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The composition, nutritional status and digestibility of the diets of *Sarotherodon mossambicus* from nine man-made lakes in Sri Lanka

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Synopsis

The dietary composition and the nutritional status and the digestibility of the diets of *Sarotherodon mossambicus* from nine reservoirs in Sri Lanka were evaluated. The feeding habits of *S. mossambicus* were variable from reservoir to reservoir; they ranged from herbivory to total carnivory. The protein, total lipid, carbohydrate and total organic matter content of the ingested material were related to the dietary composition and ranged from 18.53% to 35.15% ($\bar{x}$-24.18%), 5.94% to 9.84% ($\bar{x}$-7.91%), 11.6% to 34.7% ($\bar{x}$-22.34%) and 34.4% to 64.4% ($\bar{x}$-45.71%), respectively. Irrespective of the feeding habits, the diet contained a significant proportion of organic material which cannot be accounted for by protein, total lipid and carbohydrate. As much as the ingested material was related to the feeding habit, the digestibility of the nutrient components was related to the food material devoured. For example, the mean digestibility of the total organic matter in *S. mossambicus* feeding on detritus, plants and animal were 36.85, 33.5 and 29.5 respectively, and compared well with observations from elsewhere. It is hypothesised that the favourable nutrient quality of the available dietary material in the reservoirs of Sri Lanka, which could be and is effectively utilized by *S. mossambicus,* may have been, at least partially, responsible for its almost unprecedented success in Sri Lanka.

Introduction

Much has been written about the success of the exotic cichlid, *Sarotherodon mossambicus* (Peters), in the man-made lakes of Sri Lanka (Fernando & Indrasena 1969, Fernando 1973, De Silva & Fernando 1980, 1984). A number of reasons has been postulated as responsible for its success, although very little direct evidence has been forthcoming for any of the hypotheses (De Silva 1984). On the other hand, the nutritional constraints in detritivory which resulted in stunted populations of the species (Bowen 1979) and the importance of the detrital non-protein amino acids which results in rapid growth in *Tilapia* (Bowen 1980) have been recognised.

In Sri Lanka the *S. mossambicus* fishery in the different reservoirs is known to simulate the characteristics of a single, large fishery (De Silva 1984). It has been argued that this simulation could partly be due to the food availability in the reservoirs being non-limiting both in quality and quantity. The present investigation reports the results of studies carried out to test the validity of

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this hypothesis. Also, as the investigation included a number of water bodies with widely different morphometric and hydrological regimes, it is thought the information will provide further insight into the feeding habits of *S. mossambicus* which are known to be very variable (Bowen 1982).

Materials and methods

The reservoirs were selected from different geographical areas of the Island and belonging to four irrigation systems, for their close proximity to a laboratory, to which the samples of fish could be brought in a satisfactory condition within an hour of landing, for the initial analyses. Morphometric, hydrological and historical aspects of the selected reservoirs are described elsewhere (Arumugam 1969, De Silva & Fernando 1984) and so are the general features of the reservoir fishery (De Silva & Fernando 1984, De Silva 1984). Briefly, the fishery is uniform throughout the country, in the type of craft, the gear (gillnets of 8–10 cm stretched mesh), and time of laying of nets. The limnological features of most of the reservoirs are little known (see Mendis 1965, Gunatileke & Senaratne 1981).

The samples of fish from individual fisheries of the reservoirs were selected for freshness at the landing sites, only those individuals which showed some signs of life being selected. Some of the relevant morphometric and hydrological characteristics with the mean and the range in total length and weight of the samples analysed are given in Table 1.

Samples of *S. mossambicus* were brought to the laboratory, packed in ice. The total length and somatic weight were determined to the nearest 0.5 cm and 1.0 g respectively, the body cavity opened and the gut uncoiled. The intestine was divided into three equal parts considered to be the fore-, mid- and hindgut while the last 3 cm from the distal end was considered as the rectum. The contents of the middle 4 cm of the mid- and hindgut and that of the rectum and stomach were teased out and kept separately. This procedure was repeated for 20–30 fish, from each reservoir and the contents of each section were pooled. The stomach contents were mixed thoroughly, and a portion (about one third) was fixed in 4% formalin for determination of the qualitative and quantitative make-up of the diet of *S. mossambicus* in individual reservoirs, using the method of De Silva (1973). In this analysis floral and faunal components were identified to the generic and/or the species level, as far as possible. In the final quantification of the dietary composition the volumetric contribution of the different components belonging to the major taxonomic groups e.g. diatoms, desmids, blue-green algae etc. were pooled (De Silva 1973, De Silva et al. 1984).

Apart from the material used in the above analysis, the rest was dried at 80°C overnight, finely

Table 1. Some characteristics of the reservoirs from which the samples of *S. mossambicus* were obtained together with the mean and the range in the total length (cm) and weight (g) of the individuals analysed (* – at the full supply level; + – data from De Silva 1984; a to d indicate the different irrigational systems).

	Reservoir	Catchment km^2	Surface area* ha	Mean depth m	Conductivity ms (25° C)	pH^+	n	Length		Weight	
								$\bar{x}$	range	$\bar{x}$	range
I	Badagiriya[a]	346	482	4.3	925^+	7.6^+	27	19.1	15.5-24.5	126	77-253
II	Chandrikawewa[b]	164	447	8.5	155	7.3	31	19.2	19.0-24.0	155	101-205
III	Giritale[c]	24	310	12.3	140	8.0	22	23.5	19.0-28.5	241	115-425
IV	Kaudulla[c]	82	2537	9.2	225^+	7.9^+	21	21.2	17.5-23.5	156	95-230
V	Kiriibbanara[b]	18	293	3.2	255	7.3	34	22.4	18.0-27.0	246	121-389
VI	Ridiyagama[b]	31	888	5.3	416^+	7.9^+	33	22.8	18.0-24.5	206	141-281
VII	Tissawewa[d]	38	234	5.0	610	8.0^+	32	22.0	17.0-28.5	221	98-435
VIII	Udawalawe[b]	1162	2382	15.3	195^+	7.7^+	19	22.5	18.5-33.0	213	112-441
IX	Yodawewa[d]	46	488	4.0	655	7.8^+	30	20.8	18.0-24.0	166	102-251

ground and sieved through a 400 mμ sieve. Aliquots of the dried material from each region of the alimentary canal from different *S. mossambicus* samples were used for subsequent analyses. Analysis carried out gave the protein content 80 to 100 mg based on the biuret method, as modified by Raymont et al. (1964) using bovine serum albumen as standard[1]; carbohydrate content 8 to 10 mg (Dubois et al. 1956), ash (150 – 200 mg) content by ignition for 16 h at 550°C in a muffle furnace; and total lipid gravimetrically 120 to 140 mg (Bligh & Dyer 1959). These determinations, except for ash, were carried out mostly in quadruplicate and always, at least, in triplicate. In addition, hydrolysis resistant ash (HRA) and hydrolysis resistant organic matter (HROM) were determined for stomach and rectal contents of the samples, at least in duplicate but mostly in triplicate based on the method of Buddington (1980). This limitation was imposed by the amount of material available.

Bowen (1981) has shown that there is no apparent assimilation in the stomach of *S. mossambicus*. As such the composition (qualitative, quantitative and nutritional) of the stomach contents was considered as that of the ingested food material while HRA and HROM were initially taken to be reference markers (Buddington 1980, Bowen 1981, De Silva & Perera 1983) for digestibility estimates. Later, however ash content was also utilized as a reference marker. Digestibility of the total organic matter (TOM) and that of different nutrient components of the ingested material were estimated according to Maynard & Loosli (1972).

Results

The qualitative make-up of the diet of *S. mossambicus* in the different reservoirs is enumerated in Appendix 1. In all 6 genera of Chlorophyceae, 2 Bacillariophyceae and 2 Cyanophyceae together with 4 genera of cladocerans, 1 genus of cyclopoid copepods and 7 genera of rotifers, were identifiable in the diet of *S. mossambicus*. In addition, unidentified macrophytes and a few protozoan types were recorded. The percentage contribution (volumetrically) of the major components to the diet of *S. mossambicus* from different reservoir populations are shown in Figure 1 and summarised in Table 2. The quantitative make-up of the diets varies from reservoir to reservoir not only in detail but also in the emphasis on different food components. In three reservoirs detritus did not occur in the diet, while in two others the diet almost exclusively consisted of plant material, of which the main component was either green algae (filamentous forms) or diatoms and desmids. Similarly in two other populations the diet was predominantly of animal matter, and cladocerans were the dominant form. Rotifers occurred in most populations but never constituted more than 5% of the total by volume. In five out of nine populations of *S. mossambicus* detritus played a dominant role in the diet, the contribution varying from 64.6% to 88.4%.

Nutritional status of the diets

The nutrient composition of the ingested food material (i.e. stomach contents) in different reservoirs is shown graphically in Figure 2. In this figure the protein, total lipid and carbohydrate contents are shown both as a percent of the total material ingested as well as in proportionate to the total organic matter (TOM) in the diet. The overall protein content of the diets varied between 18.53 to 35.15% while the total lipid and carbohydrate contents varied between 5.94 to 9.84% and 11.6 to 34.7% respectively. The mean percentages of protein, total lipid, carbohydrate and TOM content of the diets were 24.18 (±5.15), 7.91 (±1.40), 22.34 (±7.65), and 45.71 (±11.31) respectively. The mean proportion of protein, lipid and carbohydrate content of the ingested TOM amounted to 11.5 (±4.9), 3.6 (±1.3) and 10.7 (±6.0) respectively. These amounts do not repre-

[1] 60–80 mg of finely ground material was digested with 25 ml of 1 N NaOH at 110°C for 1 h and filtered through a millipore system using GF/C filter paper. To 3 ml of clear filtrate 10 ml of biuret reagent was added and allowed to develop colour for 45 min and read in 1 cm path length silica cell in a spectrophotometer at 555 nm. Bovine serum albumen was used as the standard.

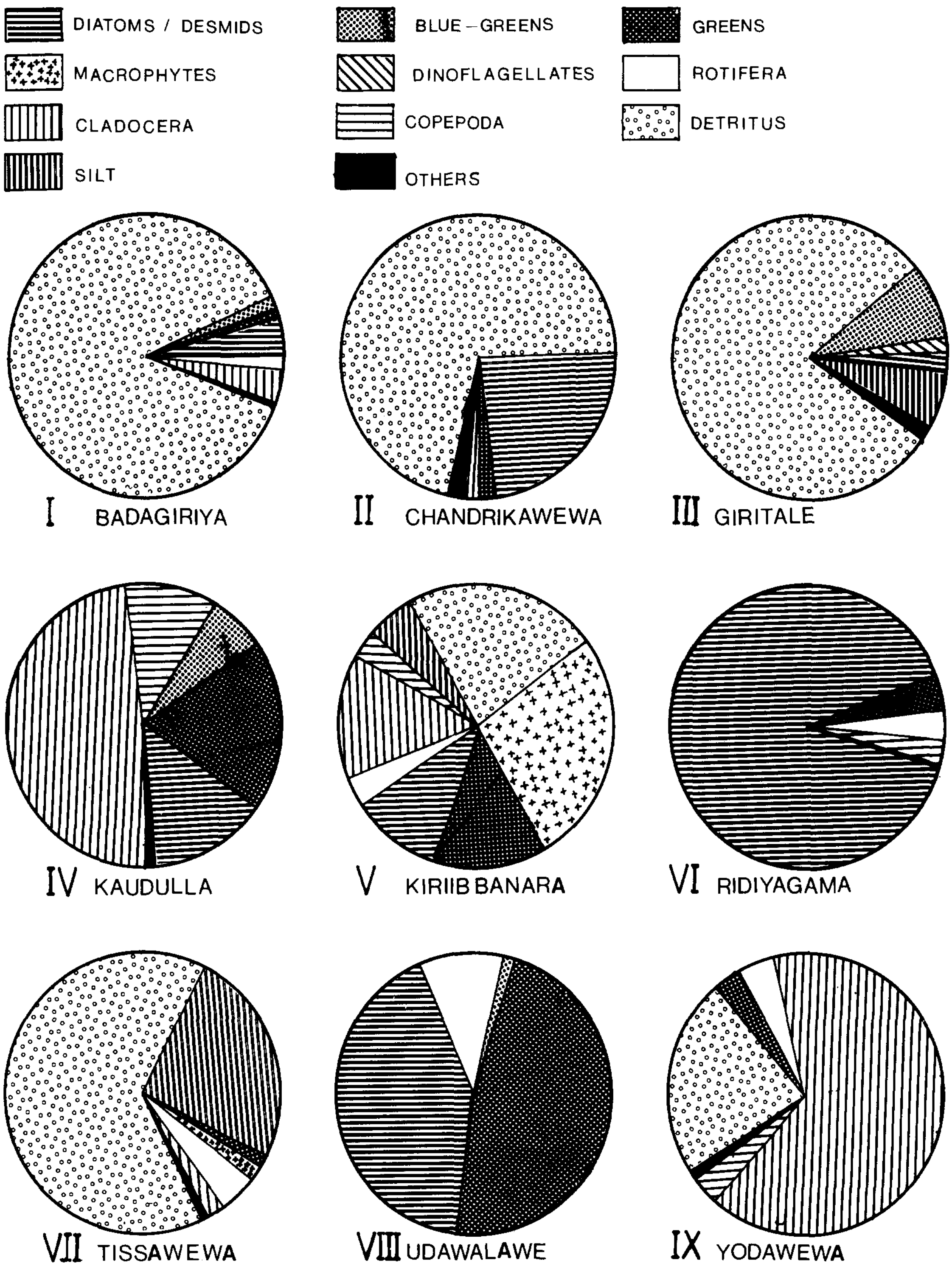

Fig. 1. The relative quantitative contribution of the major taxa to the diet of *S. mossambicus* from the different reservoirs (the category *others* refer to the aggregate of those groups of material which individually contributed less than 1% to the diet).

Table 2. The overall dietary composition of *S. mossambicus* populations from the different reservoirs (silt – non detrital sand particles).

	Reservoir	Detritus %	Plant material %	Animal material %	Silt %
I	Badagiriya	88.4	6.3	5.6	–
II	Chandrikawewa	71.3	26.2	2.2	–
III	Giritale	79.6	11.2	2.3	6.5
IV	Kaudulla	–	39.7	60.3	–
V	Kiriibbanara	22.2	51.7	20.5	5.7
VI	Ridiyagama	–	94.4	6.0	–
VII	Tissawewa	64.6	30.6	4.9	–
VIII	Udawalawe	–	90.6	9.4	–
IX	Yodawewa	22.9	3.6	73.5	–

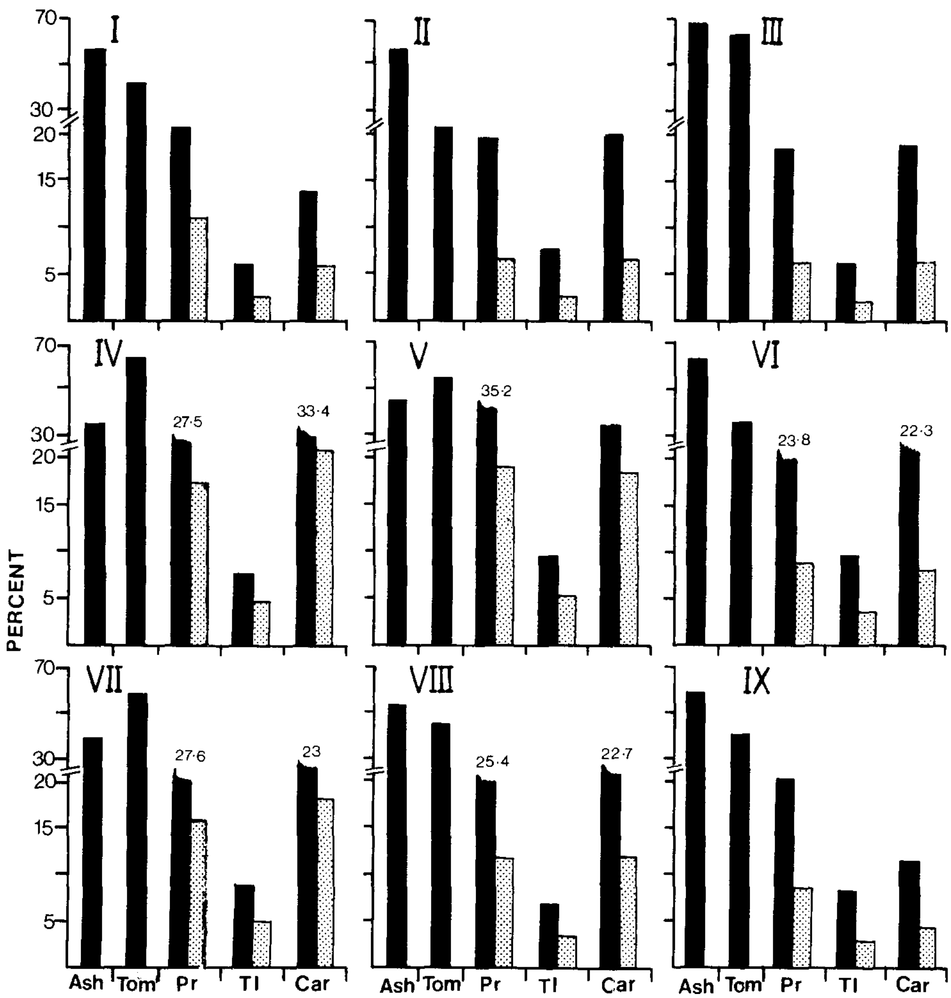

Fig. 2. The percentage content of ash, total organic matter (TOM) protein (Pr), total lipid (Tl) and carbohydrate (Car) in the diets of the different *S. mossambicus* populations (solid bars). The stippled bars indicate the proportion of protein, total lipid and carbohydrate content of the total organic matter of the ingested material (the scale is the same as for the %).

sent the percentage of each of the nutrient components in the ingested organic matter but are weighted proportions of each of the components in the organic matter in a unit of food material ingested.

Digestibility

Detailed analyses of the nutrient composition in each sector of the alimentary canal of *S. mossambicus* from the nine reservoirs are given in Tables 3 and 4. It is evident that without exception, the protein, total lipid, carbohydrate and TOM content showed a decline while the ash, HROM and HRA content was higher in the rectum than in the stomach. The mean variations in the protein, total lipid, carbohydrate and TOM content through the length of the alimentary canal of *S. mossambicus* feeding primarily on plant material, detritus and animal material are shown separately in Figure 3. The protein, total lipid and carbohydrate content here being expressed in mg in relation to the TOM present in one g of material in each sector of the alimentary canal. It is evident that the unaccountable organic matter constitutes a significant proportion of the TOM of the material, in all regions of the alimentary canal. This component varied in amount from 25.6% to 59.2% of the ingested material. It appears that assimilation of TOM, protein, total lipid and carbohydrate takes place along most of the length of the gut. In all instances, an increase in the carbohydrate content as a percent of the TOM was noticeable in the mid-intestinal region. This could indicate not an increase in the amount of carbohydrate in absolute terms but only in relative terms due to the preferential assimilation of proteins in the anterior region of the intestine.

It is evident from Tables 3 and 4 that as in the case of HROM and HRA, two of the commonly used indigenous reference markers for digestibility estimates (Buddington 1979), ash is also concentrated during the passage of food through the alimentary canal. Therefore, digestibility was also estimated using ash as a reference marker (Table 5). Clear trends were not apparent in the digestibility of TOM, protein, lipid or carbohydrate when the different markers were employed i.e. the estimates obtained from one marker did not throughout yield higher digestibility estimates for the different nutrient components in the different populations. On the other hand, the TOM, protein, total lipid and carbohydrate digestibility estimates for any one population based on the three different markers were not significantly different ($p<0.05$) except in the Kaudulla reservoir (lipid digestibility). Amongst populations, however, the protein, total lipid and carbohydrate digestibility (mean) varied between 31.2 to 60.8% ($\bar{x}$-39.8 ± 9.43), 13.6 to 59.2% ($\bar{x}$-41.6 ± 14.8) and 19.9 to 65.7% ($\bar{x}$-40.7 ± 16.3) respectively. The greatest deviation in digestibility in the different populations occurred in total lipid and carbohydrate digestibility. Digestibility of protein and TOM, amongst populations, deviated to the same extent.

Table 4. The amount of total organic matter (TOM) in mg in a g of ingested material and the weighted amount of protein (Pr.), total lipid (Tl) and carbohydrate (Car.) in mg in relation to the TOM in each sector of the alimentary canal of *S. mossambicus* from different reservoirs.

	Reservoir	*Stomach*				*Mid-intestine*				*Hind-intestine*				*Rectum*			
		TOM	Pr.	Tl.	Car.	TOM	Pr.	Tl.	Car.	TOM	Pr.	Tl.	Car.	TOM	Pr.	Tl.	Car.
I	Badagiriya	420	88	25	61	473	91	39	68	401	73	25	53	345	55	16	37
II	Chandrikawewa	327	64	25	66	–	–	–	–	277	43	17	46	250	34	12	41
III	Giritale	328	61	20	62	not sampled				not sampled				256	38	14	4
IV	Kaudulla	638	176	51	213	not sampled				not sampled				594	123	44	173
V	Kiriibbanara	544	191	52	189	576	182	60	213	492	133	42	184	423	104	26	107
VI	Ridiyagama	366	87	36	82	519	125	61	198	323	65	17	66	256	45	16	29
VII	Tissawewa	590	163	53	135	503	105	39	107	422	80	23	73	411	77	25	52
VIII	Udawalawe	466	118	32	106	608	136	51	156	437	71	21	85	399	73	14	71
IX	Yodawewa	411	86	34	48	445	59	43	116	277	41	14	26	311	34	14	17

Table 3. The percent content of ash, protein (Pr), total lipid (Tl), carbohydrate (Car), HROM and HRA of the ingested food material in the different sectors of the alimentary canal of *S. mossambicus* from different reservoirs (the SD are given for those determinations that were done in quadruplicate or more; all others were done at least in duplicate).

	Reservoir	*Stomach*						*Mid-intestine*				*Hind-intestine*				*Rectum*					
		Ash	Pr.	Tl.	Car.	HROM	HRA	Ash	Pr.	Tl.	Car.	Ash	Pr.	Tl.	Car.	Ash	Pr.	Tl.	Car.	HROM	HRA
I	Badagiriya	58.0	20.8	5.9	14.5	4.6	50.6	52.7	19.3	8.2	14.4	59.9	18.1	6.3	13.1	65.5	15.9	4.7	10.7	5.4	58.4
			±0.37		±0.30	±0.85		±0.64	±0.41		±0.5		±0.89		±0.3		±0.21		±0.9		
II	Chandrikawewa	67.3	19.5	7.6	20.1	8.4	61.2	–	16.6	8.3	25.9	72.3	15.5	6.2	16.5	75.0	13.7	4.9	16.3	9.5	70.2
		±1.05	±1.63	±0.95	±1.40	±0.30	±0.98		±0.40		±0.80		±1.21	±0.84	±1.50	±0.24	±0.19	±0.46	±1.60	±0.16	±0.11
III	Giritale	65.6	18.5	6.2	18.9	8.0	57.8		sample not taken				sample not taken			74.1	15.0	5.4	15.9	10.1	08.0
		±2.30	±0.61		±1.5											±0.88	±0.82	±1.13	±1.6		±0.33
IV	Kaudulla	35.4	27.5	7.9	33.4	6.5	31.0		sample not taken				sample not taken			40.6	20.7	7.5	29.2	6.2	33.5
		±1.12	±1.77		±0.70		±1.60										±2.78		±0.61		
V	Kiriibbanara	45.6	35.2	9.6	34.7	7.5	41.8	42.4	32.8	10.4	37.0	50.8	27.1	8.5	37.4	57.7	24.5	6.0	25.3	8.7	52.7
		±0.11	±0.76	±0.60	±1.53	±0.79	±0.20	±0.15	±0.29	±0.58	±2.14		±2.10	±0.03	±4.10		±2.03	±0.48	±1.10	±0.03	
VI	Ridiyagama	63.4	23.8	9.8	22.3	7.7	55.9	48.1	24.1	11.7	38.2	67.7	20.2	5.4	20.5	74.4	17.7	6.3	11.2	7.1	66.5
			±0.37		±1.80			±0.56	±0.42	±0.86	±4.41	±0.19	±0.59	±0.19	±2.13		±4.02				
VII	Tissawewa	41.0	26.1	9.0	22.9	5.1	35.7	49.7	20.8	7.81	21.2	57.8	19.1	5.4	17.2	59.9	18.8	6.2	12.6	6.4	49.8
			±1.58		±1.62				±1.02	±0.83	±3.1		±1.04		±1.2		±0.81	±0.16	±0.1		±1.98
VIII	Udawalawe	53.4	25.4	6.9	22.7	7.7	44.9	39.2	22.4	8.4	25.7	56.3	16.2	4.9	19.5	60.1	18.3	3.4	17.7	8.8	47.7
		±0.79	±0.91		±1.30	±0.12	±0.2	±0.89	±0.63		±4.0	±0.49	±1.07		±0.5	±0.26	±0.15		±2.5	±0.22	
IX	Yodawewa	58.9	20.8	8.2	11.6	6.5	50.8	55.5	13.2	9.7	26.1	72.3	11.3	4.9	9.4	78.9	10.8	4.5	5.3	8.3	70.8
			±0.47		±0.90				±0.21		±3.1		±0.06		±0.7		±0.13		±0.2	±0.54	

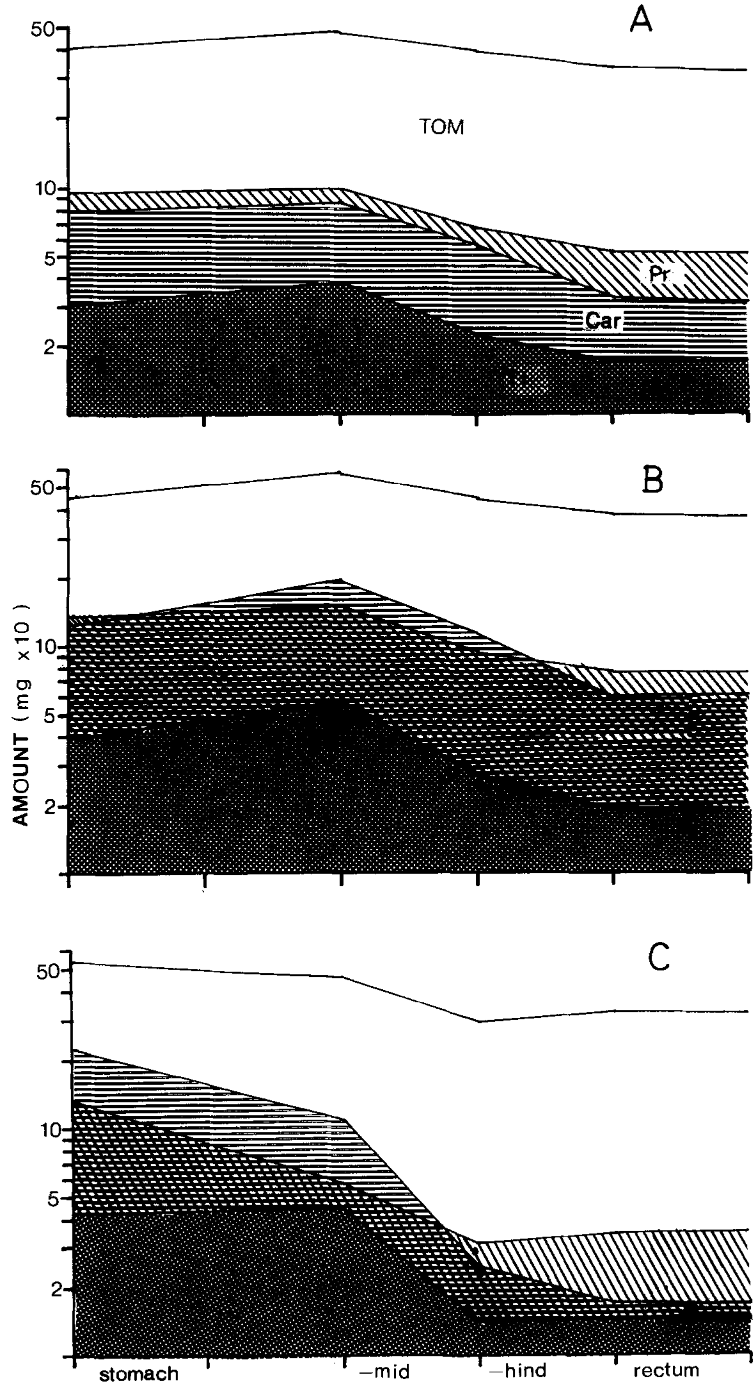

Fig. 3. The mean protein, total lipid and carbohydrate content in mg in relation to the total organic matter present in one g of material in each sector of the alimentary canal of *S. mossambicus* feeding predominantly on detritus (A), plant material (B), and animal material (C).

Table 5. Percent digestibility of the total organic matter, protein, total lipid and carbohydrate of the ingested food material in *S. mossambicus* populations from different reservoirs based on HROM, HRA and ash as reference markers.

	Digestibility of:	*TOM*				*Protein*				*Total lipid*				*Carbohydrate*			
	Reservoir/Based on:	HROM	HRA	Ash	x̄	HROM	HRA	Ash	x̄	HROM	HRA	Ash	x̄	HROM	HRA	Ash	x̄
I	Badagiriya	29.1	28.9	27.3	28.4	34.9	33.9	32.4	33.7	32.8	31.8	30.2	31.9	36.3	36.1	34.7	35.7
II	Chandrikawewa	32.4	33.4	31.5	32.4	38.3	39.2	37.5	38.3	43.0	43.9	42.3	43.1	28.2	29.3	27.2	28.2
III	Giritale	40.6	36.8	34.2	37.2	35.2	31.0	28.2	31.5	30.8	26.3	23.3	26.8	32.8	27.5	25.6	28.9
IV	Kaudulla	12.6	14.9	19.8	15.8	28.6	30.5	34.5	31.2	10.4	12.7	17.8	13.6	16.9	19.1	23.8	19.9
V	Kiriibbanara	32.9	38.2	38.4	36.5	39.9	44.6	44.8	43.1	45.6	49.9	50.1	48.5	37.1	42.1	42.3	40.5
VI	Ridiyagama	—	41.1	40.4	40.8	–	37.6	36.8	37.2	–	46.5	45.8	46.1	–	57.7	57.2	57.7
VII	Tissawewa	45.9	50.0	52.4	49.4	42.7	48.4	49.4	46.8	45.5	50.9	53.1	49.7	56.2	60.5	61.3	59.3
VIII	Udawalawe	25.1	20.7	23.8	23.2	36.8	33.1	35.7	35.2	56.9	54.4	56.1	55.8	32.2	27.8	30.6	30.2
IX	Yodawewa	40.4	45.7	43.5	43.2	58.9	62.5	61.0	60.8	57.2	61.0	59.5	59.2	64.0	67.2	65.9	65.7
	Mean digestibility	32.4	34.4	34.6	34.4	39.4	40.1	40.2	39.8	40.3	41.9	42.0	41.6	38.0	40.8	37.8	40.7
		(±10.5)	(±11.4)	(±10.3)	(±10.4)	(±8.9)	(±10.4)	(±10.5)	(± 9.4)	(15.4)	(±15.4)	(±14.9)	(±14.8)	(±15.2)	(±17.1)	(±18.5)	(±16.3)

Discussion

The feeding habits of *S. mossambicus* are known to be very diverse (Bruton & Boltt 1975, Man & Hodgkiss 1977, Weatherly & Cogger 1977, Bowen 1980) and were summarised by Bowen (1982). Bowen observed that adult tilapias characteristically devour plant matter and/or detritus of plant origin and that blue-green algae, diatoms, macrophytes and amorphous detritus are all common constituents of adult tilapia diets. Furthermore, Bowen highlighted the enigmatic role of animal matter in its diet. The work reported above is a collection of information on the diets of tilapias from different corners of the world. The present investigation provides insight into the feeding habits of *S. mossambicus* populations from a number of reservoirs in the same country, and often in systems which retain a connection through an intricate network of irrigational canals. The findings confirm the versatility of the dietary habits of *S. mossambicus* and indicate that even in the same 'water system' they could shift the dependence from the traditional plant and/or detritus diet to a predominantly carnivorous one. Although direct evidence is not available from this investigation that animal matter was selectively devoured, the almost complete absence of detritus and or algae in some populations makes us believe that in certain instances *S. mossambicus* devours animal material selectively, contrary to the belief of Spataru & Zorn (1978). The same is true for those populations feeding exclusively on plant material. The reasons for such a shift in their feeding habits is not immediately obvious but phytoplankton abundance, measured in terms of chlorophyll content (personal observations) does not indicate a limitation in the availability of the latter. Furthermore, when the number of species of diatoms, desmids, cladocerans, etc. in the diet of *S. mossambicus* is compared with species with similar feeding habits, such as for example the grey mullet (De Silva & Wijeyaratne 1977), it is apparent that the number of species in the diet of the former is much lower. Although the seasonality of the dietary changes is not presented here, data gathered up to now indicate that populations devouring a particular category of material continue to do so for most part of the year (to be published). The possibility of such a diversity resulting in differences in their gut morphology, as in the native cichlid *Etroplus suratensis* (De Silva et al. 1984), is presently being investigated.

The nutritive quality or status of the ingested food material of *S. mossambicus* is little known (Bowen 1979, 1980, Hofer & Schiemer 1983). Bowen (1980) observed that in *S. mossambicus* populations in Lake Sibaya, S. Africa, the proteins constitute less than 10% of the organic weight of the ingested food material. Recalculating from the data of Hofer & Schiemer (1983), the proportion of protein was found to be 7.92 of the organic weight in *S. mossambicus* from the Parakrama Samudra reservoir in Sri Lanka. In the Sri Lankan reservoirs the mean proportion of the protein content of the total organic weight of the ingested material was 11.48 and ranged between 6.38 to 19.11. The present data also indicate, as one would expect, that the protein content of the organic matter ingested is strongly related to the diet. The diet of populations devouring more than 50% of detritus, plant and animal material is considered to be detritivorous, herbivorous, and carnivorous respectively and their mean protein content of the total organic matter ingested varied from 93.7, 132.0 to 131 mg g^{-1} in the same order of dietary material (Table 6). The variation in the other nutritional components is also similarly related to the dietary composition. The C:N ratio is considered as an approximate index of the energy: protein ratio (Russell-Hunter 1970). Although the gross energy content of the diets was not determined in this study (due to lack of facilities, as well as the lack of material, collected from the samples were insufficient to carry out all the analyses) the comparatively high ratio of protein to TOM may indicate that the diets of *S. mossambicus* populations of reservoires in Sri Lanka are not limiting to growth. It is also important to note that the amount of utilizable protein in the diet is not significantly different in populations devouring detritus in comparison to the other food sources.

The observations that the % carbohydrate con-

Table 6. The mean nutrient composition (%) of the diets of *S. mossambicus* in relation to their food habits. The protein, total lipid and carbohydrate content as a percent of the TOM is given in parantheses (the S.D. has been calculated using all the raw data; for any one component the mean does not differ between different populations at the 1% level).

Diet	TOM	Protein	Total lipid	Carbohydrate
Detritivorous	42.0±12.0	21.2±3.4	7.2±1.4	19.1±3.5
		(9.4±4.7)	(3.1±1.5)	(6.0±0.5)
Herbivorous	45.9±8.9	28.1±6.1	8.8±1.6	26.6±7.0
		(13.2±5.3)	(4.0±1.1)	(12.6±5.6)
Carnivorous	52.8±16.6	24.2±4.7	8.1±0.2	22.5±9.2
		(13.1±6.4)	(4.2±1.2)	(13.0±11.7)

tent increases in the mid-intestine, in comparison to that of the stomach is contrary to the observations of Bowen (1981). This discrepancy could be an effect arising from the different methods of treatment of the data. However, the present data indicate that assimilation of carbohydrates does take place beyond the first quarter of the intestine, as was shown by Austreng (1978) for rainbow trout.

The assimilation efficiency or per cent digestibility of food material in cichlids has been investigated mostly in the laboratory and on food items presented singly (Van Dyke & Sutton 1977, Kirilenko et al. 1975, De Silva & Perera 1983). *S. mossambicus* is known to feed during the day (Schiemer & Hofer 1983) and as the stomach was only slightly filled at the time of sampling and also because of the expectedly fast rate of movement of food through the gut, it is assumed that the rectal contents of the individual fish represent the same dietary regime as that of the stomach contents. Contrary to the observations of Buddington (1980), it is apparent from the present data that ash is concentrated as the food passes along the gut and that ash could also be used as a reference marker, under certain conditions. The digestibility estimates for the different nutrient components estimated using the different markers did not differ significantly ($p < 0.01$) from each other, for any one population (Table 5).

As much as the nutritive quality of the ingested food material is related to the feeding habits the digestibility of the former, particularly the proteins are also related to the devoured material (Fig. 4). This however, is not exactly a direct relationship to the type of material – an increase in a single component did not necessarily result in an increase/decrease in the digestibility of the nutrient component, particularly when feeding on detritus. It appears that when the detritus component exceeds 70% the digestibility of the nutrients is significantly reduced while in the case of herbivory and carnivory the reverse appears to occur. The differences in the digestibility of the nutrient components of the reservoir populations feeding predominantly on animal matter may indirectly indicate the importance of detritus in the diet. The digestibility of all components was significantly lower in the Kaudulla population than that recorded in all the other reservoirs. This may be indicative of the importance of detritus and/or plant material in the food of *S. mossambicus*. The digestibility of the nutrient components of the naturally ingested food material in *S. mossambicus* is lower than that reported for the components when individual items were presented (Van Dyke & Sutton 1977, Caulton 1978, Buddington 1979) but compares well with that reported for *S. mossambicus* under similar conditions (Bowen 1979, Hofer & Schiemer 1983). It is also apparent that unaccountable organic material is also effectively assimilated by the *S. mossambicus* populations of the reservoirs in Sri Lanka, which would add to the nutritional quality of the food devoured.

The present study clearly shows that, irrespective of the feeding habits of *S. mossambicus* its diet almost always contains a very high proportion of organic material which is neither protein, carbohydrate, nor lipid, as was shown and discussed by Bowen (1980) and Hofer & Schiemer (1983). The possible nutritional importance of this component has been discussed by Bowen (1980). Also

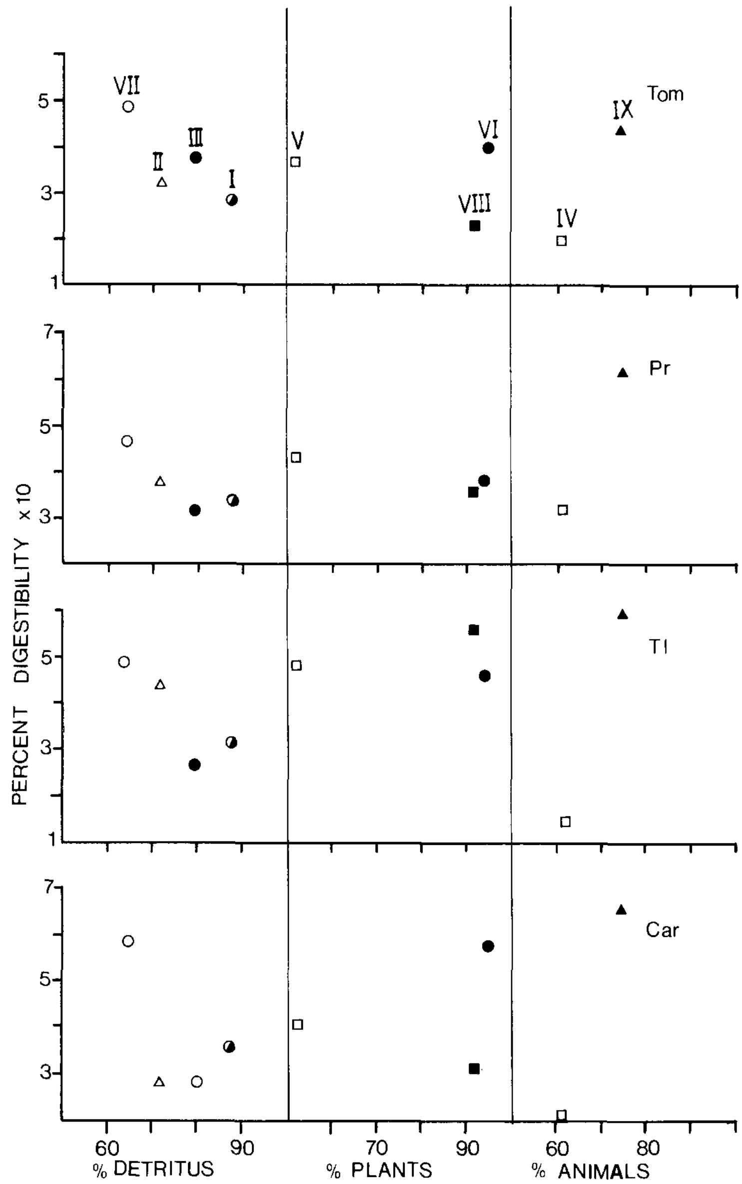

Fig. 4. The per cent digestibility of the TOM, protein, total lipid and carbohydrate in *S. mossambicus* from the different reservoirs in relation to their feeding habits. The digestibility indicated for each nutrient component is the mean of estimates using all three reference markers. The Roman numerals refer to the reservoir number given in Table 1.

the nutritional quality of the food of *S. mossambicus* from Sri Lankan reservoirs is very much comparable to and, in most cases, is better than that reported for healthy populations from elsewhere. It is believed that this evidence points to the non-limitation of the nutritional quality in the food of *S. mossambicus* in Sri Lanka reservoires despite the diversity of the latter. Moreover, the reservoirs of Sri Lanka are shallow (Arumugam 1969) and the gradients of the basin slopes are slight. This presumably means that the conditions which influence the nutritional quality of the unaccountable organic matter in the diet, as in Lake Sibaya (Bowen 1979), might not prevail in the Sri

Lankan reservoirs. Therefore, in broad terms the Sri Lankan reservoirs provide a conducive and a favourable food supply for the exotic *S. mossambicus*. This fact might have been a determining factor of the species' unprecedented success, its continuance and sustenance in Sri Lanka.

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Appendix 1. The qualitative make-up of the diets of *S. mossambicus* populations in the different reservoirs. (Relative importance by volume: + −0.05%; ++ −0.05 to 0.49%; * −5.0 to 49.99%; @ −50%). PSM and PSN refer to another reservoir not dealt with in the text.

Higher division	Family	Genus/Species	Bada	Chan	Giri	Kau	Kiri	Min	PSM	PSN	Ridi	Tissa	Uda	Yoda
FLORA														
Chlorophyceae	Hydrodictyaceae	*Pediastrum*		+	++	**	*	*	++	*	*	++	+	++
	Desmidiaceae	*Closterium*						+				++	+	
		Cosmarium		+		++		+	++	*				
		Staurastrum		++	+			++	++	++		+		
		Other genera		++					+	++		+		
	Scenedesmaceae	*Scenedesmus*			+	++		++	*	*		++		
	Zygnemataceae	*Spirogyra*											+	*
		Other genera		*			++						**	
	Other families		*	++	*	**	**	*	**	**	*	*	*	++
Dinophyceae	Glenodiscaceae	*Glenodinium*			*					*				
Bacillariophyceae	Coscinodiscaceae	*Melosira*	++	**	++	*	**	**	*	*	@	**	*	*
	Fragilariaceae	*Synedra*						++	++		+	+		
		Other genera	*	++	*	**	*	++	*	*		+	**	+
Cyanophyceae	Chroococcaceae	*Merismophedia*	+			++		++	++	*				
		Other genera	++	++	++	+	++	++	++	*	+	++		+
	Oscillatoriaceae	*Lyngbya*		+	**		+	*	**	**	+	+	*	+
		Other genera		++		**	*			+				
	Nostocaceae		**	++	+	*	*	++	**	*	+	++	*	+
Angiosperme	Graminae (?)			*	*		**		**	++		*		
FAUNA														
Cladocera	Sididae	*Diaphanosoma excisum*					**							@
	Daphnidae	*Ceriodaphnia cornuta*			++		++	++				*		
	Moinidae	*Moina micrura*	*	*				**						
	Bosminidae	*Bosminopsis dietersi*						**						
	Chydoridae					+								
	Other families			++		**	**	++		*				*
Ostracoda								*						*
Calanoida							++	++						*
Cyclopoida			++		*	**	*	*	++	++	*			*
Nauplii of copepoda						+	++	*	++	++		++		
Rotifera		*Anuraeopsis* spp.							+	++				
		Asplanchna spp.	++											++
		Brachionus calyciflorus					*			*		*		

Appendix 1 continued.

Higher division	Family	Genus/Species	Bada	Chan	Giri	Kau	Kiri	Min	PSM	PSN	Ridi	Tissa	Uda	Yoda
		B. caudatus	*						++	*				
		B. falcatus						++	++					*
		B. forficula			+	++	++	*			++	++		
		Filinia sp.	++					*			*	*		*
		Keratella tropica			++	++	++	++	++	++	++			++
		Lepedella sp.	++								+			
		Polyarthra sp.								++				
		Trichocera spp.	+			+		++	+	++				
		Other genera		++			++	++	*					++
Free eggs of rotifera				+		++	++	++	++	*				*
Rhizopoda	Arcellidae	*Arcella*	++			+								
	Difflugidae	*Difflugia*	++	++		+	++	*	++	++		+		++
Ciliophora	Vorticellidae								++					
	Other families			++						*		++	**	++
Insecta	Chaoborinae	*Chaoborus*					++							
	Chironomidae									**				
INANIMATE														
Detritus			@	@	@	+	**	@	**	*		@		**
Silt				++	*	+	**		*	++				