

Availability of animal food organisms and their utilization by cyprinids in Sri Lankan hill-stream pools

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Abstract The food and feeding of cyprinid fishes in three stream pools in South West Sri Lanka, was investigated from 29 June 1984 to 25 February 1986. S.W. Sri Lanka was chosen as a study site because the rainforest and its fish fauna are here severely threatened. Feeding ecology was studied by gut contents analysis. The availability of prey organisms in the environment was quantified and food utilization in each pool was estimated by comparing diet compositions of the fish species with the food availability. Seven cyprinid species represented more than 98% of the fish numbers caught. These were *Pethia cumingii* (PC), *Puntius dorsalis* (PD), *Dawkinsia singhala* (DS), *Pethia nigrofasciata* (PN), *Systemus pleurotaenia* (SP), *Devario malabaricus* (DM) and *Rasbora daniconius* (RD). Three of these species: the two surface feeders DM and RD and the generalist SP fed > 33 % (biovolume) on terrestrial arthropods. Since we were not able to quantify the availability of terrestrial arthropods - mainly ants falling from the trees into the stream - these three species were not included in part of the analysis. Chironomid larvae were most abundant and, on basis of biovolume, the most important animal food items of the remaining four cyprinid species (PC, PD, DS, PN). PD and PN strongly positively selected chironomid larvae, but DS and PC only weakly negatively. Although coleopterans and ephemeropterans were after chironomid larvae the most abundant food items in the environment the former were often negatively selected and ephemeropterans positively, so that the latter were generally after chironomid larvae the most frequently eaten food items.

Key words: fish community, stream fishes, fish feeding, small barbs, Sri Lanka, South East Asia

INTRODUCTION

In Sri Lanka most studies on stream fishes were carried out in the wet zone, in the South West part of the country. Most earlier studies focused on food, feeding habits, morphological features and reproduction (De Silva and Kortmulder 1977; Kortmulder et al. 1978; De Silva et al. 1977, 1980, 1985); later studies focused on niche segregation and the possible effect of competition as steering factor (Moyle and Senanayake 1984; Schut et al. 1984; Wikramanayake and Moyle 1989; Wikramanayake 1990; Vijverberg et al. 2017). In none of these studies, except Vijverberg et al. (2017), the availability of prey organisms in the environment was taken into account. The latter study focused on substrate selection, whereas in the present study we consider

whole habitats (i.e. the stream pools) and compare for the whole habitat food availability with food utilization.

Underwater observations on the feeding behaviour of cyprinid fish assemblages in stream pools of South West Sri Lanka (Vijverberg et al. 2017) showed that they were feeding on five different strata: at the bottom, close near the bottom, water column, high in the water column and at the surface. The fish assemblages could be divided into three guilds: (1) two surface feeders (*Devario malabaricus*, *Rasbora daniconius*), (2) one generalist *Systemus pleurotaenia* which fed on all five strata, and (3) four bottom feeders: *Dawkinsia singhala* (DS), *Pethia cumingii* (PC), *Pethia nigrofasciata* (PN) and *Puntius dorsalis* (PD) (Vijverberg et al. 2017). Underwater observations on the feeding behaviour showed that PC, PD, PN were exclusively feeding at or



close to the bottom and that DS was feeding for more than 20% in the middle of the water column and therefore was less benthivorous than the former three species (Vijverberg et al. 2017).

Study Area

South West Sri Lanka was chosen as a study site because the rainforest and its fish fauna are disappearing rapidly (Senanayake and Moyle 1981). Tropical forest is confined to the south-western third of the island where mountains (maximum elevation 2938 m) intercept the prevailing winds, resulting in 200-400 cm of rainfall per year. The study area (Fig. 1) is

situated in the wet zone of South West Sri Lanka close to the town of Udugama. This region is characterized by much rain fall during most months of the year. Lowest rainfall was observed in August, the highest in March and November (Vijverberg et al. 2017). Three river pools (surface area: 442-916 m², up to 2.0 m deep) in hill streams were studied (numbered A, B, C). Pool A was located in the Kondagala Ela, pools B and C in the Nannikita Ela. Both streams belong to the Gin Ganga basin. The study was conducted from 29 June 1984 to 25 February 1986. Pool A was sampled 13 times, pool B 14 times and pool C 10 times. A sampling trip took usually 2-4 days.

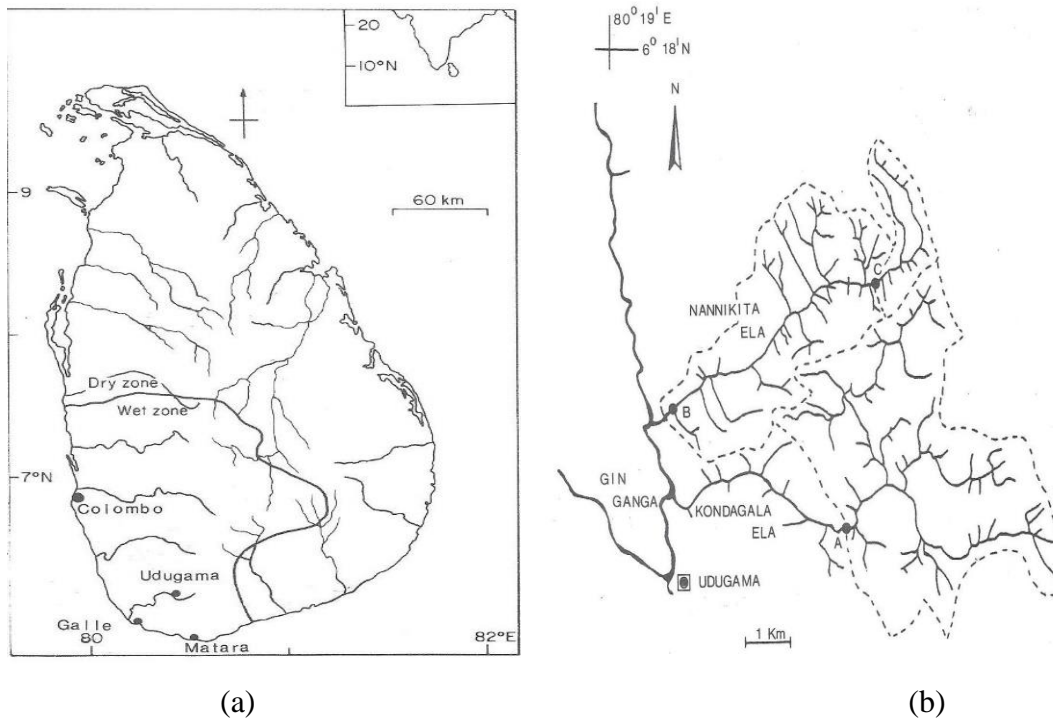


Fig 1 (a) Sri Lanka showing the position of the study site near Udugama with the Gin Ganga River. (b) Study area showing the pool A in the Kondagala Ela (K), and pools B and C in the Nannikita Ela (N), both tributaries of the Gin Ganga River. Broken lines indicate catchment boarders

All pools were surrounded by tall trees. Pool A had a surface area of 916 m² and was situated at 84 m above sea level at the border of the Kanneliya Forest and the Kondagala Tea Estate. Pool B had a surface area of 638 m², was situated 30 m above sea level, near the place where the Nannikita Ela joins the Gin Ganga. This pool was most influenced by human activities. Pool C was with a surface area of 442 m² the smallest pool of the three; it is located at 160 m above sea level in the Kanneliya Forest Reserve, a second growth

forest with almost no human influences (Table 1). Water level fluctuations were greater in the low pools A and B when compared to pool C. The water was generally very clear, visibility measured as horizontal Secchi disc distance ranged usually between 4.0 and 9.8 m. (Vijverberg et al. 2017). Flow rates ranged seasonally from 0.3 – 0.8 m.sec⁻¹; averages per pool varied from 0.40 – 0.48 m.sec⁻¹ (Vijverberg et al. 2017). Pools A and C were dominated by rocky substrates (cobble, boulders), sand was common too, occupying one third of the bottom

surface. Sand dominated in Pool B, rocky-substrates sub-dominant. After sand 'leaves' were the most common substrate; they consisted

of leaves from the surrounding trees (i.e. terrestrial material) (Vijverberg et al. 2017).

Table 1 Morphometric and physical characteristics of the study ponds.

Pond	Altitude (m)	Catchment Area (km ²)	Average Surface Area (m ²)	Average Depth \pm SD (m)	Average Water temp \pm SD (°C)
A	84	22.0	894	1.30 \pm 0.22	27.0 \pm 1.4
B	30	13.0	523	0.58 \pm 0.30	26.5 \pm 0.7
C	160	2.5	428	0.73 \pm 0.05	25.7 \pm 0.5

Since the environmental conditions were rather constant during the year, we expected not much temporal variation in both food supply and food utilization. We addressed three research questions: (1) Is the food availability in the tree ponds similar? (2) Is the food availability over time more or less constant? (3) Is food utilization of specific food items affected by their availability in the environment?

MATERIAL AND METHODS

Sampling of potential food organisms of fish

The water column and three different substrate types (rocky substrates, sand and leaves) were sampled in each pool. The water column was sampled with a standard (Hydrobios) 80 μ m mesh zooplankton net. Ten random vertical hauls from just above the bottom to the surface were taken in the deepest region of the pool. For rocky substrates (bed rock and boulders) three samples were collected by cleaning 1 dm² surface area with knife, brush and a large pipette. Sand was sampled with a Perspex tube (length 30 cm, diameter 5 cm). The tube was pushed into the sand, after which the upper cork was inserted first; then the tube was lifted slightly, and the bottom cork was inserted. This was repeated several times at randomly chosen locations until a pooled sample of 2.9 - 3.6 dm² was collected. Sampling dead leaves on the bottom of the pool was done by placing a small bucket upside down on this substrate, lifting it a little and pushing all leaves underneath inside. Two random samples were taken and pooled, representing a bottom surface area of 8.3 dm². The invertebrates were separated from the leaves by spraying each individual leaf with a washing bottle. All samples were concentrated over 80 μ m mesh plankton gauze and preserved in 4% formalin.

Fish sampling

Cyprinids were collected with monofilament gill nets (1.5 m high, 15 m long) of 6, 8, 10, 13 and 16 mm bar mesh which were operated between 10 am to 3 pm in four different locations per pool, at two different depths (surface, bottom). The exposure time per net was 15 minutes; we applied in each pool the same sampling effort. After being anesthetized with 50 ppm Benzococaine, smaller fish was preserved in 4% formalin. Guts of larger fish were removed and preserved in 4% formalin after the total length (TL) was taken. Fish specimens were classified to the species level according to Pethiyagoda (1991), Pethiyagoda et al. (2012) and FishBase (2017). Gut contents were later analysed in the laboratory.

Diet analysis

To study fish diets, the contents of the anterior 1/3 part of the gut were analysed per species and per size class (max. 10 individuals per species per size class). Diet analysis was carried out in two steps. First, the relative biovolume was estimated of plant material (mainly benthic algae), animal matter and detritus. Second, the biovolume contribution of the animal matter was analysed in more detail. We distinguished 19 different taxa, which were later pooled into 11 taxonomic groups (Table 2). Aquatic Coleoptera larvae and adults (COL L, COL AD), Chironomid larvae (CHIR), other Diptera larvae (DIP), Ephemeroptera larvae (EPHEM), Microfauna (MICRO), Oligochaeta (OLIGO), Plecoptera larvae (PLECOP), terrestrial arthropods (TA), Trichoptera larvae (TRI), macrofauna rest group (MAR). Terrestrial Arthropods (TA) were falling out of the trees into the stream.

Table 2 The eleven taxonomic groups of animal organisms distinguished in the analysis of fish diets and fish food availability with their abbreviations. Micro-fauna include: Cladocera, Copepoda, Ostracoda, Tardigrada; Rest Macrofauna includes Acari and Nematods. Terrestrial Arthropods: more than 98% of the individuals observed were ants.

Taxonomic group	Abbreviation
Coleoptera adults	COL AD
Coleoptera larvae	COL L
Chironomid larvae	CHIR
Diptera larvae rest	DIP
Ephemeroptera larvae	EPHEM
Micro-fauna	MICRO
Oligochaeta	OLIGO
Plecoptera larvae	PLECOP
Rest Macrofauna	MACRO
Terrestrial Arthropods	TA
Trichoptera larvae	TRI

Oligochaetes were quickly digested in the fish guts and could not be quantified in the guts. Therefore, oligochaetes were not included in the comparison food availability – food utilization. The relative biovolume contribution of the different food categories in the gut was estimated according to the point's method of Hynes (1950), using a dissection zoom microscope or a standard compound light microscope when small food items dominated.

Data analysis

Biomass of animal organisms was estimated by measuring the organisms under the microscope and applying published length-weight relationships from the literature to dry weight or fresh weight (Smock, 1980; Culver et al., 1985; Amarasinghe et al., 2008). To convert dry weight

to fresh weight we multiplied microfauna dry weight by 10 and macrofauna dry weight by 5 (Winberg, 1971).

RESULTS

Seven cyprinid species represented more than 98% of the fish numbers caught. These were *Pethia cumingii* (PC), *Puntius dorsalis* (PD), *Dawkinsia singhala* (DS), *Pethia nigrofasciata* (PN), *Systemus pleurotaenia* (SP), *Devario malabaricus* (DM) and *Rasbora daniconius* (RD). For author's names and overview of abbreviations see Table 3. Of the seven study species, four were endemics of Sri Lanka (DS, PC, PN, SP) and three were vulnerable for extinction (PC, PN, SP) (IUCN, 2018).

Table 3 List of common fish species with their abbreviations and number of fish caught (N) in the three stream pools. *= endemic. Species names are as given in FishBase 2017.

Species	Abbrev.	Number of fish caught (N)		
		Pool A	Pool B	Pool C
<i>Dawkinsia singhala</i> * (Duncker, 1912)	DS	277	29	0
<i>Devario malabaricus</i> (Jerdon, 1849)	DM	228	2	1
<i>Pethia cumingii</i> * (Guenther, 1868)	PC	0	121	0
<i>Pethia nigrofasciata</i> * (Guenther, 1868)	PN	237	10	173
<i>Puntius dorsalis</i> (Jerdon, 1849)	PD	40	0	245
<i>Rasbora daniconius</i> (Hamilton, 1822)	RD	156	96	66
<i>Systemus pleurotaenia</i> * (Bleeker, 1863)	SP	44	2	12
Total		982	259	497

Not all seven species occurred in all pools. In Pools A and C species PC, and in Pool B species PN was absent (Table 3). Furthermore, in pool B we collected only two specimens of DM and SP, and in Pool C only one specimen of DM. These were not used for further calculations. Fish densities and species abundance also varied among ponds. Higher fish densities were observed in pool A, which was dominated by three species (DS, DM, PN). Pool C showed two times higher fish densities than in pool B; the latter was dominated by PC and RD whereas Pool C was dominated by PD and PN (Table 3).

More than 98 % of the terrestrial arthropods (TA) falling out of the trees onto the water surface was ants. This is an important food source especially for the surface feeding fishes. To our regret we were not able to quantify the availability of this food source.

Diet composition

Of the three main food types, animal food and detritus were eaten most (Table 4). Algae were generally eaten in small quantities, and they represented on average less than 5% biovolume of the total diet. Less than 20% was higher plants including macrophytes. However there were two exceptions; in pool B both DS and PC ate substantial amounts of phytoplankton. This was the pool which was most influenced by human activities, making it possible that elevated

nutrient concentrations stimulated production of benthic algae. The highest proportions of animal food and the lowest proportions of detritus were eaten by the surface feeding minor carps (DM, RD) (Table 4). PD ate substantial amounts of animal food. In DS, PN and SP proportions of

ingested animal food varied strongly among pools.

Two surface feeders *Devario malabaricus* and *Rasbora daniconius* and the generalist *Systemus pleurotaenia* were feeding ≥ 33 %g (biovolume) of terrestrial arthropods (Fig. 2). Since we were not able to quantify the availability of terrestrial arthropods these three species were not included in the analysis.

Most benthic feeding species (DS, PC, PD, PN) fed predominantly on chironomid larvae and ephemeropteran larvae came second (Fig. 3). The variation among pools was relatively small. In pool A DS ate less chironomids and more ephemeropterans relative to the other two species, whereas PD ate less ephemeropterans and more coleopteran larvae. In Pool B DS ate relatively less chironomids and more macrofauna rest (MAR) which was dominated by nematods and micro-fauna. In pool C, PD and PN ate mainly chironomids; ephemeropterans came second; other food organisms were insignificant or not eaten at all.

Table 4 Average diet composition in percentages per fish species per pool during the study period June 1984 until February 1986. Nf= number of fish diets analysed, Ns = number of sampling dates. Three food categories: Algae, Detritus, Animal Matter. For abbreviations of fish species names see Table 2.

Pond	Fish Species	Algae (%)	Detritus (%)	Animal Matter (%)	Nf	Ns
A	DM	0.3	6.3	93.4	178	11
	DS	7.2	88.4	4.4	261	10
	PD	0.3	74.4	25.3	276	11
	PN	0.0	75.2	24.8	51	8
	RD	0.2	10.1	89.7	157	10
	SP	1.5	70.1	28.4	52	8
B	DM	0.0	10.0	90.0	2	1
	DS	35.6	24.7	39.7	23	3
	PC	26.3	67.8	5.9	85	3
	PD	0.3	73.7	26.0	15	3
	RD	3.3	5.3	91.4	87	5
	SP	0.0	95.0	5.0	2	3
C	PD	1.5	52.0	46.5	137	6
	PN	4.6	89.6	5.8	215	5
	RD	0.0	9.0	91.0	57	6

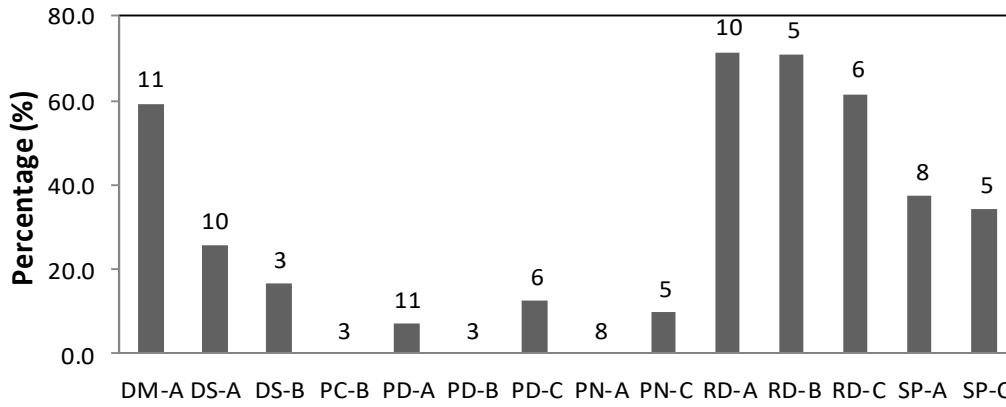


Fig 2 Average percentage of terrestrial arthropods (TA) relative to the total biovolume of animal organisms in the diets of the fish species in the three stream pools A, B, C. For abbreviations of fish species names see Table 2, for abbreviations of names of invertebrate taxa see Table 3. Number of observations above columns.

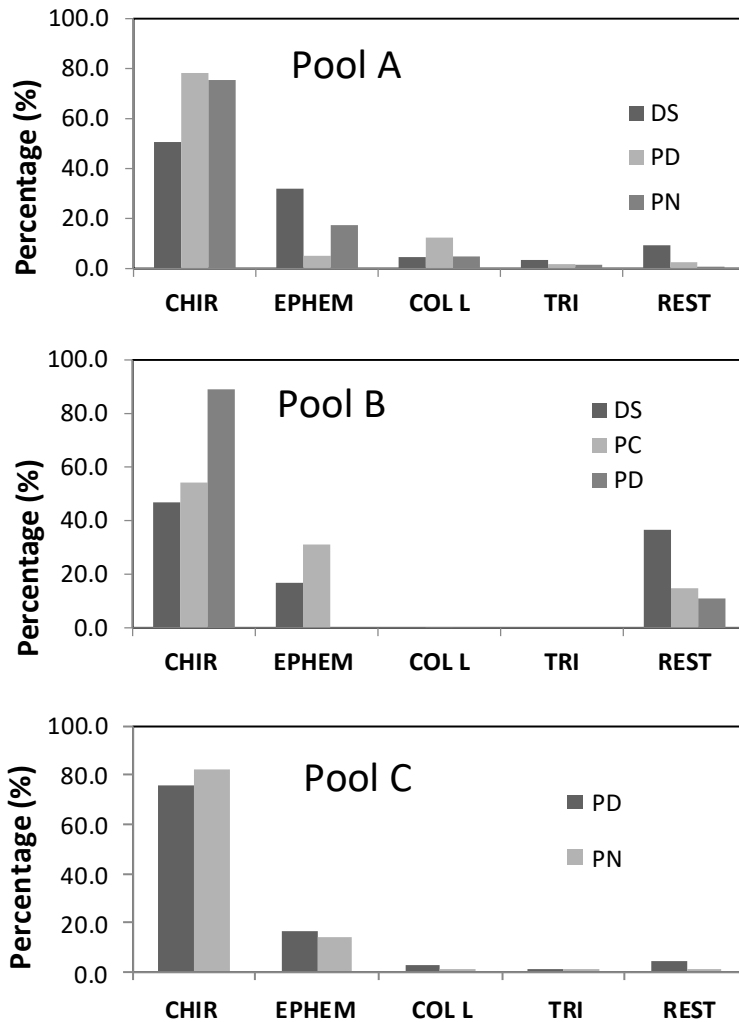


Fig 3 Average percentage (biovolume, %) of animal food taxa relative to the total biovolume of animal organisms in the diets of the fish species in the three stream pools. (a) In pool A, (b) in pool B and (c) in pool C. For abbreviations of fish species names see Table 2, for abbreviations of names of invertebrate taxa see Table 3.

Food availability

The average animal food availability (mg fresh wt dm⁻²) over the study period in the three stream pools A, B, C, varied in time and among pools (Fig. 4). Especially food availability in pools A and C varied substantially, we could not relate this variation to rainfall patterns. The lowest food availability was observed in pool B, which also

showed the lowest variation in food supply levels. On average, food values in pool C are similar to those in pool A.

Chironomid larvae were the dominant food items, generally followed by Coleoptera larvae, oligochaetes and ephemeropteran larvae (Fig. 5).

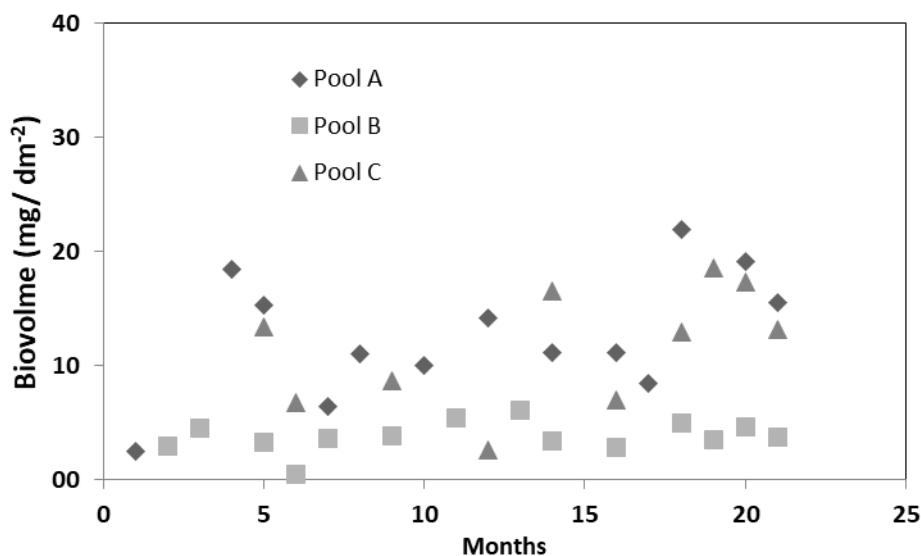


Fig 4 The average animal food availability (mg fresh wt dm⁻²) over the study period in the three stream pools A, B, C.

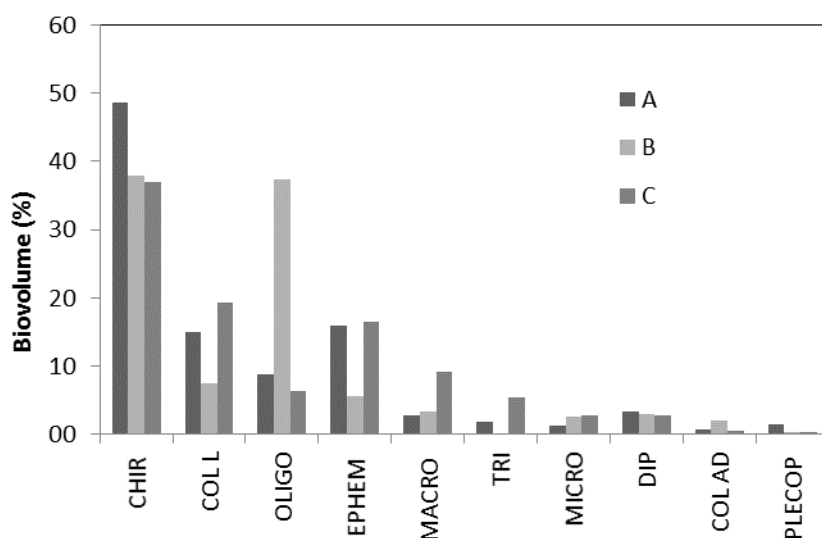


Fig 5 The mean relative food availability (biovolume, %) over the study period for the different food taxa in the three stream pools A, B, C. Food abundance per taxa in sequence of relative abundance. For abbreviations of the names of invertebrate taxa see Table 3.

Food utilization

Food utilization was studied by calculating the ratio between a fish species diet and the food availability in the pond. A value of 1.0 means no preference. The ratio above 1.0 shows positive selection, i.e., they eat more than expected from a specific food item assuming random feeding. The ratio below 1.0 shows avoidance or negative selection.

DS in pools A and B and PC in pool B showed no clear selection for chironomid larvae, but a positive selection for ephemeropterans in both pools. DS also showed a clear positive

selection for TRI in pool A but not in pool B (Fig. 6a). DS fed on coleopterans only in pool A, but selection was negative; in pool B both DS and PC did not feed on coleopterans at all. DS showed a positive selection in pool B for the rest of the groups, mainly micro-fauna and nematods.

The bottom feeders, PD and PN showed a clear positive selection for chironomid larvae (Fig. 6b). This was a strong indication that both species were real benthivores. PD in pool C, PN in pool A and PN in pool C fed randomly on ephemeropterans. All other potential food organisms were avoided in different degrees.

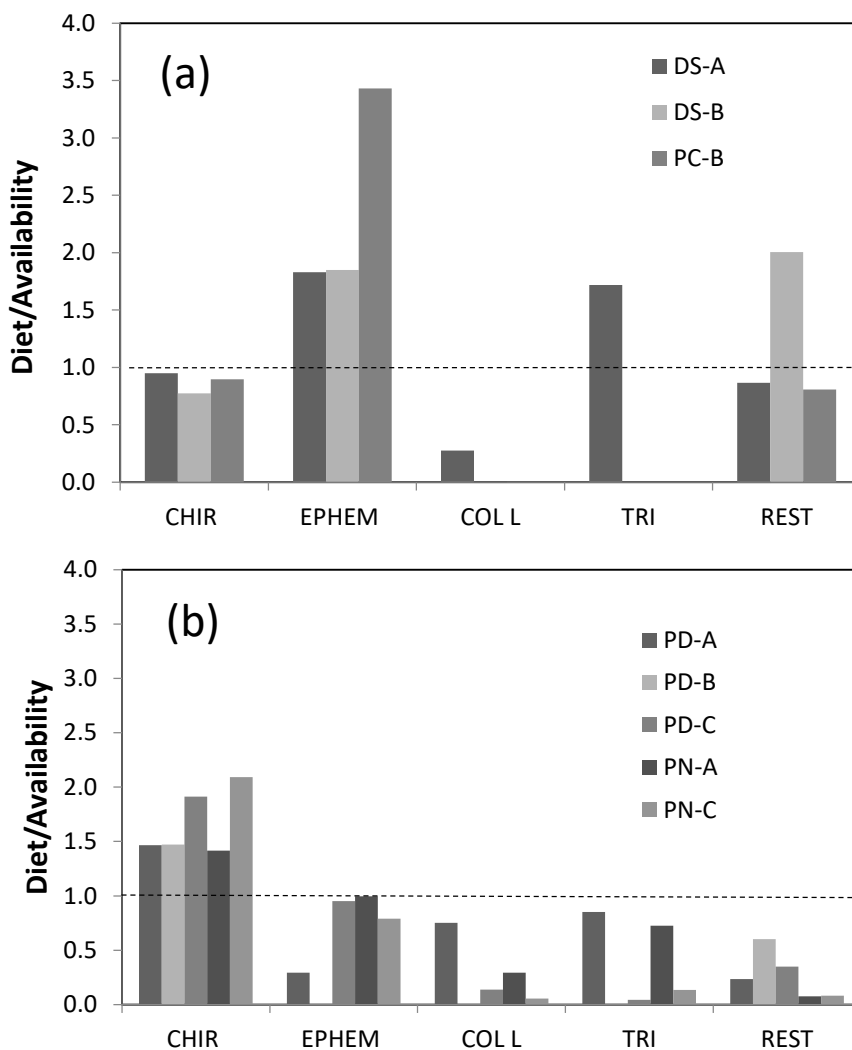


Fig 6 Selectivity (Ratio: diet/availability) of bottom feeding carps feeding on animal food taxa in the three stream pools A, B, C. The horizontal dashed line depicts selectivity equals 0, above the line selectivity is positive, below the line negative. (a) *D. singhala* (DS) and *P. cumingii* (PC); (b) The bottom feeding species: *P. dorsalis* (PD) and *P. nigrofasciata* (PN). The Ratio indicates the percentage of animal food of a taxon in the gut divided by the percentage availability of that same taxon in the environment. For abbreviations of names of invertebrate taxa see Table 2.

DISCUSSION

We found a high degree of endemism (57%) in the hill-streams of South West Sri Lanka and no exotics. This agreed with Amarasinghe *et al.* (2006) for this region, but was in contrast with Jayaratne & Surasinghe (2010) who found in the hill-streams of the Rawan Oya (Kandy District) a much lower degree of endemism (13%) and a much higher degree of exotic fish species (26%).

Diet composition

Of the three main food types, animal food and detritus was eaten most, and algae represented only a low proportion of the diet. The most available food items were eaten most by all fish species; since fish were opportunistic feeders this was according to expectation. The water column was very poor in food items, thus it was not surprising that five of the six fish species were either eating benthic invertebrates, mainly chironomids, at or near the bottom, or terrestrial invertebrates, falling out of the trees at or near the surface. Only one fish species (SP) ate in all five strata. The highest proportions of animal food were eaten by the surface feeding minor carps (DM, RD) and to a lesser degree by PD. High proportions of terrestrial insects in the diets of DM and RD were also reported by De Silva & Kortmulder (1977) and De Silva *et al.* (1980). The other species showed a considerable variation in consumption of animal food among ponds.

In contrast to those reported by most other authors (De Silva and Kortmulder 1977; De Silva *et al.* 1980), we found a relative small contribution of algae (generally < 5%, biovolume) and a relative high contribution of detritus for all species except for the two surface feeders. This may be caused by differences in interpretation of the gut contents by us and the other authors. The detritus that we observed in the guts of the benthivorous feeding species existed for a large part of what we believed to be dead benthic diatoms. Since the cobbles and boulders were covered by a thick crust of benthic algae with detritus it was difficult to decide what was already dead when ingested and what was alive. Therefore, we may have underestimated the proportion of algae, and may have overestimated the proportions of detritus in the diets.

In the present study most benthic feeding species were feeding predominantly on chironomid larvae; ephemeropteran larvae came

second. Earlier studies did not report any ephemeropterans in the diets (De Silva and Kortmulder 1977; De Silva *et al.* 1980), but found substantial amounts of Trichoptera in the guts of PD and SP.

Food availability

The animal food availability in the three stream pools varied in time and among pools, but was the highest in pools A and C and the lowest in pool B. The relatively low animal food availability in pool B was probably caused by its sand substrate. In contrast with pools A and C, which were dominated by rocky substrates, sand substrate dominated in pool B. This substrate contained lower densities of chironomids and ephemeropterans than the rocky substrates (Vijverberg *et al.* 2017). Contrary to expectations on basis of the stable climatic conditions, availability levels in two of the three pools (A and C) showed substantial variations. In all three the pools chironomid larvae were the dominant food items, generally followed by coleopteran larvae and ephemeropteran larvae. Oligochaetes were also largely available, but were not taken into further account in this study because these soft bodied worms were quickly digested in the fish guts, leaving behind only bristles which made it impossible to estimate its biovolume.

Food utilization

Chironomids were always abundant in the fish diets; they were not always positively selected. DS and PC showed no clear selection for chironomid larvae, but instead preferred ephemeropterans, micro-fauna and nematods whereas coleopterans were often negatively selected. PD and PN, however, show a clear positive selection for chironomid larvae. This indicates that PD and PN in contrast with DS and PC are real benthivores, i.e. predominantly feeding at the bottom substrates and less in the stratum low in the water column. A previous study showed that PC, PD, PN were exclusively feeding at or close to the bottom and that DS was also feeding in the middle of the water column (Vijverberg *et al.* 2017). That agrees with the results of the present study, but since Vijverberg *et al.* (2017) pooled the observation for feeding “low in the water column” and “at substrate” they were not able to distinguish in more detail the benthivorous feeding behaviour of the bottom feeding fishes.

CONCLUSION

Chironomid larvae and ephemeropteran larvae are, on basis of biovolume, the most important animal food items for the benthic feeding cyprinids in the hill stream pools of South West Sri Lanka, but only two of the four benthic species strongly positively selected chironomid larvae. These two species, PD and PC, are the real benthivores. Coleopterans, with ephemeropterans, were after chironomid larvae, the most abundant food items in the environment. However, the former was often negatively selected, while the latter was selected positively.

ACKNOWLEDGEMENTS

The study was a scientific cooperation between the Zoology Department of the Ruhuna University in Matara (Sri Lanka), the Zoology Department of the Leiden University (The Netherlands) and the Netherlands Institute of Ecology (NIOO) of the Royal Netherlands Academy of Sciences. The financial assistance by the Office of International Cooperation of the Leiden University to Dr. Kortmulder is gratefully acknowledged. We thank Dr. Sena S. De Silva, who at the time of the study was the Professor of Zoology at the University of Ruhuna, for research facilities, helpful support and scientific discussions. Messrs J.G. Sevenster, J. Heidweiller, T.R. Locher and R.J.J. de Klerk carried out part of the field work within the framework of a MSc project; their contributions are greatly appreciated. It is publication no. 6807 of the Netherlands Institute of Ecology (NIOO-KNAW).

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