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Relationship between Body Shape and Food Habits of Fish from Three Reservoirs of Sri Lanka

W.S. WELIANGE and U.S. AMARASINGHE*

Department of Zoology
University of Kelaniya
Kelaniya 11600
Sri Lanka

Abstract

In the present paper, an attempt is made to investigate whether the body shape indices can be used to predict food habits of fish species in three reservoir fish communities of Sri Lanka. The present analysis is based on the studies on food and feeding habits of fish species and their body shape indices in three Sri Lankan reservoirs, namely Minneriya, Udawalawe and Victoria. Body proportions of individual fish species were determined as P_1 (= Maximum height of the body/ Maximum width of the body) and P_2 (= Total length/ Maximum height of the body), which were found to be negative curvilinearly related. Trophic indices (T_i) of individual fish species were determined on the basis of trophic level of each food item and the fractions of all food items consumed by fish species, which ranged from 1 for exclusively herbivorous species to 3 for carnivorous species. A negative logarithmic relationship between P_1 and T_i indicates that laterally compressed fish species with deep bodies feed on lower trophic levels in the food web. On the other hand, dorso-ventrally flattened species with low P_1 have higher trophic indices than those with high P_1. The positive logarithmic relationship between P_2 and T_i also indicates that short, deep-bodied fish species representing low P_2 values feed on lower trophic levels whereas slender, long-bodied species with high P_2 values feed on higher trophic levels. The body shapes, measured as simple body proportions of the definitions of P_1 and P_2, can therefore be used to predict feeding habits of fish.

* Corresponding author. Tel./Fax: +94 11 291 4479
E-mail address: zoousa@kln.ac.lk

Introduction

Since the pioneering study by Keast and Webb (1966) on body morphology relative to feeding ecology in the fish species of a small Canadian lake, and introduction of the term ecomorphology by Karr and James (1975), there has been a steady growth in the interest in this concept (Gatz 1979; De Silva et al. 1980; Lauder 1983; Motta 1988; Wainwright 1988; Winemiller 1991; Douglas and Mathews 1992; Norton 1995; Winemiller et al. 1995; Wainwright and Richard 1995; Hugueny and Pouilly 1999). According to the concept of ecomorphology, the morphological differences in animal species are said to be due to the action of several environmental pressures, which are related to resource uses from the environment (Karr and James 1975). Therefore, the ecology of organisms can be predicted from their morphological characteristics based on the correlation between the ecological and morphological variables (Weins and Rotenberry 1980). Many studies reported on ecomorphological relationships of fish assemblages have been based on the identification of prominent ecological and morphological variables, determination of interspecific patterns of variation for the ecological and the morphological variables and their correlation (Norton 1995; Winemiller et al. 1995; Piet 1998; Hugueny and Pouilly 1999). Catella and Petrere (1998) have shown that body shapes, measured as simple body proportions, i.e. the proportions of body width and height relative to total length, of fish species from Baía da Onça, a floodplain lake in Brazil, are related to their feeding habits. In the present paper, an attempt is made to investigate whether the body shape indices can be used to predict food habits of fish species in three reservoir fish communities of Sri Lanka. This study forms part of a detailed study on feeding ecology of fish assemblages in three Sri Lankan reservoirs (Weliange and Amarasinghe 2003a; 2003b; Weliange et al. 2006).

Materials and Methods

The present analysis is based on the studies on food and feeding habits of fish species in three Sri Lankan reservoirs, viz. Minneriya (8°02' N; 80°53' E), Udawalawe (6º27' N; 80º50' E) and Victoria (7º13' N; 80º47' E). Some morphometric and physico-chemical characteristics of the three reservoirs are given in table 1. Fish were sampled bi-monthly from August 1998 to August 2000. On each sampling date, fishes were sampled from morning until late dusk using beach seines (1, 5 and 7 mm mesh size) and multi-mesh, mono-filament gillnets (12.5, 16, 20, 25, 33, 37, 50, 60, 76 and 90 mm stretched mesh size). Gillnets were exposed maximum of 30 minutes in order to prevent deterioration of the ingested food items during sampling, and fish samples were preserved in 10% buffered formalin immediately after capture. Before preservation, each fish was laterally dissected near the body cavity to facilitate penetration of the preservative. Fish samples were taken to laboratory for further analysis. In the laboratory, preserved specimens were identified, sorted into species and total length, maximum body width and maximum body height of individual fish were measured to the nearest 0.1 cm using a vernier caliper.

Table 1. Some morphometric and physico-chemical characteristics of three reservoirs studied (after Silva and Gamlath 2000)

Parameter	Minneriya	Udawalawe	Victoria
Year of construction	276-303 AD (Restored in 1903)	1967	1986
Altitude (m)	96	80	438
Catchment (km^2)	249	1164	1891
Area (km^2)	25.5	34.08	22.7
Mean depth (m)	5.8	7.9	30.5
Temperature °C	27.0-31.5	27.8-29.5	25.5-30.0
pH	7.32-8.35	7.33-8.58	7.09-7.89
Alkalinity (mg l^{-1})	56-132	61-89	33-52
Conductivity (µS cm^{-1})	98-213	102-134	66-93
Secchi Depth (cm)	45-280	50-205	95-280
Dissolved Oxygen (mg l^{-1})	6.84-8.11	7.11-8.02	6.31-8.78

Preserved specimens were dissected and all food contained in the stomach or anterior part of the gut were removed and placed into a beaker with water to create a suspension of known volume. Stomach contents were extracted by dissecting individual fish. As cyprinids do not have stomachs, contents first one-third of the intestine were considered as ingested food items. Empty stomachs or stomachs with almost fully digested contents were eliminated. Subsamples (1 ml) of the suspension were examined under a light microscope using a Sedgwick Rafter cell for quantitative determination of stomach/gut contents. Relative volumes of each food item were determined using arbitrary size such as a *Pinnularia* cell as the standard, and expressed as percentage of the total food items in the gut contents (Hynes 1950; Hyslop 1980). Relative volume of each diet item was summed across all samples for each species for the final analysis. Relative volumes of 96 food items were regrouped into 12 food categories of broader taxonomic groups, which were thought to represent food of fish with different trophic categories (Table 2).

Table 2. Food categories, their trophic classes and components of each of the food categories

Food category	Abbreviation	Trophic class	Food components
Phytoplankton	PP	0	Diatoms, blue greens, green algae, uncommon algae, filamentous algae
Macrophytes	MP	0	Terrestrial and aquatic plants
Detritus	DE	0	Soft sediments, particulate matter
Mollusks	ML	1	Aquatic gastropods, bivalves
Macrobenthos	MB	1	Nematodes, annelids and *Caridina*
Small zooplankton	SZ	1.5	*Brachionus*, *Trichocerca*, *Keratella*, dinoflagellates (e.g. *Phacus* and *Peridinium*)
Cladocerans	CD	1.5	*Bosminopsis*, *Moina*, *Daphnia*, *Diaphanasoma*, *Ceriodaphnia*
Copepod zooplankton	CP	1.5	Calanoid and cyclopoid copepods, body parts
Ostracods	OST	1.5	Chydorids, *Macrothrix* and *Cypridopsis*
Insects	IN	1.5	Flying insects, other terrestrial insects, aquatic insects
Insect larvae	IL	1.5	Larval stages of Chironomidae, Ephrmeroptera and Odonata
Fish	FH	2	Fish scales, fish eggs, small juvenile fish, fish skeletons

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

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

where T_j is the trophic level of prey species j and p_{ij} is the fraction of food (proportion by volume) consumed by species i consisting of prey species j (Adams et al. 1983; Winemiller 1990). The use of this measure implies that ecological pyramids are more accurately represented by a trophic continuum rather than by consumers at discrete levels (Adams et al. 1983; Cousins 1985; 1987). The T_i values were computed sequentially from the bottom of the food web to the top. Unidentified food items were omitted from the trophic classification, since they could not be assigned to a trophic level. They represented very small volumetric proportions of the gut contents and therefore, it was assumed that omitting these food items would not affect final results. The T_i values ranged from 1 for exclusively herbivorous species to 3 for carnivorous species.

The following two body proportions were also defined (Catella and Petrere 1998) in order to investigate whether there is a broad relationship between body morphology and feeding habits.

P_1 = Maximum height of the body/Maximum width of the body

P_2 = Total length/ Maximum height of the body

The relationship between P_1 and P_2 was determined. Also, the relationships of these body proportions with T_i were determined separately to investigate whether they could be used to predict feeding habits of fish.

Results

Trophic classes of the 12 categories of food items are given in table 2. The T_i values of individual fish species in the three reservoirs were estimated based on these trophic classes and volumetric proportions of food items of fish. Volumetric proportions of food items of fish, P_1 and P_2 values and trophic indices of individual species in Minneriya, Udawalawe and Victoria are presented in tables 3, 4 and 5, respectively.

When the fish is observed from the head aspect, species with high P_1 are laterally compressed with deep bodies such as cichlids and species with low P_1 are dorso-ventrally flattened (e.g. snakeheads and gobies). P_2 values exhibit side aspect of fish. Species with high P_2 values are slender, long-bodied individuals such as *Glossogobius giuris*, *Ophicephalus striatus*, *Ompok bimaculatus*, *Hyporhamphus gaimardi*, whereas those with low P_2 are short, deep-bodied fish such as *Etroplus suratensis*, *Oreochromis mossambicus* and *O. niloticus.*

The relationship between P_1 and P_2 of the fish species in the three reservoirs is negative curvilinear (Fig. 1). Predominantly phytoplanktivorous and detritivorous fish species such as cichlids are with high P_1 and low P_2. The other extreme is represented by predominantly piscivorous fish species such as *G. giuris* and *O. striatus*, which have low P_1 and high P_2.

Table 3. Number of fish examined, their size ranges, P1 and P2 values, volumetric proportions (%) of food items of fish species in Minneriya reservoir

Family/species	N	Total length range (mm)	P1	P2	Food items (%)												T_i
					PP	MP	DE	ML	MB	SZ	CD	CP	OST	IN	IL	FH	
Cyprinidae																	
Amblypharyngodon melettinus	297	27-91	2.16	4.71	26	0	67	0	0	1	0	0	4	2	0	0	1.10
Chela laubuca	258	32-71	2.29	4.80	1	0	4	1	1	0	7	0	2	45	38	1	2.43
Danio malabaricus	88	39-83	2.37	4.11	1	1	8	0	0	0	1	0	1	73	12	3	2.37
Esomus danrica	46	46-88	1.90	5.37	12	0	77	0	0	0	1	2	0	0	0	8	1.96
Garra ceylonensis	14	25-135	1.36	5.22	3	0	77	0	0	0	0	0	0	20	0	0	1.30
Puntius bimaculatus	13	30-56	1.85	4.40	11	10	49	0	0	0	0	0	1	9	20	0	1.45
P. chola	151	62-154	2.11	3.53	1	5	57	0	0	0	1	11	6	8	11	0	2.41
P. dorsalis	41	65-193	2.00	3.84	0	0	21	0	0	0	2	16	8	4	48	1	2.19
P. filamentosus	439	59-162	2.24	3.70	8	38	10	0	0	0	9	2	0	22	6	5	1.69
P. sarana	16	58-218	1.95	3.51	0	3	19	30	25	0	4	0	1	8	10	0	2.02
P. ticto	77	35-126	2.57	3.58	8	9	66	0	0	0	1	0	1	7	8	0	1.26
Rasbora daniconius	428	27-126	1.78	5.56	5	24	5	0	0	0	6	6	0	29	9	16	2.07
Anabantidae																	
Anabas testudineus	17	95-178	1.45	3.31	21	20	7	0	0	0	0	0	0	6	10	36	1.96
Bagridae																	
Mystus keletius	45	217-230	1.40	5.38	1	4	7	2	13	0	3	4	0	25	17	24	2.41
M. vittatus	93	72-107	1.29	5.49	0	1	4	1	0	0	2	28	1	33	26	4	2.44
Belontidae																	
Trichogaster pectoralis	8	141-156	2.58	3.33	44	0	52	0	0	4	0	0	0	0	0	0	1.04
Cichlidae																	
Etroplus maculatus	234	19-89	2.83	2.51	8	31	14	0	0	0	1	0	1	10	19	16	1.79

Table 3. Number of fish examined, their size ranges, P1 and P2 values, volumetric proportions (%) of food items of fish species in Minneriya reservoir (continued)

Family/species	N	Total length range (mm)	P1	P2	Food items (%)												T_i
					PP	MP	DE	ML	MB	SZ	CD	CP	OST	IN	IL	FH	
E. suratensis	113	47-62	3.15	2.52	37	43	7	0	0	0	0	0	0	6	3	4	1.22
Oreochromis mossambicus	74	81-176	2.44	3.02	11	25	64	0	0	1	0	0	0	0	0	0	1.01
O. niloticus	151	27-185	2.51	3.09	26	13	51	0	0	1	0	0	0	5	4	0	1.15
Tilapia rendalli	264	24-210	2.47	3.03	11	58	16	0	0	0	0	0	0	10	1	4	1.25
Channidae																	
Ophicephalus striatus	16	230-254	1.25	4.92	0	0	0	0	47	0	0	0	0	3	0	50	2.75
Cobitidae																	
Lepidocephalich-thys thermalis	6	38-59	1.59	6.21	6	0	19	0	0	0	0	5	0	0	70	0	2.13
Mastacembelidae																	
Mastacembelus armatus	2	146-225	0.81	7.45	30	0	0	0	0	0	0	0	0	20	0	50	2.30
Gobiidae																	
Glossogobius giuris	165	23-217	1.05	7.24	0	0	11	0	1	0	0	3	2	22	24	37	2.52
Heteropneustidae																	
Heteropneustes fossilis	45	113-315	1.35	6.87	1	9	5	4	1	0	2	2	3	8	5	60	2.56
Hemirhamphidae																	
Hyporhamphus gaimardi	476	94-142	1.40	11.78	3	1	0	2	2	0	55	16	1	13	7	0	2.43
Siluridae																	
Ompok bimacula-tus	12	250-296	2.22	4.89	0	3	1	0	29	0	0	0	0	29	0	38	2.63

Ti values of each species are also given here. P1 and P2 are mean values of measurements from several fish (ranging 2 fish of *M. armatus* to 90 fish of *R. daniconius*). Abbreviations for food items are as given in Table 2.

Table 4. Number of fish examined, their size ranges, P1 and P2 values, volumetric proportions (%) of food items of fish species in Udawalawe reservoir

Family/species	N	Total length range (mm)	P1	P2	Food items (%)												T_i
					PP	MP	DE	ML	MB	SZ	CD	CP	OST	IN	IL	FH	
Cyprinidae																	
Amblypharyngodon melettinus	250	54-91	2.15	4.66	12	0	82	0	0	1	5	0	0	0	0	0	1.09
Catla catla	25	205-305	1.96	3.64	3	2	77	0	0	0	5	12	0	1	0	0	1.27
Labeo dussumieri	17	190-315	1.66	4.45	10	1	89	0	0	0	0	0	0	0	0	0	1.00
L. rohita	17	158-178	2.06	3.96	7	42	49	0	0	0	0	0	0	2	0	0	1.03
P. chola	111	76-128	2.04	3.59	1	5	37	0	0	0	2	3	34	3	15	0	1.86
P. dorsalis	65	120-200	2.02	4.47	1	5	37	0	0	0	6	1	15	20	15	0	1.86
P. filamentosus	465	21-152	2.15	3.91	6	27	19	0	0	0	24	3	4	11	6	0	1.72
P. sarana	17	85-270	1.89	3.80	3	0	46	0	0	0	0	0	0	51	0	0	1.75
Rasbora daniconius	217	61-130	1.56	5.58	1	1	2	0	0	0	14	5	0	48	27	2	2.44
Bagridae																	
Mystus keletius	5	99-245	1.32	5.59	0	1	2	0	0	0	2	0	6	28	10	51	2.71
Cichlidae																	
Etroplus suratensis	297	31-141	3.04	2.35	22	63	11	0	0	0	0	0	0	2	2	0	1.06
Oreochromis mos-sambicus	6	118-180	2.16	3.09	12	0	88	0	0	0	0	0	0	0	0	0	1.00
O. niloticus	101	115-145	2.14	3.13	8	1	69	0	0	1	2	4	4	1	10	0	1.33
Tilapia rendalli	82	16-194	2.32	3.30													1.05
Gobiidae																	
Glossogobius giuris	264	44-240	1.01	7.35	2	1	16	0	4	0	1	10	4	17	18	27	2.35
Heteropneustidae																	
Heteropneustes fossilis	18	117-220	0.94	7.65	1	0	8	0	0	0	7	9	11	9	45	10	2.42
Hemirhamphidae																	
Hyporhamphus gaimardi	625	94-164	1.32	11.21	2	4	0	2	0	1	59	11	1	11	8	1	2.40
Siluridae																	
Ompok bimaculatus	4	165-310	1.76	6.19	0	0	0	0	0	0	0	0	0	0	0	100	3.00

Ti values of each species are also given here. P1 and P2 are mean values of measurements from several fish (ranging 4 fish of *C. catla* to 125 fish of *E. suratensis*). Abbreviations for food items are as given in Table 2.

Table 5. Number of fish examined, their size ranges, P1 and P2 values, volumetric proportions (%) of food items of fish species in Victoria reservoir

Family/species	N	Total length range (mm)	P1	P2	Food items (%)											T_i
					PP	MP	DE	ML	SZ	CD	CP	OST	IN	IL	FH	
Cyprinidae																
Amblypharyngodon melettinus	193	24-86	2.16	4.71	24	0	74	0	0	2	0	0	0	0	0	1.03
Danio malabaricus	337	60-92	2.44	4.59	0	0	2	0	0	7	0	0	67	22	2	2.45
Esomus danrica	55	84-97	1.84	5.50	15	1	49	0	4	0	2	0	26	3	0	1.51
P. chola	174	60-114	2.22	3.81	1	18	52	0	0	2	2	8	5	12	0	1.44
P. dorsalis	60	131-194	1.80	4.15	0	6	42	0	0	4	1	16	11	20	0	1.78
P. filamentosus	674	59-171	2.35	3.91	2	39	13	0	0	5	2	0	29	3	7	1.73
Rasbora daniconius	45	69-126	1.89	5.12	0	5	0	0	0	1	1	14	77	0	2	2.44
Bagridae																
Mystus vittatus	23	74-115	1.17	5.89	0	3	1	3	0	4	43	3	13	22	8	2.47
Cichlidae																
Etroplus maculatus	11	58-76	3.00	2.52	6	10	29	0	0	0	40	0	0	0	15	1.90
E. suratensis	3	91-147	2.52	2.77	1	95	4	0	0	0	0	0	0	0	0	1.00
Oreochromis mossambicus	26	146-191	2.40	3.17	20	0	80	0	0	0	0	0	0	0	0	1.00
O. niloticus	96	112-196	2.26	3.26	32	2	52	0	0	0	11	0	3	0	0	1.21
Tilapia rendalli	85	14-218	2.50	3.02	3	59	36	0	0	1	0	0	0	1	0	1.03
Gobiidae																
Glossogobius giuris	71	28-101	0.99	8.25	0	0	0	0	0	2	10	9	14	18	47	2.74
Heteropneustidae																
Heteropneustes fossilis	5	146-260	1.38	6.07	1	8	9	0	0	6	2	0	16	3	55	2.51

Ti values of each species are also given here. P1 and P2 are mean values of measurements from several fish (ranging 3 fish of *E. suratensis* to 84 fish of *P. filamentosus*). Abbreviations for food items are as given in Table 2.

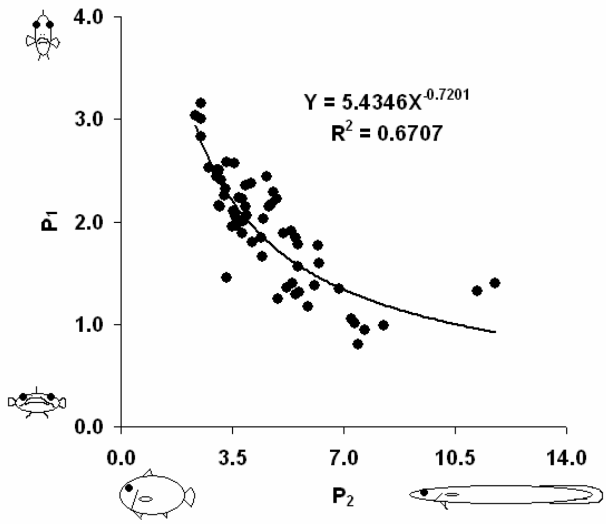

Fig. 1. The relationship between P_1 and P_2 of the fish species in three reservoirs of Sri Lanka. The approximate body shapes of fish of the extremes of P_1 and P_2 values are also diagrammatically shown here.

H. gaimardi in Minneriya and Udawalawe, which feed exclusively on zooplankton are represented by high P_2 and low P_1 values. Fish species with intermediate P_1 and P_2 values are mainly cyprinids and are of mixed feeding habits ranging from detritivory, herbivory to omnivory.

A negative logarithmic relationship is evident between P_1 and T_i (Fig. 2A). This indicates that laterally compressed fish species with deep bodies feed on lower trophic levels in the food web. On the other hand, dorso-ventrally flattened species with low P_1 have higher trophic indices than those with high P_1.

The relationship between P_2 and T_i is a positive logarithmic one (Fig. 2B). This also indicates that short, deep-bodied fish species representing low P_2 values feed on lower trophic levels whereas slender, long-bodied species with high P_2 values feed on higher trophic levels.

Discussion

The hyperbolic relationship between P_1 and P_2 indicates that in the three fish assemblages studied, there is no any species with laterally flattened, long bodied species with high P_1 and high P_2 which do not fit into this relationship. Catella and Petrere (1998) have also found a similar pattern for fish species in Baía da Onça, a floodplain lake in Brazil.

Present analysis clearly indicates that the body proportions measured as P_1 and P_2 are related to feeding habits of fish in the three Sri Lankan reservoirs. Catella and Petrere (1998) also found that the body shapes of fish in a floodplain lake in Brazil are broadly related to their feeding habits.

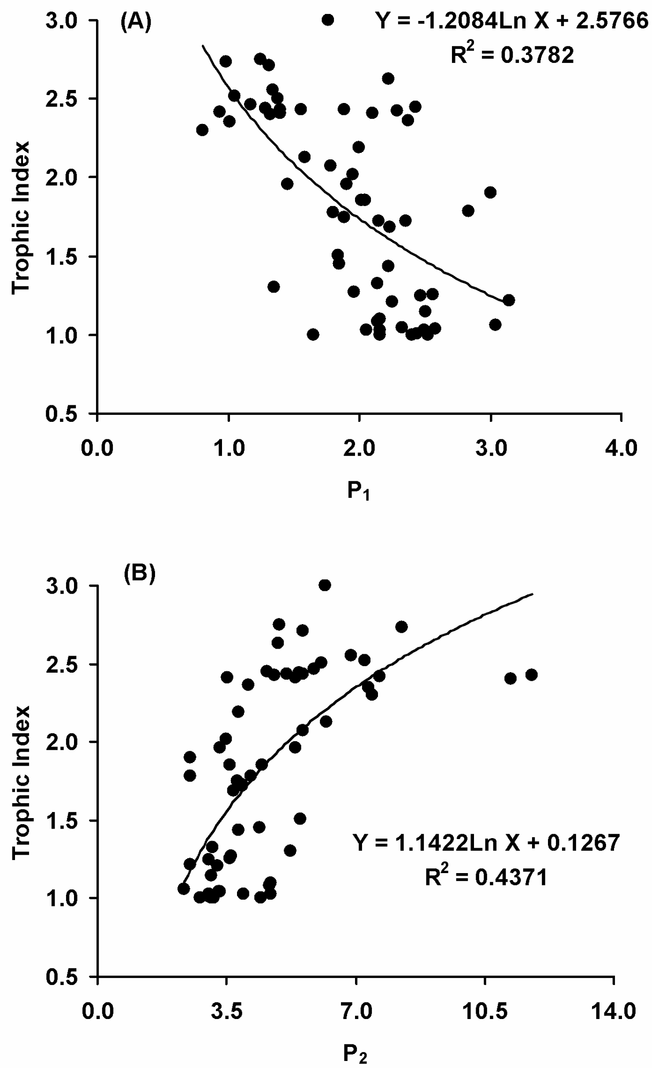

Fig. 2. (A) The negative logarithmic relationship between P_1 and T_i and (B) the positive logarithmic relationship between P_2 and T_i.

As suggested by Bond (1979), the close relationship between body shape and feeding habits may be associated with the behavioural patterns of fish. Bond (1979) has indicated that laterally compressed and short fishes which are not good swimmers but can make quick turns, possess the body shapes which are probably important in escaping from the predators. These fishes with high P_1 and low P_2 and with limited activity, feed on non-evasive food such as phytoplankton, higher plants and the detritus.

Winemiller et al. (1995) have suggested that the percomorph body plan of cichlids makes them suitable for life in slack water and vegetated habitats. The moderate T_i values of cichlids in the three Sri Lankan reservoirs studied indicate that they feed on a wide range of food items, possibly due to their slow activity patterns associated with percomorph body plan.

The body shapes of *G. giuris* and *O. striatus*, which have flattened head equipped with a large mouth, fall under the category of 'lie-in-wait predators' (Moyle and Cech 2000) which are essentially piscivores. *H. gaimardi* in Minneriya and Udawalawe reservoirs feed mainly on zooplankton. Moyle and Cech (2000) also stated that the morphology of 'surface-oriented fishes' such as halfbeak, which are characterized by upward-pointing mouth, a dorso-ventrally flattened head with large eyes, is well suited for capturing plankton.

The present analysis indicates that there is strong evidence that the gross body proportions, measured as P_1 and P_2, can be used to predict feeding habits of fish. It must be noted however, that the food consumption patterns of fish are related to other morphological variables such as size of mouth, and shape of the caudal fin. Norton (1995) has shown that large-mouthed cottids had significantly higher capture success on *Heptacarpus* shrimp than did small-mouthed species. It is also well-known that as swimming speed is related to aspect ratio of caudal fin i.e., ratio of square value of height of caudal fin to its surface area, in most fish species, amount of food consumed is related to this ratio (Palomares and Pauly 1998). While it has been shown that species having similar diets tend to converge for some morphological attributes of a broad range (Hugueny and Pouilly 1999), from the present analysis it is evident that the body shapes, measured as simple body proportions of the definitions of P_1 and P_2, can be used to predict feeding habits of fish.

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