GENETIC STRUCTURE OF WHITE SEABASS POPULATIONS FROM THE SOUTHERN CALIFORNIA BIGHT REGION: APPLICATIONS TO HATCHERY ENHANCEMENT

DEVIN M. BARTLEY
Department of Animal Science
University of California
Davis, California 95616

DONALD B. KENT
Sea World Research Institute
1700 South Shores Drive
San Diego, California 92109

ABSTRACT

Although some fisheries biologists have expressed concern over the practicality of hatchery enhancement of marine fisheries, hatchery technology has advanced significantly during the 1980s. Marine hatchery enhancement programs are now addressing ecology and genetics as well as animal husbandry. To describe the genetic structure of white seabass and apply the information to hatchery enhancement, we used starch-gel electrophoresis to assess the level and distribution of genetic variability of seabass from nine areas in the Southern California Bight. Average heterozygosity per sample estimates ranged from 0.024 to 0.064. Indices of genetic identity between samples were greater than 0.99. Because only 3% of the total gene diversity was due to intersample differences, and because an estimate of number of migrants exchanging genes among samples was approximately 9 per generation, we believe little population subdivision exists within the study area. Genetic diversity in six hatchery samples of white seabass was 15% lower than that found in the wild, possibly because small numbers of brood stock contribute to mass spawns. Although the genetic structure of progeny from a single mass spawn may differ from wild samples, successive mass spawns increased the genetic variability of the entire hatchery product. Therefore, continuous mass spawning of white seabass over the course of the spawning season appears to be an effective means of preserving genetic diversity.

RESUMEN

A pesar de las dudas expresadas por los biólogos pesqueros con respecto a la utilidad de las piscifactorías para el mejoramiento de las pesquerías marinas, la tecnología de estos criaderos ha mostrado avances significativos en la última década. Hoy día los programas de mejoramiento dirigen su atención hacia la ecología y la genética, así como también hacia la cría de los animales. El nivel y la distribución de la variabilidad genética del róbalo blanco fueron evaluadas con "starch gel" electroforesis horizontal en nueve áreas costeras del sur de California (Southern California Bight). El propósito de este estudio es el de describir la estructura genética del róbalo blanco y utilizar esta información en el mejoramiento de los criaderos. La heterocigosidad promedio observada en cada muestra fue de 0.024 a 0.064. Los índices de identidad genética entre muestras fueron mayores de 0.99. Dado que el 3% de la heterocigosidad total se debió a las diferencias entre las muestras y dado que el número estimado de individuos migratorios con intercambio genético entre las muestras fue aproximadamente de 9, creemos que existe muy poca subdivisión en la población del área estudiada. La diversidad genética en seis muestras de róbalo de criadero fue 15% menor que la observada en la población silvestre. Esto se debe probablemente al número reducido de reproductores utilizados en los desoves en masa. A pesar de que la estructura genética de la progenie obtenida en cada desove en masa pueda diferir de las muestras de poblaciones silvestres, desoves consecutivos incrementaron la variabilidad genética cuado se considera la producción total del criadero. Por lo tanto, los desoves consecutivos durante el período del desove del róbalo blanco parece ser un método efectivo para mantener la diversidad genética en los criaderos.

INTRODUCTION

At the 1988 meeting of the California Cooperative Oceanic Fisheries Investigations, some attendees expressed concern about the practicality of hatchery enhancement of marine fisheries. In light of past attempts at enhancement, much of this concern is justified. Many early hatchery enhancement programs had no demonstrable effect on the target population (see references in MacCall 1989). In the case of Pacific salmon, many hatchery programs were developed to mitigate habitat degradation resulting from water development projects (Netboy 1974). Clearly, failing to evaluate a hatchery's contribution to the target population, and using hatcheries to justify habitat destruction are unacceptable.

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However, hatchery enhancement programs are now addressing ecological and genetic concerns as well as animal husbandry, and evaluation programs are being implemented (Rutledge 1989). Biochemical genetics has become one important tool in the study of fishery biology and aquaculture (Ryman and Utter 1987). Applying biochemical genetic techniques to hatchery enhancement will help the hatcheries produce viable fish by preserving genetic diversity (Kincaid 1983; Allendorf and Ryman 1987). At the same time, the use of genetic markers will increase fishery scientists' ability to evaluate hatchery contribution to wild populations (Murphy et al. 1983; Seeb et al. 1986).

The objective of the research reported here is to apply biochemical and population genetic techniques to hatchery enhancement efforts on white seabass, *Atractoscion nobilis* (Scianidae), in the Southern California Bight region. Numbers of this species in the Southern California Bight have been declining, and the species has almost completely disappeared from the central California waters that historically supported the center of the commercial fishery (Skogsberg 1939; Vojkovich and Reed 1983). We use allozyme data from horizontal starch-gel electrophoresis of soluble proteins to describe the level and distribution of genetic diversity in natural and cultured populations of white seabass. Although these techniques have been used to describe the population genetic structure of Gulf of Mexico Scianidae (Ramsey and Wakeman 1987), genetic studies of marine fish in the Southern California Bight have, until now, neglected white seabass (Waples 1987).

METHODS

Collections and Samples

We collected 13 samples of juvenile and adult white seabass from the Southern California Bight region using gill nets of approximatley 3.8-, 7.6-, and 8.9-cm mesh. Specific locations and dates of collections were: Point Loma 1988 (Sample size [N] = 40); Point Loma 1987 (N = 50); Mission Bay, San Diego 1988 (N = 36); La Jolla 1988 (N = 23); La Jolla 1987 (N = 90); Encinitas 1988 (N = 5); Encinitas 1987 (N = 100); San Onofre 1988 (N = 35); San Onofre 1987 (N = 16); Seal Rock, San Clemente 1988 (N = 51); San Mateo Point, San Clemente 1988 (N = 34); Dana Point 1988 (N = 17); and Laguna Beach 1988 (N = 13). Muscle and liver tissue were dissected from the fish in the field and frozen in liquid nitrogen. Fish from Mission Bay were dissected at Sea World Reseach Institute, and tissue samples were frozen and stored at −70° C.

We also collected juvenile white seabass from six separate mass spawns at Sea World Research Institute (SWRI): one sample in 1985 (N = 21); one sample in 1986 (N = 72); and four samples in 1988 (N's = 30, 26, 27, and 36). These hatchery samples were designated SWRI-1 through SWRI-6. All six hatchery samples of white seabass descended from approximately 20 brood stock maintained in a 3.0 x 6.0 x 1.2-m pool (19,000 liters) with recirculating seawater. Adult white seabass were induced to spawn by photoperiod and temperature manipulation. Eggs were collected by siphon, and larvae hatched after 2–3 days. White seabass progeny were fed a combination of rotifers, *Artemia*, and commercially available trout feed until they were approximately 9 cm long, at which point they were frozen whole and stored at −70°C. Muscle and liver tissues were dissected and stored at −70°C before electrophoresis.

Electrophoresis

Horizontal starch-gel electrophoresis followed standard procedures (Aebersold et al. 1987). Enzyme systems, tissue distribution, and number of loci are presented in table 1. Gels were made with 12% hydrolyzed potato starch (Sigma Chemical Co.) combined with one of the following buffer systems: AC, an amine citrate buffer from Clayton and Tretiak (1972) adjusted to pH 7.0; R, a discontinuous buffer system (pH 8.0) described by Ridgeway et al. (1970); and MF, a boric acid-Tris system (pH 8.4) from Markert and Faulhaber (1965).

For histochemical staining procedures we followed Shaw and Prasad (1970) and Harris and Hopkinson (1976). For nomenclature we followed Allendorf and Utter (1979); in this system, the most common allele at a locus is designated the 100 allele, and variant alleles are assigned numeric values based on their anodal migration distance relative to the 100 allele. Enzyme abbreviations are in uppercase letters; alleles are designated by the italicized enzyme abbreviation followed by locus number with allelic mobility in parentheses.

Data Analysis

We assessed genetic variability of each fish sample by calculating the frequencies of alleles at each locus, the percentage of polymorphic loci (P), and average heterozygosity (H) (Nei 1973). A locus was considered polymorphic if we observed one variant allele. We calculated genetic identities (I) for each pair of

TABLE 1
Enzyme Systems and Isozyme Loci Analyzed from Liver (L) and Muscle (M) Tissue of White Seabass

Enzyme system	Abbreviation	E.C. number	Number of loci	Tissue	Buffer*
Acid phosphatase	*Acp*	3.1.3.2	2	M,L	MF
Aconitate hydratase	*Ah*	4.2.1.3	2	L	AC
Adenylate kinase	*Ak*	2.7.4.3	1	M	AC
Alcohol dehydrogenase	*Adh*	1.1.1.1	1	L	AC,MF
Aspartate amino transferase	*Aat*	2.6.1.1	2	M,L	AC,R
Creatine kinase	*Ck*	2.7.3.2	1	M	R
Esterase	*Est*	3.1.1.1	2	M,L	R
Glyceraldehyde-3-phosphate dehydrogenase	*Gapdh*	1.2.1.12	2	M	AC
Glycerol-3-phosphate dehydrogenase	*Gpd*	1.1.1.8	2	M	AC
Glucose phosphate isomerase	*Gpi*	5.3.1.9	3	M	R
Iditol dehydrogenase	*Iddh*	1.1.1.14	1	L	R
Isocitrate dehydrogenase	*Idh*	1.1.1.42	2	M,L	AC
Lactate dehydrogenase	*Ldh*	1.1.1.27	1	M	R
Malate dehydrogenase	*Mdh*	1.1.1.37	1	M,L	AC
Malic enzyme	*Me*	1.1.1.40	1	M,L	MF
Mannose phosphate isomerase	*Mpi*	5.3.1.8	1	M,L	R,MF
Phosphogluconate dehydrogenase	*6 Pdg*	1.1.1.44	1	M,L	AC
Phosphoglucomutase	*Pgm*	5.4.2.2	1	M,L	AC
Superoxide dismutase	*Sod*	1.15.1.1	1	M,L	MF,R
Triosphosphate isomerase	*Tpi*	5.3.1.1	2	M	MF
Peptidase					
Glycyl leucine	*Dpep*	3.4.13.11	2	M	R
Leucyl glycyl glycine	*Tapep*	3.4.11.4	1	M	R

*Described in text

samples (Nei 1978) and constructed a dendrogram from estimates of I with the unweighted pair-group method (UPGMA; Sneath and Sokal 1973) to examine the relative similarities among populations.

We partitioned total gene diversity (H_T) of wild and hatchery samples to estimate within-sample (H_S) and between-sample (D_{ST}) components and relative gene diversity (G_{ST}) (Nei 1973; Chakraborty and Leimar 1987). To ascertain significant subpopulation structure within the study area, we used a chi-square test to determine if Wright's F_{ST} (1943) was significantly different from zero, as described by Waples (1987). We used G_{ST} to approximate F_{ST} (Nei 1977; Slatkin and Barton 1989). Tests of independence between allelic frequency and location were performed by log likelihood G test (Sokal and Rohlf 1981). G tests were also performed on allelic frequencies and mass spawning samples to determine if significant genetic differences existed among the six hatchery samples. Quantitative estimates of gene flow were calculated from Wright's (1943) fixation index

$$F_{ST} = 1/(4Nm + 1) \quad (1)$$

where Nm is the average number of migrants per generation. Equation 1 was solved for Nm by setting F_{ST} equal to the relative gene diversity (G_{ST}) estimate (Nei 1977). Equation 1 will provide an estimate of the number of migrant fish exchanging genes among samples per generation under the assumptions of selective neutrality of alleles and Wright's (1943) island model of migration. Slatkin and Barton (1989) discussed the sensitivity of equation 1 to various methods of estimating F_{ST}, some selection, and population structure, and found it to be fairly robust.

RESULTS

Allozyme Variation of Wild Samples

We detected allozyme variation in 19 of 33 loci (table 2). The distribution of alleles in wild samples of white seabass was generally homogeneous throughout the study area, except for rare alleles in specific locations. For example, we observed the *Gpd-2 (−133)* allele only in the 1987 sample from San Onofre. In addition, IDH, ME, and MPI polymorphisms were observed in 1988 and not in 1987 samples. The distribution of rare alleles did not follow an obvious pattern. Heterozygosity estimates ranged from 0.033 in the Encinitas 1988 sample to

TABLE 2

Allelic Frequencies at 19 Polymorphic Gene Loci from 13 Wild and 6 Hatchery Samples of White Seabass

		Pt. Loma 1988	Pt.Loma 1987	Mission Bay 1988	La Jolla 1988	La Jolla 1987	Encinitas 1988	Encinitas 1987	San Onofre 1988	San Onofre 1987
Aat-1	(100)	0.975	0.906	0.930	1.000	0.909	0.900	0.870	0.886	0.860
	(115)	0.025	0.021	0.028		0.025	0.100	0.019	0.071	0.031
	(50)		0.073	0.042		0.066		0.111	0.043	0.109
	N*	40	48	36	23	90	5	79	35	16
Aat-2	(100)	0.872	0.995	0.944	0.935	0.945	1.000	0.992	0.914	1.000
	(125)	0.103	0.005	0.028	0.043	0.049		0.004	0.086	
	(65)	0.026		0.028	0.022	0.006		0.004		
	N	39	50	36	23	86	5	100	35	16
Adh	(−100)	0.462	0.443	0.486	0.304	0.543	0.500	0.438	0.443	0.385
	(−200)	0.487	0.534	0.514	0.652	0.429	0.500	0.531	0.557	0.615
	(−300)	0.051	0.023		0.043	0.028		0.031		
	N	39	44	36	23	35	5	81	35	13
Est-4	(100)	0.936	0.896	0.861	0.978	0.927	1.000	0.950	0.914	0.962
	(89)		0.010	0.056		0.028		0.025		0.038
	(115)	0.064	0.094	0.083	0.022	0.045		0.025	0.086	
	N	39	48	36	23	89	5	40	35	13
Est-5	(100)	0.938	1.000	0.875	0.957	0.925	1.000	1.000	0.900	0.937
	(103)	0.063		0.083	0.043	0.050			0.071	
	(95)			0.042		0.025			0.029	0.063
	N	40	20	36	23	40	5	40	35	16
Gpd-2	(−100)	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.967
	(−133)									0.033
	N	40	50	36	23	90	5	100	35	16
Gpi-1	(100)	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(−140)									
	N	40	50	36	23	90	5	80	35	16
Gpi-2	(100)	0.975	1.000	0.958	1.000	0.994	1.000	1.000	1.000	1.000
	(85)	0.025				0.006				
	(122)			0.042						
	N	40	50	36	23	90	5	80	35	16
Gpi-3	(100)	1.000	1.000	1.000	1.000	0.994	1.000	0.987	1.000	1.000
	(78)					0.006		0.013		
	(112)									
	N	40	50	36	23	90	5	80	35	16
Iddh-1	(100)	0.988	0.970	1.00	0.957	0.970	1.000	0.990	0.943	1.000
	(−400)				0.043	0.030		0.005	0.043	
	(700)	0.012	0.030					0.005	0.014	
	N	40	50	36	23	50	5	100	35	16
Idh-1	(100)	1.000	1.000	0.986	0.978	1.000	1.000	1.000	0.986	1.000
	(82)			0.014	0.022				0.014	
	N	40	50	36	23	90	5	100	35	16
Idh-2	(100)	0.975	1.000	0.986	1.000	1.000	1.000	1.000	0.986	1.000
	(119)	0.025		0.014					0.014	
	(62)									
	N	40	50	36	23	90	5	100	35	16
Ldh-3	(100)	0.950	1.000	0.972	0.978	0.983	1.000	0.980	0.986	0.934
	(40)	0.025		0.014		0.017		0.015	0.014	0.033
	(150)	0.025		0.014	0.022			0.005		0.033
	N	40	50	36	23	88	5	100	35	16
Me-1	(100)	0.975	1.000	1.000	0.935	1.000	1.000	1.000	1.000	1.000
	(116)	0.025			0.065					
	N	40	50	36	23	90	5	100	35	16
Mpi	(100)	0.949	1.000	0.917	0.978	1.000	1.000	1.000	0.971	1.000
	(110)	0.051		0.083	0.022				0.029	
	N	39	50	36	23	90	5	100	35	16
6Pgd	(100)	1.000	0.980	1.000	1.000	1.000	1.000	0.995	1.000	1.000
	(95)		0.020					0.005		
	N	40	50	36	23	90	5	90	35	16
Pgm-1	(−100)	0.224	0.410	0.403	0.239	0.250	0.300	0.237	0.371	0.447
	(−167)	0.750	0.590	0.555	0.761	0.750	0.700	0.750	0.586	0.553
	(−200)	0.026		0.042				0.013	0.043	
	N	38	50	36	23	10	5	40	35	16
Sod	(100)	0.988	1.000	0.986	1.000	0.989	1.000	1.000	1.000	1.000
	(109)	0.012		0.014		0.011				
	N	40	48	36	23	88	5	100	35	16
Ah-2	(100)	1.000	1.000	1.000	1.000	1.000	1.000	0.990	1.000	1.000
	(98)							0.010		
	N	40	50	36	5	90	5	99	35	16
H		0.056	0.045	0.064	0.043	0.048	0.033	0.041	0.060	0.048
P		0.39	0.21	0.36	0.30	0.33	0.09	0.30	0.33	0.21

*Sample size

H = average heterozygosity; *P* = proportion polymorphic loci

(*continued on next page*)

TABLE 2 (*continued*)

		Seal Rock 1988	San Mateo Pt. 1988	Dana Pt. 1988	Laguna Beach 1988	SWRI-1 1985	SWRI-2 1986	SWRI-3 1988	SWRI-4 1988	SWRI-5 1988	SWRI-6 1988
Aat-1	(100)	0.800	0.783	0.941	1.000	0.658	1.000	0.917	0.923	0.833	0.853
	(115)	0.030	0.152	0.059		0.250		0.033		0.019	0.015
	(50)	0.170	0.065			0.092		0.050	0.077	0.148	0.132
	*N**	50	23	17	13	21	72	30	26	27	34
Aat-2	(100)	0.908	0.912	0.969	0.923	1.000	1.000	0.967	1.000	0.963	0.686
	(125)	0.071	0.059	0.031	0.077					0.037	0.300
	(65)	0.020	0.029					0.033			0.014
	N	49	34	16	13	21	35	30	26	27	35
Adh	(−100)	0.357	0.411	0.375	0.538	0.833	0.910	0.517	0.923	1.000	0.588
	(−200)	0.633	0.574	0.594	0.462	0.167	0.090	0.483	0.077		0.412
	(−300)	0.010	0.015	0.031							
	N	51	34	16	13	21	72	30	26	27	34
Est-4	(100)	0.930	0.941	0.938	0.962	1.000	1.000	1.000	1.000	1.000	0.958
	(89)	0.020	0.029								
	(115)	0.050	0.029	0.062	0.038						0.042
	N	50	34	16	13	21	72	30	26	27	36
Est-5	(100)	0.940	0.958	0.912	1.000	1.000	1.000	1.000	1.000	1.000	0.771
	(103)	0.040	0.021	0.088							
	(95)	0.020	0.021								0.229
	N	49	24	17	13	21	72	30	26	27	35
Gpd-2	(−100)	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(−133)										
	N	51	34	17	13	21	72	30	26	27	35
Gpi-1	(100)	1.000	1.000	1.000	1.000	1.000	0.708	1.000	1.000	1.000	1.000
	(−140)						0.292				
	N	51	34	17	13	21	72	30	26	27	36
Gpi-2	(100)	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(85)										
	(122)										
	N	51	34	17	13	21	72	30	26	27	35
Gpi-3	(100)	1.000	0.971	0.971	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(78)		0.029								
	(112)			0.029							
	N	51	34	17	13	21	72	30	26	27	35
Iddh-1	(100)	0.979	0.985	1.000	0.924	1.000	1.000	1.000	1.000	1.000	1.000
	(−400)	0.021	0.015		0.038						
	(700)				0.038						
	N	48	34	16	13	21	72	30	26	27	35
Idh-1	(100)	1.000	0.957	1.000	1.000	1.000	1.000	0.983	1.000	0.870	1.000
	(82)		0.043					0.017		0.130	
	N	51	23	17	13	21	72	30	26	27	36
Idh-2	(100)	1.000	0.979	1.000	1.000	1.000	1.000	1.000	1.000	0.944	1.000
	(119)										
	(62)		0.021							0.056	
	N	51	24	17	13	21	72	30	26	27	36
Ldh-3	(100)	0.990	1.000	0.941	1.000	1.000	0.972	1.000	1.000	1.000	1.000
	(40)	0.010		0.029			0.028				
	(150)			0.029							
	N	51	34	17	13	21	72	30	26	27	36
Me-1	(100)	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(116)										
	N	51	34	17	13	21	72	30	26	27	36
Mpi	(100)	0.957	0.850	0.969	1.000	1.000	0.965	1.000	1.000	1.000	1.000
	(110)	0.043	0.150	0.031			0.035				
	N	47	30	16	13	21	72	30	26	27	36
6Pgd	(100)	0.990	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(95)	0.010									
	N	50	34	17	13	21	72	30	26	27	36
Pgm-1	(−100)	0.352	0.221	0.406	0.192	0.857	0.743	0.283	0.462	0.442	0.750
	(−167)	0.637	0.735	0.594	0.769	0.143	0.257	0.667	0.538	0.558	0.250
	(−200)	0.011	0.044		0.038			0.050			
	N	44	34	16	13	21	72	30	26	26	32
Sod	(100)	1.000	0.985	0.971	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	(109)		0.015	0.029							
	N	38	34	17	13	21	72	30	26	27	36
Ah-2	(100)	1.000	1.000	1.000	0.923	1.000	1.000	1.000	1.000	1.000	1.000
	(98)				0.077						
	N	49	29	11	13	21	72	30	26	27	36
H		0.056	0.064	0.052	0.042	0.033	0.03	0.037	0.024	0.036	0.060
P		0.30	0.36	0.30	0.18	0.09	0.15	0.15	0.09	0.15	0.18

0.064 in the San Mateo Point and the Mission Bay samples. The proportion of polymorphic loci was lowest in the Encinitas 1988 sample and highest in the Point Loma 1988 sample. However, because only five fish were collected from Encinitas in 1988, the estimates of genetic variability may be inaccurate.

Cluster analysis based on Nei's genetic identity estimates failed to reveal any geographic structure to the genetic variation in white seabass (figure 1). Genetic identity values between wild samples were all greater than 0.99.

To determine if population substructuring was occuring in natural populations of white seabass, we examined gene diversity analysis quantifying the amount of genetic variation between (D_{ST}) and within (H_S) samples. For natural populations of white seabass sampled in 1987 and 1988, approximately 97% of the variation was derived from within-sample variability (D_{ST} = 0.0017; H_S = 0.0535; H_T = 0.0552 for 1987 samples, and D_{ST} = 0.0013; H_S = 0.0487; H_T = 0.0500 for 1988 samples) and 3% was due to between-sample differences (G_{ST} = 0.304 for 1987 and 0.0259 for 1988).

In spite of this low level of intersample variability, we did find statistical evidence of differences in genetic variability. Wright's (1943) F_{ST} statistic measures the reduction in heterozygosity observed in a population due to population subdivision and is one method of assessing genetic differences between subpopulations. We used G_{ST} to approximate F_{ST} (Nei 1977) and found highly significant F_{ST} values in both the 1987 (F_{ST} = 0.0304; d.f. = 72; X^2 = 247.953) and 1988 (F_{ST} = 0.0259; d.f. = 240; X^2 = 399) samples. However, tests of independence of allele frequency and location on the 1987 and 1988 data sets revealed significant association of alleles and location only for *Aat-1* in 1988 (G = 29.391; d.f. = 16).

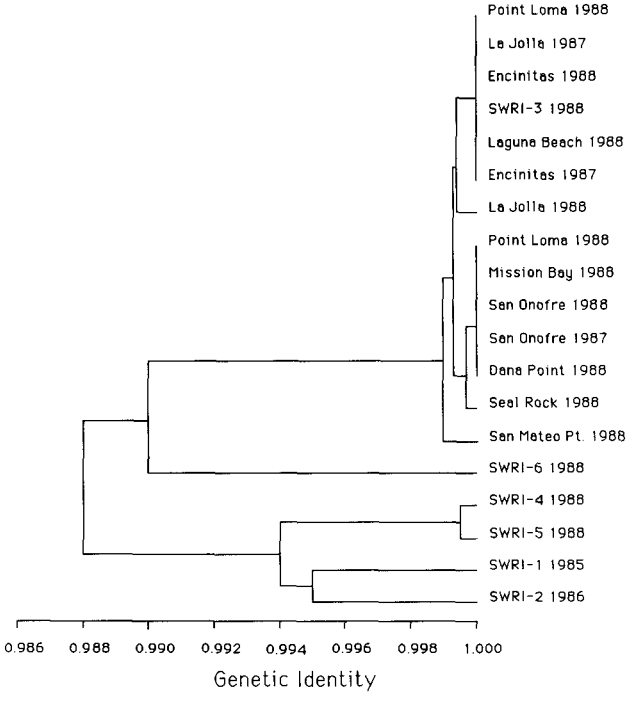

Figure 1. Cluster analysis (UPGMA) of genetic identity values among 19 samples of white seabass.

To determine if significant allele frequency differences existed between samples taken at different years from the same location, tests of independence of allele frequencies and sample year were performed on collections from Point Loma, La Jolla, Encinitas, and San Onofre. Although the summary indices of genetic variation changed between years (H and P, table 2), only the *Aat-3* locus from the Point Loma samples displayed significant temporal heterogeneity (G = 8.518; d.f. = 1).

Estimates of gene exchange were high among wild samples. We estimated the level of gene flow among wild samples to be 8.0 individuals per generation in 1987, and 9.4 in 1988 (equation 1).

Allozyme Variability in Hatchery Samples

We observed eleven polymorphic loci in six hatchery samples of white seabass. However, individual samples had as few as three, and no more than six polymorphic loci (table 2). Heterozygosity levels ranged from 0.024 to 0.060 and were comparable to levels in natural samples.

Although white seabass progeny all came from a common brood stock, differences in allelic variability were apparent. For example, SWRI-2 was the only hatchery sample in which we observed the *Ldh-3(40)*, *Gpi-1(−140)*, and *Mpi-(110)* alleles. However, no *Aat-1* or *Aat-2* polymorphisms were seen in this sample. SWRI-5 was fixed for the common *Adh* allele, whereas other hatchery samples were variable at this locus. The *Est-5* locus was polymorphic only in SWRI-6 sample.

Gene diversity analysis of hatchery samples indicated 84% of the total heterozygosity was due to differences within samples, whereas 16% (G_{ST} = 0.157) originated from between-sample differences, i.e., differences in mass spawnings (D_{ST} = 0.0069; H_S = 0.0370; H_T = 0.0440). Furthermore, significant heterogeneity in allelic frequencies existed among the hatchery groups at six loci: *Aat-1* (G = 20.545; 5 d.f.); *Aat-3* (G = 43.801; 5 d.f.); *Adh* (G = 41.125; 5 d.f.); *Idh-1* (G = 15.934; 5 d.f.); *Pgm-1* (G = 40.031; 10 d.f.); and *Gpi -1* (G = 50.031; 5 d.f.).

Genetic identities between hatchery samples were slightly less than those between wild samples (data not shown). However, all but one of the hatchery samples clustered together in figure 1. The genetic similarity between the cluster of wild samples and a single composite hatchery sample (produced by averaging allelic frequencies from all hatchery samples) was 0.994.

DISCUSSION

The electrophoretic analysis of wild samples of white seabass revealed more genetic variability than was previously reported for this species. Soulé and Senner (unpublished report to California Department of Fish and Game) detected polymorphisms only in alcohol dehydrogenase and phosphoglucomutase enzyme systems. Levels of heterozygosity reported here were slighly higher than the range of values (0.009–0.043) reported for other members of the Scianidae (Ramsey and Wakeman 1987). Waples (1987) reported a range of heterozygosity values of 0.009 to 0.087 (mean = 0.031) for ten species of Southern California Bight marine shorefishes that display diverse life-history characters. Average heterozygosity values of white seabass were similar to two of the species studied by Waples: the wooly sculpin, *Clinocottus analis* (H = 0.046), and the ocean whitefish, *Caulolatilus princeps* (H = 0.049).

Subpopulations of white seabass appear to be genetically similar in the Southern California Bight region. However, significant subpopulation differentiation was discovered among the samples in 1988, and significant allelic frequency heterogeneity existed between sampling years at Point Loma. We do not infer that discrete subpopulations of white seabass exist in the Southern California Bight area. The reasons for these differences are unclear at present, but may be an effect of the rare alleles, nonrandom sampling of the populations, temporal instability of allele frequencies, or selection, as well as discrete subpopulation structure. Hedgecock and Bartley (1988) found significant allelic frequency differences between juvenile California halibut from Mission Bay, San Diego, and adults from Marina del Rey, and discussed several testable hypotheses to account for genetic differences within a theoretically panmictic population. Unfortunately, we do not have size or age data on the present collections of white seabass; therefore a more detailed analysis of the causes of genetic heterogeneity, as was done in studies of northern anchovy (Hedgecock et al. 1989) is not possible at present.

We could detect no consistent geographic, clinal, or temporal component to the observed genetic variation in wild populations of white seabass from the Southern California Bight region. This result was not unexpected, given the past history of genetic studies on pelagic marine fishes (Gyllensten 1985; Waples 1987; Hedgecock et al., 1989). In highly mobile species such as white seabass (Vojkovich and Reed 1983), gene flow among localities is apparently sufficient to homogenize the genetic structure.

The significant F_{ST} values and the occurrence of variant alleles in specific samples suggested that the population of white seabass in the study area may not be panmictic, but rather a dynamic mosaic of very similar subpopulations. Hedgecock et al. (1989 and unpublished data) observed an extremely complex population genetic structure in northern anchovy; allelic heterogeneity existed between sexes, locations, and age classes. Campton and Utter (1987) stated that gene frequencies in subpopulations may randomly fluctuate around a global mean for the population. The random fluctuations may be statistically significant even with substantial levels of gene flow (Allendorf and Phelps 1981). Waples (1987) observed isozyme loci with significant F_{ST} values (i.e., subdivision) in two marine shorefishes with limited dispersal capabilities — the viviparous black perch, *Embiotica jacksoni* (average F_{ST} = 0.444), and the wooly sculpin (average F_{ST} = 0.042). Marine species that Waples judged to have high dispersal capabilities showed a lower range of F_{ST} values (0–0.028) than we observed in white seabass.

The results of this study have favorable implications for hatchery enhancement programs. Levels of genetic variability detected here are similar to levels in other species to which genetic marking techniques have been applied (Murphy et al. 1983; Seeb et al. 1986). Furthermore, we detected several alleles that could be used as genetic markers to differentiate hatchery stocks from wild stocks. Frequencies of alleles such as *Ldh-3(40* or *150)*, *Mpi-(110)*, or *Aat-1(115* or *50)* could be increased in hatchery populations through selective breeding, and used to quantify hatchery contribution to a target population (Pella and Milner, 1987).

Hydrologic and zoogeographic data suggest that the Southern California Bight represents a zoogeographic province bounded by Magdalena Bay, Baja California, to the south, and by Point Conception to the north (Briggs 1974). The province is characterized by fish fauna that show little regional genetic differentiation (Waples 1987). Although our initial description of the population genetic structure of

white seabass suggests that brood stock could be collected and progeny released at convenient locations within the study area, one should proceed carefully before implementing such a hatchery program. Life-history data on spawning patterns, migration, age of maturity, and growth rate must be collected throughout the Southern California Bight region to determine if the allozyme similarity in the area is reflected by phenotypic similarity. We do not know if mixing the populations of white seabass in the Southern California Bight through transfers of hatchery-produced fish would cause problems of hybridization of locally adapted stocks and result in outbreeding depression (Altukhov and Salmenkova 1987). In addition, we know nothing of the contribution of subpopulations from the offshore islands. Genetic analyses of samples from offshore islands and samples outside the Southern California Bight may reveal more genetic differences that may be a consideration in white seabass enhancement efforts in lower Baja California or northern California.

The progeny groups produced from a single brood stock at SWRI were more different from each other than were the wild populations from separate locations. Furthermore, the hatchery populations were slightly differentiated from natural populations. The differences in genetic variability among hatchery samples are most likely due to different adults contributing to successive mass spawns. The relative contribution of adult brood stock to mass spawnings may also change over time. For example, the fish contributing to the 1986 mass spawn possessed the *Gpi-1(−140)* allele. Because this allele was not seen subsequently, we presume the adult (or adults) made little or no further contribution to the progeny samples. Sampling error and small sample sizes may also account for some differences in allelic frequency or presence of rare alleles in hatchery samples.

It is important to note that progeny from a single mass spawn have a different genetic profile and may have less variability than natural populations; when additional progeny samples are analyzed, the genetic variability of the entire hatchery product is increased. However, there is a limit to the genetic variability in progeny from a limited number of adults. We observed a 15% decrease in total gene diversity in hatchery samples compared to wild samples (0.0440/0.0516). A founding population of $N = 15$ individuals (such as in a mass spawning tank) should preserve $1\text{-}1/2N$ or 97% of the variation of the original population. This relation will only hold if N is the effective population size (N_e). N_e of the white seabass brood stock may be much less than N because of different reproductive output and unequal sex ratio of adults (Allendorf and Ryman 1987). We should point out that the progeny groups we analyzed represent a small proportion of the progeny produced at SWRI.

The precise number of adults participating in the spawns could not be determined, because the genotypes of the brood stock are unknown and because spawning is difficult to see. If all adults contributed equally to each spawn, we would expect to see the same alleles in each hatchery sample. Because we observed different alleles in successive progeny groups, we believe that only a few adults are involved. Mass spawns result when one or two females ovulate, and each female is fertilized by one to four males (personal observation). Therefore, although a single mass spawn may represent a genetic contribution of only a few spawners, a series of mass spawns, each with different brood stock contributing gametes, may represent a genetic contribution of a large number of brood stock. Furthermore, a production hatchery may be able to have several tanks of brood stock spawning, thereby increasing the effective population size of adults and the genetic variability of the progeny. In a hatchery enhancement program for white seabass in the Southern California Bight region, the genetic profile of progeny from mass spawnings should be monitored over extended periods of time to insure that levels of genetic variability are maintained. Although white seabass brood stock are adapted to current hatchery conditions, dominance hierarchy or reproductive senescence in certain individuals may reduce the number of adults spawning and thus decrease the genetic diversity of progeny.

Technology now exists for producing large numbers of white seabass in a hatchery environment. But the feasibility of enhancing a depressed natural population of white seabass is still controversial. The allozymic data presented in this paper address genetic considerations associated with hatchery enhancement. Recently developed molecular genetic techniques can also be applied to fishery analyses. DNA-level polymorphisms from mitochondrial DNA, and DNA fingerprints may reveal additional markers for hatchery fish and may provide a means to follow the contribution of individual brood stock (Hallerman and Beckman 1988). We recommend the continued collection of allozyme data from offshore islands and areas outside the Southern California Bight, as well as the incorporation of DNA analyses to better understand the population genetic structure of natural and hatchery populations of white seabass.

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