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Journal:	<i>Lakes & Reservoirs: Research and Management</i>
Manuscript ID:	LRE-11-066.R1
Manuscript Type:	Original article
Date Submitted by the Author:	n/a
Complete List of Authors:	Amarasinghe, Upali; University of Kelaniya, Department of Zoology Vijverberg, J.; Netherlands Institute of Ecology (NIOO-KNAW), Department of Aquatic Ecology Weliange, Wasantha; Postgraduate Institute of Archaeology, University of Kelaniya Vos, Matthijs; Institute of Biochemistry and Biology, Department of Ecology and Ecosystem Modeling
Keywords:	fish community, biotic interactions, trophic index, food web statistics, Southeast Asia

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Food web patterns and diversity in tropical fish communities

Upali S. Amarasinghe^{1*}, Jacobus Vijverberg², Wasantha S. Weliange^{1‡} and Matthijs Vos³

¹Department of Zoology, University of Kelaniya, Kelaniya 11600, Sri Lanka

²Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW),
Droevendaalsesteeg 10, 6708 PB Wageningen, The Netherlands

³Department of Ecology and Ecosystem Modeling, University of Potsdam, Institute of
Biochemistry and Biology, Am Neuen Palais 10, D-14469 Potsdam, Germany

*Corresponding author

‡ Present address: Postgraduate Institute of Archaeology, University of Kelaniya, 407,
Buddhaloka Mawatha, Colombo 7, Sri Lanka

ABSTRACT

We compared the food webs of three Sri Lankan reservoirs: Minneriya (ancient and shallow; Udawalawe (young and shallow) and Victoria (young and deep). Species richness of the fish community was highest in Minneriya (30 species), intermediate in Udawalawe (21 species) and lowest in Victoria (18 species). Fish species belonged to 11 families, with Cyprinidae dominating the community both in terms of abundance and species richness. We used the daily amount of food consumed per fish species to distinguish weak from strong trophic interactions in these food webs. The fish community consumption pattern was characterized by a few strong interactions and many weak ones. The number of major consumers (contributing > 5% of the total fish community consumption) in each reservoir was small and similar for the three reservoirs. *Puntius filamentosus*¹ and *Amblypharyngodon melettinus* were the two major consumers in all three food webs. *Puntius chola* was a major consumer in Minneriya and Victoria, but not in Udawalawe, where it was feeding less on detritus than in the other two food webs. In all three reservoirs was the fish community mainly feeding at the bottom of the food web, on algae, macrophytes and detritus, with very little piscivory taking place. Average food web length was measured as the mean trophic index weighted for the consumption rates of the various fish populations which together compose the fish community. In comparison with most other tropical lake/reservoir food webs in Asia and Africa, of which data were available, was the average food web length in the Sri Lankan reservoirs relatively short. Furthermore, traditionally unexploited species, as opposed to species of commercial fisheries interest, *Oreochromis mossambicus* and *O. niloticus*, are major role players in trophic dynamics of reservoir ecosystems. As such, the potential of their exploitations should be considered in the management of reservoir fisheries.

Keywords fish community, biotic interactions, trophic index, food web statistics, Southeast Asia

INTRODUCTION

¹ This species is renamed as *Puntius singhala* (Pethiyagoda and Kottelat, 2005)

Freshwater fish communities are generally considered to be complex, highly structured, and characterized by the presence of many specialized, presumably co-evolved species (Lowe-McConnell 1987). Reservoir fish communities in South and Southeast Asia on the other hand consist predominantly of fish species that were drawn from associated river systems, often augmented with a few introduced lacustrine species for various purposes (Welcomme 2001). Major uses of almost all reservoirs in the tropics are for irrigation and/or hydroelectricity generation which bring about heavy drawdown. The fisheries production is essentially a secondary use of reservoirs, especially in Asia except in a few countries like China and the fisheries are mainly based on a few species of their fish communities (De Silva 1996). Many Sri Lankan reservoir fish communities are dominated by traditionally unexploited fish species (De Silva & Sirisena 1987, 1989; Amarasinghe 1990; Pet *et al.* 1996; Schiemer *et al.* 2008). Before starting a fishery on such unexploited species, the impact of exploiting these species on the trophic dynamics of the community should be understood. Due to the complex species interactions this is however not an easy task. Food web studies are therefore essential as holistic tools for planning reservoir fisheries management.

Investigating food web dynamics is a formidable challenge, especially since the strength of feeding links may be context-dependent. Diets may change as relative resource species change in abundance over the season and as water levels are changing. Patterns in food webs are generally studied in terms of food web statistics such as web connectance, linkage complexity, linkage density and compartmentation (Pimm 1982; Winemiller 1990). Comparison of these patterns in real and theoretical food webs may increase our understanding of the ecological mechanisms that underlie these patterns and the persistence of complex communities in nature.

Even though the reservoir fish communities have not co-evolved for more than a few thousands of years, they are of interest as they provide the opportunity to study how these food webs are organised according to abiotic factors such as reservoir age and depth and to what extent the community may organise itself according to the diversity and identities of the species comprising it. We studied Minneriya (an ancient, > 2000 years, shallow irrigation reservoir), Udawalawe (a young, <50 year, shallow irrigation reservoir), Victoria and (a young, <30 year, deep hydroelectric reservoir) in Sri Lanka. As in almost all major reservoirs of the country, the fisheries of the three reservoirs are dominated by two exotic cichlid species, *Oreochromis mossambicus* and *O. niloticus* (Sricharoendham *et al.* 2008), despite the presence of small-sized

cyprinid species in abundance (Ajith Kumara *et al.* 2009). The objectives of the present study are: (1) to identify the food web structure of the three reservoir food webs; (2) to ascertain if food web structure is predominantly affected by reservoir age, size, morphometry or hydrological regime, (3) to ascertain in which respects Sri Lankan reservoir food webs differ from other lake/reservoir food webs in the tropical region and (4) to determine whether exploitation of traditionally unexploited fishery resources in Sri Lankan reservoirs is ecologically justifiable.

MATERIALS AND METHODS

Study area

The present analysis is based on the studies of food and feeding habits of fish species in three Sri Lankan reservoirs, viz. Minneriya (8°02' N; 80°53' E), Udawalawe (6°27' N; 80°50' E) and Victoria (7°13' N; 80°47' E). Locations of the three reservoirs in Sri Lanka are shown in Figure 1. Minneriya and Udawalawe are located in the dry zone, Victoria in the wet zone of the island. Some morphometric and physico-chemical characteristics of the three reservoirs are given in Table 1. Minneriya is an ancient reservoir, whereas the other two are relatively young. Two reservoirs are eutrophic and one (Udawalawe) shows a seasonal shift from mesotrophic to eutrophic (Silva & Schiemer 2008). Minneriya and Udawalawe are irrigation reservoirs whereas Victoria is exclusively a hydroelectric reservoir. Minneriya and Udawalawe reservoirs, which are located in the lowland region of the country, are shallow whereas Victoria reservoir, being located in the central massif at a higher altitude, is relative deep. In Minneriya and Udawalawe reservoirs, water level fluctuations are mainly influenced by the release of water for irrigation. The hydrological regimes in these two irrigation reservoirs are characterized by high water levels from December to April due to inter-monsoonal rains from November to January when the water is not released for irrigation and low water level from June to October resulting from water release for irrigation of agricultural lands. In Victoria reservoir, there are drastic fluctuations in water level due to hydroelectricity generation. Natural processes such as evaporation and seepage also contribute to water level fluctuations in the reservoirs.

The changes in reservoir volumes with decreasing water level are markedly different among the reservoirs and are dependent on their depth and bathymetric shape. For example, in Minneriya reservoir almost half of the reservoir area dries up when the water level recedes by 7.25 m. This is similar in Udawalawe reservoir, when the water level drops by 8.25 m, the

reservoir area has been reduced to half its size. However, in Victoria reservoir, water level has to decrease by 72.0 m to reduce the reservoir area to half its size.

Field work

In the three reservoirs, we studied in the period January 1999 to March 2000 a complete hydrological cycle i.e., from high water level via lowest water level to high water level. Since local weather conditions were slightly different and the function of Victoria (hydro power) differed from the other two (irrigation), the study periods for the three reservoirs were also slightly different. Fish were sampled approximately once every two months, which resulted in 6 (Minneriya) or 5 (Udawalawe, Victoria) sampling dates. On each sampling date, fishes were sampled from morning until late dusk using beach seines (1, 5, and 7 mm mesh size) and multi-mesh, mono-filament gillnets (12.5, 16, 20, 25, 33, 37, 50, 60, 76, 90 mm stretched mesh size). Gillnets were exposed maximum of 30 minutes in order to prevent deterioration of the ingested food items during sampling, and fish samples were preserved in 10% buffered formalin immediately after capture. Before preservation, each fish was laterally dissected near the body cavity to facilitate penetration of the preservative. Fish samples were taken to laboratory for further analysis.

Preserved specimens were dissected and all food contained in the stomach or anterior part of the gut was removed and placed into a beaker with water to create a suspension of known volume. Stomach contents were extracted by dissecting individual fish. As cyprinids do not have stomachs, contents first one-third of the intestine were considered as ingested food items. Empty stomachs or stomachs with almost fully digested contents were eliminated. Sub-samples (1 ml) of the suspension were examined under a light microscope using a Sedgwick Rafter cell for quantitative determination of stomach/gut contents. Relative volumes of each food item were determined using arbitrary size such as a *Pinnularia* cell as the standard, and expressed as percentage of the total food items in the gut contents (Hynes 1950; Weliange & Amarasinghe 2003). Relative volumes of 96 food items were regrouped into 18 food categories of broader taxonomic groups, which were thought to represent food of fish with specific trophic categories (Table 2). Terrestrial spiders, belonging to the category ‘Adult insects and terrestrial spiders’ (AIN) were very rare, and therefore, this category was mainly represented by small adult insects (predominantly chironomids), which after swarming, were floating on the water surface.

Unidentified fish in the fish gut contents were assigned to prey fish species according to their relative abundance in the reservoir over the study period. Analysis of stomach/gut contents of fish was done for pre-determined 3-cm size classes separately. Fishes < 3 cm were assigned as size class 1, 3-6 cm as size class 2, 6-9 cm as size class 3 and so-on.

Food consumption

Amount of food consumed per fish species were determined as follows. Firstly, the gillnet catch per unit effort (CPUE) and expressed as numbers per 100 m² per hour (Table 3) was used as the relative abundance of each species. Secondly, for each size class of each fish species, relative abundance was determined from CPUE values and relative importance of each size class as estimated from the length frequency distributions of fish caught in gillnets and beach seines over the study period. Thirdly, daily ration of fish species (see Table 4 for references) were used to estimate amount of food consumed by abundant fish species of different size classes. For those species that daily ration values were not available, daily ration values were approximated on basis of data from other tropical freshwater species of similar size and food habits. Finally, based on the total amount of food consumed, percentage amount consumed by each species was determined and the total amount consumed by each species per reservoir was calculated. Some species however, were not caught in sufficient numbers and were disregarded in the analysis.

Trophic index and trophic classes

Food items of fish species in the three reservoirs were classified into trophic levels (T, Winemiller 1990). According to this classification, plant material (primary producers) were coded as T = 0.0, herbivores as T = 1.0, a consumer eating approximately half plant material and half herbivore tissue (e.g., crustaceans) as T = 1.5 and so on (see Table 2). The trophic indices (T_i) of fish species in the three water bodies studied were estimated using the following equation.

$$T_i = 1.0 + \sum_{j=1}^n T_j(P_{ij}) \quad (1)$$

where T_j is the trophic level of prey species j and P_{ij} is the fraction of food (proportion by volume) consumed by species i consisting of prey species j (Winemiller 1990). The use of this measure implies that ecological pyramids are more accurately represented by a trophic continuum rather than by consumers at discrete levels (e.g., Cousins 1987). The T_i values were

computed sequentially from bottom of the food web to the top. Unidentified food items were omitted from the trophic classification. Since they represented very small volumetric proportions of the gut contents, it was assumed that this had no effect on the final results. The T_i values ranged from 1 for exclusively herbivorous species to 3 for a top carnivore. T_i values of non-piscivorous fishes were first determined and then mean values of these estimated T_i values of prey fishes were used as trophic classes to estimate T_i values of piscivorous fishes.

In the literature trophic level is often defined differently, especially by researchers using the ECOPATH model (Pauly & Palameres 2006):

$$TROPH_i = 1 + \sum_{j=1}^G DC_{ij} * TROPH_j \tag{2}$$

where $TROPH_j$ is the fractional trophic level of prey (j), DC_{ij} represents the fraction of j in the diet of i and G is the total number of prey species. Here, in contrast to equation (1) of our study in which trophic class of plant matter was assigned as zero, DC_{ij} of plant matter (primary producers) is considered as 1. In order to make T_i of equation (1) comparable with the $TROPH_i$, the following conversion was used.

$$T_i = TROPH_i - 1 \tag{3}$$

Based on the proportion of plant material ($T = 0$) in the diet, T_i scores were used to assign fish species to five trophic classes (TC) as follows:

- TC 1 = >50% plant material consumed (T_i score = 1.00 -1.74)
- TC 2 = 25-50% plant material consumed (T_i score = 1.75-2.19)
- TC 3 = <25% plant material consumed (T_i score = 2.20-2.74)
- TC 4 = mostly animal prey (T_i score = 2.75-2.99)
- TC 5 = consuming non-herbivorous fish (T_i score = >3.00).

Food web diagrams

Based on the amount of food consumed as estimated from daily ration and CPUE of different species, percentage amount of food consumed by each species was determined. Species which consumed over 5% of the total amount of food were considered as major consumers, food categories that formed over 1% of the total consumed food items in the total fish diet were considered major food items. Food categories and major consumer categories were then plotted to construct a two-dimensional food web diagram for the study period. Proportion of each prey

item consumed by fish species and the trophic position (T_i) of each prey were the basic information used in constructing the food web figures. The vertical position of the species along the y-axis of T_i is ecologically important, but the horizontal position of the fish and its prey species along the x-axis was chosen arbitrarily and was not quantified. We have chosen to position algae on the left, macrophytes in the middle and detritus on the right and each fish species was placed in a central position above the distribution of its main prey (Winemiller 1990).

In the food web diagrams, all fish nodes were plotted against T_i values on a two-dimensional plane. On basis of the consumption rates of the fish populations three classes of consumers were distinguished: minor consumers = fish species consuming < 1%, intermediate consumer = fish species consuming 1-5% and major consumers = fish species consuming >5% of the total amount of food consumed by the fish community. To keep the food web simple only the interaction between major consumer species and major food categories were indicated. The strength of the interaction is indicated by the width of the line. Five line widths from thin to thick indicate 1-15% food, 15-20% food, 20-25% food, 25-30% food and > 30% total food consumed.

The consumption rates in the food web per trophic class, but irrespective of consumer species and food categories, were arranged in the form of food pyramid, to illustrate in comparative terms, number of species responsible for individual trophic classes in the food web. As fish were assigned to trophic classes on the basis of the proportion of plant material in the diets, the class intervals were bound to be unequal.

RESULTS

Fish community

The species richness of the fish communities was highest in Minneriya (30 species), lowest in Victoria (18 species) and intermediate in Udawalawe (21 species). Fish species belonged to 12 different families, but Cyprinidae dominated both in number of species and as major consumers in the communities (Table 3; Fig. 2). In contrast, the number of major consumers (feeding > 5% of the total consumption of the fish community) in each reservoir was relatively small (3-4 spp.) and similar for the three reservoirs (Fig. 2). The number of intermediate consumers (feeding > 1%, but < 5% of the total consumption of the fish community) was also small relative to the total

number of species present (3-5 spp. per reservoir). The majority of fish species (9-19 spp.) were minor consumers (feeding < 1% of the total consumption of the fish community).

The three reservoirs had more or less similar species flocks, but in terms of species composition, the Minneriya fish community was more similar to that in Udawalawe, than to that in Victoria (Fig. 2). The major consumer species in the three reservoir communities were also similar. *Puntius filamentosus* was the most important and *Amblypharyngodon melettinus* the second most important consumer species in all three reservoirs (Fig. 2). *Puntius chola* was the third most important consumer in Minneriya and Victoria, and of intermediate importance in Udawalawe. *Puntius dorsalis* as consumer was of third importance in Udawalawe and of intermediate importance in the two other two reservoirs. There are only two clear differences. *Tilapia rendalli* in Minneriya, and *Labeo dussumieri* in Udawalawe belonged to the major consumers, but in Victoria reservoir *T. rendalli* belonged to the minor consumers and *L. dussumieri* was not present.

Food Web structure

In Fig. 3, we present the mean food web diagrams over the study period. Interactions between major consumers and major food items are shown and their trophic position (T_i) indicated. Minor consumer and intermediate consumers are indicated but without their interaction with food items. For each major consumer node, the amount of food consumed is indicated by the width of the line, the thicker the line the more food consumed. If we omit the interactions of the minor and intermediate consumers with their resources, all three food webs are rather simple, with a limited number of consumer nodes and a small number of quantitatively important consumer-resource interactions.

The Minneriya food web is characterised by four fish species, *A. melettinus*, *T. rendalli*, *P. filamentosus*, *P. chola*, 3 basic food categories ($T_i = 0$) and 3 food categories belonging to the secondary producers ($1 \leq T_i \leq 1.5$). The main basic food categories are: non-filamentous blue-green algae, macrophytes and detritus, whereas the secondary producers are represented by cladocerans, copepods and adult insects. There are 3 strong, 2 intermediate and 7 weak consumer-resource interactions. All strong consumer-resource interactions are low in the food web with basic food categories: *A. melettinus* and *P. chola* with detritus and *P. filamentosus* with macrophytes.

The characteristics of the food web in Udawalawe reservoir are the importance of three fish species, *A. melettinus*, *P. dorsalis* and *P. filamentosus*, 3 basic food categories and 5 food categories belonging to the secondary producers. The main basic food categories are: non-filamentous green algae, macrophytes and detritus, whereas the secondary producers are represented by molluscs, cladocerans, insect larvae and adult insects. There are 2 strong, 3 intermediate and 8 weak consumer-resource interactions. All strong consumer-resource interactions are low in the food web with basic food categories: *A. melettinus* with detritus and *P. filamentosus* with macrophytes. This food web in Udawalawe is very similar to that of Minneriya, the main difference is that in Minneriya the consumer role of *P. chola* is more important than in Udawalawe.

The food web of Victoria reservoir is characterised by three fish species, *A. melettinus*, *P. filamentosus* and *P. chola*, 4 basic food categories and 4 food categories belonging to the secondary producers. The main basic food categories are: non-filamentous blue-green algae, non-filamentous green algae, macrophytes and detritus, whereas the secondary producers are represented by molluscs, cladocerans, insect larvae, copepods and adult insects. There are 2 strong, 2 intermediate and 6 weak consumer-resource interactions. All strong consumer-resource interactions are low in the food web with basic food categories: *A. melettinus* with detritus and *P. filamentosus* with macrophytes. This food web is very similar to that of Minneriya and Victoria, the main difference is that in Victoria the consumer interaction of *P. chola* with detritus is less important than in Minneriya, but more important than in Udawalawe.

In Figure 4, we show the consumption rates in the food web per trophic class, but irrespective of consumer species and food categories. There were two clear differences. Firstly, Minneriya was the only food web with measurable consumption in trophic index (T_i) class 2.75 – 2.99, in the other two food webs measurable consumption stopped at $T_i \geq 2.75$. This means that the food chain length is highest in Minneriya. Secondly, the shape of the pyramid of Udawalawe differed substantially from those of Minneriya and Victoria. In Udawalawe the consumption on the lowest trophic level (T_i : 1.00 - 1.74) was much less, whereas consumption on the second trophic level (T_i : 1.75 – 2.19) was much higher than in the Minneriya and Victoria food webs. When the number of species that contributed to each of the trophic levels is compared, in all three reservoirs, lowest trophic level was formed by the highest number of species. Interestingly in Minneriya, the second trophic level, which is much narrower than in Udawalawe in terms of

percentage food consumed, was formed by 10 species whereas 3 species consumed a significant proportion of food in the second trophic level in Udawalawe.

In all three reservoirs, at least three major consumers were unexploited cyprinid species, indicating that unexploited species in the reservoir fish communities have a significant contribution to trophic interactions.

DISCUSSION

Fish community

The fish communities in the three reservoirs studied were similar. The food web in ancient Minneriya reservoir contained more fish species than the other two food webs, but the number of major fish species (3-4) was similar and the quantitatively most important two species, *P. filamentosus* and *A. melettinus*, were the same in all three reservoirs. We did not find any affect of reservoir age or altitude/water depth on the structure of fish communities. Reservoir fish communities are essentially drawn from associated rivers (Yap 1999) and as such, the differences in species richness in the three reservoirs might be due to the differences in species flocks in associated riverine habitats. The complexity of trophic interactions is *inter alia* governed by the structure of fish communities (Winemiller 1990).

Food web structure: differences among 3 Sri Lankan reservoirs

If the interactions of minor intermediate consumer species are ignored, all three food webs are simple and very similar. All strong consumer-resource interactions are low in the food web, and the fishes mainly feed on detritus, algae and macrophytes. There are only minor differences among the reservoir food webs. The most important difference is the consumer role of *P. chola* which mainly feeds on detritus and to a lesser extent also on macrophytes. Although *P. chola* is present in all three reservoirs, its interaction with detritus is weak in Udawalawe, intermediate in Victora and strong in Minneriya reservoir. It is known that detrital materials in fish diets are associated with bio-films (Burns & Walker 2000; Burns & Ryder 2001) and strong interaction of some constituent species with detritus, making them a prominent component in the food webs is explainable.

Food web structure: differences between Sri Lankan reservoirs and other tropical lakes/reservoirs

We compared the mean trophic indices of different lakes/reservoir food webs with those of the three food webs in the present study (Table 5). In total we compared 13 food webs; 4 in Sri Lanka, 2 in other Asian countries, and 7 in Africa (Table 5). Average food web length ranged between 1.1 in the Parakrama Samudra reservoir in Sri Lanka (PS, Fig. 5) and 2.54 in Lake Malawi in Africa (MA, Fig. 5). All four food webs in Sri Lanka have relatively short food chain lengths. Interestingly, the food web of Veli Lake (VE) in South India falls within the same range of food chain lengths as observed for the Sri Lankan reservoirs. This South Indian Lake is located in the same geographical region as Sri Lanka, approximately 100 km far from the island's most northern tip. The second Asian reservoir in NE Thailand, Ubolratana reservoir (UBR), has a longer food chain length than the Sri Lankan and South Indian food webs, most probably because it is part of a different geographical region with a different fish species composition. Nguyen & De Silva (2006) have reported that regional differences in fish biodiversity in Asia were related to habitat size. With the exception of Lake Chad (CHA), all African food webs are clearly longer than the Sri Lankan food webs (Fig. 5). Therefore, we conclude that the food webs in Sri Lankan reservoirs are relatively short as compared to most webs in other tropical regions with the possible exception of South India where they probably have a similar length.

Role of traditionally unexploited species in food web dynamics

In terms of amount of food resources consumed, the two species of commercial importance, *O. mossambicus* and *O. niloticus* rank much lower than the small cyprinid species such as *A. melettinus*, *P. chola* and *P. filamentosus* (Fig. 2), which are not traditionally exploited in Sri Lankan reservoir fisheries. They essentially occupy lower trophic levels (Figs 3 and 4). Despite their small body size, compared to commercially exploited cichlid species (Table 4), these traditionally unexploited species play a significant role in the trophic dynamics in reservoirs. This evidence strongly suggests that present means of exploitation of fishery resources in Sri Lankan reservoirs targeting only exotic cichlid species, largely leads to incomplete exploitation of prevailing fishery resources. Pet *et al.* (1996, 1999) and Piet & Vijverberg (1998) have also indicated that in Tissa wewa, another Sri Lankan reservoir, indigenous small-sized cyprinid

species should be exploited to ensure more complete utilization of the fishery resources. Fernando & Holčík (1982, 1991) have shown, based on the data of commercial fisheries, that African cichlid species were able to colonize lacustrine habitats in tropical lakes and reservoirs. De Silva (1983, 1988) and Piet *et al.* (1999) however, have shown that although indigenous cyprinid species require riverine habitats for spawning, they exploit as the African cichlid species, the lacustrine habitats of reservoirs as feeding grounds. As shown in the present analysis, these species play a major role in trophic dynamics by consuming a significant amount of food items, which are also shared by the commercially important exotic cichlid species. As such, any strategy for lowering the population sizes of these unexploited species, through fishing seems to be a suitable management option. Amarasinghe *et al.* (2002) have shown that as these species are of high turnover rates, they can withstand high levels of exploitation. Present study therefore, further provides an insight into viewing the importance of reservoir fisheries management from the entire fish community which plays a major role in trophic dynamics in the reservoir ecosystems, rather than treating only part of the fish community that is exploited by reservoir fishers. The approach that Fernando & Holčík (1991) have adopted to highlight their opinion that higher fish yields are achieved from reservoirs when there are lacustrine and/or lacustrine-adapted fish species are found in fish communities, has been based on the exploited component of the fish assemblage. This opinion has unfortunately institutionalized, but present analysis indicates that unexploited species in the reservoir fish communities also play a major role in trophic dynamics.

ACKNOWLEDGEMENTS

This study was part of the FISHSTRAT project which was supported by contract no. ERB 3514 PL 961695 of the European Commission's INCO-DC Programme. The Schure-Beijerinck-Popping Fund of the KNAW supported the sabbatical stay of the first author (USA) during the period of data analysis and writing up of major part of this manuscript. The first author was also supported travelling in the region by a regional project on reservoir fisheries management in Asia, funded by Icelandic Agency for International Development Administration (ICEIDA), administered by Network of Aquaculture Centres in Asia-Pacific (NACA), Bangkok, which enabled him to make thought-provoking discussions the reservoir fisheries scientists in the

region. The authors thank P.A.D. Ajith Kumara, C. Nissanka and R.P.P.K. Jayasinghe for helping with the field work.

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Table 1. Morphometrical and hydrological characteristics of the three reservoirs (Silva et al. 2008). Altitude (m amsl) = metres above mean sea level; MCM = million cubic metres. Mean depth = volume at full supply level divided by area at full supply level. Dead storage = Non-drainable volume or water below the sill of the sluice. a = Silva & Schiemer (2008)

Parameter	Minneriya	Udawalawe	Victoria
Year of impoundment	276 (restored in 1903)	1969	1988
Productivity ^a	Eutrophic	Mesotrophic - Eutrophic	Eutrophic
Function	Irrigation	Irrigation	Hydropower
River basin	Mahaweli	Walawe	Mahaweli
Altitude (m amsl)	95	88.4	438
Catchment (km ²)	249	1164	1891
Area at full supply level (ha)	2860	3408	2430
Mean depth (m)	6.0	7.9	30.3
Volume at full supply level (MCM)	135	268	783
Dead storage (MCM)	3.2	26.26	34
Shoreline (km)	60.4	53.0	261.0

Table 2. Approximate trophic classes of the various food categories observed in the fish diets and used to estimate the trophic indices of fish species in the three reservoirs.

Abbreviation	Food category	Trophic class
AIN	Adult insects and terrestrial spiders	1.5
BG	Non-filamentous blue-green algae	0
CD	Cladocerans	1
CP	Copepods	1.5
CR	Shrimps (caridians, decapod crustaceans)	1
DE	Detritus	0
DF	Dinoflagellates	1
DT	Diatoms	0
FA	Filamentous algae	0
FWS	Freshwater sponges	1
GA	Non-filamentous green algae	0
IL	Insect larvae-littoral & benthic	1.5
MB	Microbenthic invertebrates	1
ML	Molluscs (bivalves, gastropods)	1
MP	Macrophytes	0
OA	Other algal groups	0
RT	Rotifers	1
WM	Worms (nematods, annelids, oligochaetes)	1

Table 3. Mean catch per unit effort (Nos 100 m⁻² hr⁻¹) in experimental gillnet fishing carried out from January 1999 to January 2001 (Sources: Silva *et al.* 2008; Ajith Kumara *et al.* 2009; Amarasinghe & Ajith Kumara, unpublished data). Only species caught in sufficient numbers were used to estimate amount of food consumed.

Family/species	Minneriya	Udawalawe	Victoria
Cyprinidae			
<i>Amblypharyngodon melettinus</i>	88.961	37.325	38.570
<i>Catla catla</i>		0.013	
<i>Chela laubuca</i>	0.396		
<i>Danio malabaricus</i>	0.043		2.719
<i>Esomus danrica</i>	0.071	0.048	0.384
<i>Garra ceylonensis</i>	0.120		
<i>Labeo dussumieri</i>	0.012	0.098	
<i>L. rohita</i>		0.060	
<i>Puntius bimaculatus</i>	0.107		
<i>P. chola</i>	19.948	1.356	14.607
<i>P. dorsalis</i>	0.561	0.926	0.452
<i>P. filamentosus</i>	8.942	7.260	15.325
<i>P. sarana</i>	0.010	0.003	
<i>P. ticto</i>	0.043		
<i>P. vittatus</i>	1.300		
<i>Rasbora daniconius</i>	8.067	2.240	0.061
<i>Tor khudree</i>			0.003
Bagridae			
<i>Mystus kelatius</i>	0.002	0.002	
<i>M. vittatus</i>	1.665	0.084	0.515
Cichlidae			
<i>Etroplus maculatus</i>	0.406		0.018
<i>E. suratensis</i>	0.048	0.255	0.002
<i>Oreochromis mossmbicus</i>	0.252	0.037	0.381
<i>O. niloticus</i>	0.359	0.085	0.074
<i>Tilapia rendalli</i>	1.407	0.004	0.023
Gobiidae			
<i>Glossogobius giuris</i>	0.335	0.273	0.128
Hemirhamphidae			
<i>Hyporhamphus limbatus</i>	0.947	0.625	
Anabantidae			
<i>Anabas testudineus</i>	0.088		
Siluridae			
<i>Ompok bimaculatus</i>	0.033	0.022	0.012

Mastacembelidae			
<i>Mastacembelus armatus</i>	0.052	0.001	0.001
Ophicephalidae			
<i>Ophicephalus striatus</i>	0.002		
Osphronemidae			
<i>Trichogaster pectoralis</i>	0.014		
Heteropneustidae			
<i>Heteropneustes fossilis</i>	0.208	0.014	0.045
Cobitidae			
<i>Lepidocephalus thermalis</i>	0.012		
Number of species	30	21	18

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Table 4. The fish species of the three reservoirs, their abbreviations, family, maximum length (TL, cm), and references for the daily ration used for the calculation of consumption per fish species per reservoir. Abbreviations used: M = Minneriya, U = Udawalawe, V = Victoria. References are: a = De Silva et al., 1996; b = Weliange *et al.* 2006; c = Weliange & Amarasinghe, unpublished; * = approximations on the basis of freshwater species from the tropical region of similar size and food habits (source: Froese & Pauly 2011).

Species	Abbreviation	Family	Present in Reservoir	Total Length Max (cm)	Daily ration References
<i>Amblypharyngodon melettinus</i>	AM	Cyprinidae	M, U, V	10.6	a, b
<i>Anabas testudineus</i>	AT	Anabantidae	M	17.0	*
<i>Catla catla</i>	CC	Cyprinidae	U	30.0	c
<i>Chela laubuca</i>	CL	Cyprinidae	M	8.6	*
<i>Danio malabaricus</i>	DM	Cyprinidae	M, V	10.2	b
<i>Esomus danrica</i>	ED	Cyprinidae	M, U, V	12.0	*
<i>Etroplus maculatus</i>	EM	Cichlidae	M	12.1	c
<i>E. suratensis</i>	ES	Cichlidae	M, U, V	19.8	b
<i>Garra ceylonensis</i>	GC	Cyprinidae	M	12.0	*
<i>Glossogobius giuris</i>	GG	Gobiidae	M, U, V	22.1	c
<i>Heteropneustes fossilis</i>	HF	Heteropneustidae	M, U, V	29.0	*
<i>Hyporhamphus limbatus</i>	HL	Hemiramphidae	M, U	13.2	c
<i>Labeo dussumieri</i>	LD	Cichlidae	U	30.0	c
<i>L. rohita</i>	LR	Cichlidae	U	30.0	b
<i>Lepidocephalus thermalis</i>	LT	Cobitidae	M	6.4	*
<i>Mastacembelus armatus</i>	MA	Mastacembelidae	M	36.0	*
<i>Mystus keletius</i>	MK	Bagridae	M, U	27.0	*
<i>M. vittatus</i>	MV	Bagridae	M, U, V	15.0	*
<i>Ompok bimaculatus</i>	OB	Siluridae	M, U, V	30.0	*
<i>Oreochromis mossambicus</i>	OM	Cichlidae	M, U, V	18.4	*
<i>O. niloticus</i>	ON	Cichlidae	M, U, V	16.0	b
<i>Puntius bimaculatus</i>	PB	Cyprinidae	M	6.6	*
<i>P. chola</i>	PC	Cyprinidae	M, U, V	15.0	a, b
<i>P. dorsalis</i>	PD	Cyprinidae	M, U, V	23.1	a
<i>P. filamentosus</i>	PF	Cyprinidae	M, U, V	18.0	a, b
<i>P. sarana</i>	PS	Cyprinidae	M, U	21.0	*
<i>P. ticto</i>	PT	Cyprinidae	M	9.0	*
<i>Rasbora daniconius</i>	RD	Cyprinidae	M, U, V	12.9	a, b
<i>Tilapia rendalli</i>	TR	Cichlidae	M, U, V	18.0	b, *

Table 5. Weighted mean trophic indices (Mean T_i) of food webs in tropical lakes and reservoirs according to information from the literature and the present study. Lake abbreviations refer to Figure 5. For each fish species we converted the $TROPH_i$ given in the literature to T_i values using equation 3 and weighted them by their relative consumption per species (proportion of i^{th} species consumption to total fish consumption) to calculate the mean T_i for the fish community. In the literature, consumption (Q) was given as Q/B, the ratio of food consumption to biomass, consumption (Q) was defined as total production divided by the gross growth efficiency. To calculate Q we multiplied Q/B by the biomass (B) both given in the cited papers. For the present study we used the percentage amount consumed per fish species per reservoir given in Fig. 2.

Lake/Reservoir (Abbreviation)	Country	Mean T_i	Authority
Parakrama Samudra Res. (PS)	Sri Lanka	1.11	Moreau <i>et al.</i> (2001)
Minneriya Res. (MIN)	Sri Lanka	1.34	Present study
Victoria Res. (VIC)	Sri Lanka	1.35	Present study
L. Veli (VE)	India	1.45	Aravindan (1993)
Udawalawe Res. (UDA)	Sri Lanka	1.49	Present study
L. Chad (CHA)	Chad	1.53	Palomares <i>et al.</i> (1993)
Ubolratana Res. (UBR)	Thailand	1.62	Villanueva <i>et al.</i> (2008)
L. Victoria (1985-1986) (LV1)	Kenya	1.63	Moreau <i>et al.</i> (1993a)
L. Victoria (1971-1972) (LV2)	Kenya	1.77	Moreau <i>et al.</i> (1993a)
Kariba Res. (KAR)	Zimbabwe	1.80	Machena <i>et al.</i> (1993)
L. Turkana (TUR)	Kenya	2.02	Kolding (1993)
L. Tanganyika (TAN)	Burundi	2.10	Moreau <i>et al.</i> , 1993b.
L. Malawi (MA)	Malawi	2.54	Degnbol (1993)

List of Figures

Fig. 1 Map of Sri Lanka showing locations of the three study reservoirs Minneriya (M), Udawalawe (U) and Victoria (V), and the shape and size of the reservoirs. Abbreviations used: DRY = Dry Zone, WET = Wet Zone.

Fig. 2 Percentage amount of food consumed per fish species (i.e., percentage of the total amount consumed by the fish community) in each of the three reservoirs over the study period. For abbreviations of species names see Table 4. In each reservoir, species were ranked according to the percentage amount of consumption. The fish consumers that ate over 5% of the total amount of food were considered as major consumers, the others intermediate (1-5%) or minor consumers (< 1%).

Fig. 3 Mean food web diagrams of each of the three reservoirs over the study period. Interactions between major fish consumers (open spheres) and major food items (closed spheres). The food items that formed over 1% of the total consumed food items were considered major food items. Three bubble sizes (○, small, medium, large) represent fish species consuming < 1% (minor consumer), 1-5% (intermediate consumer) and >5% (major consumer), respectively, of the total amount of food consumed. For each major consumer node, the amount of food consumed is indicated by the width of the line. Five line widths from thin to thick indicate 1-15% food, 15-20% food, 20-25% food, 25-30% food and > 30% total food consumed. For abbreviations of major fish consumers see Table 4 and for abbreviations of prey categories see Table 2.

Fig. 4 Mean pyramids of percentage of food consumed by the whole fish community at different trophic levels over the study period: **(a)** Minneriya, **(b)** Udawalawe and **(c)** Victoria reservoir. Number of species per trophic level is given on the right-hand side of each pyramid.

Fig. 5 Weighted mean trophic indices (Mean T_i) of food webs in tropical lakes and reservoirs in Sri Lanka (SL reservoirs), the rest of SE Asia and Africa according to information from the literature and the present study. The lakes are arranged in order of increasing T_i . For calculations, identification of lakes/reservoirs, location and authorities see Table 5. Abbreviations used: CHA = L. Chad, KAR = L. Kariba, LV1 = L. Victoria 1985-1986, LV2 = L. Victoria 1971-1972, MA = L. Malawi, MIN = Minneriya Res., PS = Parakrama Samudra Res., TAN = L. Tanganyika, TUR = L. Turkana, UBR = Ubolratana Res., UDA = Udawalawe Res., VE = L. Veli and VIC = Victoria Res.

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