RUHUNA JOURNAL OF SCIENCE
Vol. 2, September 2007, pp. 70-81
http://www.ruh.ac.lk/rjs/rjs.html
ISSN 1800-279X

Morphological heterogeneity and population differentiation in the green chromid *Etroplus suratensis* (Pisces: Cichlidae) in Sri Lanka

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Abstract. Morphological variation of the euryhaline cichlid fish *Etroplus suratensis* (Bloch) from six geographically apart estuarine localities along the southern and western coasts of Sri Lanka was studied. Significant heterogeneity in morphology of the cichlid were found with respect to nine morphometric characters (n=218). Fish of Nilwala estuary and Garanduwa lagoon were not significantly different in morphology, yet they show discernible differences from the other four samples (Kahanda lagoon, Chilaw lagoon, Walawe estuary and Koggala lagoon) with respect to the most of the studied characters. Concordant results were found by multivariate analysis of the size-corrected morphological data as well. Three functions were significant in discriminating the populations of which the first two functions accounted for 95% of the covariance (CV1 85.4 % and CV2 9.7%). The function with the greatest discriminatory power (CV1) can clearly separate samples of Nilwala estuary (L5) and Garanduwa lagoon (L6) from the rest of the samples, while the magnitude of the discrimination between the latter samples is much smaller. Classification functions could correctly classify an average of 65.7% of the individuals into their respective *a priori* population units. No evidence was found for isolation-by-distance model. The results suggest that *E. suratensis* populations in some of the studied estuarine localities maintain significant morphological heterogeneity, and the morphological variation can be used to differentiate some of these populations.

Keywords: Cichlid, morphometry, phenotypic variation, partial isolation.

1 Introduction

The green chromide, *Etroplus suratensis* (Bloch) is an indigenous cichlid fish restricted in distribution to Sri Lanka and India (Ward & Wyman, 1977). It is euryhaline, commonly occurring in riverine estuaries and coastal lagoons, and in natural and man-made freshwater habitats in Sri Lanka (Pethiyagoda, 1991). Some aspects of its biology including the length-weight relationship, diet and feeding, and aspects of reproductive biology have been studied (Ward & Wyman, 1977; Costa, 1983; De Silva *et al*., 1984). It is an important food fish in Sri Lanka, being caught mainly as a part of subsistence fishery (De Silva, 1988).

Sri Lankan fishermen have noted markedly decreasing catches of the green chromide in some estuarine habitats, and attribute this to a decline in population density (Pers. Comm.). As human populations tend to concentrate close to estuaries, anthropogenic threats to that environment are unavoidable. Moreover, estuaries naturally receive large amounts of allochthonous material including domestic wastes and other pollutants. Thus, the estuarine ichthyofauna seems to be threatened by factors like habitat degradation and pollution. Reportedly declining stocks of *E. suratensis* indicate that it is becoming increasingly important to study the existing levels of genetic and phenotypic variation, with regard to conservation planning. Any management and conservation practice should be based upon prior knowledge of the existing natural variation, in order to preserve any adaptive variation that might be present.

Although estuaries are not closed hydrological systems like lakes, it is hypothesized that fish in different estuaries may have adapted to maintain their stocks largely within each estuary, resulting in some degree of isolation and an identifiable phenotypic differentiation. Morphological characters for many fishes, including highly dispersible marine and estuarine species have revealed spatial separation of populations (Schaefer, 1991; Elliott *et al.*, 1995; Uiblein, 1995; Hurlbut & Clay, 1998; Jerry & Cairns, 1998). Intra-specific phenotypic or genetic variation of the green chromide has not been studied previously, yet intra-specific variation has been indicated in the other extant species of the genus in Sri Lanka, *E. maculatus* (Bloch) (Pethiyagoda, 1991). The present work aims to test the hypothesis of intraspecific phenotypic variation for *E. suratensis* by studying the morphology of the fish among six geographically discrete estuarine localities in Sri Lanka. The null hypothesis of no population heterogeneity in morphology is statistically tested, and the possibility of differentiating the estuarine populations using morphological variation is assessed.

2 Materials and methods

2.1 Samples

Six estuarine localities including two riverine estuaries and four coastal lagoons in Sri Lanka were selected for sampling (Fig. 1). Adult fish were collected using various sized gillnets (mesh size range 4.0-6.0 cm) while a few samples were collected from fishermen. As the sex of individual fish was indistinguishable externally, a random sample of fish (n=104) from all six locations was sex-determined internally, and preliminary testing was carried out to see whether there was any sexual dimorphism. No significant sexual dimorphism with respect to the selected morphometrics was observed, therefore the data analysis was performed without taking the sex of the individuals into consideration.

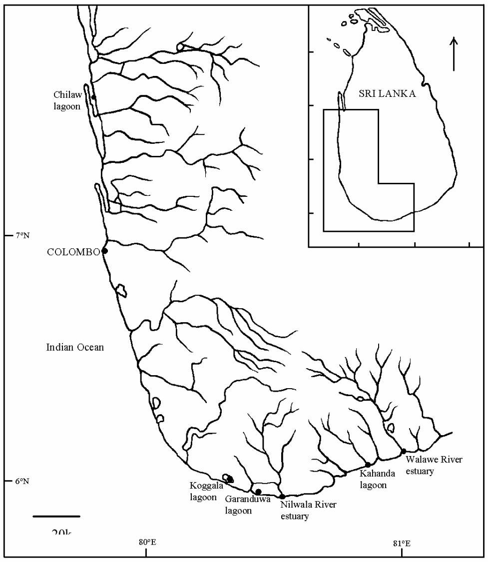

Figure. 1. Map of the collection localities of *Etroplus suratensis*.

2.2 Morphometrics and meristic measures

Standard length (L_S) was used as the measure of overall fish size. Twelve reliably measurable morphometric characters were selected for the study (Table 1).

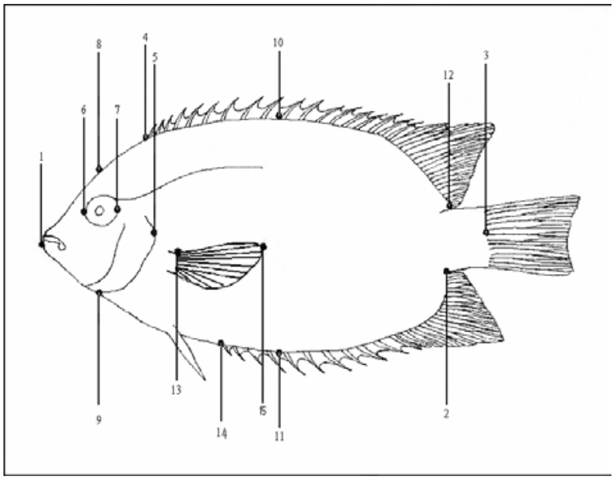

Figure. 2. Schematic diagram of the fish showing the positions of the superficial points used to collect data in *Etroplus suratensis* (see Table I for description).

All body measurements were taken from the lateral side of the fish to the nearest 0.1 mm using a Vernier caliper, and were the distance between the verticals or horizontal lines made across the identified superficial landmark points (Fig. 2). These landmark points were utilized to maintain the character homology between specimens as much as possible. All length measurements (*L*) were taken parallel to the antero-posterior body axis.

Head depth (HD) was taken perpendicular to the body axis between dorsal and ventral margins of the head, starting from the point where the ventral edge of the operculum intersects the ventral body margin. Maximum body depth (MBD) was measured between the two visually detectable widest points of the trunk, perpendicular to the body axis. Mouth gape (MG) was measured vertically between the mid points of upper and lower jaws of the fully-opened mouth. The length of the fin bases of dorsal and anal fin was measured between the verticals made across the externally visible origins of the first spine and the last ray of the fin.

Table 1. Morphometric characteristics of *Etroplus suratensis* studied.

Character	**code**	**description**	**Number code (Fig. 2)**
Standard length	L_S	mouth tip to the mid point of caudal fin origin	1-3
Caudal peduncle length	L_{CP}	length from the anal fin insert to the midpoint of the caudal peduncle	2-3
Pre-dorsal length	L_{PRD}	mouth tip to the origin of dorsal fin	1-4
Head length	L_H	mouth tip to the posterior edge of operculum	1-5
Orbital length	L_O	length (along axis) of the orbit	6-7
Post-orbital length	L_{PO}	posterior edge of orbit to posterior edge of operculum	5-7
Pre-orbital length	L_{PRO}	mouth tip to anterior edge of orbit	1-6
Mouth gape	MG	height between the mid points of the upper and lower jaws of the fully opened mouth	not shown
Head depth	HD	depth from the ventral point of intersection of the outer operculum edge to the dorsal head margin (measured vertically)	8-9
Maximum body depth	MBD	distance between points at deepest part of body (measured vertically)	10-11
Dorsal fin base	FBDO	length between the visible origins of the first spine and the last ray of the dorsal fin	4-12
Anal fin base	FBAN	length between the visible origins of the first spine and the last ray of the anal fin	2-14
Pectoral fin length	L_{PECF}	length of the fin from dorso-posterior part of fin base to the edge of the fin	13-15

2.3 Data and statistical analysis

As the fish exhibiting allometric growth show a strong correlation in shape measurements to body size (Reist, 1985, 1986), raw data of each morphometric character were standardized to standard length (L_S) to obtain data sets with means of zero and unit standard deviation using the following equation (Elliott *et al*., 1995).

$$M_S = M_O \, (L \,/\, L_S)^b$$

The working formula for each specimen for a given morphometric character is:

$$\log_{10} M_S = \log_{10} M_O + b \log_{10} L - b \log_{10} L_S$$

where M_S is the standardized character measurement, M_O is the observed character measurement, L is the mean standard length for all fish from six collections, L_S is the standard length of the specimen, and b is the slope of the regression of $\log_{10} M_O$ on $\log_{10} L_S$ for all fish. Correlation analysis of the standardized data against size showed that the allometric transformation successfully removed size dependence.

The standardized data were analyzed by univariate and multivariate methods. Differences among geographic samples were tested by one-way analysis of variance (ANOVA) followed by Newman-Keuls multiple comparison test (Zar, 1984). Tests were considered significant at 0.05 probability level with the sequential Bonferroni adjustment (Rice 1989). Discriminant function analysis (DFA) was performed to identify the characters that were important in distinguishing population groups, and to formulate classification functions for each location. Based on these functions, DFA classifies individual fish into a group, which is then compared with the *a priori* group of that individual to get the percentage of classification success. Pair-wise squared Mahalanobis distance (D^2) among 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 (approx. distance derived from a scaled map). All data analysis and statistical analyses were carried out by using the software package STATISTICA v 7.0 (Statsoft, USA).

3 Results

Table 2. Collection localities, sample sizes (n) and size statistics (standard length L_S) of adult *Etroplus suratensis* samples.

Location	**estuary type**	**n**	**Size range (L_S) (mm)**	**Mean L_S (mm)**	**SD**
L1: Kahanda Lagoon	Coastal lagoon	32	66.5- 128.4	90.6	17.6
L2: Chilaw lagoon	Coastal lagoon	32	75.6- 116.3	93.5	9.2
L3: Walawe estuary	Riverine estuary	31	77.2- 154.2	110.0	21.7
L4: Koggala lagoon	Coastal lagoon	35	110.6- 143.6	125.2	8.5
L5: Nilwala estuary	Riverine estuary	38	85.5- 174.0	126.5	28.4
L6: Garanduwa lagoon	Coastal lagoon	49	52.6- 130.0	89.8	12.1

The size statistics of the fish samples is given in Table 2. Significant differences in size were found among samples where the largest fish were recorded from Koggala lagoon and Nilwala estuary ($p<0.05$, ANOVA). The mean L_S (± SD) for all fish analyzed is 105.3 ± 23.8 mm (n=218). The sex ratio was male biased (1.2:1). Univariate ANOVA revealed highly significant differences ($p<0.05$, with Bonferroni adjustment) in nine of the studied morphometric characters leading to the rejection of the null hypothesis of 'no heterogeneity in fish morphology among estuarine populations'. There were no significant differences in caudal peduncle length, pre-orbital length, and length of dorsal fin-base among samples (Table 3). Fish from Nilwala estuary and Garanduwa lagoon share several of the morphometric characters that are significantly different from those in the other four locations. In this respect, they have shorter pre-dorsal lengths, shorter post-orbital lengths, smaller mouth gape, deeper heads, and shorter anal fin bases. The samples from Nilwala estuary and Garanduwa lagoon are not differentiable from each other by any of the morphometrics. Fish from Koggala lagoon have the largest maximum body depth. Slight, yet significant differences in most of the other morphometric characteristics were found among the studied populations (Table 3).

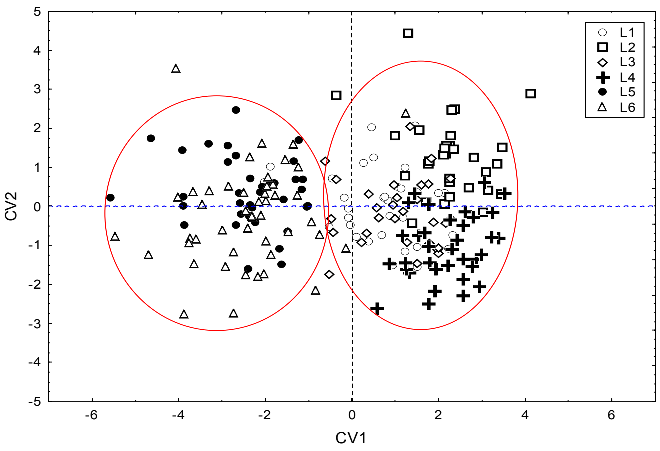

Figure. 3. Plot of the first and second canonical variate (CV) scores for the six collections of *Etroplus suratensis*. CV1 and CV2 explain 85.4% and 9.7% of the variation among the individuals respectively. (○ L1: Kahanda lagoon; □ L2: Chilaw lagoon, ◊ L3: Walawe estuary, + L4: Koggala lagoon, • L5: Nilwala estuary, Δ L6: Garanduwa lagoon).

Discriminant function analysis (DFA) for size-standardized data identified eleven characters that contribute significantly for the derived functions (Wilks' Lambda= 0.106; n= 218; approximate $F_{(60,\ 921)}= 9.43$; $p<0.001$) (Table 4). Head depth of the fish is the character that contributed most to the discrimination among groups while length of the pectoral fin had the least contribution (p=0.103). Among the five functions (canonical roots or covariates) derived, only three were statistically significant (chi square tests, $p<0.05$) (Table 5). According to the standardized coefficients for roots (Table 6), first function is weighted most heavily by MG, HD, L_O, L_{PRO}, L_{PO} and FBAN while the second function is weighted mostly by MBD, L_{CP}, FBDO and L_{PECF}. About 85.5% of all discriminatory power is explained by the first function, and therefore it is clearly the most important discriminant function. As detected by the respective eigen values, the first two canonical variables (CV) in the DFA collectively account for 95.1% of the variance in the data (Table 6).

According to the canonical means, first function can clearly discriminate Nilwala (L5) and Garanduwa (L6) populations from the rest of the groups (by having larger negative means), and Chilaw (L2) & Koggala (L4) samples from Kahanda (L1) & Walawe (L3) samples to a lesser degree (Table 7). Accordingly, the plot of the first two CV's separates the data into two discernible clusters (Fig. 3) in which the CV1 has the most important power in discriminating L5 and L6 from the rest. Although the magnitude of the discrimination is much smaller, CV2 seems to discriminate L2 from L4 in the latter cluster based on positive and negative canonical means respectively (Table 7). The studied characters are not able to discriminate L5 from L6, or L1 from L3 adequately. The derived classification functions could correctly classify an average of 65.7% of the individuals into their respective *a priori* groups (Table 8). The pair-wise squared Mahalanobis distance (D^2) for all pairs of populations were highly significant (Table 9) yet there was no agreement to the isolation-by-distance model (Pearson's r = -0.05, p>0.05).

Table 3. Summary of the morphometrics of *Etroplus suratensis* presented as percentages of L_S (mean ± SD). Superscripts indicate test results of the ANOVA followed by Newman-Keuls multiple comparison tests on size-adjusted characters (any measurements with shared superscript letters are not significantly different from each other at P<0.05 with sequential Bonferroni adjustment).

Character length (mm)	Kahanda lagoon (L1) n= 32	Chilaw lagoon (L2) n= 32	Walawe estuary (L3) n= 31	Koggala lagoon (L4) n= 35	Nilwala estuary (L5) n= 40	Garanduwa lagoon (L6) n= 50
L_{CP}*	10.2 ± 1.4^{a}	11.4 ± 1.4^{a}	10.3 ± 1.4^{a}	10.2 ± 1.4^{a}	10.8 ± 1.7^{a}	10.3 ± 2.1^{a}
L_{PRD}	33.6 ± 1.5^{a}	33.8 ± 2.2^{a}	33.2 ± 1.5^{a}	34.1 ± 1.7^{a}	30.5 ± 2.3^{b}	31.3 ± 2.5^{b}
L_H	30.0 ± 1.0^{ab}	29.9 ± 1.4^{ab}	30.6 ± 1.5^{a}	30.0 ± 1.4^{a}	28.0 ± 2.4^{b}	30.2 ± 2.4^{ab}
L_O	8.5 ± 0.8^{ad}	8.1 ± 0.6^{bd}	8.2 ± 0.9^{acd}	7.2 ± 0.6^{b}	8.2 ± 0.6^{ac}	9.2 ± 1.0^{c}
L_{PO}	12.6 ± 1.1^{a}	12.7 ± 0.9^{a}	12.9 ± 1.2^{a}	13.0 ± 0.8^{a}	10.7 ± 1.1^{b}	11.4 ± 1.4^{b}
L_{PRO} *	9.2 ± 1.1^{a}	9.2 ± 1.3^{a}	9.5 ± 1.4^{a}	9.6 ± 1.0^{a}	9.9 ± 1.3^{a}	10.0 ± 1.4^{a}
MG	10.8 ± 0.9^{a}	11.3 ± 0.9^{ac}	11.1 ± 0.8^{ac}	11.6 ± 0.8^{c}	9.6 ± 0.9^{b}	9.8 ± 1.1^{b}
HD	45.3 ± 2.0^{a}	41.2 ± 3.1^{c}	44.5 ± 2.8^{a}	46.2 ± 2.3^{a}	48.8 ± 2.0^{b}	49.0 ± 5.0^{b}
MBD	57.1 ± 3.4^{a}	55.9 ± 2.8^{a}	56.8 ± 2.3^{a}	58.8 ± 1.8^{b}	55.9 ± 2.1^{a}	56.6 ± 2.9^{a}
FBDO*	59.9 ± 3.6^{a}	60.4 ± 3.2^{a}	59.7 ± 2.2^{a}	60.0 ± 1.9^{a}	58.7 ± 2.7^{a}	58.7 ± 3.3^{a}
FBAN	43.1 ± 3.0^{ac}	43.8 ± 2.0^{ac}	42.5 ± 3.2^{a}	44.8 ± 2.0^{c}	39.7 ± 2.9^{b}	39.9 ± 3.3^{b}
L_{PECF}	26.7 ± 2.8^{ab}	25.5 ± 2.8^{a}	27.2 ± 2.0^{b}	27.0 ± 1.6^{b}	25.6 ± 2.0^{ab}	26.7 ± 1.8^{ab}

* not significant

Table 4. Summary results of the forward stepwise discriminant function analysis of standardized morphological data of *Etroplus suratensis*. The characters are listed in the descending order of contribution to the discrimination between locations (Wilk's partial Lambda).

character	Wilk's Lambda	Partial Wilk's Lambda	F-to remove	p-level
HD	0.148	0.716	15.564	<0.001
MG	0.142	0.748	13.214	<0.001
L_{O}	0.130	0.817	8.780	<0.001
L_{PRD}	0.119	0.896	4.563	0.001
FBDO	0.117	0.910	3.899	0.002
FBAN	0.116	0.913	3.750	0.003
L_{H}	0.116	0.914	3.686	0.003
L_{PRO}	0.116	0.917	3.525	0.004
MBD	0.116	0.919	3.433	0.005
L_{CP}	0.114	0.934	2.748	0.020
L_{PO}	0.113	0.937	2.629	0.025
L_{PECF}*	0.111	0.955	1.863	0.103*

* not significant

Table 5. Results of the Chi square analysis to determine which roots are statistically significant (a step-down table for all roots; asterisks indicate significant tests with p<0.05).

Roots removed	Eigen value	Canonical R	Wilk's Lambda	χ^2	df	p-level
0	4.137	0.897	0.106	455.0	60	<0.001*
1	0.469	0.565	0.546	122.8	44	<0.001*
2	0.173	0.384	0.802	44. 8	30	0.040*
3	0.045	0.207	0.941	12.1	18	0.825
4	0.018	0.132	0.983	3. 6	8	0.894

Table 6. Standardized coefficients for the three significant discriminant functions (roots) derived for morphology of *Etroplus suratensis*.

character	Root 1	Root 2	Root 3
MG	0.575	-0.132	-0.068
HD	-0.544	-0.504	0.370
L_{PO}	0.299	-0.131	-0.172
L_{O}	-0.480	0.303	-0.276
FBAN	0.327	0.104	0.183
L_{CP}	-0.038	0.420	0.047
L_{PECF}	-0.070	-0.326	-0.089
L_{H}	0.180	-0.322	-1.008
L_{PRD}	0.345	0.111	0.580
L_{PRO}	-0.426	0.049	0.212
FBDO	0.308	0.392	0.086
MBD	-0.155	-0.499	0.279
Eigen value	4.137	0.469	0.173
Cumulative proportion	0.855	0.951	0.987

Table 7. Means of canonical variables (roots) for each locality based on the discriminant functions derived for morphology of *Etroplus suratensis*.

Location/ group	**Root 1**	**Root 2**	**Root 3**	**Root 4**	**Root 5**
L1	-0.681	0.042	0.259	-0.450	-0.090
L2	2.246	1.278	-0.018	0.178	-0.072
L3	1.098	-0.203	-0.757	-0.090	0.180
L4	2.171	-1.035	0.373	0.178	-0.0002
L5	-2.416	0.365	0.448	0.035	0.183
L6	-2.384	-0.240	-0.280	0.088	-0.147

Table 8. Proportion of *E. suratensis* correctly classified into groups by classification functions based on the *a priori* knowledge of their original location. Group numbers refer to the respective location number (rows: observed classification, columns: predicted classification).

Group	**Percent correct**	**Groups**					
		L1	**L2**	**L3**	**L4**	**L5**	**L6**
1: L1	59.4	19	3	3	5	1	1
2: L2	74.2	0	23	2	6	0	0
3: L3	54.8	4	4	17	5	0	1
4: L4	82.9	2	2	2	29	0	0
5: L5	58.3	0	0	0	0	21	15
6: L6	64.6	1	1	1	0	14	31
total	65.7	26	33	25	45	36	48

Table 9. Squared Mahalanobis distance between pairs of populations (below diagonal) and the probability values (above diagonal) (asterisks indicate tests that are not significant at $p<0.05$ with sequential Bonferroni adjustment).

	L1	L2	L3	L4	L5	L6
L1	-	<0.0001	0.046 *	<0.0001	<0.0001	<0.0001
L2	4.45	-	<0.0001	<0.0001	<0.0001	<0.0001
L3	1.47	4.19	-	<0.0001	<0.0001	<0.0001
L4	3.80	5.51	3.23	-	<0.0001	<0.0001
L5	10.04	22.87	14.14	23.06	-	0.084 *
L6	10.05	23.82	12.49	21.83	1.01	-

4 Discussion

Results from both univariate and multivariate analyses provide congruent evidence for the existence of significant intraspecific morphological heterogeneity in *E. suratensis* among selected estuarine localities of Sri Lanka. Derived classification functions provide moderate percentage of classification success (ranging from 54.8% to 82.9%), indicating that the morphological characters used in this analysis provide some discriminatory power for the *E. suratensis* populations studied. Few population-specific characteristics are also evident including the largest body depth (MBD) of fish in Koggala lagoon and the shortest head depth (HD) of fish in Chilaw lagoon.

Among three significant functions in discriminating the populations, the first function (CV1) is clearly the most important one, and the magnitude of discrimination of the other two functions is comparatively much smaller. The close affinity of the fish populations between Garanduwa lagoon and Nilwala estuary is evident. Of the characters identified as being most weighted for CV1, Nilwala estuary and Garanduwa lagoon shared four characters that are also significantly different from those of the other four samples (smaller MG, larger HD, and shorter L_{PO} and FBAN). In addition, L_{PRD} which is weighted most heavily for the CV3 is also a shared character between Nilwala estuary and Garanduwa lagoon yet differs from all samples of the second cluster. Overall, the close affinity between L5 and L6 suggests that the two samples represent similar geographical existence and origin, and the subsequent population intermixing is the likely explanation for the observed morphological homogeneity. In fact, the Garanduwa lagoon receives freshwater influxes originating from 'Polwatta Ganga' that has a hydrological connection to the River Nilwala before discharging to the sea at Modara in Weligama (Annon. 1988). Such hydrographical connectivity between the two water bodies is likely to facilitate the intermixing of pelagic fish populations, disrupting any potential mechanisms of population divergence.

Wide overlap exists in the CV values among the samples of the second cluster as well, although discrimination to a lesser degree is possible. The morphological heterogeneity observed has no significant correlation to the geographical distance between estuaries, as evidenced by the negative results from the isolation-by-distance model. Chilaw lagoon represents the geographically most remote location among the studied estuarine populations, yet the pair-wise Mahalanobis distances involving the Chilaw lagoon sample are not systematically large. This is also displayed by the clustering of the Chilaw population together with three other geographically remote populations in the second cluster.

Morphometric measurements have been widely used to discriminate populations of various fish species (Elliott, *et al*., 1995; Uiblein, 1995; Hurlbut & Clay, 1998). The conventional approach for such analysis is based on measurements along the antero-posterior body axis and the depth measurements. However, no previous investigation on morphology of *E. suratensis* populations has been reported so far. In this study, variation in various morphological characters of the fish is found between geographically separated estuarine localities. The reasons behind such variability might include geographic isolation, phenotypic plasticity and local adaptation. The waters off the south coast of Sri Lanka contribute to the overall current regime around the island having a direction closely connected with the Indian Ocean monsoons (Schott *et al*., 1994, Shankar *et al*., 2002). This coastal current regime is likely to impose tidal currents in and out of coastal lagoons and riverine estuaries, allowing some interchange between drift-vulnerable life stages of fishes. However, *E. suratensis* is a substrate spawner that has a specialized life history strategy to protect the young during their early stages (Ward & Wyman, 1977). Such life strategy is likely to contribute to the retention of early stages that may be vulnerable to tidal flow, largely within the estuarine habitat, and consequently facilitating their populations to maintain to some extent separately from other neighboring populations. 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, including cichlids (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 differentiable variation in morphology among fish populations has been suggested as indicative of the presence of stock structuring and restricted movement among geographically isolated populations (Uiblein, 1995; Roby *et al.*, 1991; Palumbi, 1994; Jerry & Cairns, 1998). In *E. suratensis*, presence of such population subdivision or strong stock structure is not supported due to the low degree of differentiation detected.

Morphological divergence has been reported in estuarine fish populations that are not completely geographically separated, suggesting that partial isolation may play a role in population subdivision (Roby *et al.*, 1991, Suneetha & Naevdal, 2001). The results of the present study can also be explained by a similar postulate of partial isolation as the studied estuarine habitats are not completely isolated. Population differentiation may also occur despite opportunity for extensive gene flow between populations when there are relatively strong differential selective pressures exerted on the different populations by local environmental factors, such as temperature (Verspoor & Jordan, 1989). As the present analysis does not include environmental data for the sample localities, it is not possible to confirm whether the observed variation is associated with local environmental conditions, and therefore, further environmental comparisons of these estuaries would be worthwhile. In addition, genetic investigations of the variation and population differentiation involving more estuarine samples of *E. suratensis* will be useful in substantiating the findings of the present study. Knowledge of the genotypic and phenotypic variation of species is a pre-requisite in conserving them, particularly where populations with subtle adaptive variation are likely to exist.

Acknowledgements

This study was funded by the National Science Foundation (Sri Lanka) grant number RG/2003/BT/03. The technical assistance provided by S. Kapukotuwa and A.G. Samanthi, and assistance in preparation of Fig.2 by Anuradha De Silva is acknowledged.

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