

Genetic relationship in goatfishes (Mullidae: Perciformes) of the Red Sea and the Mediterranean, with remarks on Suez Canal migrants*

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SUMMARY: An electrophoretic examination of 21 presumptive loci was used to analyze the genetic relationship in the fish family Mullidae. The present study included seven species from the Red Sea and two from the Mediterranean. Two of the Red Sea species (*Upeneus pori* and *U. moluccensis*), which had colonized the Mediterranean via the Suez Canal, were also sampled in their new habitat. The electrophoretic results support the taxonomy which is based on morphomeristic measurements, with the exception of *U. pori*, the genetic distance of which with its congeneric species is at a level which is attributed to different genera. No discernible genetic difference was found between the populations of the colonizing species in both seas ($D=0.004$ for *U. moluccensis*, $D=0.081$ for *U. pori*), as well as between colonizing and non-colonizing species. The average heterozygosity of Mullidae is lower than the average known for other fishes.

Key words: Mullidae, genetic relationship, Red Sea, eastern Mediterranean, migration.

INTRODUCTION

The goatfish family (Mullidae) can be easily distinguished from all other percoids by their unique hyoid barbels, used in trophic foraging. This circumtropical family includes about 50 species belonging to six genera.

Most goatfish inhabit inshore areas and are commercially important throughout their distribution. Due to their economic value, goatfish have been the subject of rather intense biological and taxonomic studies (e.g., Lee, 1974; Munro, 1976; Papaconstantinou *et al.*, 1981; Sorden, 1983; Gosline, 1984; Wahbeh, 1992a,b; Golani, 1994).

The taxonomy of Mullidae in the Red Sea has received considerable attention (Dor and Ben-Tuvia, 1984; Al-Absey, 1988; Ben-Tuvia and Kissil, 1988). Thirteen species have been reported from the Red Sea region, belonging to three genera: *Mulloid*es Bleeker, 1849, *Parupeneus* Bleeker, 1863 and *Upeneus* Cuvier, 1829. Electrophoretic analysis can add a different dimension, which provides insight into the interrelationship of species and genera, to these taxonomic studies (Avise, 1974; Buth, 1984; Bolch *et al.*, 1994). Regarding the Red Sea Mullidae, electrophoretic studies may be of particular interest, since two members of this family, the brownband goatfish *Upeneus pori* Ben-Tuvia and Golani, 1989 (previously known in this area as *U. asymmetricus*), and the goldband goatfish, *Upeneus*

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moluccensis (Bleeker, 1855), have migrated through the Suez Canal, which was opened in 1869, into the Mediterranean Sea. Colonization exposed these populations to ecological pressures that may have differed from those exerted on their original populations. Therefore, it has been hypothesized that the colonizing population would undergo some changes (Parsons, 1984). Despite the different hydrological conditions and faunistic affinities of these two seas, each of these two species succeeded to establish a large permanent population in the Mediterranean. In their new region they encountered two indigenous mullids, the red mullet *Mullus barbatus* Linnaeus, 1758, and the striped mullet, *Mullus surmuletus* Linnaeus, 1758.

Another question presented by Lessepsian migration is the association between genetic variability and success in colonization. High genetic variability has been hypothesized as a preadaptation to a heterogeneous environment (Hedrick *et al.*, 1976). Since successful colonization often requires the occupation of new and different habitats, it is expected that successful colonizer species have high genetic variability (Baker and Stebbins, 1965; Safriel and Ritte, 1980; Gray, 1986; Williamson and Fitter, 1996).

The purpose of this study is thus threefold: to determine the genetic relationship between Red Sea mullid species and their Mediterranean confamilials; to compare the genetic structure of Red Sea and Mediterranean populations of the colonizing

species; and to compare the genetic structure of colonizing and non-colonizing species.

MATERIALS AND METHODS

Collection of material

Of the 13 known species of Red Sea Mullidae, 11 reach the Gulf of Elat (Ben-Tuvia and Kissil, 1988). Seven species, representing all three genera that occur in this region, were sampled for the present study. Five of these species, *Mulloides flavolineatus* (Lacepède, 1801), *Parupeneus macronema* (Lacepède, 1801), *P. rubescens* (Lacepède, 1801), *Upeneus moluccensis* (Bleeker, 1855) and *U. subvittatus* (Temminck and Schlegel, 1843), have a wide zoogeographic distribution, including the Indian Ocean and the western Pacific. The two other species, *Parupeneus forsskali* Fourmanoir and Guézé, 1976 and *Upeneus pori* Ben-Tuvia and Golani, 1989 were considered endemic to the Red Sea until the latter extended its distribution into the Mediterranean. Of the three species that were not sampled, two, namely *Mulloides vanicolensis* Valenciennes, 1831 and *Parupeneus heptacanthus* (Lacepède, 1801), are rare in the northern part of the Gulf of Elat and never appeared in our catches. The third species, *Parupeneus cyclostomus* (Lacepède, 1801), is associated with coral reefs in which collection is prohibited by law.

TABLE 1. – Number of individuals, length range, date, method of capture and catalogue numbers.

	number of individuals	total length (mm)	date	method of capture	HUJ catalogue number*
RED SEA					
<i>Upeneus pori</i>	20	100-162	Mar. 30, 86	Beach seine	13598
“ “	30	116-149	June 21, 86	“ “	13599
<i>U. moluccensis</i>	16	99-131	Dec. 6, 86	Trammel net	13600
<i>U. subvittatus</i>	1	149	Apr. 30, 86	“ “	13601
“ “	4	119-212	Nov. 12, 86	“ “	13602
<i>Mulloides flavolineatus</i>	48	138-173	Nov. 30, 86	Beach seine	13603
<i>Parupeneus forsskali</i>	23	51- 86	Nov. 8, 86	“ “	13604
“ “	17	171-257	Nov. 15, 86	Spear gun	13605
<i>P. rubescens</i>	40	76-130	June 21, 86	Beach seine	13606
<i>P. macronema</i>	6	111-182	Nov. 15, 86	Spear gun	13607
MEDITERRANEAN					
<i>Upeneus pori</i>	50	93-153	May 4, 86	Trawl	13608
<i>U. moluccensis</i>	38	102-175	May 4, 86	“	13609
<i>Mullus barbatus</i>	38	105-202	May 5, 86	“	13610
<i>M. surmuletus</i>	14	120-205	May 5, 86	“	13611

*All studied fish are deposited in the Hebrew University Fish Collection (HUJ).

TABLE 2. – The different enzymes (including the tissue from which each was extracted, and the buffer system that was used for its analysis) that were analyzed in the present study.

enzyme	E.C. number	abbreviations	tissue*	buffer system**
Adenosine deaminase	3.5.4.4	ADA	L	1
Alkaline phosphatase	3.1.3.4	ALP	L	2
Amino peptidase	3.4.1.2	AP-1	L	1
Amino peptidase	3.4.1.2	AP-2	L	1
Esterase	3.1.1.1	EST	L	3
General Protein	—	Gen-Prot-1	M	3
“ “	—	Gen-Prot-2	M	3
“ “	—	Gen-Prot-3	M	3
“ “	—	Gen-Prot-4	M	3
“ “	—	Gen-Prot-5	M	3
Glycerate dehydrogenase	1.1.1.29	GlyDH	M	3
Glucose-6-phosphate dehydrogenase	1.1.1.46	G6PD-1	L	2
“ “	1.1.1.46	G6PD-2	L	2
Glucokinase	2.7.1.2	GK	L	2
Isocitrate dehydrogenase	1.1.1.42	IDH	L+M	3
Malic enzyme	1.1.1.40	ME-1	L+M	3
“ “	1.1.1.40	ME-1	L+M	3
6-Phosphogluconate dehydrogenase	1.1.1.44	PGD	L	2
Phosphoglucomutase	2.7.5.1	PGM-1	L	2
“ “	2.7.5.1	PGM-2	L	2
Xanthine dehydrogenase	1.2.3.2	XDH	L+M	3

* L - liver; M - muscle

** 1 - Tris-Citrate pH 6.7/6.3, 4.7 Cm/V, 6-7 h

2 - Tris-Citrate pH 8.0, 2.7-3.3 Cm/V, 6-7 h

3 - Lithium Hydroxide pH 8.1/8.4, 7.3-12.7 Cm/V, 6-7 h

In the eastern Mediterranean, populations of the two migrants, *Upeneus moluccensis* and *U. pori*, were sampled, as well as the two indigenous goatfish *Mullus barbatus* and *M. surmuletus* which extend to the northeastern Atlantic.

Fish collection was conducted in the northern tip of the Red Sea (Gulf of Elat) and the eastern Mediterranean. Details of the collection are presented in Table 1. Fishes collected by beach seine and trawl were placed on dry ice immediately upon capture. Those captured by trammel nets and spear guns were placed on dry ice no later than 45 minutes after capture. Fish were delivered frozen to the Department of Genetics at the Hebrew University and stored at -40°C.

Electrophoresis

Muscle and liver tissue were dissected from each individual and homogenized with equal volumes of 0.1 M Tris-HCl pH 7.0: H₂O: Glycerol (2:2:1) using a Sonifier Cell Disruptor, model W185 (Heat System-Ultrasonic, Inc.) (10,000 rpm). The homogenates were centrifuged at 4°C for 30 min at 14,000 g. The supernatants were run on horizontal

starch gels using 12% hydrolyzed starch (Sigma No. S-4501) at 4°C.

The enzymes analyzed are listed in Table 2. Staining procedures followed Selander *et al.* (1971) and Harris and Hopkinson (1976). Enzyme nomenclature followed the International Union of Biochemistry recommendations. Allelic designations were determined according to their electrophoretic mobility, following Buth (1983).

Genetic analysis

The genetic distances between all possible pairs were calculated using Nei's (1978) index. The DISPAN computer program (Ota, 1993), using the neighbour-joining method (Saitou and Nei, 1987), was based on genetic distances and applied in the construction of an unrooted phylogenetic tree. This program was chosen because it allows compensation for possible bias due to a small number of individuals in sample size; a few species in this study were represented by less than 20 individuals. Allele frequencies of the different enzymes were used for the calculation of the levels of polymorphism (\bar{P}) and heterozygosity (\bar{H}) for each species.

RESULTS

Gene products of 21 loci were screened. Their allele frequencies are given in Table 3. Because six loci (ADA, ALP, Gen Prot-1, ME-1, ME-2 and XDH) were monomorphic for the same allele in all species, they are not included in Table 3. Five other loci (G6PD-1, Gen Prot-3, Gen Prot-4, IDH and PGD) were also monomorphic, but not all species were monomorphic for the same allele. Ten loci (AP-1, AP-2, EST, Gen Prot-2, Gen Prot-5, G6PD-2, GlyDH, Gk, PGM-1 and PGM-2) were polymorphic in at least one species (Table 3).

The genetic distances (Nei, 1978) between all species and populations are given in Table 4. The neighbour-joining phylogenetic tree constructed by the DISPAN program is given in Fig 1. The mean levels of polymorphism and heterozygosity are listed in Table 5.

Mean polymorphism in Red Sea and Mediterranean Sea goatfish ($\bar{P} = 0.108 \pm 0.028$) was significantly lower than the value ($\bar{P} = 0.209 \pm 0.137$) found for 200 species of fishes (Nevo *et al.*, 1984), ($t = 7.692$ (209 d.f.); $p < 0.001$), but slightly higher than the value ($\bar{P} = 0.064$) found for goatfish from

TABLE 3. – Allele frequencies in Red Sea and Mediterranean goatfishes. U.p. = *Upeneus pori*, U.m. = *U. moluccensis*, U.s. = *U. subvittatus*, M.f. = *Mulloides flavolineatus*, P.f. = *Parupeneus forsskali*, P.r. = *P. rubescens*, P.m. = *P. macronema*, M.b. = *Mullus barbatus*, M.s. = *M. surmuletus*. (M) = Mediterranean, (R) = Red Sea. (Sample size is given next to species name; exceptions are indicated in the body of the table)

Locus	allele	U.p. (M) n=50	U.p. (R) n=50	U.m. (M) n=38	U.m. (R) n=16	U.s. n=5	M.f. n=48	P.f. n=40	P.r. n=40	P.m. n=6	M.b. n=38	M.s. n=14
AP-1	A	1.000	1.000	1.000	1.000	1.000				0.083		
	B						1.000	1.000	1.000	0.917	1.000	1.000
AP-2	A			1.000	1.000	1.000						
	B						1.000	1.000	1.000	1.000		
	C	0.970	0.990								1.000	1.000
	D	0.030	0.010									
EST	A	0.970	0.670	0.868	0.531	1.000	0.094	0.357	0.888		0.526	0.321
	B	0.030	0.330	0.132	0.469		0.906	0.643	0.112	1.000	0.474	0.679
Gen Prot-2	A	0.040										
	B	0.960	1.000	1.000	1.000	1.000	1.000	1.000	0.950	1.000		1.000
	C								0.050			
	D										1.000	
Gen Prot-3	A	1.000	1.000				1.000					
	B			1.000	1.000	1.000		1.000	1.000	1.000	1.000	1.000
Gen Prot-4		1.000	1.000	1.000	1.000							
Gen Prot-5	A							1.000	1.000	1.000		
	B	1.000	1.000	1.000	1.000	0.900					1.000	1.000
	C					0.100	1.000					
GlyDH	A	0.020	0.020	1.000	1.000				1.000	1.000	1.000	0.536
	B	0.980	0.980			1.000	1.000					0.464
	C							1.000				
G6PD-1	A						1.000		1.000		1.000	1.000
	B	1.000	1.000	1.000	1.000	1.000		1.000	1.000	1.000		
G6PD-2	A			n=22					1.000	0.851	1.000	
	B			1.000	1.000					0.149		1.000
	C					1.000						1.000
GK	A	0.070	0.090									
	B	0.930	0.910	1.000	1.000	1.000	1.000					
	C							1.000	1.000	1.000	1.000	1.000
IDH	A			1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	B	1.000	1.000									
PGD	A						1.000					
	B	1.000	1.000								1.000	1.000
	C			1.000	1.000	1.000						
	D							1.000	1.000	1.000		
PGM-1		n=21	n=24	n=24			n=24				n=30	
	A			0.500	0.406	0.500		0.525	0.063	0.500	0.500	0.536
	B	0.313	1.000									
PGM-2	C	0.687		0.500	0.594	0.500	1.000	0.475	0.937	0.500	0.500	0.464
	A			1.000	1.000							
	B	1.000	1.000			1.000	1.000		1.000	1.000	0.960	1.000
	C										0.040	
	D							1.000				

Hawaii (Shaklee *et al.*, 1982). The average heterozygosity of Red Sea and Mediterranean goatfishes ($\bar{H} = 0.042 \pm 0.018$) was also lower but not significantly different from the value ($\bar{H} = 0.051 \pm 0.035$) found by Nevo *et al.* (1984) for 183 species of fishes ($t=1.507$ (192 d.f.); $p>0.100$).

For each of the two migrating species, *Upeneus pori* and *U. moluccensis*, the level of genetic differ-

entiation between the Mediterranean and the Red Sea populations was estimated using both the two-tailed Fisher's exact test for independence and Wright's F_{ST} statistic. Since each polymorphic locus has only two alleles, and for each species we compare only two populations, we preferred to use the exact test over the more commonly used χ^2 test for independence. The significance of departure of F_{ST}

TABLE 4. – Standard genetic distances (Nei, 1978) among Red Sea and Mediterranean goatfishes (Abbreviations as in Table 3).

	U.p. (M)	U.p. (R)	U.m. (M)	U.m. (R)	U.S.	M.f.	P.f.	P.r.	P.m.	M.b.
U.p.(R)	0.081									
U.m.(M)	0.383	0.512								
U.m.(R)	0.395	0.515	0.004							
U.s.	0.239	0.357	0.106	0.118						
M.f.	0.431	0.557	0.602	0.561	0.428					
P.f.	0.682	0.819	0.475	0.460	0.476	0.474				
P.r.	0.618	0.804	0.461	0.469	0.451	0.336	0.199			
P.m.	0.609	0.714	0.414	0.380	0.422	0.382	0.114	0.104		
M.b.	0.477	0.509	0.461	0.456	0.470	0.483	0.458	0.250	0.319	
M.s.	0.380	0.424	0.437	0.424	0.373	0.378	0.879	0.245	0.268	0.079

TABLE 5. – Number of analyzed loci, number of polymorphic loci, mean polymorphism and mean heterozygosity in Red Sea and Mediterranean goatfishes (numbers in parentheses indicate alleles which had frequencies of less than 5%).

	No. of loci	No. of Polymorphic loci	mean polymorphism	mean heterozygosity	Heterozygosity S.E.
<i>Upeneus pori</i> (Medit.)	20	3 (3)	0.150	0.0411	0.0231
<i>U. pori</i> (R.S.)	20	2 (2)	0.100	0.0339	0.0235
<i>U. moluccensis</i> (Medit.)	21	2	0.095	0.0378	0.0280
<i>U. moluccensis</i> (R.S.)	21	2	0.095	0.0517	0.0356
<i>U. subvittatus</i>	20	2	0.100	0.0425	0.0326
<i>Mulloidis flavolineatus</i>	19	1	0.053	0.0087	0.0087
<i>Parupeneus forsskali</i>	20	2	0.100	0.0491	0.0338
<i>P. rubescens</i>	21	3	0.143	0.0211	0.0122
<i>P. macronema</i>	20	2	0.100	0.0391	0.0309
<i>Mullus barbatus</i>	20	2 (1)	0.100	0.0554	0.0353
<i>M. surmuletus</i>	20	3	0.150	0.0770	0.0422

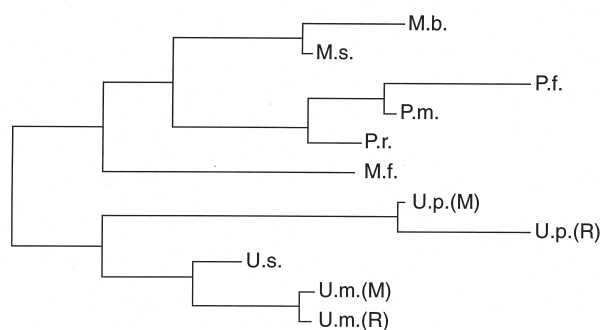


FIG. 1. – A neighbour-joining phylogenetic dendrogram of the standard genetic distances analyzed for the Red Sea and Mediterranean mullid. (Abbreviations as in Table 3).

values from zero was calculated using the χ^2 test of Workman and Niswander (1970).

The effective number of migrants per population per generation ($N_e m$) can be obtained from the F_{ST} statistic by the formula:

$$N_e m = \frac{1 - F_{ST}}{4F_{ST}} \quad (\text{Walpes, 1987}).$$

TABLE 6. – Level of genetic differentiation between Red Sea and Mediterranean populations of the colonizing goatfishes.

Species	Locus	No. of alleles	Fisher's Exact Test	F_{ST}
<i>Upeneus pori</i>	AP-2	2	P=0.3712	0.0051 (NS)
	EST	2	P=8.31x10 ⁻⁹	0.1524 (**)
	Pen Prot 2	2	P=0.0606	0.0204 (*)
	GlyDH	2	P=1.0000	0 (NS)
	GK	2	P=0.6152	0.0014 (NS)
<i>Upeneus moluccensis</i>	PGM-1	2	P=7.71x10 ⁻¹⁴	0.5232 (**)
	EST	2	P=3.31x10 ⁻⁴	0.1351 (**)
	PGM-1	2	P=0.4946	0.0089 (NS)

NS = not significant; (*) = p<0.05; (**) = p<0.01

The results of the tests of the level of genetic differentiation in *Upeneus pori* and *U. moluccensis* are given in Table 6. For *U. pori*, the mean F_{ST} over all six polymorphic loci was 0.1171.

The effective number of migrants between populations is estimated as 1.89 individuals per generation. For *U. moluccensis*, the mean F_{ST} over the two polymorphic loci was 0.0720. The effective number of migrants between populations is estimated as 3.22 individuals per generation.

Average heterozygosity for the Red Sea populations of the migrating species, for both *U. pori* and *U. moluccensis*, was 0.04283 (n=2), while the average heterozygosity for the non-migrating Red Sea species (e.g., *Upeneus subvittatus*, *Mulloides flavolineatus*, *Parupeneus forsskali*, *P. rubescens* and *P. macronema*) was 0.03212 (n=5). This difference is statistically not significant ($t=0.8022$ (5 d.f.); $p>0.400$).

DISCUSSION

The electrophoretic analysis of the Red Sea and Mediterranean goatfish generally supports the conclusions of the morphomeristic-based systematic studies of this family (Al-Absey, 1988; Ben-Tuvia and Kissil, 1988).

The only notable exception is *U. pori*, which clusters to its other congeneric species at a level which has been found in this study to distinguish between genera. This finding supports Kühlmorgen-Hille (1974), who suggested to split *Upeneus* into two subgenera; *Upeneus (Upeneus)* for species with five to seven interdorsal fin scales and 12 rows on the upper part of the peduncle (including *U. moluccensis* and *U. subvittatus*), and *Upeneus (Penon)* for species with four interdorsal fin scales and ten scale rows on the peduncle (including *U. pori*).

The interrelationship between genera found in this study agrees with that of Shaklee *et al.* (1982), who found that *Upeneus* clusters first with *Mulloidichthys* (= *Mulloides*) and later with *Parupeneus*.

The morphological similarity between *Mullus barbatus* and *M. surmuletus* has led some authors (Day, 1880-84; Lozano Ray, 1952) to treat them as different subspecies. Despite the results of our electrophoretic analysis which also found them to be very close, we refrain from drawing a categorical conclusion, especially in light of Basaglia and Callegarini (1988) and Mamuris *et al.* (1998), who also used electrophoresis and clearly distinguished these two fish as belonging to two separate species.

It has been speculated that the Red Sea fishes, found today in the Mediterranean, inhabited it prior to the opening of the Suez Canal. Unfortunately, before that event, little was known on the ichthyofauna of the eastern Mediterranean. However, due to their Atlantic origin, almost all indigenous fishes from the eastern Mediterranean are also known from the western Mediterranean. The occurrence of Red Sea fishes with Indo-Pacific distribution exclusively

in the eastern Mediterranean supports the interpretation of their recent arrival by migration through the Suez Canal. Early comparative studies of Lessepsian goatfishes in the Red Sea and the Mediterranean revealed some meristic changes, which were attributed to the adjustment of the spawning season to a more fluctuating temperature regime in the Mediterranean (Golani, 1990). The present electrophoretic study revealed a low level of genetic distance between the Red Sea and Mediterranean populations of the two colonizing species, *U. pori* ($D = 0.081$) and *U. moluccensis* ($D = 0.004$). These values are lower than those calculated in Mullidae (Stepien *et al.*, 1994) in particular, and among conspecific populations in general (Avisé, 1974; Butth, 1984). Thus, it can be concluded that the short time elapsed since the establishment of the Mediterranean populations has not been sufficient to establish discernible genetic differences. Only a single allele (PGM-1-C) detected in the Mediterranean population of *U. pori* was not found in the Red Sea (Table 3). Because of the short time since the separation, it is reasonable to assume that this allele may also occur, perhaps rarely, in the Red Sea. The low level of genetic distance and the calculated effective number of migrants between the colonizing and the source populations (1.89 for *U. pori* and 3.22 for *U. moluccensis*) indicate that the establishment of the Mediterranean populations probably involved relatively large propagules and/or continuous gene flow from the Red Sea.

Our results concerning the question, whether high genetic variability contributes to success in colonization, are negative. This conclusion was reached by many other authors (Ritte and Pashtan, 1982; Ehrlich, 1986; Holdgate, 1986; Gray, 1986; Lavee and Ritte, 1994; Williamson and Fitter, 1996). The distinction between closely-related colonizing and non-colonizing species seems rather to be associated with ecological differences (Ayal and Safriel, 1983; Golani, 1993).

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