Sri Lanka J. Aquat. Sci. **10** (2005): 19-34

Food niche segregation among co-occurring endemic fish species in Sri Lanka

R.R.A.R. SHIRANTHA*, M.J.S. WIJEYARATNE AND U.S. AMARASINGHE

Department of Zoology, University of Kelaniya, Kelaniya, Sri Lanka.

*Corresponding Author (E-mail: r_shirantha@hotmail.com)

Abstract

The food and feeding habits of six endemic freshwater fish species namely, *Belontia signata*, *Rasbora vaterifloris*, *Puntius cumingii*, *Puntius nigrofasciatus*, *Puntius titteya* and *Garra ceylonensis* inhabiting the streams of the Kalu and Kelani river basins in Sri Lanka were studied from October 1998 to September 2000 with the objective of quantifying the food niche overlap and evaluating the degree of competition for food resources among them. All fish species studied except *R. vaterifloris* were found to be omnivorous, feeding on different varieties of food items. *R. vaterifloris* was found to be strictly carnivorous. *P. titteya* and *B. signata* were highly selective for diatoms, aquatic insects and rotifers while *P. cumingii*, although highly selective for diatoms, was non-selective for aquatic insects and filamentous algae. *P. nigrofasciatus* was selective for diatoms, aquatic macrophytes and non-selective for green algae. *R. vaterifloris* and *G. ceylonensis* were selective for aquatic insects and crustaceans and non-selective for diatoms, rotifers and detritus.

P. nigrofasciatus showed a moderate dietary overlap with *P. cumingii* and a low dietary overlap with other co-occurring species. *R. vaterifloris* showed moderate dietary overlap with *G. ceylonensis* and a low dietary overlap with other co-occurring species. A moderate dietary overlap was observed among *B. signata*, *P. cumingii*, *P. titteya* and *G. ceylonensis*. The results indicated that there is very little or no interspecific competition among these species due to low or moderate dietary overlap and different degree of selectivity for different food items, which has enabled them to co-exist.

Introduction

Morphologically similar co-occurring fish species are reported to be often sharing the same resources resulting in intensive interspecific competition (Costa and Fernando 1967; Bishop 1973; Gatz 1979; Winemiller 1991). The mechanism of resource partitioning minimizes or avoids the possible intensive competition among sympatric species (Lévêque 1997).

Feeding on different food items or feeding on same food items at different intensities or at different times would reduce the intensity of competition for food resources resulting in niche segregation. Studies of food resources partitioning among the co-occurring fish species help to understand the intensity of interspecific competition for food resources and the niche segregation among co-existing species (Schoener 1970, 1974; Roughgarden 1976).

Many studies on food and feeding habits of some endemic freshwater fish species co-exiting in the freshwater bodies in Sri Lanka have been carried out (Costa and Fernando 1967; De Silva and Kortmulder 1977; Kortmulder et al. 1978; De Silva et al. 1980; Moyle and Senanayake 1984; De Silva and Somarathna 1994; Divigalpitiya et al. 1998; Samayawardena *et al.* 2000). However, only a few of them deal with food resources partitioning and food niche overlap among the endemics (Moyle and Senanayake 1984; Divigalpitiya et al. 1998; Samayawardena et al. 2000).

Present study was carried out to investigate food niche segregation of six endemic fish species co-exiting in stream habitats in the wet zone of Sri Lanka. The fish species studied were *Rasbora vaterifloris*, *Puntius cumingii*, *P. titteya*, *P. nigrofasciatus*, *Belontia signata*, and *Garra ceylonensis*. All these species are considered to be threatened and conservation dependent (IUCN 2000, Ekaratne et al. 2003). Studies on food and feeding habits, food niche segregation and degree of preference for different food items would be helpful in *ex situ* conservation practices such as rearing in aquaria for captive breeding with the objective of to releasing the offspring back into the natural environment. Further, the results of these studies would also be useful for *in situ* conservation to take necessary measures to ensure the availability of preferred food in their natural habitats.

Materials and Methods

Collection of samples

Present study was carried out in selected sampling sites the Kalu and Kelani river basins in the wet zone of Sri Lanka from October 1998 to September 2000. Fifteen sampling sites from each river basin (Figure 1) were selected randomly based on available literature on their distribution (Pethiyagoda 1991). At each sampling station, around 20 specimens of each fish species were caught at monthly intervals using a cast net of 1 cm stretched mesh and a fine meshed scoop net. Immediately after capture, fishes were preserved in 10% buffered formalin and taken to the laboratory for detailed analysis. On each sampling occasion, plankton samples were collected using a plankton net of 50 μ mesh. One plankton sample was preserved in Lugol solution for phytoplankton analysis and another sample was preserved in 5% buffered formalin for zooplankton analysis.

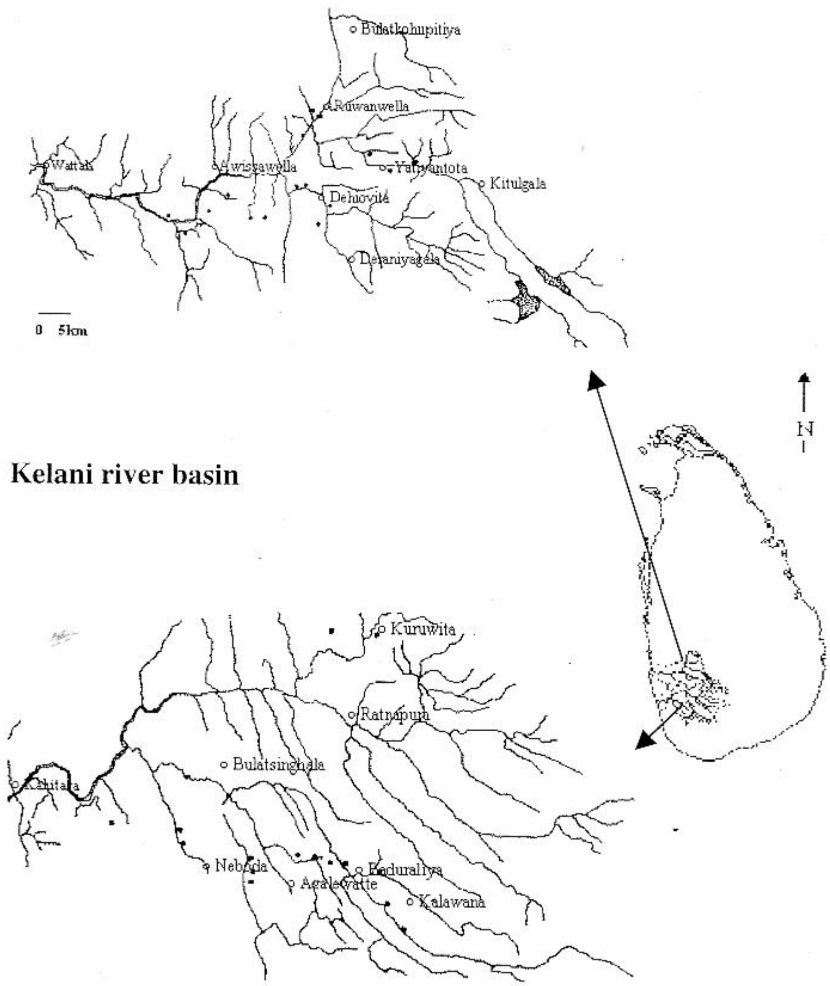

Figure 1. Map of the Kalu and Kelani river basins showing the sampling sites (•sampling sites).

In the laboratory, after measuring the total length and weight, each fish was eviscerated and the stomach contents were scooped out. Since Kalu river basin cyprinids do not process well-defined stomachs, contents in the anterior most 1 cm of the intestine were scooped out. The food items were identified under an optical microscope up to genus level using Needham and Needham (1962), and Abeywickrama (1979). The quantitative analysis of the stomach/gut contents of each fish species was carried out using the volumetric method described by Helawell and Abel (1971). A cell of *Spirogyra* was used as an arbitrary unit to determine the relative volume of each food item. The relative importance of major taxonomic groups of food items in the diet of each fish species was thus determined volumetrically.

Analysis of plankton samples

The plankton species in the samples collected from each site were identified as much as possible using Needham and Needham (1962), Mendis and Fernando (1962) and Abeywickrama (1979). The relative volumes of major taxa of plankton were estimated using a cell of *Spirogyra* as an arbitrary unit and the relative importance of each major taxon in the plankton samples was determined. These values were later used to calculate the co-efficient of electivity for different food items.

Food niche overlap

The similarities among the diets of co-existing fish species at each sampling site were determined by similarity index of Schoener (1970).

$$S = 100 - 0.5 \Sigma \, |Px_i - Py_i|$$

where,

S = Similarity index.

Px_i = Relative importance (%) of a particular food item in species x.

Py_i = Relative importance (%) of the same food item in species y.

The values for S range from 0 to 100 and give the % overlap in the diet between the two species considered. In the present study, the values less than 33.3 were considered to indicate a low overlap, the values between 33.3 and 66.7 to indicate a moderate overlap and the values higher than 66.7 to indicate high overlap as suggested by Moyle and Senanayake (1984).

Coefficient of electivity

The preference for different food items by each fish species was determined by calculating Ivlev's coefficient of electivity (E) using the following equation (Ivlev 1961).

$$E = (r_i - p_i)/(r_i + p_i)$$

where,

r_i = Relative importance of any food item in the gut/stomach (expressed as percentage volume)

p_i = Relative importance of same food item in the environment (expressed as percentage volume)

The values for coefficient of electivity range from +1.00 to −1.00. The positive values indicate selection of a certain food item and negative values indicate avoidance (Ivlev 1961).

Results

A large number of food items of different taxa were recorded in the gut/stomach contents of the fish species studied. These included 4 genera of Cyanophyceae (Blue green algae), 11 genera of Bacillariophyceae (Diatoms), 28 genera of Chlorophyceae (Green algae), one genus each in Euglenophyceae and Rodophyceae, 4 genera of Protozoans, 9 genera of rotifers, together with many crustaceans and aquatic insects. There was no apparent temporal difference in the composition of the diet of different sized individuals of any particular fish species. Therefore, data of all individuals of any one species irrespective of the size were pooled together in order to obtain a comprehensive picture on its food and feeding habits. The different taxa of food items of each fish species are listed in Table 1. The diet of all fish species was dominated either by phytoplankton or zooplankton. Of the food items, the green algae, diatoms, insects and rotifers were highly diverse groups which contributed most to the diet of many species of fish studied. The relative importance of major taxa of food items in each fish species inhabiting the two river basins are shown in Figure 2. It is evident that the food items in the diet of a particular fish species considerably differ in two river basins.

All fish species studied other than *R. vaterifloris,* were found to be omnivorous (Figure 2). *R. vaterifloris*, which was found only in some tributaries of the Kalu river basin, was observed to be carnivorous. More than 80% of the diet of this species comprised of insects. The rest of the diet consisted of crustaceans and rotifers, which contributed 16% and 3% respectively. When the mean values for the coefficient of electivity for different food items are considered, *R. vaterifloris* appeared to be selective for all food items found in their gut contents i.e. aquatic insects, crustaceans and rotifers (Table 2).

B. signata, which inhabits both river basins, was found to be feed mainly on aquatic insects and green algae (Figure 2). However, aquatic macrophytes and blue green algae, which were found in small amount in the diet of *B. signata* inhabiting Kalu river basin, were not recorded in the stomach contents of those collected from the Kelani river basin. The mean values for the coefficient of electivity indicated that *B. signata* was selective for aquatic insects, rotifers and diatoms (Tables 2 and 3). Although green algae contributed for more than 22% of the diet, the negative values for the coefficient of electivity indicated that this species is not selective for green algae.

The aquatic insects and green algae were the most important food items of *P. cumingii* in both river basins. Over 60% of its diet consisted of these food items. *P. cumingii* inhabiting Kalu river basin was found to feed on considerable amount of rotiferans (18%) and blue green algae (5%) although they were not recorded from the diet of those inhabiting in Kelani river basin.

Table 1. The food items found in the gut/stomach contents of fish species studied in the Kalu and Kelani river basins. (Bs- *Belontia signata*; Gc- *Garra ceylonensis*; Pc- *Puntius cumingii*; Pn- *Puntius nigrofasciatus*; Pt- *Puntius titteya* and Rv- *Rasbora vaterifloris*).

Food item	Kelani river basin					Kalu river basin					
	Bs	Gc	Pc	Pn	Pt	Bs	Gc	Pc	Pn	Pt	Rv
Cyanophyceae											
Anabaena			+								
Lyngbya			+	+	+	+			+		
Rivularia	+			+							
Scytonema	+		+	+	+	+		+	+		
Bacillariophyceae											
Achnanthes					+		+			+	
Asterionella		+									
Cocconeis		+	+	+	+		+			+	
Coscinodiscus	+	+	+		+			+	+	+	
Cyclotella		+	+				+			+	
Cymbella		+						+		+	
Diatoma	+	+	+	+	+	+	+	+	+	+	
Navicula	+	+	+	+	+	+		+			
Pinnularia	+		+	+	+			+			
Stauroneis			+	+	+			+			
Surirella				+	+	+					
Chlorophyceae											
Bulbochaete	+		+	+	+			+			
Chaetophora	+		+		+			+			
Cosmarium	+		+	+	+	+		+			
Closterium			+	+	+	+		+			
Cylindrocapsa			+								
Cladophora	+		+	+	+	+		+			
Desmidium			+	+	+			+			
Docidium	+		+		+			+			
Euastrum								+			
Gonatozygon								+			
Hormidium			+					+	+		
Hyalotheca				+							
Micrasterias			+	+							
Microspora	+			+	+						
Mougeotia	+		+	+							
Netrium	+										
Oedogonium	+		+	+				+			
Pediastrum					+						
Penium	+		+	+							
Rhizoclonium			+	+							
Sirogonium			+	+	+			+			
Spirogyra	+		+	+	+	+		+			
Spondylosium	+		+	+				+			
Staurastum	+										
Tetmemorus			+			+				+	
Triploceras	+		+	+	+			+	+		
Ulothrix			+	+	+	+					

Table 1. Continued.

Zygnema	+		+	+	+	+					
Euglenophyceae											
Euglena			+	+							
Rodophyceae											
Batrachospermum									+		
Protozoa											
Acanthocystis	+					+					
Actinosphaerium	+				+	+		+	+		
Paramecium	+									+	
Urolegena								+		+	
Rotifera											
Asplanchna	+							+	+	+	
Conochilus								+			+
Dicranophorus											+
Kellicittia			+					+			+
Lecane	+		+							+	+
Mytilina											+
Philodina	+		+					+	+		+
Rotaria										+	+
Trichocera							+				
Crustacea											
Branchiopoda	+	+							+		
Malacostraca											
Zoea larvae										+	+
Mysis larvae										+	+
Shrimps	+				+						+
Copepoda	+						+	+			+
Naupili larvae	+						+			+	
Insecta											
Dipteran larvae	+	+	+	+	+	+		+		+	+
Coleoptera larva	+		+	+	+	+		+		+	+
Ephemeroptera	+	+	+		+	+		+		+	+
Plecoptera	+				+	+			+		+
Hemiptera	+					+			+		+
Aquatic macrophytes	+		+	+		+			+		

P. cumingii inhabiting Kelani river basin was found to feed on detritus too. The mean values for the coefficient of electivity indicated that *P. cumingii* was selective only for diatoms and green algae (Tables 2 and 3).

P. titteya inhabiting the two river basins was found to feed predominantly on aquatic insects and diatoms. In addition, green algae also contributed for a significant portion of the diet of *P. titteya* inhabiting the Kelani river basin. However, green algae were not found in the gut contents of *P. titteya* in the Kalu river basin. The relative abundance of rotifers and crustaceans in the gut contents of *P. titteya* inhabiting Kalu river basin was very low (2%) while in those inhabiting the Kelani river basin these contributed for about 12% of the diet. The mean values for the coefficient of electivity indicated that *P. titteya* is selective for diatoms, aquatic insects and

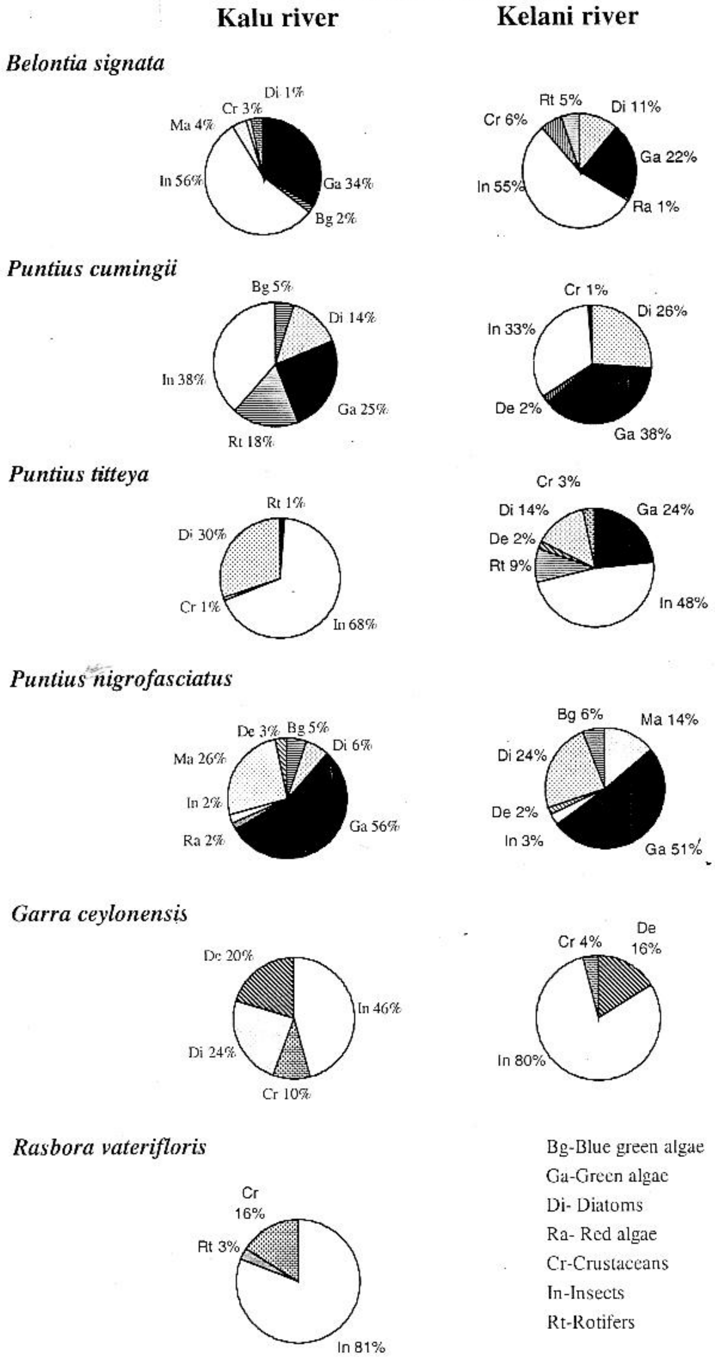

Figure 2. Relative importance of different taxa of food items found in the gut/stomach contents of each fish species studied in the Kalu and Kelani river basins.

Table 2. The mean values for the coefficient of electivity of major taxa of food items found of the in the fish species inhabiting the Kalu river basin (Bg-Cyanophyceae; Di-Bacillariophyceae; Ga- Chlorophyceae; Ra- Rhodophyceae; In- Insecta; Cr- Crustacea; Rt-Rotifera; Ma-Aquatic macrophytes; De- Detritus).

Species	Bg	Di	Ga	Ra	In	Cr	Rt	Ma	De
B. signata	- 0.73	0.02	-0.32	-0.06	0.42	-0.19	0.33	-0.82	-1.00
P. cumingii	-0.05	0.43	0.11	-	-0.03	-0.35	-0.06	-1.00	-0.52
P. nigrofasciatus	-0.68	0.18	-0.02	-0.25	-0.65	-1.00	-1.00	0.97	0.50
P. titteya	-1.00	0.66	-0.43	-	0.56	-0.18	0.19	-1.00	-1.00
R. vaterifloris	-1.00	-1.00	-1.00	-1.00	0.51	0.24	0.14	-1.00	-1.00
G. ceylonensis	-1.00	0.56	-1.00	-1.00	0.14	0.13	0.80	-1.00	-0.83

Table 3. The mean values for the coefficient of electivity of major taxa of food items found of the in the fish species inhabiting the Kelani river basin (Bg-Cyanophyceae; Di-Bacillariophyceae; Ga- Chlorophyceae; In- Insecta; Rt- Rotifera; Cr- Crustacea; Ma-Aquatic macrophytes; De- Detritus).

Species	Bg	Di	Ga	In	Cr	Rt	Ma	De
B. signata	-1.0	0.02	-0.52	0.82	-0.19	0.33	-0.82	-1.00
P. cumingii	-0.05	0.23	0.11	-0.03	-0.15	-0.06	-1.00	-0.56
P. nigrofasciatus	-0.32	0.38	-0.02	-0.62	-1.00	-1.00	0.85	0.60
P. titteya	-1.00	0.42	-0.83	0.36	-0.18	0.22	-1.00	-1.00
G. ceylonensis	-1.00	0.72	-1.00	0.58	0.24	0.60	-1.00	-0.45

rotifers. Although the considerable amounts of green algae, crustaceans and detritus were found in the gut contents, this species appeared to be non selective for them (Tables 2 and 3).

Of the fish species studied, *P. nigrofasciatus* was found to have the most diverse diet. The green algae and aquatic macrophytes were the most abundant food items in the gut contents of *P. nigrofasciatus* in the Kalu river basin while diatoms and green algae were the most important items of those inhabiting the Kelani river basin. The animal matter contributed only for a small proportion of the diet (≤3%). Although green algae is the most abundant food item in the diet, *P. nigrofasciatus* was found to be non selective for these. It was selective for diatoms, aquatic macrophytes and detritus (Tables 2 and 3). The main food items of *G. ceylonensis* were aquatic insects and detritus. In the Kalu river basin diatom also contributed for a significant proportion of the diet (24%). The mean values for the coefficient of electivity indicated that *G. ceylonensis* is selective for all food items found in their gut contents, other than diatoms.

The dietary overlap of different species that co-exist in each river basin is given in Tables 4 and 5. There was no high dietary overlap among the co-occurring fish species in both two river basins. *P. nigrofasciatus* in the Kalu river basin, showed a moderate dietary overlap with *P. cumingii* and a low overlap with other fish species. However *P. nigrofasciatus* in Kelani river basin showed a low dietary overlaps with all other co-occurring fish species. *P. cum*ingii and *P. titteya* in both river basins showed moderate dietary overlaps with other co-occurring fish species. *R. vaterifloris* showed a moderate overlap with *G. ceylonensis* and low overlap with other co-occurring fish species.

Table 4. The food niche overlap (as %) among the co-occurring fish species studied in the Kalu river basin. (Bs- *Belontia signata*; Rv- *Rasbora vaterifloris*; Pc- *Puntius cumingii*; Pt- *Puntius titteya*; Gc- *Garra ceylonensis*).

	Pc	Pt	Bs	Gc	Rv
P. nigrofasciatus	34.60	4.63	17.60	0.00	0.00
P. cumingii	-	Nc	46.50	38.20	Nc
P. titteya	-	-	49.70	35.46	Nc
B. signata	-	-	-	56.20	Nc
G. ceylonensis	-	-	-	-	53.04

Nc- Not co-occurring

Table 5. The food niche overlap (as %) among the co-occurring fish species studied in the Kelani river basin. (Bs- *Belontia signata*; Pc- *Puntius cumingii*; Pt- *Puntius titteya* and Gc- *Garra ceylonensis*).

	Pc	Pt	Bs	Gc
P. nigrofasciatus	28.98	18.60	32.64	0.00
P. cumingii	-	39.51	57.80	42.32
P. titteya	-	-	44.19	46.83
B. signata	-	-	-	38.50

Discussion

The feeding habit of a particular fish species is closely related to its morphological features (Lagler et al. 1977). All fish species used in the present study except *B. signata* are of the same family, i.e. Cyprinidae and are morphologically similar. The results of the present study revealed that, although they are morphologically similar and co-exist in the same habitat, the composition of the diets varies considerably (Table 1 and Figure 2). The composition of the diet of the same species living in two river basins also varied. These differences may have resulted due to the different degree of selectivity of different food items by different fish species although they are morphologically similar. Most of the fish species studied are euryphagous, i.e. they depend on variety of food resources. This euryphagous habit and selectivity for different food items minimize the competition for food and also result in niche segregation.

Results of the present study indicate that *R. vaterifloris* feeds predominantly on aquatic insects. Geisler (1967) cited by Pethiyagoda (1991), reported that *R. vaterifloris* mainly fed on dipterans and coleopterans, has observed similar results. Moyle and Senanayake (1984) reported that diet of *R. vaterifloris* comprised mainly terrestrial insects and detritus. However, no detritus was found in the gut of *R. vaterifloris* during the present study. The results of the present study also indicates that *R. vaterifloris* is highly selective in its food habit.

P. cumingii inhabiting the streams of both river basins were found to feed mainly on aquatic insects, green algae and diatoms while *P. nigrofasciatus* mainly feed on green algae, diatoms and aquatic macrophytes (Figure 2). However, De Silva and Somarathna (1994) have reported that diet of *P. cumingii* and *P. nigrofasciatus* inhabiting the Mahaweli river basin mainly consisted of detritus, sand and diatoms. According to Geisler (1967) cited by Pethiyagoda (1991), green algae, aquatic macrophytes and detritus are the important food items of *P. cuminigii*. The results of the present study indicate that there is only a low dietary overlap between *P. cumingii* and *P. nigrofasciatus* although they feed more or less on the same food items. De Silva and Somarathna (1994) also reported that the dietary composition of these two species were more or less similar. Moyle and Senanayake (1984) stated that filamentous algae and detritus were the important food items of *P. nigrofasciatus* found in the Mahaweli river basin. The coefficient of electivity indicates that *P. cumingii* is selective only for green algae and diatoms. Although aquatic insects account for a considerable percentage of the diet, *P. cumingii* is not selective for them. Similarly, although present in considerable amount in the diet, *P. nigrofasciatus* is not selective for green algae but highly selective for aquatic macrophytes.

De Silva et al. (1977) reported that *P. titteya* in the Mahaweli river basin is predominantly omnivorous, feeding mainly on detritus, green algae and animal matter. The results of the present study also indicates that *P. titteya* in Kalu and Kelani river basins are omnivorous. However, *P. titteya* in these two river basins mainly feed selectively on diatoms and aquatic insects.

The results of the present study also indicate that *B. signata* in the Kalu and Kelani river basins is omnivorous feeding mainly on aquatic insect larvae such as ephemeropteran and dipteran larvae (Table 1 and Figure 2). Similar results have been reported by several workers (Costa and Fernando 1967; Geisler 1967 cited by Pethiyagoda 1991; Molye and Senanayake 1984). High value for the coefficient of electivity for aquatic insects indicates that *B. signata* is selective for aquatic insects. This species is not selective for green algae, although they contributed for a significant percentage of its diet.

The main food items of *G. ceylonensis* in both river basins were found to be aquatic insects and detritus. Considerable amount of diatoms was also recorded in the gut contents *G. ceylonensis* in the Kalu river basin. Costa and Fernando (1967) have reported that diet of *G. ceylonensis* comprised of detritus and diatoms. This species is found to be selective for diatoms and insects but not for detritus.

The results of the present study indicate that these six endemic species feed on variety of food items. Even *R. vaterifloris*, a strictly carnivorous species, feeds on different types of animal matter such as aquatic insects, crustaceans and rotifers. The omnivorous feeding habit is attributed to the limited supply of food in the environment (Suyehiro 1942). The omnivorous habit allows the survival of fish even if any food item is scarce in the environment. The result of the present study indicated that the food and feeding habit of any particular species vary with the locality. The reason for this is that the fish being omnivorous, are able to feed on variety of food items that are available in the environment although some of these food items are not selected by the fish. Therefore, it is likely that the type of food ingested by omnivorous fish is considerably influenced by what is available or abundant in the habitat (Schut et al. 1984). All fish species studied inhabit riverine habitats, which are highly dynamic. Therefore, these fish have to mainly depend on autochthonous food resources whose availability also varies frequently.

The Ivlev's index of food electivity indicated that fish were selective only for some food items. These selective items need not be the most abundant food items in the environment. Further, they need not be the most abundant food items of the diet. This selectivity also helps in the food niche segregation.

The present study shows that although the fish species studied are mostly omnivorous; they do not show high dietary overlap. Moyle and Senanayake (1984) has also shown that despite the use of broad categories of food items there was low dietary overlaps among some co-occurring fish species in rain forest streams in Sri Lanka. They also stated that those species heavy rely on autochthonous material, mainly the algae and aquatic invertebrates. Among some of the co-existing fish species, moderate overlap in the diets was evident. Differences in the selectivity for various food items may have helped the co-existence of such species by further segregating the food niches.

In animal communities, resource partitioning among members is known to occur along trophic, spatial and temporal dimensions (MacArthur 1965; Levins 1968; Ross 1986). Present study also indicates that food resource partitioning occurred among constituted species of the endemic fish communities in the two river basins substantiating that resource partitioning along tropic dimension is important for their co-existence. It appears that extensive studies on food resource partitioning among endemic and non-endemic fish species along all three dimensions might be useful to define objective methodologies for conservation of threatened species.

Acknowledgements

The financial assistance provided by the National Science Foundation (Research Grant No. RG/98/MAB/03) is gratefully acknowledged.

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