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Accounting for Diel Feeding Periodicity in Quantifying Food Resource Partitioning in Fish Assemblages in Three Reservoirs of Sri Lanka

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Abstact

Most investigations on food resource partitioning in fish along the temporal dimension are based on the diet composition of constituent species in fish assemblages, pooled over a longer time lapse, but variation within 24-hour cycle is not considered. In the present study, an attempt was made to account for diel feeding periodicity in fish species in quantifying dietary overlaps among constituent species in fish assemblages in three reservoirs of Sri Lanka. The dietary overlap of fish species estimated as a mean for short time intervals in three reservoirs is significantly lower than that is based on the sum of all time intervals, especially for pairs with moderate and high overlaps. Furthermore, the dietary overlaps estimated for short time intervals, which indicate moderate and high dietary overlaps between pairs, exhibit negligible overlaps of peak feeding period indicating the necessity to account for diel feeding periodicity in quantification of food resource partitioning.

Introduction

Ecologists have concentrated on resources partitioning among the species living in the same community, which is useful to understand the limits of inter-specific competition (MacArthur 1965; Schoener 1974; Roughgarden 1976, 1983). Ross (1986) reviewed the work on resource partitioning in fish communities and distinguished three resource dimensions along which segregation can be observed: trophic, spatial and temporal. Constituent species in fish communities can therefore be expected to minimize inter- and intra-specific competition for resource utilization along these three dimensions.

Freshwater fish assemblages in the tropics are generally considered to be complex, highly structured, and characterized by the presence of many specialized, presumably co-evolved species (Fryer and Iles 1972; Welcomme

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1979; Goulding 1980; Lowe-McConnell 1987). Reservoir fish communities on the other hand consist of fish species, which are essentially drawn from associated river systems and introduced species for various purposes (Welcomme 2001).

In Sri Lankan reservoirs, the commercial fishery is almost entirely based on two exotic cichlid species, *Oreochromis mossambicus* and *O. niloticus* that account for over 90% of the total landings (Amarasinghe 1998). In addition, small-sized indigenous cyprinid species such as *Amblypharyngodon melettinus*, *Puntius dorsalis*, *P. chola*, and *P. filamentosus*, which are presently unexploited due to poor consumer preference, and gear restrictions and mesh regulations in the commercial fisheries, are dominant in Sri Lankan reservoirs (Fernando 1967; Schiemer and Hofer 1983; De Silva and Sirisena 1987; Amarasinghe 1990). High abundance of these small-sized, indigenous fish species in reservoirs of Sri Lanka is probably due to the resource partitioning along the three dimensions and, as shown by Amarasinghe et al. (2002), their high turn-over rates. According to Piet et al. (1999), the fish assemblages in a shallow irrigation reservoir of Sri Lanka, survive during the periods of low water level, when food is scarce, by partitioning of food resources not only in the axis of the habitat but also time. As fish species are known to exhibit diel patterns of feeding (Jarre et al. 1990), it can be expected that diel feeding periodicity has some bearing on the food resource partitioning among constituent species in a given fish assemblage.

In the present study, an attempt is made to quantify dietary overlap between fish species and between different size classes of each species. An attempt is also made to investigate whether the diel patterns of feeding have any influence on the food resource partitioning among fish species. This paper forms part of a detailed study directed towards trophic evaluation of reservoir and lake ecosystems in Asia (Amarasinghe et al. 2001).

Materials and Methods

Studies were carried out in three reservoirs of Sri Lanka viz. Minneriya (6° 02’ N, 80° 53’ E; Area - 25.5 km^2), Udawalawe (6° 23’ N, 80° 50’ E; Area - 34.1 km^2) and Victoria (7° 13’ N, 80° 47’ E; Area - 22.7 km^2). Eight diel surveys (3 in Minneriya; 3 in Udawalawe; and 2 in Victoria) were carried out in the three reservoirs in January, February, July 1999 and May 2000. In each diel survey, two methods of sampling of fish were carried out. Beach seines with 7 mm stretched mesh (50 x 2m), 5 mm stretched mesh (25 x 2m) and 1 mm stretched mesh (8 x 1m) were the major sampling gear. Multi-mesh monofilament gillnets (12, 16, 20, 24, 36, 50, 60, 76, 90 mm stretched mesh sizes) were also used to sample fish. Gillnets were set from surface to bottom in shallow areas. Fish were caught in regular (mostly 2-3 hourly) intervals. When the specimens of some size classes were not caught in regular sampling intervals, sampling was repeated in the following day too, during the similar time period.

The fish sampled and preserved in 10% buffered formalin, were dissected with a lateral cut immediately after capture to facilitate penetration of preservative. They were taken to the laboratory for further examination. In the laboratory, total length of each fish was measured to the nearest 0.1 cm and grouped into pre-defined size classes (Table 1). The species/size classes, which were not sampled during the same time intervals, were disregarded in the analysis. Each fish was dissected and the stomachs/guts were separated out and pooled for each species in each size class for each time interval. As cyprinids have no stomachs, the anterior one-third of the gut was separated and contents in this portion were considered as the recently consumed food. In cichlids the entire sac like stomachs were separated and in hemirhamphids, which have very short guts, food items in the first two-third were considered as recently consumed food.

In order to determine the stomach/gut content weights of fish, the stomachs/guts of all specimens in a given size class were pooled for each species, and weighed to the nearest 0.001 g. The stomach/gut contents were then extracted and the weight of empty stomachs/guts was determined. The weight difference between full and empty stomachs/guts gives the wet weight of the stomach contents (Getachew 1989). The mean stomach/gut content weight per fish was determined by dividing total stomach/gut content weight from number of stomachs/guts pooled. These stomach content weights were plotted against time to examine diel-feeding patterns.

Stomach/gut contents of individual fish species were analysed for different size classes and different time intervals separately. One ml of the suspension of stomach/gut contents with appropriate dilutions was taken to a

Table 1. Fish species caught in the three reservoirs and size classes (as defined below) used in the present analysis. Species marked as '+' were not caught in sufficient numbers in most time intervals in the diel surveys. Numbers of fish studied for individual size classes of different species in all diel surveys in each reservoir are given in parentheses. The abbreviations (codes) used in this paper are also indicated here. Definition of size classes: 1: < 3 cm; 2: 3-6 cm; 3: 6-9 cm; 4: 9-12 cm; 5: 12-15 cm; 6: 15-18 cm; 7: 18-21 cm; 8 : 21-24 cm.

Family/Species	Code	Minneriya	Udawalawe	Victoria
Cyprinidae				
Amblypharyngodon melettinus	AM	+	2 (21), 3 (55)	2(33), 3(28)
Catla catla	CC		8 (20)	
Chela labauca	CL	2 (98)		
Danio malabaricus	DM	+		3(99)
Esomus danrica	ED	+		3(28)
Labeo rohita	LR		6 (28)	
Puntius dorsalis	PD	+	6 (22)	+
P. filamentosus	PF	3 (45), 4 (63)	4 (67)	3 (55), 4 (105), 5(94)
Rasbora daniconius	RD	1(38), 2 (49), 3 (103)	2 (35), 3 (33)	+
Cichlidae				
Etroplus maculatus	EM	2 (42)		+
E. suratensis	ES	+	2 (51), 3 (43), 4 (35)	+
Oreochromis mossambicus	OM	5 (42)	+	+
O. niloticus	ON	5 (48)	5 (38)	+
Tilapia rendalli	TR	2 (73), 3 (56), 5 (32)	+	+
Gobiidae				
Glossogobius giuris	GG	2 (59)	3 (71)	+
Hemirhaphidae				
Hemirhamphus limbatus	HL	4 (105), 5 (124)	3 (43), 4 (136), 5(115)	

Sedgwick-rafter counting cell and examined under a light microscope. Likewise three sub-samples were examined from each suspension. The relative bio-volumes of food were estimated according to the point method (Hynes 1950). All the food items were identified to the lowest possible taxon. Accordingly, a total of 96 food items were identified. However, the diets of the species/size classes, which were considered in the present analysis, consisted of only 41 food items. Using approximate volumetric proportions of food items (visually judged under light microscope) in each size class of individual fish species dietary overlap was determined by the following index (Schoener 1974).

S=1-0.5(å½*Pxi* - *Pyi*½)

where *Pxi* and *Pyi* are the proportions of the resource *i* used by species *x* and *y* respectively. The values of Schoener's index (S) range from 0.0 (no overlap) to 1.0 (complete overlap). In this analysis, overlaps >0.66 were considered to be high and those <0.33 low, and overlaps in between 0.33-0.66 were considered as moderate. This analysis was performed for the data on diet composition of fish species and different size classes of a given fish species for each time interval separately and the mean value of S for all time interval was considered as the index of dietary overlap. This value is referred to as S_M hereafter. In addition, dietary overlap was also calculated for different size classes of fish species taking the proportions of food items pooled for all time intervals of the day, which is referred to as S_P hereafter.

In the species/size class pairs with >0.33 (i.e., moderate and high) dietary overlaps, feeding periods of the day, which were determined by the iterative method, MAXIMS (Jarre et al. 1990), and presented in another paper in the series (Weliange et al. in prep.), were used to investigate whether there was a temporal segregation in feeding.

Results

There were 16 fish species, which were caught in sufficient numbers during different time intervals of the 8 diel surveys in the three reservoirs (Table 1). Diel patterns of feeding periodicity of different size classes of these fish species in Minneriya, Udawalawe and Victoria reservoirs are presented elsewhere (Weliange et al. in prep.).

Of the 16 fish species considered in the present analysis, there were 9 species in Minneriya reservoir, which fed on 30 food items (Table 2). The 10 species caught in Udawalawe reservoir had 33 food items (Table 3). There were only 4 species in Victoria reservoir, which were considered in the present analysis in 2 diel surveys and 28 food items were found in these 4 species (Table 4).

The Schoener's indices calculated for pairs of different size groups of individual species and for different species for the 8 surveys separately are given in figure 1 for Minneriya, Udawalawe and Victoria reservoirs. Here

Table 2. The volumetric proportions (%) of the food items of fishes in Minneriya reservoir, which were used to estimate dietary overlaps. * - Small proportions (<1%). D1 (February 1999), D2 (July 1999) and D3 (May 2000) are first, second and third diel surveys in Minneriya reservoir respectively. Abbreviations for species and size classes are as given in Table 1.

Food items	D1										D2							D3		
	CL2	EM3	GG2	HL4	HL5	PF4	RD1	RD2	RD3	TR2	CL2	EM2	HL4	PF3	RD3	TR2	TR3	TR5	ON5	OM5
Melosira	*	*	*			*				*		*		*		*	*	*	1	1
Pinnularia		*				*				*				5		*	*	*	2	*
Other diatoms		25	*			1			*	2	*	*		1		*	2	*	1	1
Microcystis	*			*		*				*			*	*			*	3	15	1
Bulbochaete		1				*			*	*									*	
Closterium		*				*				*			*	1		*	1	*	*	*
Oedogonium		*				1			*	2				1			*	*	*	*
Oscillatoria		*								*			1							
Pediastrum		*				*				*			*	*		*	1	*	1	*
Spirogyra						*	*			2				*					*	
Filamentous algae		*				*				*		*				1	*	*	1	*
Macrophytes	1	69				68		8	18	51		1		2				93	2	2
Bosmina				3	3								*							
Chydorus			*	4	10		2	3	2	1				3	2					
Daphnia lumholtzi				7	4	5		1												
Other Daphnids	1			12	13		3	6	1		6	1	10	6	7	4			*	
Diaphanosoma				4	10		2	3	2				1	2						
Macrothrix	1		*			1								1						
Moina	3		*	24	20		2	1	1		3		39	36	23					
Parts of Cladocerans							1					11		2						
Copepods	1		*	18	6		32	30	6			1	4		4		1			*
Fish scales		2					2		7	1					11	7				
Fish eggs										4										
Fish			38				4								3				1	
Insect larvae	3	*	2	5	2			1	3		44	44	32	1	19	30	2	1		
Insects	88	*	22	21	27	11	19	36	61	22	46	30	11	31	30	9	8	*		
Caridinia			37																	
Mollusks	*			2	5	7		1		*		*	2	*		1				
Gamules and spicules						1								*			*		*	
Detritus	1	2	*			3	30		*	7	*	8		7		47	81	2	74	94

Note: Volumetric proportions of food items indicated in italics as detritus probably represent digested matter.

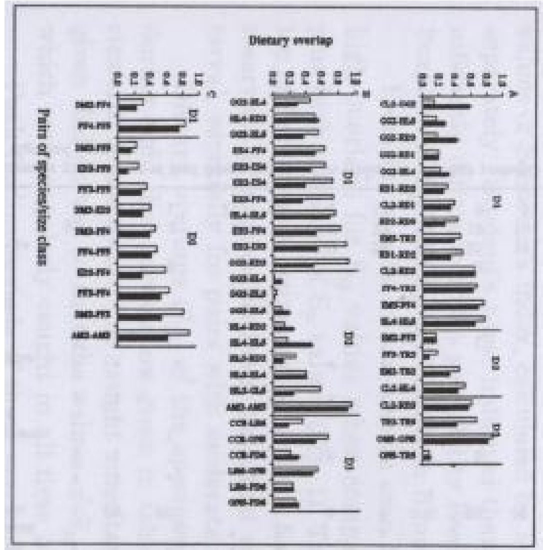

Fig. 1. The dietary overlaps calculated as S_P (open bars) and S_M (dark bars) in the three reservoirs during 8 diel surveys. Here S_P is the index of dietary overlap based on the pooled diet composition for all time intervals over a 24 h period and S_M is the mean value of indices of dietary overlap based on the observed diet compositions in specific time intervals. A - Minneriya; B - Udawalawe; C – Victoria. D1, D2 and D3 refer to the diel surveys (See tables 2,3 and 4 for abbreviations). Species abbreviations are as indicated in table 1. The numeral next to the species abbreviation is the size class as defined in table 1.

Table 3. The volumetric proportions of the food items of fishes in Udawalawe reservoir, which were used to estimate dietary overlaps. * - Small proportions (<1%). D1 (February 1999), D2 (July 1999) and D3 (May 2000) are first, second and third diel surveys in Udawalawe reservoir respectively. Abbreviations for species and size classes are as given in Table 1.

Food items	D1								D2							D3			
	ES2	ES3	ES4	GG3	HL4	HL5	PF4	RD3	AM2	AM3	GG3	HL3	HL4	HL5	RD2	CC8	LR6	ON5	PD6
Cyclotella										*	1					*		*	
Melosira	*	*	*				*+		1	1						*	*	1	*
Pinnularia	*	*	*				*								1	*	*	*	
Other diatoms	*	*	*				*	*		*						*	*	1	*
Microcystis					*				3	3						1	*	*	
Closterium	1						*		*	*					*	*	*	*	
Docidium	1	*															*	*	
Mougeotia	1		*													*		*	
Oedogonium		*														*	*	*	
Oocystis									*	*								*	
Pediastrum	2	*	*				*		8	7						*	*	4	*
Pleurotaenium																	1	*	
Spirogyra		*	*		*	*		3											
Staurastrum	*	*	*				*		*	*						*	*	*	
Filamentous algae	11	12	2			*	9		*	*						*	1	*	
Peridinium																*	*	*	
Macrophytes	73	73	93	*	3	7	53						*			3	48	13	*
Bosmina					18	22		2					*	1	1	8	*		
Chydorus											5		*	*				2	1
Daphnids					2	*				2		1	*	2	4				
Diaphanosoma												10	*	6	10	*			
Macrothrix	1															*			
Moina					9	4		1	4			16	1	32	62	*			
Copepods	*			1	12	3					1	37	96	13	13	18	+		
Cypridopsis							1				*	1	*			*	*	*	1
Fish scales		*	2	5									*	1					
Fish eggs					*	*	13												
Fish				2							82								*
Insect larvae				3	3	8					2	26	2	14					28
Insects	3	2		89	45	56	18	92			9	4	*	18	9	*	3	6	50
Caridina					5						2			1					
Mollusks					1							5	*	11					
Detritus	7	10	2				6		84	85						66	43	68	20

Note: Volumetric proportions of food items indicated in italics as detritus probably represent digested matter.

Table 4. The volumetric proportions of the food items of fishes in Victoria reservoir, which were used to estimate dietary overlaps. * - Small proportions (<1%). D1 (January 1999) and D2 (July 1999) are first and second diel surveys in Victoria reservoir respectively. Abbreviations for species and size classes are as given in Table 1.

Food items	D1			D2						
	DM3	PF4	PF5	AM2	AM3	DM3	ED3	PF3	PF4	PF5
Cyclotella				1	1		*	*	*	*
Melosira	*	*	*	3	4		1	*	*	*
Other diatoms	*			*			*	*	*	*
Coelosphaerium				1	3					
Merismopedia				1	1		*	*		
Microcystis				9	10	*	26	1	1	
Bulbochaete							*	1	*	*
Coelastrum				1	1		*			
Oedogonium							*	*	*	*
Pediastrum				1			1			
Scenedesmus				1	*		*	*	*	*
Staurastrum	*	*	*	3	4		1	*	*	*
Staurodesmus				*	*		*			
Macrophytes	1	68	92			2	2	8	30	75
Bosmina								1		
Chydorus	*	*	*							
Daphnids	2	1			2	18	2	17	3	2
Diaphanosoma			1					1		1
Macrothrix		*						1		
Moina	2	1			3	1		6		
Parts of Cladocerans	*	*			*	*	1	2		
Copepods	*	6	*				1	1	1	
Parts of Copepods		*	*				1			
Trichocerca				*	1					
Fish scales			2						9	
Insect larvae						70	28	42	32	11
Insects	91	20	4	2		8	23	15	19	10
Detritus	3	2	1	77	69	1	12	3	5	1

Note: Volumetric proportions of food items indicated in italics as detritus probably represent digested matter.

values of Schoener's index, calculated by both methods (S_M and S_P) are given separately. Student's t-test indicated that mean values S_M and S_P were significantly different at 5% probability level (t_{obs} = 2.02; df = 118; $p < 0.05$). Boxplots of S_M and S_P are shown in figure 2.

From the results, it can also be seen that 57% of pairs had moderate or high overlaps for S_M values when compared to 65% of pairs of moderate plus high overlaps of S_P values (Fig. 1). This indicates that the dietary overlap of fish species estimated as a mean for short time intervals in the three reservoirs is appreciably lower than that when it is based on a long time interval, especially for pairs with moderate and high overlaps.

Dietary overlaps (S_M) of the species/size class pairs in three reservoirs during eight diel surveys are given in table 5. It must be noted that all species/size classes were not caught simultaneously in all time intervals of a given diel survey so that the values of S_M are available only for the species, which were regularly caught in all time intervals in a diel survey.

Peak feeding periods of these species/size classes are shown in figure 3. This indicates that although these species/size classes exhibit moderate or high dietary overlaps, peak feeding periods of most of them do not overlap.

Discussion

Food resource partitioning among constituent species in fish assemblages is one of the major aspects in niche segregation in their habitats. MacArthur (1965) and Levins (1968) argued that in a competitive system, as the number of species increases, the constituent species in a community will have to segregate through resource partitioning in order to achieve minimal overlap. This argument assumes an eventual incompressibility of a species niche on trophic, spatial and/or temporal dimensions. Piet and Guruge

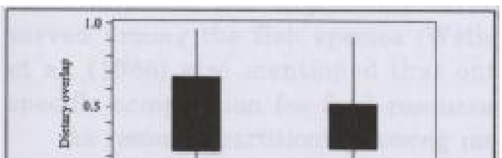

Fig. 2. Comparison of S_P and S_M estimated for 60 species/size classes. The boxplots consist of the centre-line (median) splitting the rectangle defined by the 25th and 75th percentiles. Whiskers are lines drawn from the ends of boxes to the maximum and minimum data points. The solid circles in the boxplots indicate mean values. S_P and S_M are as defined in figure 1.

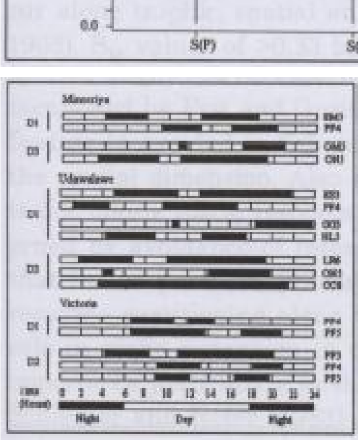

Fig. 3. Peak feeding periods of the pairs of species/size classes, which exhibit moderate and high dietary overlap. D1, D2 and D3 refer to diel surveys as indicated in the tables 2,3,and 4. The abbreviations for the species are as indicated in Table 1. The numeral next to the species abbreviation is the size class also as defined in table 1. Peak feeding periods of the day were determined by the iterative method, MAXIMS (Jarre et al. 1990), and presented in another paper in the series (Weliange et al. in prep.).

(1997), who studied diel variation in feeding and vertical distribution of 10 co-occurring fish species in a Sri Lankan reservoir, suggested that resource partitioning along the spatial dimension is mainly aimed at avoiding compe-

Table 5. Dietary overlap (S_M) matrices of different species/size classes in 8 diel surveys in the three reservoirs. Abbreviations for the diel surveys in Minneriya, Udawalawe and Victoria reservoirs are as given in Tables 2, 3 and 4 respectively. Dietary overlaps were calculated for the pairs, which were caught simultaneously in sufficient numbers in all time intervals in a given diel survey. Abbreviations for species and size classes are as given in Table 1.

(a). Minneriya (D1)

	CL2	EM3	GG2	HL4	PF4	RD1	RD2
GG2	0.58						
HL4			0.31				
HL5			0.27	0.65			
PF4		0.70					
RD1	0.34		0.20				
RD2						0.34	
RD3	0.65		0.42			0.25	0.27
TR2		0.39			0.62		

(b). Minneiya (D2)

	CL2	EM3	PF3	TR2
HL4	0.44			
PF3		0.17		
RD3	0.57			
TR2		0.320	0.07	-
TR3				0.425

(c). Minneriya (D3)

	OM5	ON5
ON5	0.80	-
TR5		0.09

(d). Udawalawe (D1)

	ES2	ES3	ES4	GG3	HL4
ES3	0.55	-			
ES4	0.39	0.45	-		
HL4				0.30	-
HL5				0.37	0.70
PF4	0.52	0.36	0.51		
RD3				0.50	0.55

(e). Udawalawe (D2)

	AM2	GG3	HL3	HL4
AM3	0.92			
HL3		0.03	-	
HL4		0.11	0.41	-
HL5		0.19	0.24	0.47
RD2			0.13	0.25

(f). Udawalawe (D3)

	CC8	LR6	ON5
LR6	0.19	-	
ON5	0.52	0.49	-
PD6	0.31	0.24	0.32

(g). Victoria (D1)

	DM3	PF4
PF4	0.22	-
PF5		0.74

(h) Victoria (D2)

	AM2	DM3	ED3	PF3	PF4
AM3	0.61				
ED3		030	-		
PF3		0.53		-	
PF4		0.40	0.30	0.52	-
PF5		0.17	0.12	0.29	0.41

tition at the time of feeding. However, studies on food resource partitioning along the temporal dimension are generally based on the stomach/gut content data pooled over a longer time lapse such as days, months, seasons or years. For example, Moyle and Senanayake (1984) studied food resource portioning among fish species of rainforest streams of Sri Lanka based on diet composition of fish species collected over a period of three months. Conversely, diel feeding patterns of fish species are known to vary having one or two peak feeding periods within a day (Jarre et al. 1990). As such, degree of food resource partitioning during peak feeding periods of the day may be different from that of non-feeding periods of the diel cycle. De Silva et al. (1996) based on this issue, have emphasized the importance of incorporating diel feeding periodicity in the quantitative analyses of food resource partitioning in fish communities. The present analysis indicates explicitly that the degree of dietary overlap measured as Schoener's index (Schoener 1974) is inconsistent when it is quantified as S_M and S_P. As shown by the differences in estimates of S_M and S_P in the present analysis, quantification of dietary overlaps based on long time lapse perhaps produces misleading results.

Present analysis also revealed that in addition to diel variations in food resource partitioning among members of fish communities, seasonal variations in resource partitioning occur, possibly due to the variations in food availability during low water level and high water level in reservoirs. This aspect has however been dealt with, in some details, by various workers (Jepsen et al. 1997; Piet et al. 1999b). Peit et al. (1999a) suggested that when resources are scarce, partitioning of these resources is an important mechanism for potential competitors in a fish assemblage to coexist. They have further stated that species with large ontogenetic changes have a higher potential for niche expansion, which helps to relax them partially from intra-specific competition. In these three reservoirs too, size dependent variations in feeding patterns were observed among the fish species (Weliange and Amarasinghe 2003). Tonn et al. (1986) also mentioned that ontogenetic dietary shifts relax intra-specific competition for food resources.

As resource partitioning among members of the animal communities occur along trophic, spatial and temporal dimensions (MacArthur 1965; Levins 1968), S_M values of >0.33 between any two species or size classes of a given species might not necessarily indicate high or moderate dietary overlap. As mentioned by Peit and Guruge (1997), exploitative competition at the time of feeding is avoided in fish communities through resource partitioning along the spatial dimension. Also as suggested by the same authors, when feeding is not taking place, resource partitioning along the spatial dimension is governed by avoidance of interference competition. Present analysis indicates that in the pairs of species/size classes with S_M values greater than 0.33, resource partitioning along the temporal dimension also plays a significant role in niche expansion in co-occurring species. However, this might be of importance particularly in the situations where food resources are not scarce. Schiemer and Hofer (1983) have also shown that *P. chola* and *P. dorsalis*, which had similar feeding habits in a Sri Lanka reservoir fed during different time intervals of the day.

Segregation of food resource uses along temporal dimensions among constituent species in the fish communities in the three reservoirs as shown by the present study might have contributed to colonization success of fish species in the reservoir ecosystems. It is known that spatial differences in environmental conditions are found in reservoir ecosystems due to the presence of lacustrine zones, riverine zones and transition zones (Thornton et al. 1990). Although not attempted in the present analysis, spatial variations in food availability for fish may also occur, which perhaps result in food resource partitioning in spatial dimensions, as shown by Peit and Guruge (1997).

When accounting for diel feeding periodicity to quantify dietary overlaps using Schoener's index (Schoener 1974), it is suggested that the mean value be estimated (S_M) for several time intervals of the day. However, at an extreme case when one species or size class in the pair is not feeding, such observations should be omitted in estimating dietary overlap through temporal dimensions.

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