Tissue-specific Isozymes in Fishes of the Subfamily Sparinae (Perciformes: Sparidae) from the Coastal Waters of Taiwan

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Chuen-Tan Jean, Sin-Che Lee, Cho-Fat Hui and Che-Tsung Chen (1995) Tissue-specific isozymes in fishes of the subfamily Sparinae (Perciformes: Sparidae) from the coastal waters of Taiwan. *Zoological Studies* **34**(3): 164-169. A total of forty-five isozymes scored from twenty-five enzyme systems in five species of the subfamily Sparinae were detected. Their distribution in twelve tissues was also delineated. The results of the present study show that there are no differences in tissue distribution among these five species, and the patterns of tissue distribution of most isozymes are similar to those of most bony fishes. From the results of the present study, the most appropriate isozymes, tissues, and buffer systems for electrophoretic analysis in future studies of interspecific phylogenetic relationships and intraspecific population genetics of fishes within the subfamily Sparinae will be determined.

Key words: Subfamily Sparinae, Isozymes, Tissue distribution.

In Taiwan, the subfamily Sparinae contains two genera and five species. The genus *Acanthopagrus* includes four nominal species, *Acanthopagrus schlegeli*, *A. latus, A. berda,* and *A. australis*. These species are also called the *Acanthopagrus schlegeli* complex because of their morphological similarities. The other genus *Sparus* includes only one species, *Sparus sarba* (Lee 1983, Jean and Lee 1992). Fishes of the subfamily Sparinae, commonly known as porgies, are important commercial species for food consumption and recreational fisheries in estuarine and coastal waters of Taiwan. Since 1980, they have become a valuable pond-cultivated species after the successful artificial mass propagation of fingerlings (Lin and Yen 1980, Lin et al. 1988, Leu et al. 1991).

In recent years, natural stocks of porgies have decreased drastically due to overfishing, pollution, and illegal fishing practices such as poisoning and electric shock. Thus, there is an urgent need to find ways to recover the original stocks such as conservation, management, and mariculture.

Knowledge of taxonomic status and population structure of a species is a basic prerequisite for making rational decisions about their exploitation and management, as well as for correct interpretation of ecological investigations (Ferguson and Mason 1981). Electrophoretic analyses of isozymes can provide criteria to clarify taxonomic status of species and evolutionary relationships of populations, species, and higher taxa (Shaklee et al. 1982). However, electrophoretic analyses of isozymes require the examination of a large number of loci in species in order to provide accurate estimates of the amount of divergence between populations or species.

On the other hand, the functions of enzymes probably diverged very early in the phyletic history of teleosts (Avise and Kitto 1973). The specific pattern of tissue expression is, therefore, indirect evidence of functional divergence. Hence, comparative studies of tissue-specific distribution of protein loci among taxa can provide valuable insights into the evolution of genomes and evolu-

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tionary divergence (Fisher and Whitt 1978).

The objectives of the present study are to investigate tissue-specificity of expression of isozymes and to provide a basis for selection of appropriate isozymes, tissues, and buffer systems for electrophoretic analysis in future studies of phylogenetic relationships and population genetics of fishes within the subfamily Sparinae.

MATERIALS AND METHODS

Five fully grown specimens of each species in the subfamily Sparinae were used in these experiments. They were caught by longline from coastal waters off Tanshui. Fresh specimens were iced immediately, then stored at -70°C.

Twelve different tissues were removed from each specimen: skeletal muscle, heart, eye, liver, brain, dorsal fin membrane, gills, intestine, kidney, testis, spleen, and stomach. Individual tissues were homogenized in two to three volumes of extraction buffer (0.01M Tris-HCl pH 7.0, 1mM EDTA, 0.05mM NADP) (Pasteur et al. 1988) using a sonicator in an ice bath. Homogenates were centrifuged at 13,500 r.p.m. for 40 minutes at 4°C, and supernatants were then stored at -70°C until electrophoresis.

A piece of Whatman No. 3 filter paper was dampened with roughly 10μl of protein extract and placed into the sample slot at the cathodal end of a 12% (w/v) starch gel. Horizontal electrophoresis was performed at 4°C under different buffer systems, electrical conditions, and running time periods.

After electrophoresis, the starch gel was sliced into several horizontal pieces (excluding the top and bottom sections) and stained with specific histochemical staining recipes described by Shaw and Prasad (1970), Siciliano and Shaw (1976), Redfield and Salini (1980), Shaklee and Keenan (1986), Pasteur et al. (1988), and/or Murphy et al. (1990). Stained gels were then fixed with acetic acid/methanol (Pasteur et al. 1988), photographed, and dried for storage.

Thirty-nine enzymes and sarcoplasmic proteins were tested in tissues from the muscle, heart, eye, liver, brain, fin, gill, intestine, kidney, testis, spleen and stomach of specimens under six buffer systems: TVB (Siciliano and Shaw 1976), TME (Shaw and Prasad 1970), TC 7.0 and TC 8.0 (Siciliano and Shaw 1976), LiOH (Redfield and Salini 1980), and CAPM (Clayton and Tretiak 1972). The resolution power in separation of the forty enzymes from fishes of the subfamily Sparinae under the six buffer systems is available from the authors upon request.

Table 1 gives the most appropriate buffer system for each particular enzyme for the subsequent investigation of tissue distribution of the twenty-five enzymes. Nomenclature of protein-coding loci was designated according to Shaklee et al. (1990).

Abbreviations for enzymes investigated in this study are listed in Table 1.

RESULTS AND DISCUSSION

A total of 45 isozyme loci scored from 25 enzyme systems were detected in the present study. Names of isozymes and their expression in twelve tissues are shown in Table 1. The results of the present study show that there are no differences in expression of these isozymes in different tissues among the five species of Sparinae. Brief descriptions of tissue expression of each enzyme is delineated below.

The electrophoretic patterns of AAT isozymes exhibit two supernatant loci and one mitochondrial locus. sAAT-1* was expressed in most tissues except eye, liver, and fin while sAAT-2* was only detectable in eye and liver. mAAT* was expressed in all tissues except fin. The relative anodal mobility of these three loci was in the order: sAAT-1* > sAAT-2* > mAAT*.

ADH was detected as a single locus ADH* in liver. It moved toward the cathodal side in the TC 8.0 buffer system as described previously by Taniguchi and Fujita (1986). When compared with other fishes, the ADH pattern of the present fish group differs from that of the guppy since the latter has more loci (Wu and Schroder 1984). Also the ADH-D* locus is considered a regulatory isozyme in cell differentiation found only in embryonic stages (Wu and Schroder 1984).

AH was appeared in a single locus AH* which was detected in heart, liver and kidney.

Four loci of AK were detected: AK-1* in liver; AK-2* in testis; AK-3* in heart, intestine, kidney, testis, spleen, and stomach; and AK-4* in skeletal muscle. The relative anodal mobility of the four AK isozymes was in the order: AK-1* > AK-2* > AK-3* > AK-4*.

A single locus of ALP was detected in heart, eye, gills, kidney, testis, spleen and stomach.

CK was dimeric with two-banded heterozygotes which appeared as three loci (Fig. 1): CK-A* isozyme in skeletal muscle; CK-B* in eye and brain; CK-C* in all tissues except skeletal muscle. They readily formed a higher level CK-BC* dimer between the B and C loci. These CK isozyme patterns are

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Table 1. Distribution and activity of isozymes in twelve tissues of fishes in the subfamily Sparinae

Enzyme (Abbreviations)	Locus	Buffer system	Tissue											
			Mu	Hr	Ey	Lv	Br	Fn	Gi	In	Ki	Te	Sp	St
Aspartate aminotransferase	sAAT-1*	TC8.0	+++	+++	−	−	+	−	+	+	++	+	+	++
(AAT)	sAAT-2*		−	−	+++	+++	−	−	−	−	−	−	−	−
	mAAT*		+++	+++	+++	+++	+	−	++	++	++	+	+	+
Alcohol dehydrogenase (ADH)	ADH*	TC8.0	−	−	−	+++	−	−	−	−	−	−	−	−
Aconitate hydrase (AH)	AH*	TVB	−	++	−	++	−	−	−	−	+	−	−	−
Adenylate kinase (AK)	AK-1*	TVB	−	−	−	+	−	−	−	−	−	−	−	−
	AK-2*		−	−	−	−	−	−	−	−	−	++	−	−
	AK-3*		−	+	−	−	−	−	−	+	+	+	+	+
	AK-4*		++	−	−	−	−	−	−	−	−	−	−	−
Alkaline phosphatase (ALP)	ALP*	LiOH	−	+	++	−	−	−	+	−	+	+	++	+
Creatine kinase (CK)	CK-A*	LiOH	+++	−	−	−	−	−	−	−	−	−	−	−
	CK-B*		−	−	+++	−	+++	−	−	−	−	−	−	−
	CK-C*		−	++	++	++	+	+	++	+	++	+	++	+++
Fumarate hydratase (FH)	FH*	TC8.0	+	++	+	++	++	+	+	+	++	+	+	++
Glucose dehydrogenase (GDH)	GDH*	LiOH	−	−	−	+++	−	−	−	−	−	−	−	−
Glutamate dehydrogenase (GLUDH)	GLUDH*	TC8.0	−	−	−	+++	−	−	−	−	++	−	−	−
Glyceraldehyde-3-phosphate dehydrogenase (GAPDH)	GAPDH*	TC8.0	−	−	+++	++	+	−	+++	++	++	++	+++	+++
Glycerol-3-phosphate	G₃PDH-1*	TVB	−	−	−	++	−	−	−	−	−	−	−	−
dehydrogenase (G₃PDH)	G₃PDH-2*		++	−	−	−	−	−	−	−	−	−	−	−
Glucose-6-phosphate	G₆PHD-1*	LiOH	−	−	−	++	−	−	−	++	++	−	−	+
dehydrogenase (G₆PDH)	G₆PDH-2*		+	++	++	+++	++	−	+++	+++	+++	+++	+++	++
Glucose-6-phosphate	GPI-A*	TVB	+++	+++	+	+	++	+	++	+	+++	+	+	+
isomerase (GPI)	GPI-B*		+	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Hexokinase (HK)	HK-1*	TVB	−	++	+	−	+	−	−	−	−	−	−	−
	HK-2*		++	−	−	−	−	−	−	−	−	−	−	−
Isocitrate dehydrogenase	IDHP-A*	TC8.0	+	+	+	+++	++	−	++	++	++	−	++	+
(NADP⁺) (IDHP)	IDHP-B*		−	−	−	+	−	−	−	−	−	−	−	−
L-Lactate dehydrogenase	LDH-A*	TC8.0	+++	++	++	++	++	++	+++	+++	+++	+++	+++	+++
(LDH)	LDH-B*		++	+++	++	++	+	+	+++	+++	+++	++	+++	+++
	LDH-C*		−	−	+++	−	−	−	−	−	−	−	−	−
Malate dehydrogenase	sMDH-A*	TC8.0	++	+	+	+	+	−	+	+	+	−	+	+
(MDH)	sMDH-B*		++	+++	+++	+++	++	+	+++	+++	+++	++	+++	+++
	mMDH*		++	+++	+++	+++	++	−	+++	+++	+++	++	++	++
Malic enzyme (NADP⁺)	MEP-1*	TVB	+++	++	++	+++	−	−	+	++	+	+	++	++
(MEP)	MEP-2*		+	+++	+	−	−	−	+	+	−	+	+	+
Mannose-6-phosphate isomerase (MPI)	MPI*	LiOH	++	++	+++	+++	++	+	+++	+++	++	++	++	++
Octanol dehydrogenase (ODH)	ODH*	LiOH	−	−	−	++	−	−	+	+	+	+	+	+
Phosphogluconate	PGDH-1*	TC8.0	+	+	+	+++	+	−	+	++	++	++	++	++
dehydrogenase (PGDH)	PGDH-2*		−	−	−	+	−	−	−	−	−	−	−	−
Phosphoglucomutase	PGM-1*	TVB	++	++	−	++	++	−	−	+	+	−	+	+
(PGM)	PGM-2*		+++	+	+	++	+	−	−	++	+	−	+	+
Sorbitol dehydrogenase (SDH)	SDH*	LiOH	−	−	−	+++	−	−	−	−	−	−	−	−
Superoxide dismutase (SOD)	sSOD*	TC8.0	+	++	+	+++	+	+	+	+	++	++	+++	++
	mSOD*		−	+	−	−	−	−	−	−	+	−	+	−
Xanthine dehydrogenase (XDH)	XDH*	LiOH	−	−	−	+++	−	−	−	−	+	−	−	−

Mu, skeletal muscle; Hr, heart; Ey, eye; Lv, liver; Br, brain; Fn, fin; Gi, gills; In, intestine; Ki, kidney; Te, testis; Sp, spleen; St, stomach.
+++, strongest expression; ++, intermediate expression; +, weak expression; −, not detectable.

similar to those of many other teleosts (Scholl and Eppenberger 1972, Fisher and Witt 1977). The relative anodal mobility of the three isozymes was in the order: $CK-B^* > CK-C^* > CK-A^*$. The dimeric CK heterozygote in black porgies is two-banded, while that in Chondrichthyes is three-banded (Ferris and Whitt 1978).

FH was detected in a single locus FH^* in all tissues, exhibiting stronger expression in heart, liver, brain, kidney, and stomach.

GDH is detected in a single locus and is expressed in liver only. A single locus for GLUDH was found only in liver and kidney.

A single locus of GAPDH was detected in all tissues except skeletal muscle, heart, and fin.

Two loci of G_3PDH were identified: G_3PDH-1^* in liver; and G_3PDH-2^* in skeletal muscle. The relative anodal mobility of these two isozymes was $G_3PDH-1^* > G_3PDH-2^*$.

Two loci for G_6PDH were detected: G_6PDH-1^* in liver, intestine, kidney, and stomach; while G_6PDH-2^* was found in all tissues except fin. The relative anodal mobility of these two isozymes was $G_6PDH-1^* > G_6PDH-2^*$. Only one band (locus) of G_6PDH was detected in the liver of the guppy (Wu and Schroder 1984), but that is apparently not the case in the present fish species investigated.

As for GPI (or PGI), with the exception of the Clupeomorpha, there are two loci (Dando 1974), which is in agreement with the results of the present study (Fig. 2). $GPI-A^*$ showed the highest degree of apparent expression in skeletal muscle, heart and kidney, and various lower levels of expression in other tissues. $GPI-A^*$ moved cathodally, while $GPI-B^*$ moved anodally with strong expression in

all tissues except skeletal muscle. $GPI-A^*$ and $GPI-B^*$ readily associated to form a GPI-AB dimer.

Two loci for HK were detected: $HK-1^*$ exhibited moderate expression in heart and lesser expression in eye and brain. $HK-2^*$ was found in skeletal muscle only. The relative anodal mobility of these two isozymes was $HK-1^* > HK-2^*$.

IDHP appeared at two loci: $IDHP-A^*$ was found in all tissues except fin and testis with strongest expression in liver; $IDHP-B^*$ was in liver only. The presence of a three-banded heterozygote indicated a dimeric structure of this enzyme. The relative anodal mobility of these isozymes was $IDHP-A^* > IDHP-B^*$.

LDH is tetrameric in structure with three loci detected: $LDH-A^*$ was present in all tissues with an almost equally high level of concentration; $LDH-B^*$ was found in all tissues with highest expression in heart; and $LDH-C^*$ was in eye only. The patterns of tissue distribution of LDH in the present study are similar to those of many other teleosts (Markert and Faulhaber 1965), as well as of the remaining vertebrates in general. The relative anodal mobility of the three LDH isozymes was in the order: $LDH-C^* > LDH-B^* > LDH-A^*$. In all five species examined, $LDH-A^*$ and $LDH-B^*$ subunits were not able to associate at random to form five isozymes $LDH-A_4$, $LDH-A_3B_1$, $LDH-A_2B_2$, $LDH-A_1B_3$, and $LDH-B_4$ in all tissues. Only two or three tetrameric isozymes were observed. According to Markert et al. (1975), the restricted assembly of heteropolymers containing $LDH-A^*$ and $LDH-B^*$ subunits could probably be due to the evolutionary divergence of subunits $LDH-A^*$ and $LDH-B^*$. The $LDH-C^*$ in the teleost eye has been localized in the neural retina (Witt 1970) and, more specifically, in the inner segments of the photoreceptor cells (Whitt and Booth 1970, Miller and Whitt 1975).
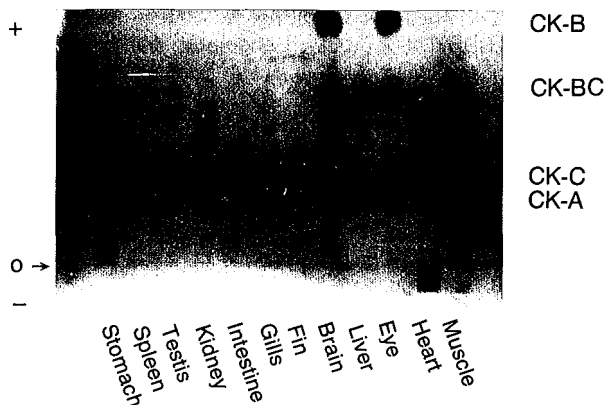

Fig. 1. CK isozymes of *Acanthopagrus schlegeli*. Starch gel was performed using LiOH pH 8.31 buffer at 4°C for 18 hours at 180V.
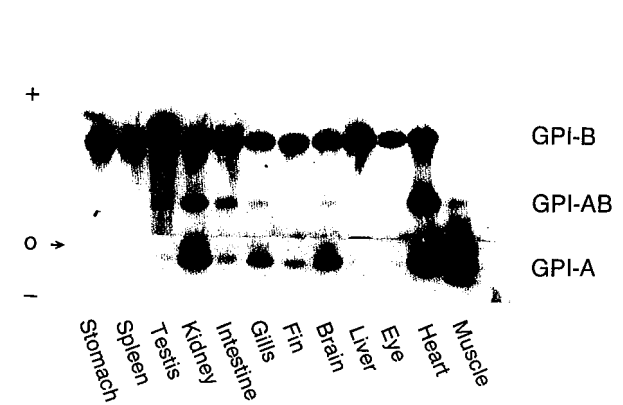

Fig. 2. GPI isozymes of *Acanthopagrus schlegeli*. Starch gel was performed using TVB pH 8.0 buffer at 4°C for 18 hours at 180V.

MDH is dimeric in structure with two supernatant loci and one mitochondrial locus. *sMDH-A** showed high resolution in skeletal muscle but faint resolution in other tissues except fin and testis where none was detected. *sMDH-B** was distributed in all tissues and showed higher resolution in heart, eye, liver, gills, intestine, kidney, spleen, and stomach. *sMDH-A** and *sMDH-B** interacted to form a heterodimeric sMDH-AB. The isozyme *mMDH** was found in all tissues except fin, showing higher resolution in heart, eye, liver, gills, and kidney. The relative anodal mobility of these isozymes was in the order: *sMDH-A** > *sMDH-B** > *mMDH**.

For the enzyme MEP, two loci were detected: *MEP-1** was found in most tissues except brain and fin, with higher resolution in skeletal muscle and liver; while *MEP-2** exhibited higher resolution in heart, and lesser resolution in skeletal muscle, eye, gills, intestine, testis, spleen, and stomach. The relative anodal mobility of these isozymes was *MEP-1** > *MEP-2**.

MPI is monomeric in structure with a single locus detected in all tissues. ODH is dimeric, which is usually present in the tail muscle of decapods (Mulley and Latter 1981). However, porgies present a single locus in liver, gills, kidney, intestine, testis, spleen, and stomach.

Two loci are appeared at PGDH: *PGDH-1** was found in all tissues except fin, with higher resolution in liver; *PGDH-2** was in liver only. The latter migrated anodally more slowly than *PGDH-1**.

PGM is a monomer with two loci expressed: *PGM-1** was detected with higher resolution in skeletal muscle, heart, liver, and brain; while *PGM-2** was in skeletal muscle, heart, eye, brain, intestine, kidney, spleen, and stomach. The electrophoretic mobility of *PGM-1** was more anodal than that of *PGM-2**.

SDH appeared at a single locus in liver only. SOD presented a supernatant locus and a mitochondrial locus: *sSOD** was expressed in all tissues; *mSOD** was expressed in heart, kidney, and spleen with a uniformly faint resolution. The electrophoretic bands of SOD appeared white against the blue-stained gel background. XDH was appeared with a single locus in liver and kidney.

The results of the tissue-specific profile of the isozymes scored above can serve as standards for evaluating electrophoretic analyses for future comparative studies of fish systematics at populational, species, or even higher taxonomic levels. We think that the experimental tests that we conducted are essential before more formal experiments can be undertaken.

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臺灣沿岸海域鯛亞科魚類同功酶之組織分布特性

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本文記述屬於25種酶系統之45種同功酶在黑鯛、黃鰭鯛、灰鰭鯛、澳洲黑鯛及黃錫鯛等五種鯛亞科魚類之骨骼肌、心肌、眼睛、肝臟、腦、背鰭鰭膜、鰓、腸肌、腎臟、精巢、脾臟、及胃肌等12種組織之分布特性。研究結果顯示鯛亞科魚類同功酶之組織分布特性並無種間之差異，且與大多數真骨魚類相似。此研究結果亦可提供將來以同功異構酶澱粉凝膠電泳法探討鯛亞科五種魚種間親緣關係，及種內族群遺傳時選擇合適之同功酶及組織部位、緩衝液系統等之依據。

關鍵詞：鯛亞科, 同功酶, 組織分布特性。

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