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Allozyme Variation in the Large-scale Mullet *Liza macrolepis* (Perciformes: Mugilidae) from Coastal Waters of Western Taiwan

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Sin-Che Lee, Hui-Ling Cheng and Jung-Ti Chang (1996) Allozyme variation in the large-scale mullet *Liza macrolepis* (Perciformes: Mugilidae) from coastal waters of western Taiwan. *Zoological Studies* **35**(2): 85-92. Allozyme variation was studied in the large-scale mullet *Liza macrolepis* collected from 4 sites: 3 sites on the west coast of Taiwan, the Tanshui estuary, the Kaohsiung River (Love River) and Dapong Bay (Tungkang); and 1 site about 50 km off the west coast of Taiwan, the Penghu Islands. The genetic similarities among these 4 localities are rather high (0.992-0.999), indicating that they belong to the same population. The inter-sample comparisons of heterozygosity based on 10 polymorphic loci (*sAAT-1, CK-B, GPI-A, GPI-B, IDHP-A, LDH-C, sMDH-A, sMDH-B, ME-1* and *MPI-1*) under the 0.99 criterion revealed that most loci conform with the Hardy-Weinberg Equilibrium, except those at *GPI-B* from Dapong Bay and *IDHP-A* from the Tanshui estuary. Analysis of overall mean heterozygosities among 4 inter-sample comparisons revealed that the samples from Dapong Bay and the Tanshui estuary have higher values (0.044 and 0.043, respectively) than those from the Kaohsiung River and Penghu (0.029 and 0.028, respectively), probably due to heavy organic pollution in Dapong Bay and colder temperatures in the Tanshui estuary. Comparisons of overall F_{ST} (local subpopulation differentiation) of Dapong Bay with those of the three other locations indicate a moderate genetic differentiation which is mainly contributed by the unusually high allele frequency of the *MPI* locus. A higher inbreeding coefficient (F_{IS}) in the Dapong sample corresponds to the high inbreeding potential at this site, probably due to its nearly land-locked habitat, which limits the exchange of individual fish between the bay and the open coast.

Key words: Population genetics, Allozyme comparisons, Large-scale mullet.

The large-scale mullet *Liza macrolepis* (Smith 1846) is a wide ranging Indo-West Pacific species, with a northern limit to southern Japan and extreme western limit to southern Africa. Morphologically, it has a poorly-developed adipose eyelid, a yellowish pectoral fin base, and a short distance from the dorsal fin origin to the snout tip. There are 4 spines and 8-9 soft rays on the dorsal fin, 3 spines and 9-10 soft rays on the anal fin, 15-18 soft rays on the pectoral fin, and 30-33 longitudinal series of scales on the sides of body. It resembles the most closely related sympatric species, *L. subviridis*, but the latter has no yellowish stripe at the pectoral base and, in addition, it has a well-developed adipose eyelid.

Liza macrolepis occurs in inshore bays, estuaries and even in freshwater. It spawns in autumn, with juveniles gathering in the muddy-sand inshore bays and estuaries during April and May (Okiyama 1988). The juveniles may further spread out to tidal rocky shores. In Taiwan, *Liza macrolepis* adults are a common inhabitant of inshore waters and bays. It seems that *Liza macrolepis* is well adapted to habitats with variable environmental conditions. This species would be potential study material for detection of genetic variation in relation to the environment. The present investigation determined the level of electrophoretically detectable gene variation in *Liza macrolepis* and assessed whether different stocks of subpopulations exist in the waters of Taiwan. Furthermore, *Liza macrolepis* is a medium-sized food fish in Taiwan; thus, an understanding of the genetic basis of its variation will aid the future management of

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this commerically important fish resource.

MATERIALS AND METHODS

A total of 106 *Liza macrolepis* collected from the Tanshui estuary (16 specimens ranging 66.7-122.2 mm in standard length, SL), Penghu (30 specimens ranging 166.6-227.8 mm in SL), Kaohsiung River (31 specimens ranging 140.3-220.0 mm in SL) and Dapong Bay (29 specimens, ranging 140.0-212.9 mm in SL) were used for this study (Fig. 1).

Samples of skeletal muscle, eye and liver of roughly 0.2-0.3 g each were removed and homogenized with 2 to 3-fold extraction buffer (0.01 M Tris-HCL pH 7.0, 1 mM EDTA, 0.05 M NADP) (Pasteur et al. 1988). Samples were centrifuged at 13 500 rpm at a temperature of 4 °C for 40 min, and supernatants were then applied on 12% starch gel for horizontal electrophoresis. The electrical conditions and running times depended upon the buffer systems used: 300 V, 75 mM for 6 hours with Tris-citrate buffer (Shaw and Prasad 1970); 180 V, 50 mM for 18 hours with Tris-versene-borate buffer (Selander et al. 1971); or 350 V, 140 mA for 6 hours with Lithium-borate/Tris-citrate buffer (Selander et al. 1971). Procedures for enzyme staining followed Shaw and Prasad (1970) and Pasteur et al. (1988).

Allozyme data were obtained for samples from all 4 localities. Allele frequencies, mean expected heterozygosity (H_e), and the level of local subpopulation differentiation (F_{ST}) were calculated using the statistical package, BIOSYS-1 software (Swofford and Selander 1989). D values (Nei 1972 1978) were calculated from the allele frequency of each locus. Finally, a UPGMA phenogram (Sneath and Sokal 1973) was constructed by means of NTSYS-pc software (Rohlf 1987). F statistics, including F_{IS}, F_{IT} and F_{ST}, were used to represent the genetic differentiation of the population. F_{IS} is the

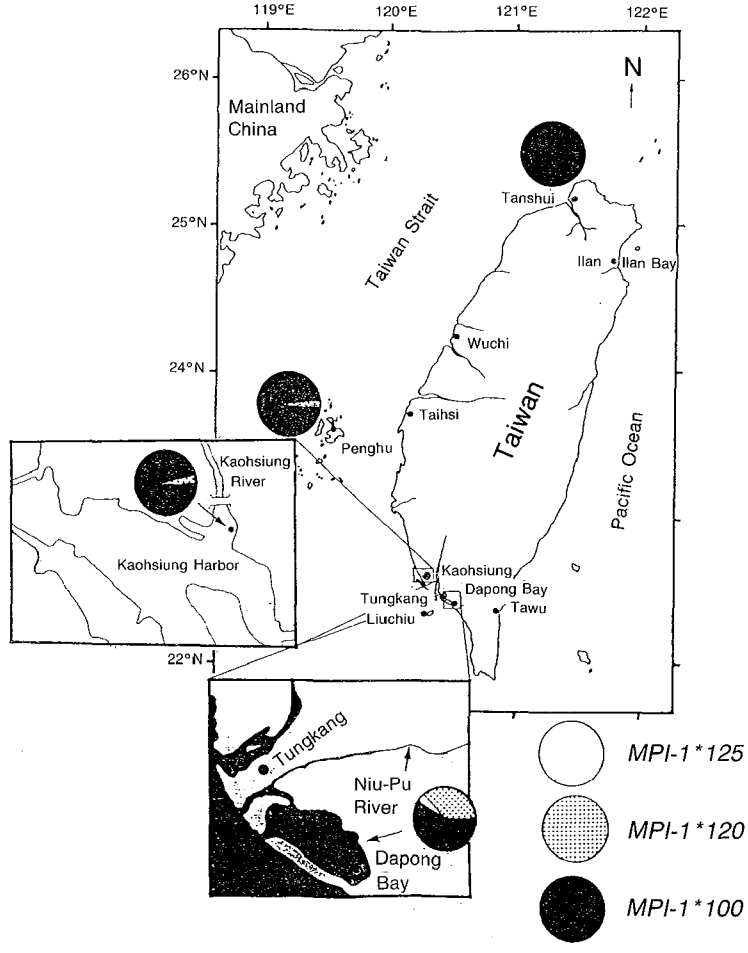

Fig. 1. Map showing allele frequencies of the *MPI* locus in samples collected from 4 different localities.

mean value of genetic differentiation or inbreeding coefficient within a subpopulation, F_{IT} is the mean value of genetic differentiation over the entire population, and F_{ST} is the genetic differentiation between any two subpopulations. P_{99} is the proportion of polymorphic loci under the 0.99 criterion.

RESULTS

The ten polymorphic loci analyzed were sarcoplasmic aminotransferase-1 (*sAAT-1*), Creatine kinase (*CK-B*), Glucose-phosphate isomerase (*GPI-A*), Glucose-6-phosphate dehydrogenase-B (*GPI-B*), Isocitrate dehydrogenase (*IDHP-A*), Lactate dehydrogenase-C (*LDH-C*), sarcoplasmic malate dehydrogenase-A (*sMDH-A*), sarcoplasmic malate dehydrogenase-B (*sMDH-B*), Malic enzyme-1 (*ME-1*) and Mannose-6-phosphate isomerase (*MPI-1*) (Table 1; Fig. 2). Samples from 4 localities showed no differences in their very close genetic identity values (I) of 0.992-0.999 (or D = 0.001-0.008) (Table 2) . Contingency X^2 tests were used to examine the stability of allele frequency among the 4 collecting sites. The allele frequencies of the samples from all 4 localities show no obvious differences for the 10 polymorphic loci except the *MPI-1* locus. The *MPI-1* locus shown in the Fig. 1 indicates allele

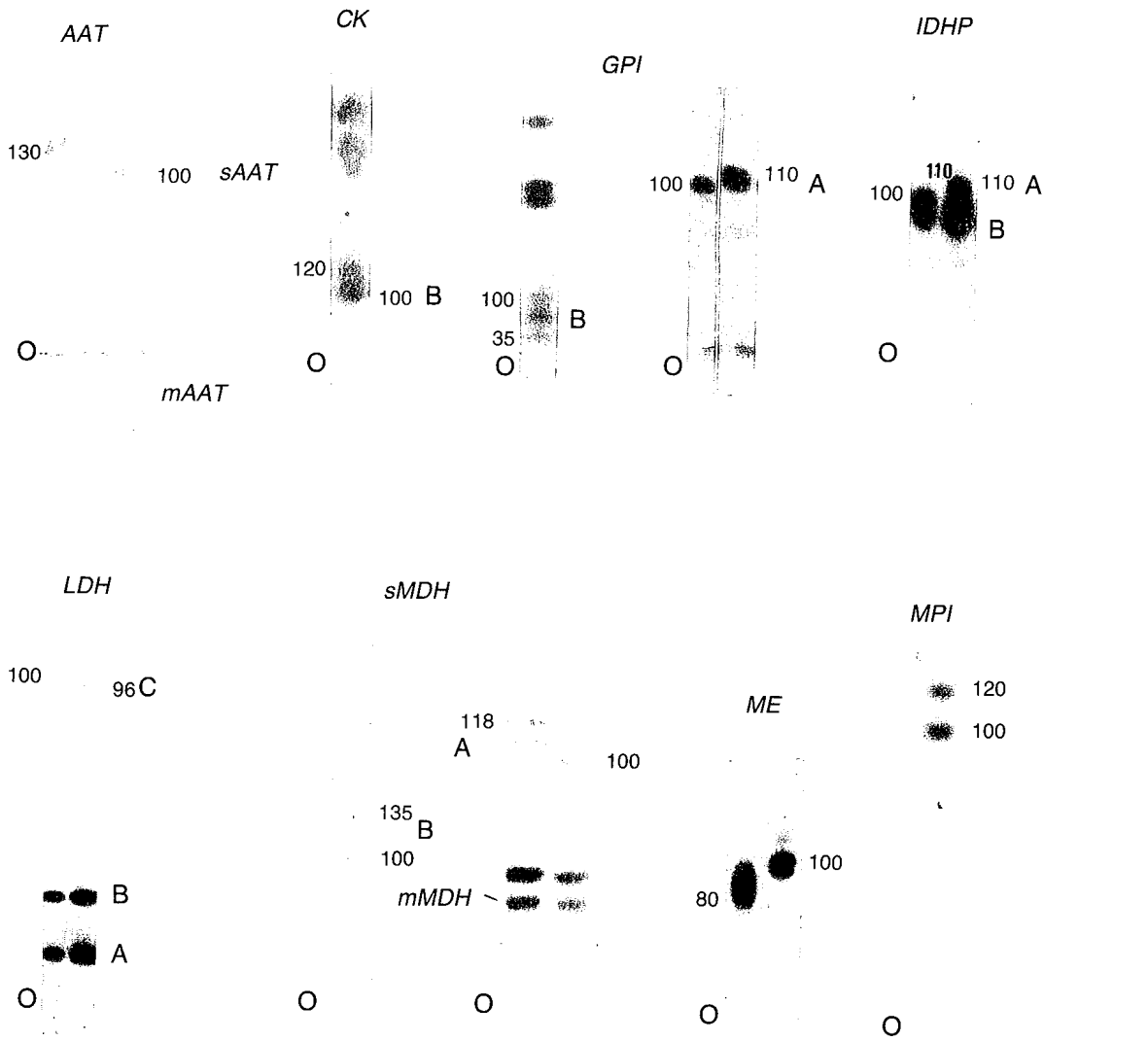

Fig. 2. Allozyme patterns of 10 polymorphic loci scored in *Liza macrolepis*. *sAAT-1*, sarcoplasmic aminotransferase-1; *CK-B*, creatine kinase; *GPI-A*, glucosephosphate isomerase-A; *GPI-B*, glucosephosephate isomerase-B; *IDHP-A*, isocitrate dehydrogenase-A; *LDH-C*, lactate dehydrogenase-C; *sMDH-A*, sarcoplasmic malate dehydrogenase-A; *sMDH-B*, sarcoplasmic malate dehydrogenase-B; *ME-1*, malic enzyme-1; and *MPI-1*, mannose-6-phosphate isomerase-1.

Table 1. Allele frequencies, observed heterozygosity (H_o) and deficiency of heterozygosity (D) of polymorphic loci under the 0.99 criterion in *Liza macrolepis*, collected from the Kaohsiung River (KS), Penghu (PH), Dapong Bay, Tungkang (DP), and Tanshui estuary (TS)

Locus	*Allele*	Locality KS ($n = 31$)	PH ($n = 30$)	DP ($n = 29$)	TS ($n = 16$)
sAAT-1	*130*	0.113	0.033	0.086	0.125
	100	0.887	0.950	0.897	0.875
	70	0.000	0.017	0.017	0.000
	H_o	0.161	0.100	0.138	0.250
	D	−0.208	0.023	−0.281	0.107
CK-B	*120*	0.000	0.017	0.000	0.000
	100	1.000	0.983	1.000	1.000
	H_o	0.000	0.033	0.000	0.000
	D		0.000		
GPI-A	*110*	0.000	0.000	0.000	0.031
	100	1.000	1.000	1.000	0.969
	H_o	0.000	0.000	0.000	0.063
	D				0.000
GPI-B	*100*	0.936	0.800	0.862	0.844
	35	0.000	0.017	0.018	0.000
	−10	0.016	0.017	0.034	0.063
	−65	0.048	0.166	0.086	0.094
	H_o	0.129	0.267	0.207**	0.313
	D	0.038	−0.209	−0.180	0.099
IDHP-A	*110*	0.032	0.000	0.017	0.063
	100	0.968	1.000	0.983	0.937
	H_o	0.065	0.000	0.034	0.125**
	D	0.017		0.000	−1.000
LDH-C	*100*	0.984	1.000	1.000	1.000
	96	0.016	0.000	0.000	0.000
	H_o	0.032	0.000	0.000	0.000
	D	0.000			
sMDH-A	*118*	0.016	0.000	0.000	0.063
	100	0.984	1.000	1.000	0.937
	H_o	0.000	0.067	0.000	0.125
	D	0.000			0.033
sMDH-B	*135*	0.032	0.017	0.034	0.031
	100	0.968	0.983	0.966	0.969
	H_o	0.065	0.033	0.069	0.063
	D	0.017	0.000	0.018	0.000
ME-1	*100*	1.000	0.967	1.000	1.000
	80	0.000	0.033	0.000	0.000
	H_o	0.000	0.067	0.000	0.000
	D		0.017		
MPI-1	*125*	0.000	0.000	0.017	0.000
	120	0.032	0.017	0.362	0.000
	100	0.968	0.938	0.621	1.000
	H_o	0.065	0.033	0.379	0.000
	D	0.017	0.000	−0.229	
Mean heterozygosity (direct-count H_o)		0.029	0.028	0.044	0.043
Hdy-Wbg Expected H_e		0.034	0.032	0.055	0.046
Percentage of polymorphic loci (P_{99})		10.5	10.5	15.8	21.1

**significant at the 0.01 level indicating departure from Hardy-Weinberg expectation.

frequency differences among the 4 localities. The allele *MPI-1*120* (0.362) from Dapong Bay showed higher frequencies than those of the 3 other localities, being 0.032, 0.017, and 0.000 for the Kaohsiung River, Penghu and Tanshui estuary, respectively. On the contrary, the Dapong Bay sample showed lower frequencies at allele *MPI-1*100* (0.621) than those of the Tanshui estuary (1.000), Kaohsiung River (0.968) and Penghu (0.938). In addition, the Dapong Bay sample was the only sample to contain an *MPI-1*125* allele with the rather low frequency of 0.017. The allele frequencies of all studied loci obeyed the Hardy-Weinberg law except those of the *GPI-B* locus from Dapong Bay and the *IDHP-A* locus from the Tanshui estuary.

F_{ST} values help elucidate the genetic differentiation among the 4 localities (Tables 3-5). The pairwise F_{ST} between the Dapong Bay sample and 3 other samples ranged 0.068-0.077 (Table 3). Thus, according to Wright (1978), they can be classified as having a moderate degree of differentiation. The pairwise F_{ST} among the samples from the Kaohsiung River, Penghu and Tanshui estuary ranged 0.011-0.012, indicating a very slight differentiation (Table 3). Considering the *MPI-1* locus alone, the Dapong Bay sample exhibits a rather high value (0.174-0.222) when compared to the other 3, in contrast to the values obtained among the latter 3 samples themselves (0.003-0.016) (Table 4). When the *MPI-1* locus data were excluded from the statistics, the F_{ST} between the Dapong Bay sample and the 3 other samples combined became 0.006-0.008 while F_{ST} among the 3 latter samples themselves became 0.011-0.012 (Table 5). These results suggest that the *MPI-1* locus is the main locus having genetic differentiation in the Dapong sample. The overall mean F_{IS} value among samples from Dapong Bay, Kaohsiung River, Penghu and Tanshui estuary was 0.103 (Table 6), however, when the Dapong Bay sample was removed from the statistics, the mean F_{IS} value was reduced to nil (0.000). The subsequent summarization in the same table indicates that the Dapong Bay sample has a higher proportion of inbreeding with restricted gene flow. The observed (H_o) and expected (H_e) mean heterozygosities, and proportion of polymorphic loci (P_{99}) differed among localities (Table 1): the highest H_o being 0.044 in Dapong Bay, 0.043 in the Tanshui estuary and the lowest being 0.028 in Penghu. The highest P_{99} was found in the Tanshui estuary (P_{99} = 21.1%) followed in order by Dapong Bay (15.8%), Kaohsiung River (10.5%) and Penghu (10.5%).

Table 2. Nei's genetic identity (I) and distance (D) among four samples

	I Value			
	KS	PH	DP	TS
D Value				
KS	—	0.999	0.994	0.999
PH	0.001	—	0.993	0.999
DP	0.006	0.007	—	0.992
TS	0.001	0.001	0.008	—

(DP, Dapong Bay, Tungkang; KS, Kaohsiung River; PH, Penghu; TS, Tanshui estuary.)

Table 3. Genetic differentiation (F_{ST}) value among 4 samples, calculated from all scored loci

	DP	KS	PH	TS
DP	—	0.068	0.077	0.072
KS	0.068	—	0.012	0.011
PH	0.077	0.012	—	0.016
TS	0.072	0.011	0.016	—

(DP, Dapong Bay, Tungkang; KS, Kaohsiung River; PH, Penghu; TS, Tanshui estuary.)

Table 4. Genetic differentiation (F_{ST}) value among 4 samples, calculated from the *MPI-1* locus alone

	DP	KS	PH	TS
DP	—	0.174	0.196	0.222
KS	0.174	—	0.003	0.016
PH	0.196	0.003	—	0.008
TS	0.222	0.016	0.008	—

(DP, Dapong Bay, Tungkang; KS, Kaohsiung River; PH, Penghu; TS, Tanshui estuary.)

Table 5. Genetic differentiation (F_{ST}) value among 4 samples, calculated from loci with the exclusion of the *MPI-1* locus

	DP	KS	PH	TS
DP	—	0.006	0.007	0.008
KS	0.006	—	0.012	0.011
PH	0.007	0.012	—	0.016
TS	0.008	0.011	0.016	—

(DP, Dapong Bay, Tungkang; KS, Kaohsiung River; PH, Penghu; TS, Tanshui estuary.)

DISCUSSION

Nei's genetic identity values of 0.992-0.999 among the fish sampled from Dapong Bay, Kaohsiung River, Penghu and Tanshui estuary confirm that these fish are a panmictic species belonging to the same population. *L. macrolepis* spawns during January and April in deeper waters outside the estuaries of different localities. The freshly hatched pelagic larvae may drift randomly in the Kuroshio current and Taiwan coastal current in the waters surrounding Taiwan (Fan 1982, Wang and Chern 1989), resulting in a mixing of larvae. Once the young enter the nearly enclosed Dapong Bay, their populational exchange with those individuals on the open coast elsewhere would be limited. The adaptation of the population remaining inside the bay to environmental conditions there results in a slight population divergence from populations at the Kaohsiung River, Penghu and Tanshui estuary. Dapong Bay is isolated from the other 3 localities which has resulted in a higher inbreeding coefficient (F_{IS}, 0.103) compared with the other three locations. F_{IS} equals 0 (0.000) when the Dapong Bay sample is excluded from those of the remaining 3 samples (Table 6). The overall mean polymorphic loci per population (P_{99} = 0.15) and mean heterozygosity (H_e = 0.036) estimated for the Taiwanese *Liza macrolepis* in this study are within the ranges observed for other bony fishes (P_{99} = 0.000-0.560, H_e = 0.000-0.180) (Nevo 1978). Heterozygosity estimates are a measure that can predict stress resistance of individuals fish. It is known that genetic variation will persist at a locus if there is some advantage for heterozygosity. For example, heterozygotes have greater stress resistance than homozygotes in an organism (Hoffman and Parsons 1991). The higher overall mean heterozygosities of the samples from Dapong Bay (H_o = 0.044) and the Tanshui estuary (0.043) as compared to the Kaohsiung River (0.029) and Penghu (0.028), indicate that fish from the former 2 localities have a greater resistance to environmental stress than those from the latter 2 localities. Although the overall mean H_o of Dapong Bay and Tanshui estuary samples are quite close, the 4 individual loci (*sAAT-1, GPI-A, GPI-B, IDHP-A*) reveal a higher H_o in the Tanshui sample. This higher heterozygosity is correlated with its higher proportion of polymorphic loci. A slightly lower monthly mean temperature of 22.2-23.7°C near the Tanshui estuary compared to 26.0-26.5°C near the Dapong Bay area (Chen and Chen 1978) is considered one of the factors affecting H_o differences, resulting in a possible selection for some enzymes. The organisms living in climatically extreme environments provide examples of basic mechanisms of thermal adaptation (Maresca et al. 1988). Mechanisms of thermal adaptation are evident at all levels of biological organization from the morphology of organic systems down to molecules. Such adaptation provides rates of catalysis and stability of biological structures appropriate for local temperature compensation (Hazal 1993). The thermal regime of 22.2 to 23.7°C at the Tanshui estuary and 26.5°C at Dapong Bay are equivalent to subtropical and tropical temperatures, respectively, in the habitats for the barracudas, *Sphyraena lucasana* and *S. ensis* (Graves and Somero 1982). Temperature differences of only a few degrees C are sufficient to select for temperature-compensatory differences in enzyme kinetic properties (Graves and Somero 1982). A possible cold adaptation of the *GPI* locus in *Acanthopagrus schlegeli* (Jean et al. unpublished) and the *IDHP* locus in *Anguilla japonica* (Chan pers. comm.) can be explained in the same way. The exact roles of these enzymes in cold adaptation in fish should be tested experimentally in the future. The *MPI* product is involved in carbohydrate metabolism (catalyzing the conversion of D-mannose-6-phosphate into D-fructose-6-phosphate)

Table 6. Comparisons of *F* statistics and contingency X^2 analyses between all 4 samples and those excluding the Dapong Bay sample

Samples	F_{IS}	F_{IT}	F_{ST}	X^2	*p*
Dapong, Kaoshiung River, Penghu, Tanshui estuary	0.103	0.166	0.071	93.442	0.000 01**
Kaohsiung River, Penghu, Tanshui estuary	0.000	0.019	0.019	31.174	0.221 86 ns

F_{IS}, mean value of genetic differentiation or inbreeding coefficient within a subpopulation.
F_{ST}, genetic differentiation between subpopulations.
F_{IT}, mean value of genetic differentiation among total populations.

(Slein 1955). It has been postulated that *MPI* is related to the high heterozygosities in the widespread brackish-water and limnic gammarids (Bulnheim and Scholl 1982). The proper explanation of such a higher H_o (0.397) at the *MPI-1* locus in the Dapong Bay sample is probably a reflection of environmental stress such as temperature or pollution. The currently available data indicate that contamination by ammonia, nitrate, phosphate, silicate, etc., in Dapong Bay is worse than in the Kaohsiung River or at Penghu (Tan and Tzeng 1988, Hsieh et al. 1991, Chen pers. comm.). The contamination in Dapong Bay has been reported to have damaged the local mariculture industries (Hsieh et al. 1991). Heavy metals are other factors which increase heterozygosity, such as exposure to the stress of mercury pollution (Nevo et al. 1981). Though Kaohsiung harbor has greater heavy metal pollution than other areas (Chen and Wu unpublished data), the harbor provides good water circulation during the rising and receding tides. In general, heterozygosity in marine fish is higher than that of freshwater fish due to extensive gene flow (Ward et al. 1994). In other words, a lower probability of inbreeding would increase the heterozygosity estimates. However, F statistics for the Dapong Bay sample indicate a rather high inbreeding coefficient (0.103) which would be expected to decrease heterozygosity values. On the contrary, the expected heterozygosity in Dapong Bay sample is unusually higher (H_o = 0.044) than that of the Kaohsiung River (0.029) and Penghu (0.028). This may be due to pollution in Dapong Bay having an overriding effect. The higher H_o (0.043) in samples from the Tanshui estuary than those from the Kaohsiung River and Penghu samples is probably due to the lower temperature at Tanshui which again might have an overriding effect.

It is concluded that the samples from Dapong Bay, Kaohsiung River, Penghu and Tanshui estuary belong to the same population, as evidenced by a very low level of genetic differentiation among them. However, a minor divergence of samples from certain localities may have entirely resulted from metabolic isozymes such as those of *GPI* and *MPI*, which are, in turn, environmentally dependent.

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臺灣沿海岸大鱗鰄異構酶之變異

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本文報導採自臺灣西海岸淡水河口、澎湖、高雄愛河及東港大鵬灣大鱗鰄異構酶之分析比較。上述四個地區樣品間所估算出之遺傳相似度(I=0.992-0.999)極高，足證彼應同屬一族群。由*sAAT-1*、*CK-B*、*GPI-A*、*GPI-B*、*LDH-C*、*IDHP-A*、*sMDH-A*、*sMDH-B*、*ME-1*及*MPI-1*等十個基因座雜合率(P_{99})之比較，發現除了大鵬灣之*GPI-B*及淡水河口之*IDHP-A*外，其餘八個基因座均符合哈溫定律。綜合比較四個樣品之雜合率，大鵬灣(0.044)及淡水河口樣品(0.043)遠高於高雄愛河(0.029)及澎湖(0.028)，可能緣於大鵬灣受到較嚴重的污染衝擊(尤其是有機性的)及淡水河口之較低溫環境。再則由於大鵬灣樣品*MPI-1*基因座之高頻度現象可能引致大鵬灣魚群與其它三處間有明顯的遺傳變異現象。大鵬灣因屬半封閉之瀉湖，內中魚群與外海魚群間之基因交流不若其它三處顯著，使得大鵬灣大鱗鰄呈現偏高之近交係數。

關鍵詞：族群遺傳，異構酶比較，大鱗鰄。

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