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INTRASPECIFIC VARIATION IN MORPHOLOGY AND SEXUAL DIMORPHISM IN *PUNTIUS SINGHALA* (TELEOSTEI: CYPRINIDAE)

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ABSTRACT

Intraspecific morphological variation and differentiation among six populations of the endemic freshwater fish *Puntius singhala* (Cyprinidae) were investigated. There is significant sexual dimorphism in three morphometric characters (pectoral-fin length, caudal-peduncle length, and length of dorsal-fin base), where males have slightly longer measures than females, indicating adaptive significance related to dispersal. Significant heterogeneity and differentiation was found only among some of the populations studied (Wilk's λ for males = 0.079 and for females = 0.129) indicating limited geographic variation, as suggested by relatively large overlap in canonical scores among most of the samples. No significant correlation between the pair-wise differences and inter-locality geographic distances was found, thus isolation-by-distance was not a plausible explanation for the observed variation. The present results show that *P. singhala* is not phenotypically homogenous. The absence of differences between population samples that experience highly limited present-day interchange may be partly explained by colonization history.

Key words: Geographic variation, morphometry, multivariate analysis, population differentiation

INTRODUCTION

Populations of a species represent units that, when sufficiently isolated from each other, may have independent dynamics (Brown & Ehrlich, 1980). Measures of gene flow and genetic differentiation are typically used to distinguish one population from another. Populations can also be distinguished with the use of other measures such as differences in morphology or phenology (Luck *et al*., 2003). Identification of populations is important from the perspectives of species conservation and evolution. Evolutionary units (EUs) are populations with independent evolutionary dynamics so that an EU consists of a group of interbreeding individuals sharing a common gene pool (Luck *et al*., 2003). For example, recently colonized island populations may form separate EUs that differ from the mainland populations from which they originated (Cody & Overton, 1996). The existence of differentiable populations of a species may also represent the existence of adaptive variation. The study of existing phenotypic and genotypic intraspecific variation is also significant in problems of species delineation, where it is acknowledged that insufficient information on intraspecific variation may lead to ambiguous species identifications (Ishihara, 1987), particularly when external morphologies alone are used for the purpose.

Being inhabitants of a small island, Sri Lankan freshwater ichthyofauna provide good examples to assess whether individual species are comprised of multiple evolutionary units. In this study, the hypothesis that different geographic samples may belong to a single, homogenous population unit was tested for the cyprinid fish *Puntius singhala* using morphological characters. *Puntius singhala* Duncker (1912), a barb with an elongate, filamented dorsal fin, is a widely distributed endemic freshwater species (previously known as *P. filamentosus*) in Sri Lanka (Pethiyagoda, 1991), while its closest relative, *P. filamentosus*, occurs in India (Pethiyagoda & Kottelat, 2005). Apart from recent taxonomic studies (Pethiyagoda & Kottelat, 2005), no other work has focused on its geographic variation within the island. A detailed study of morphometric characters of *P. singhala* is presented here, to reveal the existing intraspecific variation, sexual dimorphism and level of differentiation using several geographic population samples from freshwater bodies in Sri Lanka.

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MATERIALS AND METHODS

Adult specimens of *P. singhala* were collected from six freshwater bodies, namely Pattiyapola tank (hydrologically connected to Walawe Ganga) (L1), Godapitiya Wewa, a small waterlogged area (directly fed by the Nilwala Ganga) (L2), a stream at Dediyagala (hydrologically connected to Nilwala Ganga) (L3), Kirindi Oya (L4), Kuru Ganga (connected to Kalu Ganga) (L5), and Hiyare tank (hydrologically connected to Gin Ganga) (L6). Sex was determined by morphology of the dorsal fin (only the males have filamentous rays), while a sub-sample of fish was dissected to confirm the external sex determination. Individual fish were digitally imaged together with an mm-rule, and horizontal and vertical dimensions between identified points were converted to mm-scale in order to record individual data on standard length (SL) and 11 other morphometric characters: caudal-peduncle length (CPL), pre-dorsal length (PrDL), head length (HL), orbital length (OL), post-orbital length (PsOL), pre-orbital length (PrOL), head depth (HD), maximum body depth (MBD), dorsal fin-base length (FBD), anal fin-base length (FBA) and pectoral-fin length (PFL) (Table 1).

Morphometric character measurements as well as the relative lengths (% SL) showed significant correlation with size, therefore, measurements of each morphometric character made were standardized to fish size (SL) to remove size-effect using Reist (1985) methods as described in Gunawickrama (2007). Size-corrected data were analyzed by t-test, one-way ANOVA, and multivariate methods including Discriminant Function Analysis (DFA). Preliminary data analysis for maximum body depth (MBD) found a large within-group variation not related to the sex in some population samples introducing unexplainable variance component, and thus MBD was removed from further statistical analysis. Sexual dimorphism was tested on size-corrected morphometrics by t-test (for independent groups). Differences among population samples were tested by one-way analysis of variance (ANOVA) followed by Tukey HSD (for unequal sample size) post-hoc test (Zar, 1999) using the size-corrected variables for the males and females separately. Tests were considered significant at 0.05 probability level with the sequential Bonferroni adjustment (Rice, 1989). DFA was performed to generate multivariate discriminant functions (Wilk's λ ranges between 0-1.0; values closer to zero indicate greater discrimination) that can identify the characters that were most important in distinguishing population groups. Pair-wise squared Mahalanobis distance (D^2) among population samples were calculated and tested for their significance, and the agreement to the isolation-by-distance model (Slatkin, 1993) was tested by Pearson correlation analysis using pair-wise D^2 and pair-wise geographic distance (approximate distance derived from a scaled map). All data analysis and statistical analyses were carried out by using STATISTICA v 7.0 (Statsoft, USA).

Table 1. **Morphometric characters of *P. singhala* measured for comparison of populations in different geographical locations. (all measurements were made parallel to the antero-posterior body axis, except HD and MBD).**

Character	code	Description
Standard length	*SL*	mouth tip to the last perforated scale of the lateral line
Caudal-peduncle length	*CPL*	posterior end of anal-fin base to the last perforated scale of the lateral line
Pre-dorsal length	*PRDL*	mouth tip to the origin of dorsal-fin
Head length	*HL*	mouth tip to the posterior edge of operculum
Orbital diameter	*OL*	diameter of the orbit
Post-orbital length	*PsOL*	posterior edge of orbit to posterior edge of operculum
Pre-orbital length	*PrOL*	mouth tip to anterior edge of orbit
Head depth	HD	depth from the ventral point of intersection of the outer operculum edge to the dorsal head margin (measured perpendicular to body axis)
Maximum body depth	MBD	distance between points at deepest part of body (measured perpendicular to body axis)
Dorsal-fin base	FBD	distance between the visible origins of the first spine and base of the last ray of the dorsal-fin
Anal-fin base	FBA	distance between the visible origins of the first spine and base of the last ray of the anal-fin
Pectoral-fin length	*PFL*	length of the fin from dorso-posterior part of fin base to the distal edge of the fin

RESULTS

The size composition of the fish examined from each population is given in Table 2. The mean SL (± SD) for all fish analyzed is 64.5 ± 12.0 mm (n=246). The sex ratio is female-biased in the pooled sample (1.8:1) while it varied in separate samples (Table 2). All ten size-corrected morphometric characters were not significantly correlated to SL of fish, proving that the size-effect had been successfully removed.

Testing for differences between sexes in the pooled sample revealed slight, yet significant dimorphism (t-test for independent samples) in three of the size-corrected measures, i.e. CPL (p= 0.023), FBD (p= 0.002) and PFL (p< 0.001), where the males had slightly longer measures than females. In males (n= 89), relative (%SL± SD) CPL, FBD and PFL were 16.7±1.5, 19.0 ± 1.3 and 21.7 ±1.3 respectively. In females (n=156), relative (%SL± SD) CPL, FBD and PFL were 16.4± 1.5, 18.4 ± 1.1 and 20.9 ± 1.6, respectively.

In males, univariate ANOVA revealed significant differences (p<0.05 with sequential Bonferroni correction) in PrOL, PsOL and HL rejecting the H_0 of ‘no heterogeneity in fish morphology among studied populations’ (Table 3). L2 and L4 (i.e. not different from each other) differ from all other population samples with respect to PrOL. PsOL in L1 fish differs from those of L2, L3 and L5, while the HL only differs between L1 and L2. Male fish from L2 and L3 (both have hydrological connection to the River Nilwala) were different in respect to PrOL where L3 fish had about 1% (of SL) longer PrOL than the L2 fish. Discriminant Function Analysis (DFA) using size-corrected characters of males, derived a model (Wilk’s λ = 0.079, p<0.001) where PrOL, PsOL, OL, FBA, CPL and HD contribute significantly (in descending order) for discrimination between population samples. The most important contribution for discrimination was by PrOL (Partial Wilk’s λ = 0.51). The first two canonical variates (CV) accounted for 78.7% of the variation in size corrected data while three other less important functions were also significant (CV1: 46.6%, CV2: 32.1%, CV3: 13.5%, CV4: 6.6%, CV5: 1.2%). CV1 was most heavily weighted by PrOL and PsOL. Average classification success using derived classification functions was 79.8%, with 82-90% success recorded for L1, L2 and L6 fish, 67% for L4 and L5 fish, and 57% for L3. The plot of the canonical scores for the first two CV showed considerable overlap between some of the populations (Fig. 1). However, considerable separation of L1 from L2 and L4 is seen along the CV1. Other three population samples (i.e. L3, L5 and L6) showed wide overlap indicating poor differentiation.

In females, univariate ANOVA revealed significant differences (p<0.05 with sequential Bonferroni correction) in CPL, HL, OL, PrOL, PsOL, FBD, FBA and PFL rejecting the H_0 of ‘no heterogeneity in fish morphology among studied populations’ (Table 3). DFA using size-corrected characters of females, derived a model (Wilk’s λ = 0.129, p<0.001) where CPL, FBA, PrDL, PFL, PsOL, FBD and HL contribute significantly (in descending order) for discrimination between population samples. The most important contribution for discrimination was by CPL (Partial Wilk’s λ = 0.76). The first two canonical variates (CV) accounted for 77.0% of the variation in size corrected data while three other less important functions were also significant (CV1: 51.4%, CV2: 25.6%, CV3: 12.5%, CV4: 6.4%, CV5: 4.1%). CV1 was most heavily weighted by FBA and PFL. Average classification success using derived classification functions was 71.9%. The plot of the canonical scores for the first two CV showed considerable overlap between some of the populations (Fig. 1). However, some discrimination of L1 from some other population samples (i.e. L3, L5 and L6) is seen despite poor differentiation. Overall, close affinities in L3, L6 and L5 than with others are apparent both in males and females.

Table 2. Collection localities, sample size (n) and size statistics (SL) of adult *P. singhala* samples.

Location	Altitude (m)	Male %	Female %	Total n	Size range (SL) (mm)	Mean SL (mm)	SD
L1: Pattiyapola tank [a] (Walawe Ganga)	0 – 50	49.4	49.4	83	49.6 – 81.7	63.9	7.1
L2: Godapitiya wewa [a] (Nilwala Ganga)	0 – 50	61.1	38.9	18	49.5 – 84.6	61.6	8.5
L3: Dediyagala stream [b] (Nilwala Ganga)	0 – 50*	25.5	74.5	55	44.7 – 96.4	71.5	14.7
L4: Kirindi Oya	0 – 50	21.4	78.6	42	42.0 – 86.3	61.7	7.6
L5: Kuru Ganga [b] (Kalu Ganga)	50 – 100*	46.2	53.8	13	67.5 – 91.7	83.7	7.3
L6: Hiyaare tank [a] (Gin Ganga)	0 – 50*	22.6	77.1	35	43.3 – 87.1	52.8	8.6

[a] irrigation tank/ waterlogged area hydrologically connected to the stated river; [b] an uphill stream connected to the main body of the stated river, * upper range

Table 3. Descriptive statistics of the morphometric characters for female and male (within brackets) *P. singhala* (% SL; mean ± SD).

	Pattiyapola (L1) n= 41 (=41)	Godapitiya (L2) n= 7 (=11)	Dediyagala (L3) n= 41 (=14)	Kirindi Oya (L4) n= 33 (=9)	Kuru Ganga (L5) n= 7 (=6)	Hiyare tank (L6) n= 27 (=8)
SL	60.8 ± 6.2 (67.1 ± 6.7)	55.0 ± 5.2 (65.8 ± 7.5)	71.6 ± 15.4 (71.1 ± 12.9)	60.7 ± 7.9 (65.0 ± 5.6)	80.4 ± 7.4 (87.6 ± 5.5)	53.5 ± 8.8 (50.4 ± 8.1)
CPL	16.0 ± 1.2 ^{a} (16.4 ± 1.2)	16.6 ± 1.9 ^{ab} (17.9 ± 1.2)	15.6 ± 1.4 ^{a} (16.0 ± 1.8)	16.5± 1.2 ^{ab} (16.2 ± 1.0)	16.8 ± 1.5 ^{ab} (17.1 ± 0.9)	17.9 ± 1.3 ^{b} (18.4 ± 1.0)
PrDL*	48.2 ± 1.2 (47.9 ± 1.1)	47.5 ± 1.3 (46.7 ± 1.3)	47.7 ± 1.5 (48.0 ± 1.5)	48.7 ± 1.6 (48.2 ± 1.6)	47.1 ± 0.9 (47.0 ± 1.5)	48.9 ± 1.3 (48.3 ± 0.7)
HL	26.7 ± 1.5 ^{a} (26.6 ± 1.1 ^{b})	25.2 ± 1.3 ^{ab} (24.5 ± 1.3 ^{a})	25.8 ± 2.0 ^{a} (25.7 ± 1.7 ^{ab})	25.1 ± 1.9 ^{b} (24.9 ± 1.4 ^{ab})	22.9 ± 1.5 ^{ab} (23.4 ± 0.8 ^{ab})	27.6 ± 1.5 ^{a} (28.0 ± 0.6 ^{ab})
OL	9.3 ± 0.7 ^{a} (9.0 ± 0.7)	10.0 ± 0.6 ^{ab} (9.4 ± 0.5)	9.5 ± 1.2 ^{b} (9.4 ± 0.9)	9.2 ± 0.8 ^{a} (9.4 ± 1.1)	8.0 ± 0.4 ^{ab} (8.1 ± 0.6)	10.6 ± 0.9 ^{b} (10.9 ± 0.5)
PsOL	11.4 ± 0.6 ^{c} (11.5 ± 0.5 ^{b})	10.4 ± 0.6 ^{abc} (10.5 ± 0.6 ^{a})	10.4 ± 0.6 ^{a} (10.5 ± 0.6 ^{a})	11.1 ± 0.7 ^{bc} (11.0 ± 0.5 ^{ab})	9.7 ± 0.6 ^{ab} (10.1 ± 0.6 ^{a})	10.7 ± 0.9 ^{ab} (10.6 ± 0.4 ^{ab})
PrOL	6.0 ± 0.9 ^{a} (6.1 ± 0.6 ^{a})	4.8 ± 0.5 ^{ab} (4.5 ± 0.6 ^{b})	5.9 ± 0.9 ^{a} (5.7 ± 0.9 ^{a})	4.7 ± 1.1 ^{b} (4.4 ± 0.9 ^{b})	5.2 ± 0.8 ^{ab} (5.2 ± 0.5 ^{a})	6.3 ± 1.0 ^{a} (6.6 ± 0.4 ^{a})
HD*	21.9 ± 1.3 (21.5 ± 1.1)	23.3 ± 3.2 (20.5 ± 0.9)	21.2 ± 1.4 (21.6 ± 1.6)	21.9 ± 1.1 (21.8 ± 0.7)	20.0 ±1.2 (20.8 ± 1.0)	22.8 ± 1.1 (22.4 ± 0.6)
MBD	37.7 ± 1.4 ^{ab} (37.1 ± 1.6 ^{abc})	38.0 ± 4.0 ^{abc} (36.6 ± 1.5 ^{ab})	37.8 ± 1.6 ^{a} (38.7 ± 1.7 ^{bc})	38.9 ± 1.5 ^{b} (39.8 ± 1.3 ^{c})	37.7 ± 1.4 ^{abc} (38.0 ± 1.5 ^{abc})	35.1 ± 1.7 ^{c} (34.1 ± 1.8 ^{a})
FBD	18.3 ± 0.8 ^{ab} (19.1 ± 1.1)	18.5 ± 1.1 ^{ab} (19.8 ± 1.6)	19.1 ± 1.1 ^{b} (19.0 ± 1.1)	18.5 ± 0.9 ^{ab} (19.1 ± 1.5)	18.1 ± 1.1 ^{ab} (17.9 ± 0.9)	17.6 ± 1.1 ^{a} (18.1 ± 1.1)
FBA	8.8 ± 0.9 ^{ab} (9.3 ± 0.8)	9.0 ± 0.8 ^{ab} (9.3 ± 0.6)	9.6 ± 0.9 ^{a} (9.6 ± 1.0)	8.6 ± 0.7 ^{b} (8.5 ± 0.9)	9.2 ± 0.6 ^{ab} (9.4 ± 1.3)	9.3 ± 0.9 ^{a} (9.4 ± 0.7)
PFL	20.2 ± 1.2 ^{a} (21.7 ± 1.2)	21.9 ± 1.3 ^{ab} (21.5 ± 1.4)	20.9 ± 1.3 ^{ab} (21.3 ± 1.3)	20.6 ± 1.6 ^{ab} (21.5 ± 1.3)	20.6 ± 0.8 ^{ab} (22.8 ± 1.3)	22.1 ± 2.0 ^{b} (22.5 ± 1.3)

Results of the ANOVA and Tukey HSD (for unequal N) post-hoc tests on size-corrected characters that are significant are indicated by superscript letters, where no shared letter between the superscripts for a given row indicates significant differences among populations at $p<0.05$ with sequential Bonferroni adjustment for multiple tests.

* not significant

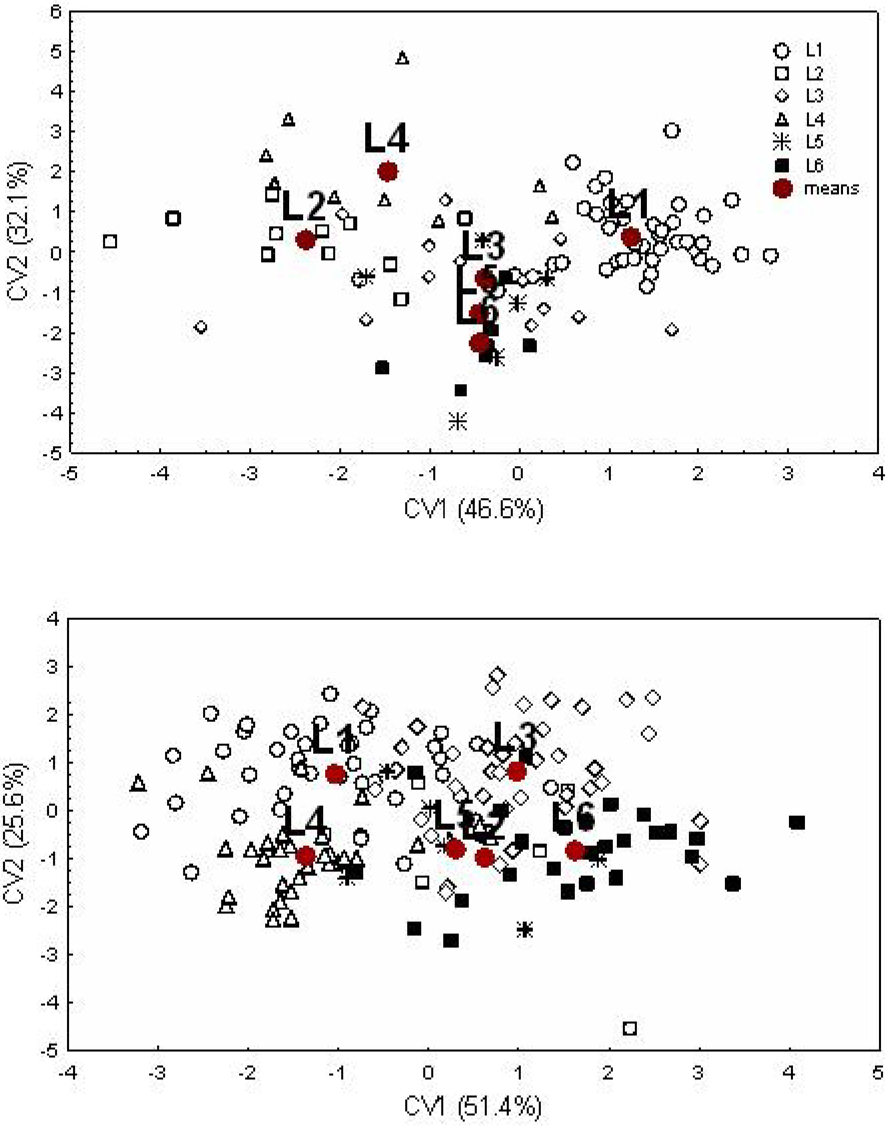

Figure 1. Plot of the first and second canonical variate (CV) scores and the CV means for the six collections of *Puntius singhala* using all morphometrics excluding body depth for males (top), and females (bottom) separately (location codes are as in Table 2).

DISCUSSION

Population structuring in freshwater fish species is expected to be greater than that in marine species, implying minimized intermixing among different rivers (Ward *et al*., 1994). Geographic variation and other forms of intraspecific phenotypic differences in freshwater fishes among different river/ lake systems have been documented by Guenette *et al*. (1992), Jerry & Cairns (1998), Hänfling & Brandl (1998) and Dynes *et al*. (1999). If a species has a life history that leads to restricted dispersal, maintenance of local populations in different rivers may be likely (Jerry & Cairns, 1998). Under continued spatial separation and isolation, accumulated genetic differences may lead to differentiable phenotypic outcomes in addition to what is resulted from mere phenotypic plasticity (Thompson, 1991). Differentiable variation in morphology among fish populations has been suggested as indicative of the presence of stock structuring (Hurlbut & Clay, 1998) and restricted movement among geographically isolated populations (Roby *et al*., 1991; Palumbi, 1994; Elliott *et al*., 1995; Uiblein, 1995; Jerry & Cairns, 1998). Presence of local populations within the same river system with significant phenotypic heterogeneity has been documented for some fishes (Guenette *et al*., 1992, Hänfling & Brandl, 1998).

In *P. singhala*, significant morphological heterogeneity was evident among some of the six population samples, although the level of differentiation between most of them was small as evidenced by wide overlap of data. The observed inter-location affinities were not strictly concordant between males and female fish, which make it rather complex to explain the observed variation. Slight differences in morphometrics between different geographic populations are likely to be observed due to the inherent natural variation in quantitative data, as well as phenotypic plasticity (Thompson, 1991). Genetic polymorphism or environmental factors may induce morphological variability among spatially separated fish populations (Carvalho, 1993), and phenotypic plasticity in fish morphology has been documented for various species (Wimberger, 1991, 1992). Fishes are considered to be phenotypically more variable than most other vertebrates, having relatively higher within-population coefficients of variation of phenotypic characters (Carvalho, 1993). The studied aquatic environments represent two major habitat types, lentic (L1, L2 and L6) and lotic (L3, L4 and L5) in which environmental conditions that may affect life history, growth and behaviour of fishes are expected to be different. If the observed morphological differences have resulted from mere phenotypic plasticity in response to different environs, these two groups of samples should have clustered separately. The variation observed also has no significant correlation to the inter-locality geographic distance, thus isolation-by-distance was not a plausible explanation.

It is accepted that if localized populations inhabit similar environments, or remain interconnected through gene-flow, they may fail to display great heterogeneity in phenotypic or genetic traits (Carvalho, 1993). Although there is some significant heterogeneity in morphology in *P. singhala*, the degree of differentiation is somewhat low between most of the population samples (e.g. L3, L5 & L6), as evidenced by the results of the discriminant analysis. Natural present-day dispersal between the populations in three distinct river systems (i.e. L3, L5 & L6) is possible only if these rivers hydrologically connect at termination in the same lowland floodplain in extreme pluvial periods. Therefore, the phenotypic affinities between them are likely to have resulted from some historical dispersal events in addition to inter-locality dispersal during rare extreme events. Present-day population structure shaped by historical gene flow and other processes has been suggested for many animals (Avise *et al*., 1988; Kvist *et al*., 1999; Monaghan *et al*., 2001). Sri Lanka is a small island with historical geological connection to the mainland India about 500,000 years ago (Rohling *et al*., 1998), and thus many faunal affinities have been established between the two landmasses (Pethiyagoda, 2005). Common ancestry can be assumed for *P. singhala* and its mainland relative *P. filamentosus*, as the latter is believed to be the species common to both regions prior to Pethiyagoda & Kottelat's (2005) description of the island form as a separate species, i.e. *P. singhala*. Accordingly, present-day phenotypic affinities seen in *P. singhala* among geographically distant rivers may be partly explained by assuming historical colonization from a common source, and relatively less subsequent diversification during evolutionary history of the species. *P. filamentosus* may have historically colonized the island and subsequent geographic isolation of the island population and cessation of its geneflow with the mainland may have led to its divergence from the ancestral form.

Sexual dimorphism in the dorsal fin of *P. singhala* is well known: only mature males have discernibly long filamentous rays (Pethiyagoda, 1991; Pethiyagoda & Kottelat, 2005). As the length of the ray-filaments apparently depends on reproductive status, the height of the dorsal fin is not a suitable quantitative character to assess geographic variation. The results indicate sexual dimorphism in three other characters, PFL, CPL, FBD where the males were found to have longer lengths than females. Sexual dimorphism in external body form or coloration, if present, plays an important evolutionary role in mate selection and reproductive fitness (Van Alphen & Seehausen, 2001). All three sex-based morphometrics in *P. singhala* are related to the fin characters that may have some adaptive significance for male fitness as well as for dispersal capabilities. Relatively longer pectoral fin (PFL) and dorsal-fin base as well as the longer caudal peduncle may give more maneuverability and swimming power to the male fish compared to the female fish so that the males may have better powers of dispersal. Sex-biased dispersal where individuals of one sex are more prone to disperse while those of the other sex stay at their natal site is seen in many animal groups including mammals, birds and fishes

(Prugnolle & de Meeus, 2002). In salmonids and some other fishes, male-biased dispersal has been suggested (Hutchings & Gerber, 2002), where the dispersing sex should be less structured genetically (Goudet *et al*., 2002). Evidence for sex-biased dispersal are generally obtained from biparentally inherited genetic markers (Goudet *et al*., 2002) or mark-recapture experiments (Hutchings & Gerber, 2002). Although no direct comparison is intended in the studied phenotypic traits with genetic data, indications of male-biased dispersal in *P. singhala* may be found by studying the patterns of phenotypic heterogeneity between the sexes. Significant heterogeneity in male morphometry among geographic samples was not found for any of the fin characters but only for PrOL, PsOL and HL, indicating that regardless of the present-day geographic location, *P. singhala* males share rather homogenous phenotypic traits that may have some adaptive significance particularly for dispersal. In contrast, female fish showed significant population heterogeneity in all characters except PrDL and HD. This indicates that females may have experienced less dispersal, creating opportunities to retain the incipient phenotypic variation received during historical colonization, and to intensify subsequent diversification. Most of the fin characters such as CPL, FBD, FBA and PFL in the females were found to be heterogeneous among the population samples. A study of genetic markers will be useful to investigate this proposition further.

Body depth of fishes mostly depends upon the stage of reproduction (ripe, spawning, or spent), especially in females, and therefore, caution should be taken on defining it as a particularly important shape variable. If the majority of the fish were of ripe/ spawning state, large mean BD’s would have resulted introducing another component of variation into the data. In that case, the Discriminant Function Analysis carried out without body depth (BD) data may represent a better picture of the population interrelationships.

A low level of variability in genetic makeup and phenotypes can be expected in island populations if the initial colonization occurred through a small number of founder individuals (Frankham, 1997). Extremely low genetic variability that resulted from founder events have been seen in fishes (Carlson *et al*., 1982). Moreover, potential inbreeding and associated loss of genetic variation has been linked particularly to island populations, so that the published data points to the conclusion that island populations have less genetic variation than mainland populations (Frankham, 1997). Such a postulate may be tested for small cyprinid populations in Sri Lanka as an island inhabitant that had separated from Indian mainland a long time ago.

In conclusion, the results suggest that the *P. singhala* populations show significant morphological variability among some of the discrete geographic localities, although the level of differentiation seems to be modest. Closer affinities of the sample populations representing geographically distinct locales (different river systems) that have very limited opportunities for present-day intermixing, may have been caused by phenotypic homogeneity resulting from historical dispersal events. Sexual dimorphism could be seen in fin characters including caudal-peduncle length, dorsal-fin base length and pectoral-fin length that may represent some adaptive significance for male-biased dispersal.

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