periodic drying, create fluctuating habitats that influence fish population structures and trophic interactions. The controlled stocking and harvesting of CBF species in both types of reservoirs contribute significantly to inland fish production, enhancing food security and providing economic benefits to local communities (Chandrasoma and Pushpalatha 2018; De Silva et al. 2006).

Despite the growing importance of CBF in Sri Lanka, there is a lack of research to examine reservoir food webs and utilise the knowledge on species interactions for better management of CBF. Using novel techniques like SI analysis to understand feeding relationships in these ecosystems is non-existent. SI analysis is a powerful tool for examining energy flow and nutrient pathways in aquatic food webs (Fry 2006; Peterson and Fry 1987). The SIs of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are widely used to assess dietary variability, feeding strategies, trophic positions, trophic niche shifts and nutrient sources in ecosystems (Layman et al. 2012; Post 2002). Generally, $\delta^{15}N$ serves as an indicator of trophic position, as it reflects an organism's resource use and increases predictably with each trophic level (Post 2002). In contrast, $\delta^{13}C$ is used to trace the original source of carbon in food webs, distinguishing between different basal energy sources such as planktonic and benthic production (Peterson and Fry 1987). Advances in Bayesian mixing models and isotopic niche analysis have further enhanced the application of SI analysis, allowing for precise estimations of prey contributions and the trophic niche space occupied by consumers within an ecosystem (Layman et al. 2007; Parnell et al. 2010; Abrantes, Barnett and Bouillon 2014). These advancements provide a robust framework for understanding species interactions, energy transfer and ecosystem stability.

Understanding the trophic interactions between CBF species and native species is essential for sustainable fisheries management, as food web dynamics influence species competition, resource partitioning and ecosystem resilience (Córdova-Tapia, Contreras and Zambrano 2015). This study aims to address this knowledge gap by determining the trophic interconnectedness of CBF species with native species, assessing the contributions of pelagic and benthic nutrient pathways in structuring reservoir food webs, and investigating the dietary contributions

of various prey sources to economically important CBF fish species and indigenous species. Additionally, this research seeks to identify potential predators of CBF species, especially the high-valued GFP (*M. rosenbergii*), providing insights into their ecological role within the reservoir ecosystem. Therefore, the primary objective of this study is to construct the food web of Sri Lankan reservoirs using SI analysis with a specific focus on CBF and economically important GFP. The findings of this study are expected to contribute to improved CBF management strategies and sustainable utilisation of reservoir resources ensuring long-term productivity and ecological balance.

Material and methods

We studied freshwater fish communities and their dietary sources in 6 perennial reservoirs located in the dry zone of Sri Lanka. These reservoirs included 4 medium-sized ones as classified by NAQDA: Weerawila in Hambantota District, Tabbowa and Vijayakatupotha in Puttalam District, and Urusitawa in Monaragala District. Additionally, 2 minor reservoirs – Maha Aluthgam Ara in Hambantota District and Siyabalangamuwa in Kurunegala District – were also studied (Table 2.5.1). These reservoirs were multifunctional, serving as sources of irrigation, water supply and CBF. Medium reservoirs exhibited diverse habitat characteristics, including vegetation cover and mixed substrate types (sandy, muddy and rocky), whereas minor reservoirs were less diverse in habitat features. The NAQDA stocks these reservoirs annually with GFP post larvae and fingerlings of various exotic CBF species, including *O. niloticus*, *L. rohita*, *C. mrigala*, *C. catla* and *H. molitrix*. Samples were collected from all 6 reservoirs every 3 months from May 2023 to June 2024 to ensure sufficient replication for SI mixing model analysis.

Sampling and preparation of fish and GFP for SI analysis

Fish and GFP were collected either using gillnets deployed by local fishers or multi-mesh gillnets set by us in specific microhabitat locations within each reservoir. The gillnets were deployed at designated sites in the evening prior to each sampling day. The following morning, after sampling potential food resources from the same habitats, the overnight catch from the nets was retrieved. For each fish, total length, standard length and weight were recorded. A sample of dorsal white muscle tissue (approximately 1% of body weight) was dissected from the left side of the body and preserved in 70% ethanol.

Table 2.5.1: Location and features of the 6 study reservoirs and their trophic difference represented by mean values of the chlorophyll-a content

Reservoir	Latitude and longitude	Max surface area (km^2)	Max depth (m)	Mean (±SE) Chl-a ($\mu g.L^{-1}$)
Weerawila	6.29 °N, 81.24 °E	5.011	13	4.91±2.50
Tabbowa	8.07 °N, 79.96 °E	5.372	19	11.05±9.07
Vijayakatupatha	7.72 °N, 79.90 °E	1.615	13	11.74±7.73
Urusitawa	6.33 °N, 80.93 °E	1.410	23	17.17±8.97
Maha Aluthgam Ara	6.37 °N, 81.09 °E	0.820	12	20.23±26.34
Siyabalangamuwa	7.94 °N, 80.46 °E	0.792	18	32.64±30.47

For fish samples less than 3 cm in standard length, the whole bodies of fish were used after removing the head, intestine and scales. For GFP, morphometric and meristic parameters, as outlined by Munasinghe and Thushari (2010) were recorded. GFP were then dissected, and tail muscle tissue (2–5 g) was taken for SI analysis, removing shell material, which can be enriched in $\delta^{13}C$ and would not reflect the actual assimilated diet of consumers (Kirby, Soniat and Spero 1998). For the time between sampling and sample preparation for SI analysis at the laboratory, all samples were preserved in 70% ethanol to ensure consistency (Hobson, Gibbs and Gloutney 1997). Since ethanol preservation was applied to all fish and GFP samples, it was assumed that any preservation effects on isotopic values would be consistent across species. Samples were sent to the SI analysis facility at James Cook University, Australia, and before sending, muscle tissues were washed 3 times with distilled water and oven-dried at 60 °C for several days until they could be easily powdered using a ceramic mortar and pestle (Hobson, Gibbs and Gloutney 1997; Vander Zanden et al. 1998).

Sampling potential basal resources and other consumers for SI analysis

Basal resources sampled for SI analysis included plankton (categorised into 2 size classes: 35–100 µm and >100 µm), detritus, emergent aquatic plants, submerged aquatic plants and riparian plants. Plankton samples were collected using 2 types of plankton nets: one with a 20 cm diameter and 100 µm mesh size, and another with a 30 cm diameter and 35 µm mesh size.

To prepare plankton samples in the 35–100 µm size range, approximately 25 L of surface water was collected at a depth of 0.5 m in the water column with a measuring basket and pre-filtered through the 100 µm mesh net to remove larger plankton and other debris. Then, the filtrate was passed through a 35 µm mesh net to remove tiny particles. The resulting filtrate was filtered again through a pre-combusted GF/C filter using a Buchner funnel fitted to a vacuum pump. Plankton larger than 100 µm was directly collected by dragging the 100 µm plankton net horizontally at a depth of 0.5 m in the water column. Debris and filamentous algae in the sample were removed by filtering through a 1 mm mesh before final filtration was passed through a pre-combusted GF/C filter. All GF/C filters containing plankton were oven-dried at 50 °C for 8 hours to prepare them for SI analysis (Keough, Sierszen and Hagley 1996; Mateo et al. 2008).

Detritus, emergent aquatic plants, submerged aquatic plants and riparian plants were handpicked from the littoral zones of the reservoirs. These samples were thoroughly rinsed with distilled water several times to remove sediments, organisms and other attachments. Detritus samples were further treated with 1 $mol.L^{-1}$ HCl to remove carbonates before drying. Mollusks and aquatic insects were collected from the littoral zone using a hand net. Depending on the time required for transport to the laboratory, mollusks and aquatic insects were kept alive in distilled water for 24 hours either in situ or in the laboratory to allow gut clearance. Mollusks were dissected to extract adductor muscle tissue, while the entire bodies of aquatic insects were prepared for SI analysis. All collected samples were oven-dried at 60 °C for at least 48 hours and then ground into a homogeneous fine powder using a mortar and pestle. The powdered samples were stored in clean containers in a desiccator until they were ready for SI analysis.

SI analysis

SI analysis was done using a Smart EA isolink elemental analyser connected to a Delta V Plus isotope ratio mass spectrometer via a ConFlo IV interface. Samples (0.8–1.2 mg) were combusted at 1020 °C, and the resulting CO_2 and N_2 gases were analysed for $\delta^{13}C$ and $\delta^{15}N$ values. International standard USGS40 (L-glutamic acid) and laboratory standards chitin and taipan were used for calibration. Data processing included drift and linearity corrections, with normalisation to Viana Pee Dee belemnite for carbon and to atmospheric nitrogen for nitrogen. The instrument had a precision of ≤0.06‰ (1σ) for isotope ratio measurements. SI ratio was expressed as:

$$\delta X\ (‰) = [((R\_sample)/(\ R\_standard\ ))-1] \times 1000$$

Where X is either ^{13}C or ^{15}N SI ratio, and R is either the ^{13}C: ^{12}C ratio for carbon or ^{15}N: ^{14}N ratio for nitrogen.

Arithmetic lipid correction

All fish and GFP samples were lipid-corrected following the method described by (Taylor et al. 2017). The equation, which adjusts for lipid-related $\boldsymbol{\delta^{13}C}$ depletion based on the C:N ratio is:

$$\delta^{13}C_{normalized} = \delta^{13}C_{bulk} + (93/(1+(C:N)^{3.4}))$$

Where $\boldsymbol{\delta^{13}C_{bulk}}$ is the measured $\boldsymbol{\delta^{13}C}$ value of the untreated sample, $\boldsymbol{\delta^{13}C_{normalised}}$ is the lipid corrected $\boldsymbol{\delta^{13}C}$ value, **C:N** serving as a proxy for lipid content. The empirically derived constants 93 (scaling factor) and 3.4 (exponent) account for the nonlinear relationship between C: N and lipid depletion. This model was selected for its broad applicability across taxa and greater accuracy than previous lipid normalisation equations (McConnaughey and McRoy 1979; Kiljunen et al. 2006; Post et al. 2007), as it was developed using a large dataset, including freshwater aquatic organisms.

Food-web structure and SI mixing models

This study aimed to develop a conceptual food web with an emphasis on CBF in Sri Lanka. The Tabbowa, Weerawila and Siyabalangamuwa reservoirs were selected for food web construction, as they encompass most of the fish species found in Sri Lankan reservoir ecosystems. To determine whether these reservoirs share similar isotopic baselines, multivariate statistical analyses were conducted using R statistical software (version 4.4.2). PERMANOVA was performed with $\delta^{13}C$ and $\delta^{15}N$ isotope values as response variables and reservoirs and basal resource groups (plankton, detritus, submerged plants, emergent plants and benthic algae) as grouping factors. Analyses were conducted on Euclidean distance measures using untransformed data. Levene's test confirmed the homogeneity of variances, and PERMANOVA ($\alpha = 0.05$) was used to assess significant differences among reservoirs and basal resource groups, with significance determined using Type I (sequential) sums of squares and 999 unrestricted permutations. Given the observed isotopic similarity across reservoirs, the data from these 3 reservoirs were combined to establish a consistent baseline for food web construction, ensuring a comprehensive representation of ecological patterns in $\delta^{13}C$ and $\delta^{15}N$ values.

The assessment of food web structure was based on trophic enrichment factors of 1.5±0.5 ‰ for $\delta^{13}C$ and 3.2±0.5 ‰ for $\delta^{15}N$ (Sweeting et al. 2007). SI Mixing Models in R (R 4.2.2) with the SIMMR package were used to estimate the contribution of multiple sources to each consumer species. SIMMR is a package designed to solve mixing equations for stable isotopic data within a Bayesian framework using Markov Chain

Monte Carlo (MCMC) fitting algorithms (Parnell et al. 2013; Phillips et al. 2014). The model generates posterior probability distributions described by average estimates of the source contributions and their associated credible intervals. Convergence and diagnostic statistics were evaluated using the Gelman-Rubin test, with all variables achieving values close to one, indicating convergence. Thereafter, the model fit was checked with a posterior predictive check, and it was investigated if all data points would fall approximately within the fitted value intervals. Within the SIMMR package, the program JAGS was used to run the mixing model (Parnell et al. 2013).

Consumer trophic positions

Consumer trophic levels (TL) were calculated based on the formula proposed by (Post 2002) and based on fractionation of 3.2±0.5 ‰ for $\delta^{15}N$ (Sweeting, Polunin and Jennings 2006):

$$TL=(\lambda+ (\delta^{15}N_{consumer} - \delta^{15}N_{base})/TEF)$$

Where $\delta^{15}N_{base}$ is the mean $\delta^{15}N$ value for a representative primary consumer, and TEF is the mean trophic fractionation which is 3.2 ‰. In this study, freshwater mollusks were used as baseline primary consumers to estimate trophic positions, with bivalves (*Lamellidens marginalis*, Unionidae) representing pelagic primary production and gastropods (Viviparidae) representing benthic primary production (Winemiller et al. 2011). Primary consumers were selected over primary producers due to their ability to integrate isotopic signals from multiple sources, providing a more stable and ecologically relevant baseline (Anderson and Cabana 2007). The mean $\delta^{15}N$ values of these mollusks were used to establish the baseline trophic level ($\lambda = 2$) for calculating the trophic positions of higher consumers. Using primary consumers as baselines reduces isotopic variability caused by environmental fluctuations, and simplifies food web reconstruction (Peterson and Fry 1987; Post 2002) Their filter-feeding and grazing habits make them reliable indicators of energy flow pathways, ensuring more accurate estimations of trophic interactions in reservoir ecosystems (Cabana and Rasmussen 1996).

Results

SI signatures of basal resources and consumers

A total of 515 samples were checked for SI ratios to investigate the trophic structure of Sri Lankan reservoir ecosystems. The dataset includes 4 basal resource types, 6 invertebrate groups, 27 fish species and GFP along with apex predators such as the great cormorant and crocodile (Table 2.5.2). This paper primarily emphasises CBF species with GFP along with their indigenous competitors and predators for food web construction. Apart from *Oreochromis niloticus*, which belongs to the family Cichlidae, all other CBF species – *C. catla, C. mrigala, L. rohita* and *H. molitrix* – belong to the family Cyprinidae. These fish species primarily inhabit benthopelagic zones, utilising both the water column and bottom habitats within the reservoir ecosystem.

Table 2.5.2: Carbon and nitrogen SI ratios (mean±standard deviation) of fish species, invertebrate groups, and basal carbon sources sampled from Weerawila (H2), Tabbowa (P4), Vijayakatupatha (P5), Urusitawa (Mo5), Maha Aluthgam Ara (H3), and Siyabalangamuwa (Ku5), Iranamadu (Ki2)

Species	Family	Reservoir	N	δ13C	δ15N
Fish species					
Oreochromis niloticus	Cichlidae	H3	7	-23.57±2.12	9.85±1.26
		Ku5	12	-26.20±1.14	7.63±0.94
		P4	12	-26.30±1.66	7.94±0.94
		Mo5	9	-31.79±0.35	6.93±1.29
		P5	12	-28.63±1.19	6.83±1.24
		H2	10	-27.13±2.96	10.12±0.85
Cirrhinus mrigala	Cyprinidae	H3	6	-26.64±0.82	5.05±1.08
		Ku5	4	-28.34±2.75	3.64±0.90
		P4	8	-28.52±2.05	3.64±1.48
		Mo5	10	-32.75±1.19	7.43±0.79
		P5	10	-29.83±1.38	4.41±0.57
		H2	8	-28.44±2.15	8.66±1.39
Labeo rohita	Cyprinidae	H3	6	-22.11±0.86	8.76±0.75
		Ku5	5	-25.88±1.38	5.86±0.10
		P4	1	-26.43	6.84
		Mo5	6	-32.24±0.35	5.58±0.86
		P5	11	-29.05±1.22	6.37±0.46
		H2	5	-25.54±2.01	7.77±0.52
Hypophthalmichthys molitrix	Cyprinidae	Ku5	4	-24.22±1.05	6.87±0.11
		P4	4	-26.62±0.49	7.43±0.37
		Mo5	7	-31.53±0.43	9.55±0.30
Catla catla	Cyprinidae	Ku5	6	-27.04±1.17	9.25±0.63
		P4	1	-30.51	7.99
		Mo5	8	-31.63±0.36	7.74±0.92
		P5	4	-30.76±1.09	8.28±0.11
Amblypharyngodon melettinus	Cyprinidae	P4	3	-26.93±0.33	6.74±0.14
Awaous grammepomus	Gobiidae	H3	3	-23.91±1.79	9.57±1.17
		Ku5	4	-25.51±0.73	10.36±0.32
		P4	8	-26.36±0.57	9.49±0.58
		P5	5	-29.27±1.25	8.89±0.93
		H2	1	-28.01	11.59

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Species	Family	Reservoir	N	δ13C	δ15N
Coptodon rendalli	Cichlidae	Ku5	2	-25.95±0.82	7.82±0.21
		P4	7	-19.35±0.94	9.90±0.30
Cyprinus carpio	Cyprinidae	P4	1	-27.32	7.24
Dawkinsia sp.	Cyprinidae	P4	2	-24.82±1.36	9.03±0.25
Dawkinsia singhala	Cyprinidae	P4	4	-26.0±1.36	9.03±0.25
Etroplus suratensis	Cichlidae	Ku5	10	-24.93±0.99	9.556
		P4	12	-26.45±0.47	8.56±0.17
		Mo5	2	-34.25±6.11	7.59±1.88
		P5	5	-25.51±2.09	9.26±0.91
Heteropneustes fossilis	Heteropneustidae	P4	5	-25.62±1.13	9.12±0.71
		P5	1	-31.67	5.65
Labeo dussumieri	Cyprinidae	H2	1	-27.84	6.59
Mystus ankutta	Bagridae	P4	3	-26.90±1.46	11.53±3.95
Oreochromis mossambicus	Cichlidae	H3	2	-24.88±0.22	9.18±0.38
		Ku5	6	-26.73±0.67	7.84±0.49
		P4	3	-23.27±5.24	8.72±1.14
		Mo5	1	-31.70	8.5
Pseudotroplus maculatus	Cichlidae	P4	6	-26.73±0.67	7.84±0.49
Pterygoplichthys gibbosus	Loricariidae	P4	2	-27.73±1.28	5.69±0.13
		Mo5	3	-31.38±0.63	7.68±0.29
		P5	4	-29.34±1.11	8.21±1.01
Puntius bimaculatus	Cyprinidae	P4	3	-24.0±0.7	9.02±0.64
Puntius dorsalis	Cyprinidae	Ku5	1	-25.36	8.03
		P4	3	-25.09±0.97	7.80±0.19
		P5	1	-28.42	7.08
Puntius sarana	Cyprinidae	H3	2	-22.26±0.61	10.31±0.19
		P4	4	-26.59±0.07	7.34±0.59
		Mo5	7	-30.98±0.76	9.66±0.77
		P5	2	-28.82±1.39	8.19±0.72
		H2	6	-27.68±1.06	11.41±0.59
Rasbora microcephalus	Cyprinidae	H3	1	-25.15	8.44
		P4	4	-25.67±0.33	9.89±0.42
Channa marulius	Channidae	Ku5	1	-24.18	10.64
Ompok bimaculatus	Siluridae	Ku5	2	-25.63±0.05	9.98±0.54
		P4	5	-27.26±2.21	9.32±0.88
		P5	5	-25.19±1.05	10.19±0.55

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Species	Family	Reservoir	N	δ13C	δ15N
Channa striata	Channidae	P4	1	-25.06	10.42
		Mo5	2	-30.39±0.57	10.95±0.77
		P5	1	-27.61	11.24
		H2	9	-26.7±1.37	12.14±1.95
Anguilla bicolor	Anguillidae	H2	1	-23.55	13.02
Mastacembellus armatus	Mastacembelidae	P4	6	-25.19±1.05	10.19±0.55
Invertebrates					
Macrobrachium rosenbergii	Palaemonidae	H3	5	-23.43±0.52	11.09±0.44
		Ku5	8	-25.26±0.68	10.08±0.65
		P4	10	-25.81±1.40	9.70±0.80
		Mo5	2	-29.39±1.00	10.52±1.55
		P5	8	-28.30±1.29	9.37±0.56
		H2	10	-28.78±2.24	11.39±0.98
Aquatic insect larvae	-	H3	2	-32.61±1.36	5.92±0.71
		Ku5	2	-32.71±0.93	5.66±0.26
		P4	4	-27.29±5.50	6.41±0.78
		Mo5	3	-33.39±2.37	4.42±0.88
		P5	5	-32.21±3.2	4.64±1.15
		H2	2	-28.56±1.53	7.36±0.92
Freshwater shrimp *(Caridina simoni)*	Atyidae	P4	3	-27.58±1.35	5.89±0.58
		Mo5	2	-31.29±0.69	7.56±1.82
		P5	3	-29.67±1.6	7.68±0.89
		H2	1	-25.86	8.3
Freshwater crab	Gecarcinucidae	Mo5	2	-31.5±0.07	8.12±1.80
		P5	1	-31.64	10.08
Plankton >100 µm	-	Ku5	3	-30.09±0.75	8.02±0.31
		P4	3	-32.76±0.86	8.36±0.47
		H2	3	-32.76±1.15	8.02±0.31
Freshwater bivalves *(Lamellidens marginalis)*	Unionidae	P4	2	-29.35±0.41	4.72±0.02
		P5	1	-32.61	4.37
Freshwater snails	Viviparidae	H3	3	-32.71±0.35	5.58±0.90
		Ku5	3	-34.16±1.22	6.40±1.92
		P4	3	-31.09±1.85	5.51±1.30
		Mo5	6	-33.00±0.53	6.4 ±1.10
		P5	3	-34.59±0.25	5.63±2.14
		H2	3	-27.62±1.55	6.43±1.37

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Species	Family	Reservoir	N	δ13C	δ15N
Basal resources					
Plankton (35–100 µm)	-	Ku5	3	-29.10±1.14	5.53±1.01
		P4	4	-30.23± 0.16	5.49±0.15
		H2	2	-30.68±0.94	7.49±0.15
Detritus	-	H3	2	-24.56±0.23	4.51±1.62
		Ku5	3	27.37±2.04	3.18±0.64
		P4	4	-24.57±4.16	3.35±1.48
		Mo5	3	-28.62±0.59	6.97±2.39
		P5	3	-24.91±6.62	2.51±1.05
		H2	4	-25.32±4.86	4.61±2.06
Emergent plants	-	P4	2	-18.65±6.99	4.59±0.76
		Mo5	1	-17.48	6.02
		H2	6	-18.44±3.32	5.16±2.41
Submerged plants	-	H3	1	-32.71±0.35	5.58±0.90
		Ku5	2	-28.01±2.28	4.05±0.57
		P4	6	-29.22±1.62	2.93±3.02
		Mo5	3	-31.31±0.60	2.81±2.79
		P5	4	-28.19±0.72	3.49±1.77
		H2	3	-29.53±0.46	6.15±1.00
Benthic algae	-	P4	3	-13.87±1.82	3.41±3.16
		H2	2	-30.93±0.64	5.73±0.42
Other species					
Phalacrocorax carbo	Phalacrocoracidae	P5	1	-26.33	9.96
Crocodile	Crocodylidae	Ki2	1	-21.57	9.37

Tabbowa (P4), Weerawila (H2) and Siyabalangamuwa (Ku5) reservoirs were selected for the conceptual food web development of Sri Lankan reservoirs. Across these reservoirs, the $\delta^{13}C$ values of basal resources ranged from -30 ‰ to -11 ‰ (Figure 2.5.1). Among these, submerged plants exhibited the lowest $\delta^{13}C$ values, while detritus showed relatively enriched $\delta^{13}C$ values ranging from -28 ‰ to -24 ‰. Statistical analysis using the Kruskal-Wallis test ($H = 18.47$, $df = 2$, $p<0.001$) and Dunn's post-hoc test indicated that detritus was not significantly different from submerged or emergent plants (Detritus vs. Emergent plant: $Z = -2.218$, $p = 0.0797$; Detritus vs. Submerged plant: $Z = 2.253$, $p = 0.0727$). These findings suggest that a significant portion of detritus is likely derived from macrophyte-derived organic matter.

The 35–100 µm plankton size group exhibited more enriched $\delta^{13}C$ values compared to the >100 µm size group, suggesting differences in carbon sources between these fractions. In contrast, the >100 µm plankton group displayed higher $\delta^{15}N$ values (8.02–8.36 ‰) than the 35–100 µm group (5.49 – 7.48 ‰), indicating a clear trophic separation

between these size classes. The >100 µm fraction likely consists of larger herbivorous and omnivorous zooplankton, such as copepods, cladocerans and large rotifers, which feed on smaller phytoplankton and microzooplankton. This trophic enrichment follows the established pattern of nitrogen isotope fractionation, where $\delta^{15}N$ values increase by approximately 2–4 ‰ per trophic level due to stepwise nitrogen assimilation and excretion processes (Minagawa et al. 1984). These results align with the expected food web structure, where phytoplankton (35–100 µm) serve as primary producers with lower $\delta^{15}N$ values, while larger zooplankton (>100 µm) occupy a higher trophic level due to their consumption of microzooplankton and phytoplankton. The $\delta^{13}C$ values of consumer fish and GFP in the reservoirs ranged from -23 ‰ to -30 ‰, while $\delta^{15}N$ values ranged from 3 ‰ to 13 ‰ (Figure 2.5.1) indicating diverse nutrient pathways and trophic positions. The variation in $\delta^{15}N$ values reflects different trophic levels, from primary consumers to higher-level predators.

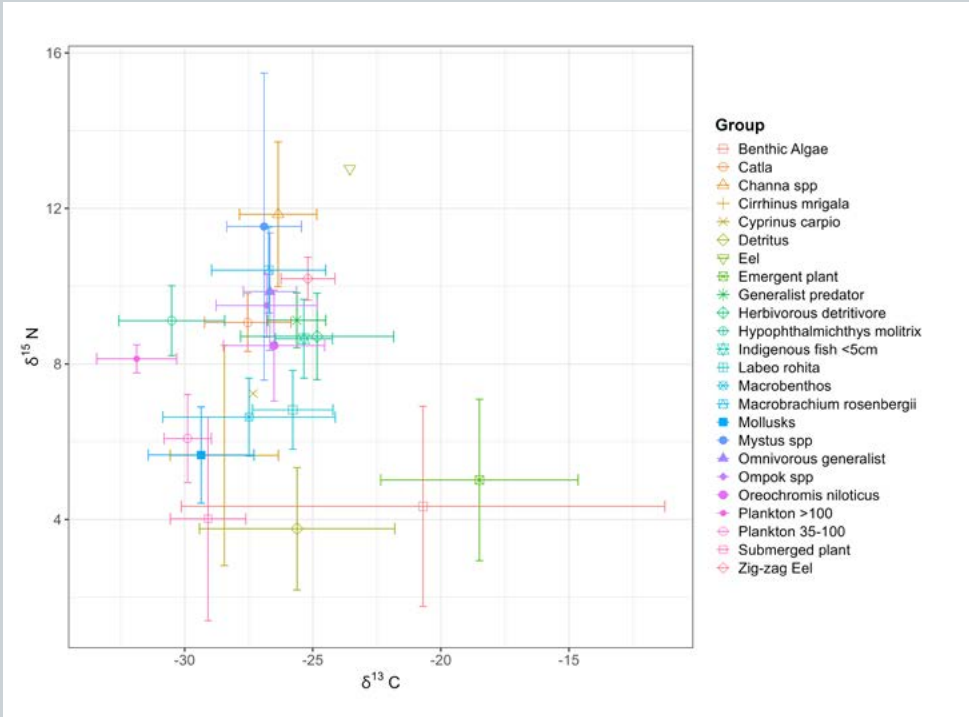

Figure 2.5.1: Stable $\delta^{13}C$- $\delta^{15}N$ isotopic biplot of consumers and their potential basal resources pooled from 3 reservoirs (Tabbowa (P4), Weerawila (H2) and Siyabalangamuwa (Ku5)) in 2023 to 2024

Note: Data points represent the mean±standard deviation for each species or group of species.

The differences in SI values ($\delta^{13}C$ and $\delta^{15}N$) among reservoirs were analysed using PERMANOVA, considering the basal resource groups: plankton, detritus, submerged plants, emergent plants and benthic algae. The analysis, conducted using Euclidean distance with 999 permutations, revealed that reservoir location had no significant effect on isotopic composition ($F = 1.2335$, $p = 0.306$), explaining only 4.9% of the total variance ($R^2 = 0.04888$), with the remaining 95.1% attributed to within-reservoir variation.

These results suggest that the isotopic composition of basal resources is relatively uniform across reservoirs (Figure 2.5.2), therefore combining basal resource data from different reservoirs for food web construction is feasible. Pooling the data can provide a representative baseline for food web analysis without introducing significant spatial bias, as the isotopic differences are primarily driven by within-reservoir factors rather than reservoir location.

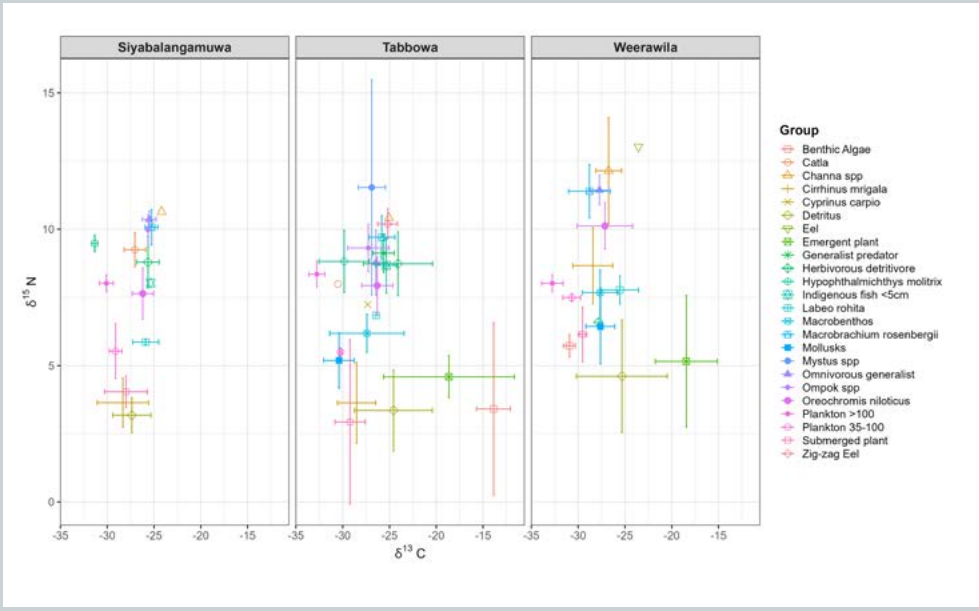

Figure 2.5.2: Separate stable $\delta^{13}C$ - δ15N isotopic biplots of Tabbowa (P4), Weerawila (H2) and Siyabalangamuwa (Ku5)

Note: Data points represent the mean±standard deviation for each species or group of species.

Feeding ecology of GFP

The SIMMR model utilised SI values ($\delta^{13}C$ and $\delta^{15}N$) and trophic enrichment factors (Sweeting et al. 2007) of GFP muscle tissue to estimate the proportional contributions of potential dietary sources, which included benthic algae, detritus, emergent plants, macrobenthos, mollusks, indigenous fish species (<5 cm) and submerged plants. It revealed that indigenous fish species (<5 cm) contributed the highest proportion to the diet (mean = 0.402±0.124), followed by mollusks (mean = 0.255±0.150) and macrobenthos (mean = 0.196±0.189) (Figure 2.5.3 b). These findings suggest that GFP primarily shows carnivorous behaviour, relying heavily on animal-based food sources, which is consistent with previous studies indicating its opportunistic feeding behaviour and preference for protein-rich prey (Kurup, Harikrishnan and Sureshkumar 2000; New 2002). The relatively minor contributions from submerged plants (mean = 0.063±0.053), detritus (mean = 0.035±0.026) and benthic algae (mean = 0.025±0.017) align with earlier observations that plant material and organic detritus are secondary dietary components, often consumed when preferred prey is scarce (Mariappan et al. 2000).

The posterior density plots and credible intervals (Figure 2.5.3 a) indicate variability in dietary intake, highlighting the species' ability to adjust its feeding strategy based on resource availability. Compared to previous studies in natural freshwater ecosystems, which reported a higher reliance on detritus and plant matter in heavily vegetated habitats (Bakhtiyar, Lakhnotra and Langer 2013), the present findings suggest that in the studied reservoirs, carnivorous feeding predominates, likely due to the greater availability of small fish species and mollusks.

The SIMMR matrix plot (Figure 2.5.3 c) presents the pairwise relationships between dietary sources of GFP, revealing strong negative correlations between Macrobenthos and small indigenous fish species <5 cm (-0.692), as well as between Macrobenthos and Mollusks (-0.682). These negative correlations suggest potential dietary trade-offs, indicating that GFP may dynamically adjust its diet in response to prey availability. In contrast, a weak positive correlation (0.264) is observed between indigenous fish species <5 cm and submerged plants, suggesting some degree of simultaneous consumption. The small fish species collected from these reservoirs – such as *Pseudetroplus maculatus, Puntius dorsalis, Puntius bimaculatus, Rasbora microcephalus, Dawkinsia singhala* and *Amblypharyngodon melettinus* – are often found in the littoral zone, where dense vegetation is prevalent. This habitat overlap may explain the observed co-occurrence in the diet of GFP. However, the relatively low correlation value (0.264) suggests that GFP does not heavily rely on submerged plants when consuming small fish species, and the association may be incidental rather than a primary dietary preference.

Feeding ecology of CBF fish species

The primary CBF fish species in Sri Lankan reservoirs include tilapia species such as *Oreochromis niloticus* and various carp species, including *L. rohita*, *C. mrigala*, *C. catla*, *H. molitrix*, *H. nobilis*, *Ctenopharyngodon idella* and *Cyprinus carpio*. However, due to the unavailability and insufficient sample number of *H. nobilis*, *C. idella* and *C. carpio* from the sampled reservoirs, these species were not included in the SIMMR Bayesian mixing model analysis. The analysis focused on the remaining species, with most sampled individuals being adults (Table 2.5.3), thereby providing insights into the feeding ecology of their adult life stage in reservoir ecosystems.

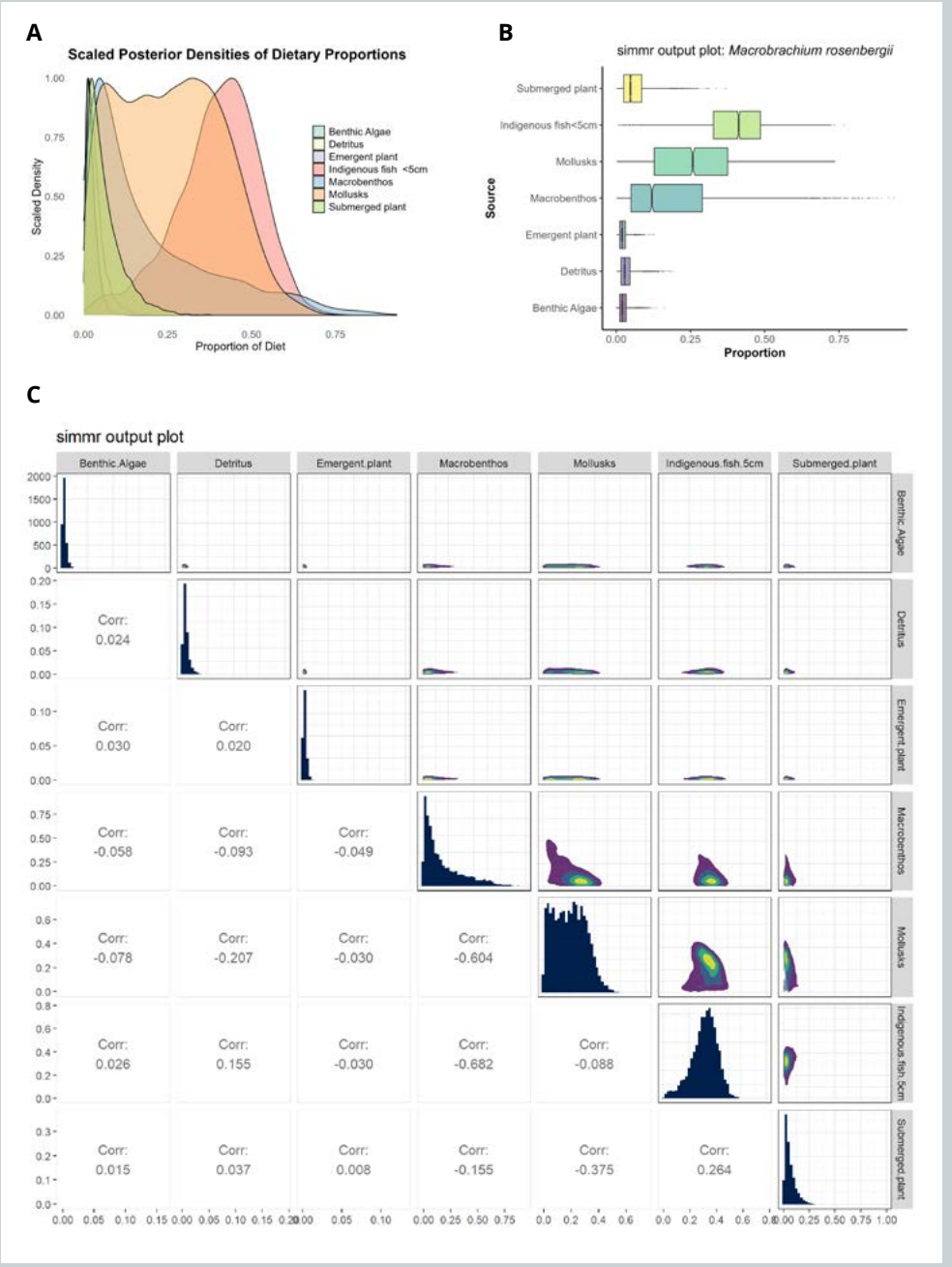

Figure 2.5.3: Posterior distributions of dietary source proportions for GFP estimated using SIMMR

Note: (a) Scaled Density Plot, (b) Boxplot of Relative Proportions (c) Matrix plot showing correlations between dietary components.

Table 2.5.3: Total length (TL), standard length (SL) and weight of culture-based fish species sampled from 3 reservoirs (Ku5=Siyabalangamuwa, P4=Tabbowa, H2=Weerawila)

Species	Reservoir	TL range (cm)	SL range (cm)	Weight range (g)
Catla catla	Ku5	34.1–53.5	25.8–44.1	410–2,495
	P4	22.5	18.7	198
Cirrhinus mrigala	Ku5	45.8–49	38–41.2	1,096–1,391
	P4	42.7–57.8	35–48.7	853–1,803.8
	H2	32.7–52.1	27.1–42.3	411.8–1,362
Labeo rohita	Ku5	29.5–50.8	19.7–40.5	307–1,685.8
	P4	48.5	39.3	979
	H2	28.5–46.2	22.6–36.8	276–1,252.6
Hypophthalmichthys molitrix	Ku5	45.2–57.5	38.1–48.4	899–2,096
	P4	40.3–54.1	34.1–46.2	680–1,402
Oreochromis niloticus	Ku5	17.5–26.3	14–21.9	109–394.4
	P4	21–35.7	17.2–29.4	197–879
	H2	15.1–40.1	16.7–34.2	162.2–516.2

The SIMMR model was applied to *O. niloticus* using 4 basal dietary sources: detritus, plankton (35–100 µm), plankton (>100 µm) and macrobenthos. The macrobenthos category included insect larval stages, which were directly observed in the gut contents of the sampled *O. niloticus*. These dietary sources, confirmed through gut content analysis, represent the primary food items utilised by the species in the studied environment. A related study by Temesgen et al. (2022) reported a diverse range of dietary components in the gut contents of *O. niloticus*, including phytoplankton, zooplankton, insects, detritus, macrophytes, fish parts and nematodes. The results of the SIMMR model indicated that *O. niloticus* predominantly feeds on detritus (40.9%), followed by plankton (35–100 µm) (29.7%). Macrobenthos contributed 16.6%, while plankton (>100 µm) accounted for 12.8% (Figure 2.5.4 a). Among the dietary sources, detritus exhibited the highest proportion with the lowest uncertainty, with a 95% credible interval ranging from 24.5% to 55.9%. The density distribution for detritus displayed a narrow peak, indicating greater confidence in its contribution. In contrast, plankton (35–100 µm) exhibited a broader peak, suggesting higher uncertainty in its dietary contribution (Figure 2.5.4 b). The posterior predictive check revealed that 42.7% of the observed data fell outside the predicted range, indicating a moderate model fit with some unexplained variation.

The SIMMR model was applied to culture-based cyprinid species, with dietary sources identified through gut content observations and validated using secondary literature. For *H. molitrix*, the dietary sources included plankton (35–100 µm), plankton (>100 µm) and detritus (Jayasinghe et al. 2015; Tumolo and Flinn 2019). A similar composition was applied to *C. catla* (Lalit 2015; Mishra 2020). For *C. mrigala* and *L. rohita*, submerged plants were also included as dietary sources (Soni and Ujjania 2018; Mishra 2020). The results showed that plankton (35–100 µm) contributed 48.7% of *H. molitrix*'s diet (Figure 2.5.5 a) and 40% of *C. catla*'s diet (Figure 2.5.5 b). *C. mrigala* primarily relied on submerged plants (55.9%, Figure 2.5.5 c), while *L. rohita* showed a strong dependence on macrophytic detritus (46.5%, Figure 2.5.5 d).

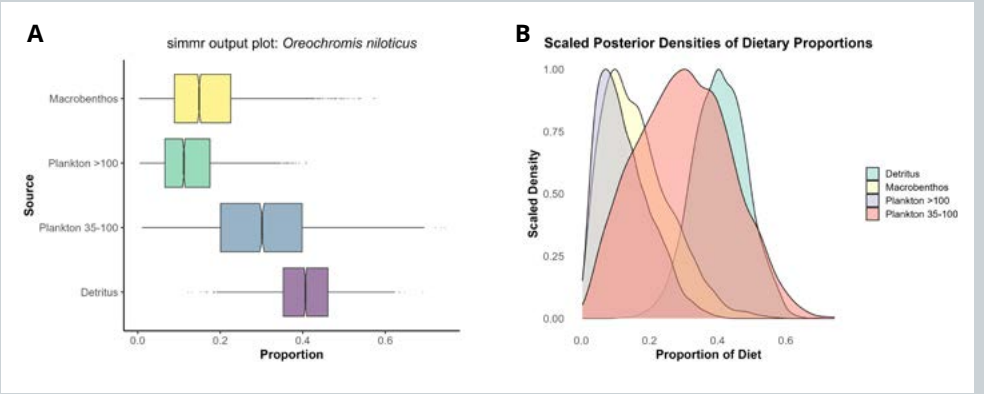

Figure 2.5.4: Relative dietary proportions of *Oreochromis niloticus* (a) dietary boxplot (b) scaled density plot resulted from SIMMR model

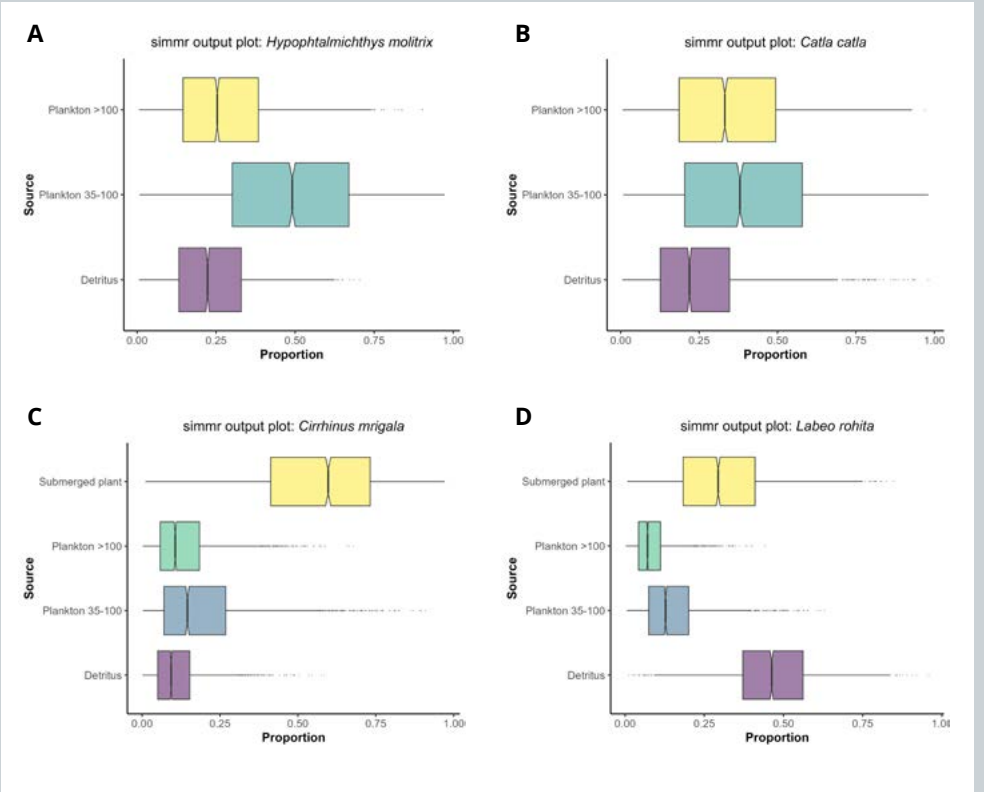

Figure 2.5.5: Dietary boxplots of (a) *Hypophthalmichthys molitrix* (b) *Catla catla* (c) *Cirrhinus mrigala* (d) *Labeo rohita* resulted from SIMMR model

Feeding ecology of potential predators of CBF species

Piscivorous fish species, including *C. striata* and *C. marulius*, along with generalist predators such as *A. bicolor*, *M. armatus* and *O. bimaculatus* were incorporated into the model based on ecological evidence supporting their predation on CBF species. Additionally, local fishers' observations suggest that these predators actively prey on GFP, particularly when they are entangled in gillnets. These species are known to feed on fingerling and juveniles of CBF fish, as well as the post-larval stages of GFP highlighting their role as key predators within the reservoir ecosystem.

The SIMMR model was used to determine the dietary contributions of piscivorous and generalist predator species by incorporating each CBF species as an individual dietary source, while indigenous fish species smaller than 5 cm were pooled together with mollusks, macrobenthos and other relevant dietary sources as a single category as appropriate. The selection of dietary sources for each predator was based on gut content observations, fishers' ecological knowledge and experience, and existing literature to ensure a comprehensive understanding of their trophic interactions. *Channa* spp. was modelled with macrobenthos, mollusks and indigenous fish species less than 5 cm in standard length, along with an assessment of their predation on GFP. Only small fish species were incorporated into the model, as existing literature does not indicate that *Channa* spp. prey on adult cyprinids and cichlids (Das et al. 1998; Amin et al. 2005) and no evidence of such predation was observed in their gut contents. The SIMMR model results indicate that *Channa* spp. exhibits a generalist predatory feeding strategy, with GFP contributing the highest proportion (34.7%) to their diet, followed by mollusks (25.0%), indigenous fish species <5 cm (21.0%) and macrobenthos (19.3%) (Figure 2.5.6 a).

For the SIMMR model of *A. bicolor, O. niloticus* was incorporated as a dietary source along with other potential prey items based on gut content observations (Rupasinghe and Attygalle 2006; Sidqi et al. 2018). The model results indicate that

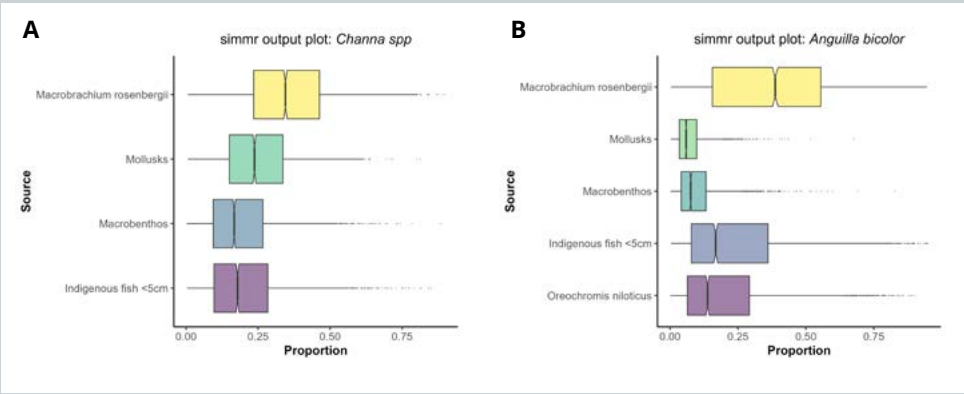

Figure 2.5.6: Relative dietary boxplots of (a) *Channa* spp. (b) *Anguilla bicolor* as explained by the SIMMR model

A. bicolor exhibits a generalist predatory feeding strategy, with GFP contributing the highest proportion (37.3%), followed by indigenous fish species <5 cm (24.0%) and *O. niloticus* (21.6%). Macrobenthos (9.6%) and mollusks (7.4%) contributed to a lesser extent (Figure 2.5.6 b), suggesting occasional consumption of benthic invertebrates. The relatively high reliance on GFP and small fish species aligns with its piscivorous tendencies, where it actively preys on available fish and crustaceans, demonstrating opportunistic feeding behaviour influenced by the prey availability within the reservoir ecosystem. The relatively high reliance on GFP suggests that it is an important prey item for *Channa* spp. and *A. bicolor.* As GFP frequently become entangled in gillnets during fishing operations they can be easily accessible to these predators.

To assess the trophic interactions and dietary composition of *M. armatus* and *O. bimaculatus,* a SIMMR Bayesian model was employed, incorporating indigenous fish species <5 cm in standard length, mollusks, and macrobenthos as dietary sources. Mollusks, including freshwater bivalves and snails, and macrobenthos, consisting of insect larvae and *C. simonii,* were selected based on existing literature (Gupta and Banerjee 2016; Kashyap et al. 2023; Serajuddin et al. 1998). Furthermore, to evaluate potential predation on GFP, it also was integrated as an additional dietary source. The SIMMR Bayesian model results indicate that *M. armatus* and *O. bimaculatus* exhibit generalist predatory feeding strategies, consuming a diverse range of dietary sources. *O. bimaculatus* primarily relied on mollusks (42.4%) and macrobenthos (22.9%), followed by *O. niloticus* (13.2%), indigenous fish species <5 cm (11.7%) and GFP (9.8%) (Figure 2.5.7 a). Similarly, *M. armatus* showed a relatively even dietary distribution, with mollusks (25.0%), macrobenthos (22.5%), indigenous fish species <5 cm (21.6%) and *O. niloticus* (18.2%), while GFP contributed 12.8% (Figure 2.5.7 b). The substantial intake of mollusks and macrobenthos in both species highlights their benthic foraging behaviour, utilising available invertebrate resources in the reservoir ecosystem. The inclusion of *O. nioticus* and GFP suggests opportunistic attacking on bigger preys, further supporting their role as mesopredators within the food web.

The SIMMR model demonstrated a moderate overall fit, with a mean proportion of observed data outside the predictive range of 41.8%, indicating some variation in model accuracy across species. *M. armatus* (16.6%) and *O. bimaculatus* (14.3%) exhibited the strongest model performance, suggesting that their dietary contributions were well represented with minimal unexplained variation. *Channa* spp. (36.4%) showed a moderate level of deviation, likely reflecting dietary flexibility or unaccounted variability in prey selection. In contrast, *A. bicolor* exhibited the highest deviation (100%), though this is likely attributable to the limited sample size (n=1) rather than actual dietary inconsistency. These findings indicate that the model effectively captured the dietary patterns of *M. armatus* and *O. bimaculatus*, while the greater discrepancies observed for *Channa* spp. and *A. bicolor* suggest the need for a more comprehensive dietary representation or increased sample sizes to enhance predictive accuracy.

Trophic structure of consumers in the reservoir ecosystem

The estimated trophic positions of consumers in the reservoirs' food web ranged from 2.0 to 4.3, with primary consumers positioned near the baseline

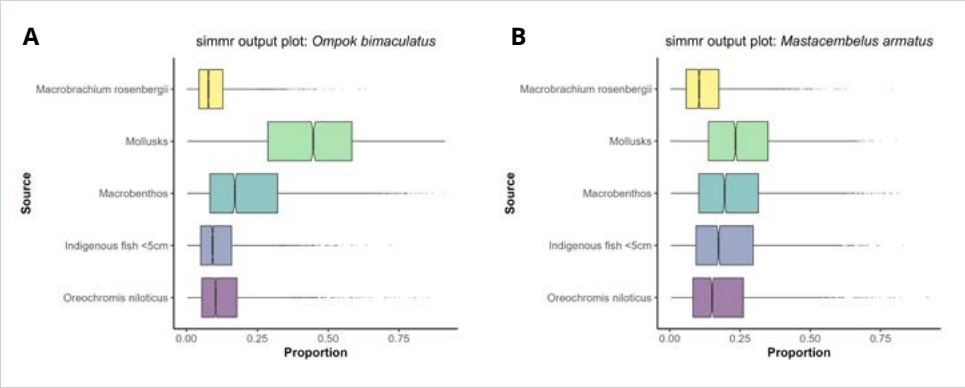

Figure 2.5.7: Relative dietary proportion boxplot of (a) *O. bimaculatus* (b) *M. armatus* as explained by the SIMMR model

(TP = 2), while top predators like *A. bicolor* and *Channa* spp. occupied higher trophic levels (~4.0). GFP (TP = 3.49) was identified as an omnivorous consumer with a carnivorous tendency (Figure 2.5.8).

Conceptual reservoir food web with an emphasis to CBF

The food web structure of the studied reservoirs was constructed using dietary proportions estimated from the SIMMR model, highlighting trophic interactions among culture-based fish species and native fish species. The dietary proportions (Figure 2.5.9) based strong trophic links (>40% contribution) were represented by double-line red arrows, while moderate contributions (20–40%) by solid blue arrows. Dietary contributions between 10–20% were represented by solid black arrows, whereas the least contributions (0–10%) were depicted using dashed black arrows. The results confirm that the reservoir ecosystem supports a complex trophic structure, with both pelagic and benthic nutrient pathways contributing to CBF fish production.

Discussion

Understanding food web structures and trophic dynamics of CBF species and non-CBF native fish species in reservoir ecosystems is essential for developing strategic improvements in fisheries management based on scientific knowledge. This study applied SI analysis to investigate trophic interactions in 6 reservoirs representing spatial differences across 4 dry zone districts in Sri Lanka. Eventually, 3 reservoirs were selected for food web construction, as they encompass most of the fish species found in Sri Lankan reservoir ecosystems. Each reservoir was differing in habitat complexity and productivity. However, those reservoirs did not show significant differences among basal resource groups, in terms of observed isotopic similarity across reservoirs, therefore could be combined to establish a consistent baseline for food web construction.

By analysing carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures, this study identified the trophic niches of various

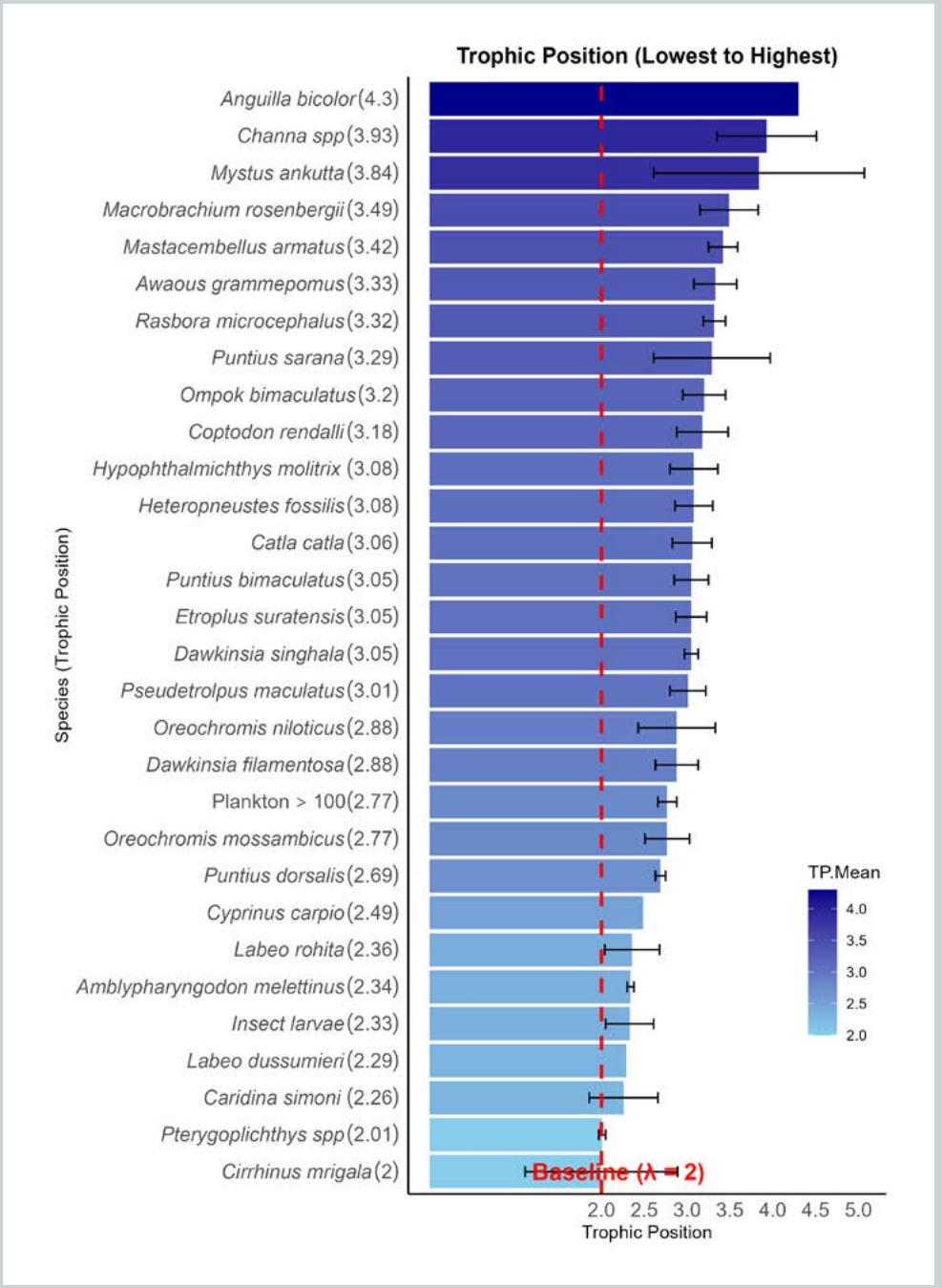

Figure 2.5.8: Mean trophic position of the consumers, with error bars indicating dietary variability

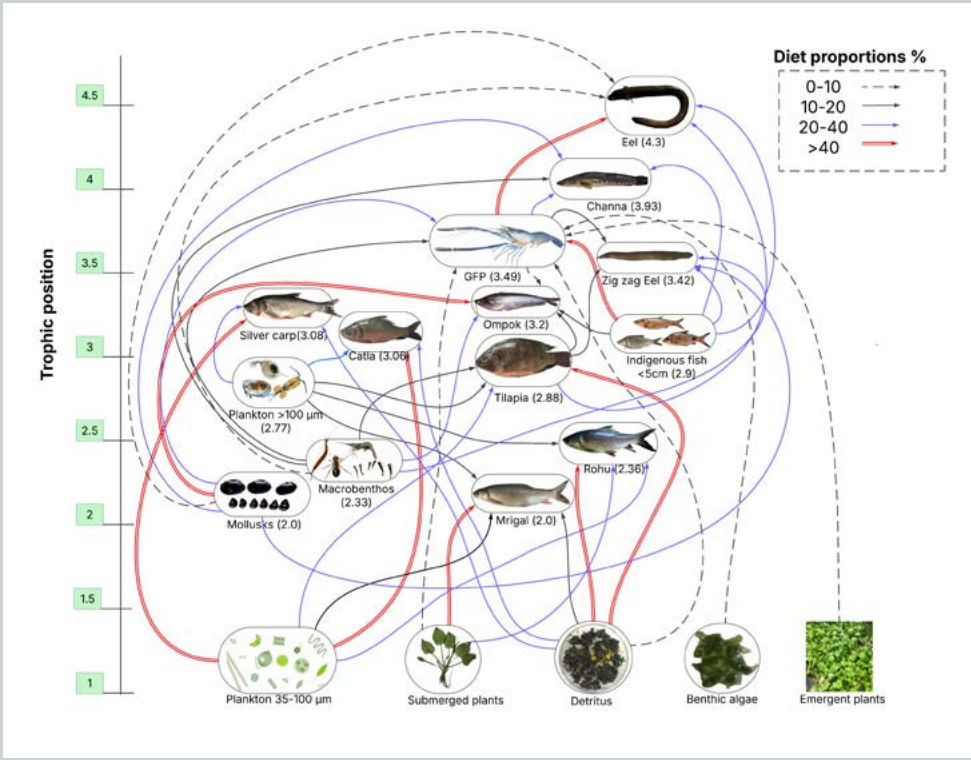

Figure 2.5.9: Conceptual reservoir food web structure and trophic interactions with an emphasis to CBF species in Sri Lankan reservoir ecosystem

consumers and quantified the contributions of basal dietary sources to CBF species. The assessment of pelagic and benthic dietary sources provides valuable insights into optimising species stocking proportions, which is an essential part of the CBF management. It ensures balanced nutrient pathways and enhanced fisheries productivity in reservoir ecosystems. In this study, a total of 515 samples were checked for SI ratios to investigate the trophic structure of Sri Lankan reservoir ecosystems. Although, species other than CBF were not abundant in the catches of fishers since those species were not their primary target. Smaller species were not in the catch due to the selectivity of fishing gear for larger individuals, therefore, needed extra effort to collect smaller indigenous fish specimens. Also, the bigger indigenous fishes like eels were not common in gillnet catches due to their specific elongated body shape. On top of that, eels were not a target species of fishers due to lack of interest, taste or mythical beliefs. Apex predators other than fish such as the great cormorant and crocodile are poorly represented here because there was no active sampling process targeting those species. For example, one tissue sample of a crocodile could be obtained since there was its carcass floating in the reservoir on that particular sampling day.

The recent introduction of GFP into CBF in many reservoirs has generated greater economic and social benefits compared to finfish, as these high-value prawns are primarily supplied to Colombo restaurants and export markets (De Silva, Amarasinghe and Nguyen 2006; Digamadulla et al. 2023) Therefore, a comprehensive understanding of GFP's feeding ecology is crucial for sustainable fisheries management. The SIMMR analysis confirmed that GFP exhibits an opportunistic omnivorous feeding strategy, with a strong preference for animal-based prey, reinforcing its carnivorous tendencies within the reservoir ecosystem. These findings align with previous studies indicating that GFP primarily consumes protein-rich prey, such as small fish, mollusks and benthic invertebrates (Kurup, Harikrishnan and Sureshkumar 2000; New 2002). Furthermore, the TP analysis, calculated using the equation proposed by (Post 2002), provided additional support for the SIMMR results, positioning GFP at a higher trophic level (TP = 3.49). This further validates GFP's role as a secondary consumer within the reservoir ecosystem, emphasising its reliance on animal-based food sources and its functional significance in the trophic structure.

According to fishers, a major constraint to GFP fisheries is predation within the reservoir, which impacts optimal harvest yields. The SIMMR model applied to piscivorous and generalist predator species, including *A. bicolor*, *Channa* spp., *M. armatus* and *O. bimaculatus,* confirmed that these species actively prey on GFP, contributing to its population decline. This predatory pressure underscores the need for effective fisheries management strategies, such as predator control measures, optimised stocking densities and habitat modifications, to enhance GFP survival and improve harvest efficiency. The trophic structure of the reservoir ecosystem suggests that GFP plays a dual role as both a predator and prey species, contributing to energy transfer between trophic levels. However, its high predation pressure from piscivorous fish species presents a significant challenge for sustainable fisheries management.

The *O. niloticus*, a cichlid fish species, was introduced to Sri Lanka in 1956 to enhance inland fisheries (De Silva 1988). Since then, it has become a dominant species in many of the country's reservoirs (Amarasinghe and De Silva 2015). Rural inland communities in Sri Lanka have shown a growing preference for *O. niloticus* over stocked cyprinid species, likely due to its high reproductive capacity, adaptability and consistent availability (Amarasinghe and De Silva 1999). Consumer preference on taste of tilapine fishes over other Chinese and Indian carps could be another reason, although it has not been empirically quantified. According to existing ecological knowledge*, O. niloticus* is omnivorous with herbivorous tendencies, feeding primarily on algae, plant material and detritus, but also consuming zooplankton and benthic invertebrates depending on availability (Moriarty 1973; Getachew and Fernando 1989). The diet of *O. niloticus* is highly plastic, shifting between phytoplankton, detritus, periphyton and zooplankton depending on food availability and environmental conditions (Attayde and Menezes 2008; Britton et al. 2007). However, based on SIMMR model, *O. niloticus* in the studied reservoirs primarily fed on detritus, followed by plankton 35–100 µm, which mainly consists of phytoplankton. Zooplankton (>100 µm) contributed the least, while macrobenthos, including insect larvae, accounted for 16.5%, reinforcing its omnivorous detritivore

classification. Findings from Temesgen et al. (2022) were partially consistent with our study, reporting that larger individuals of *O. niloticus* (total length >20 cm) primarily consumed detritus, macrophytes and fish parts. In contrast, several studies have reported differing dietary patterns for *O. niloticus*, suggesting that its diet is predominantly composed of phytoplankton (Attayde and Menezes 2008; Worie Assefa, Getahun and Workiyie Worie Assefa 2015; Tesfaye et al. 2021; Akbal Husen et al. 2024). In another case, Ethiopian lakes reported high detritus consumption in *O. niloticus*, particularly in nutrient-rich environments (Worie Assefa, Getahun and Workiyie Worie Assefa 2015), where organic matter accumulation supports microbial biofilms and decomposed macrophytes. This aligns with tilapia's ability to digest fibrous detrital material using gut microbiota, facilitating the assimilation of organic-rich detritus (Moriarty 1973). In the present study, submerged macrophytes were excluded from the model due to isotopic overlap with macrophytic detritus, which might influence dietary proportion estimates. Decomposed macrophytes often retain $\delta^{13}C$ signatures similar to live macrophytes, making them indistinguishable in isotope models (Fry 2006; Post 2002).

According to this study, the filter-feeding species *H. molitrix* and *C. catla* derived the majority of their dietary contributions from plankton 35–100 µm (phytoplankton), followed by plankton >100 µm (zooplankton), positioning them at approximately similar mid-trophic levels of 3.08 and 3.06, respectively, within the reservoir food web. These findings are consistent with previous studies, such as Tumolo and Flinn (2019), which reported a predominant reliance on phytoplankton, followed by zooplankton, in a mainstream reservoir ecosystem. This phytoplankton-dominant filter-feeding behaviour has been confirmed by multiple studies (Spataru and Gophen 1985; Xie and Yang 2000; Huang et al. 2024). Similarly, gut content analyses conducted in large river systems (Williamson and Garvey 2005; Minder et al. 2018) confirmed that *H. molitrix* primarily consumes phytoplankton, with zooplankton as a secondary dietary component. An SI study on a drinking water reservoir by Huang et al. (2024) reported similar findings, indicating that *H. molitrix* primarily feeds on phytoplankton, with zooplankton as a secondary food source, and occupies a mid-trophic level. Other SI analyses (Xie and Yang 2000; Jayasinghe et al. 2015) suggest that the diets of *H. molitrix* may consist of nearly equal proportions of phytoplankton and zooplankton. As concluded by Jayasinghe et al. (2015), the foraging behaviour of this filter feeding Chinese carp is opportunistic and might even go for macrophytic detritus in the bottom at organically polluted environments.

In the studied reservoirs, *C. catla* exhibited a more balanced dietary preference, consuming plankton 35–100 µm (40%) and plankton >100 µm (35.6%), suggesting a broader reliance on both phytoplankton and zooplankton. This pattern is consistent with the diet study conducted by Sangeetha and Susithra (2023) in the Thenpenai River, India. However, the present findings contrast with the previous gut content analyses, which typically classify *C. catla* as a zooplankton feeder (Lalit 2015; Mishra 2020; Surya Prakash 2020). Furthermore, Soni and Ujjania (2018) documented the presence of detritus in the diet of *C. catla*, which aligns with our findings, where detritus emerged as the secondary dietary source.

C. mrigala from 3 reservoirs exhibited a predominant reliance on submerged plants, contributing 55.9% to its diet.

Plankton (35–100 µm) and plankton (>100 µm) were identified as secondary dietary sources, contributing 19.4% and 13.5%, respectively, while detritus accounted for 11.2%. However, Mishra (2020) reported that *C. mrigala* primarily relies on decaying vegetation, which contrasts with our findings. In gut content analyses of the present study, we observed decaying macrophytes in the samples, indicating that submerged plants and their decomposition products form a significant portion of their diet. The predominance of submerged vegetation in the Tabbowa and Weerawila reservoirs may have influenced the dietary composition of *C. mrigala*. Habitat conditions, such as the availability of macrophytes, likely play a key role in shaping the species' feeding behaviour, emphasising the ecological variability of *C. mrigala* across different environments. According to literature, *C. mrigala* is a bottom-dwelling species with an iliophagous feeding habit and a predominantly detritivorous dietary preference (Mishra 2020). However, the present study indicates that *C. mrigala* is having a more flexible feeding strategy than previously documented. It is physiologically equipped to consume submerged plant material due to its anatomical and digestive adaptations. Its subterminal mouth allows it to forage efficiently along the substrate, where it can access fragmented macrophytes and organic detritus as part of its diet. From a digestive perspective, *C. mrigala* possesses a relatively long alimentary canal, a characteristic adaptation among herbivorous and detritivorous fish, enabling efficient digestion of plant material and organic detritus. Furthermore, the species thrives in vegetation-rich, muddy-bottomed environments, where submerged plants are abundant, making them a viable dietary component (Mishra 2020).

These physiological and behavioural traits collectively suggest that *C. mrigala* is well-adapted to utilising submerged macrophytes as a significant food source, contrary to the documented feeding habits.

In its juvenile and adult stages, *L. rohita* functions primarily as a herbivorous column feeder, demonstrating a preference for algae, periphyton and submerged vegetation. However, gut content analysis reveals the presence of decayed organic matter, sand and mud, suggesting incidental bottom-feeding, likely occurring while foraging on periphyton or detritus-associated plant material (Mishra 2020). In this study, *L. rohita* from 3 reservoirs demonstrated a significant reliance on macrophytic detritus (46.5%), with submerged plants as the second most significant dietary source (30.2%), indicating its dependence on macrophyte-derived nutrients either directly or through decomposed detritus. Anatomically, *L. rohita* possesses a nibbling-type mouth with soft, fringed lips and sharp cutting edges, along with an absence of teeth in the buccopharyngeal region, which facilitates the consumption of soft aquatic vegetation without the need for active prey seizure or crushing (Majumder et al. 2018).

The SIMMR model showed a moderate overall fit across the 4 cyprinid species, with a mean proportion outside predictive range of 0.347 (34.7%), indicating that, on average, 34.7% of the observed data fell outside the model's predictions. *C. catla* exhibited the best fit (proportion outside = 0) with consistent dietary patterns, while *L. rohita* showed a reasonable fit (proportion outside = 0.364), reflecting some variability in benthic and plant-based resource use. *H. molitrix* and *C. mrigala* had higher proportions outside predictive range (0.5 and 0.525, respectively), indicating greater dietary variability likely influenced by

habitat-specific factors such as macrophyte abundance and plankton distribution in the reservoirs.

The mean dietary contributions of the 4 dietary sources to the CBF species indicate varying reliance on pelagic and benthic nutrient pathways. The estimated mean dietary proportions show that plankton is the dominant food source, contributing 50.1% to the overall diet, highlighting the importance of pelagic nutrient pathways in sustaining the fish community. Detritus, as the primary benthic source, accounts for 29.4%, emphasising its role in the system's energy flow. Submerged plants contribute 17.2%, acting as an intermediate resource that may support both pelagic and benthic pathways (Teubner et al. 2022). According to the results, macrobenthos plays a minor role, contributing only 3.3% to the overall diet. Similarly, a study on the Lake Liambezi food web found that particulate organic matter was the primary driver of the ecosystem (Peel et al. 2019), highlighting the ecological significance of pelagic nutrient pathways. As filter-feeding cyprinids efficiently utilise planktonic resources, their feeding behaviour plays a crucial role in pelagic energy transfer supporting nutrient cycling and maintaining ecosystem productivity. However, according to Jayasinghe et al. (2015), even the filter feeder like *H. molitrix*, which has heavily specialised gill rakes for filtering smaller particles suspending in the water column, has shown opportunistic feeding on detrital macrophyte particles in an urban reservoir. It can be assumed that any fish or GFP which are highly motile, can shift their feeding strategies depending on the resources available in the vicinity.

The conceptual reservoir food web created in this study gives an emphasis to CBF species and their trophic interactions with other indigenous fish fauna. It confirms the fishers' belief that indigenous top predatory fish like *Channa* spp. and *Anguilla* spp. destroy the potential catch of high-valued GFP. But it disproves the belief that GFP reduces the catch of tilapia and other CBF species. In these man-made environments with a short history compared to the evolutionary time scale, all indigenous species can be considered as aliens as much as the exotic CBF species. While CBF species are stocked into the reservoirs time to time by NAQDA, indigenous species find their way to this lacustrine ecosystem along the ephemeral water ways in the rainy seasons. Since most of the agrarian reservoirs are scattered in the dry zone of Sri Lanka with a similar climatic environment, they can be considered within the same biome or aquatic life zones. In this way, the situation can be generalised to all dry zone reservoirs in Sri Lanka and to similar tropical lacustrine habitats around the world.

Conclusion

This study provides a comprehensive assessment of trophic interactions and food web structure in Sri Lankan reservoir ecosystems, offering valuable insights into the feeding ecology of CBF species, native fish populations, and the recently introduced CBF candidate *M. rosenbergii* (GFP). The application of SI analysis and SIMMR Bayesian mixing models has enhanced our understanding of the dietary niches of key fish species, elucidating their trophic positions, dietary preferences and interspecies interactions. Ultimately, this study underscores the importance of a balanced trophic structure in reservoir fisheries, where both culture-based and indigenous species contribute to ecosystem stability. Understanding the feeding ecology and trophic interactions of these species provides a scientific foundation for sustainable fisheries management,

ensuring the long-term productivity of Sri Lankan reservoirs while maintaining ecological integrity and resource sustainability. Future research should focus on seasonal dietary shifts, prey availability assessments and the impact of environmental changes on trophic interactions to further refine management strategies for CBF in reservoirs.

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