Genetic Isolation of Channel Islands Fish Populations: Evidence From Two Embiotocid Species

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INTRODUCTION

Islands have provided some of the most fruitful natural laboratories for the study of evolutionary phenomena. Much of the current understanding of processes such as adaptive radiation, character displacement, and speciation has resulted from observation of island populations and species. In particular, understanding of the speciation process has benefited from analyses of island biota. This is not surprising if, as is generally accepted, speciation requires allopatry between diverging groups. Islands are obvious potential isolates for terrestrial plants and animals; consequently, evolutionary literature is endowed with many well-documented examples of terrestrial island endemism and adaptive radiation.

Islands are also important in the production of new marine species. The degree to which any island or island group supports marine endemic species depends on the distance from the nearest source of immigrants, current patterns, and dispersal characteristics of individual species. Fishes are generally regarded as a highly vagile group; however, they often display a considerable degree of endemism at isolated islands. For example, Hawaiian fish species are 34 per cent endemics, Easter Island 29 per cent, Galapagos 27 per cent, and South Georgia 57 per cent (Briggs 1966). Islands that are near shore or in the direct path of currents show lower levels of fish species endemism (McDowall 1968); Bermuda, for example, has 5 per cent endemics, Cape Verde has 4 per cent, and the Azores have none (Briggs 1966).

The Channel Islands off southern California are quite close to the mainland and are in the path of the California Current; it seems unlikely, therefore, that this island group would possess endemic fish species. Under such conditions, immigration would be likely to occur at a rate sufficient to prevent genetic divergence of fish populations in island waters. However, Tarp (1952) has described an endemic species of embiotocid fish, *Cymatogaster gracilis*, from the Channel Islands. On the basis of morphologic divergence from the mainland species, *C. aggregata*, the island perch has been recognized as a distinct species. The family Embiotocidae comprises 23 species, 20 of which occur in California waters, where they are among the most commonly encountered shallow-water marine fishes. The family is particularly distinguished by viviparous reproduction; once a year mature females give birth to broods of between 10 and 50 young that are at an advanced stage of development. Since tagging studies indicate that adult embiotocids are relatively sedentary, and since there apparently is no dispersal stage in their life history, it may not be surprising that an island endemic species has occurred in that family.

Until recently, morphologic variation provided one of the only bases for taxonomic distinctions. The primary difficulty in interpreting morphologic data has always been the problem of separating genetic and environmental effects. In the last decade, the widespread availability and utilization of electrophoretic techniques have provided a source of data on geographic variation that is generally free from direct environmental effects (Avise 1974). These data also allow the direct measurement of allele frequencies at individual gene loci. Consequently, electrophoresis is a powerful tool for use in studies of genetic isolation.

In this study, two other species of embiotocid fishes, the pile surfperch (*Damalichthys vacca*)

TABLE 1. Sample locations (with abbreviations), collection dates, sample sizes, and collection method.

Population	Date	*n*	Method
	Damalichthys vacca		
Puget Sound (PS)	Sept. 74	50	Beach seine
San Francisco (SF)	Aug. 74	50	Angling
Avila (AV)	1975	50	SCUBA
Santa Barbara (SB)	1976	46	SCUBA
Santa Cruz Island (SCI)	1976	38	SCUBA
Redondo (RE)	1976	45	SCUBA
Santo Tomás (ST)	1975	47	SCUBA
	Embiotoca lateralis		
Puget Sound (PS)	Oct. 1975	38	Beach seine
San Francisco (SF)	Nov. 1975	49	Angling
Avila (AV)	1975	50	SCUBA
Santa Barbara (SB)	1976	34	SCUBA
Santa Cruz Island (SCI)	1976	43	SCUBA
Santo Tomás (ST)	1975	50	SCUBA

and the striped surfperch (*Embiotoca lateralis*), were examined electrophoretically to determine if Channel Island populations are genetically isolated from mainland populations. In addition, a number of morphologic analyses were conducted on both species to determine if any form of phenetic variation indicates results similar to those determined electrophoretically.

Materials and Methods

The time, place, sample size, and collection method for each sample are given in Table 1. Figure 1 indicates the species' geographic ranges and identifies sampling locations. The collected fish were frozen immediately on dry ice and were kept frozen until analysis in the laboratory. Horizontal starch gel electrophoresis was conducted following the basic procedures described by Ayala *et al.* (1972) or Selander *et al.* (1971). Seventeen gene loci, determined by nine enzyme assays, were used in electrophoretic analysis. The nine assays were: *general protein* (PT), *lactate dehydrogenase* (LDH), *malate dehydrogenase* (MDH), *glyceraldehyde-3-phosphate dehydrogenase* (GAP), *tetrazolium oxidase* (TO), *glutamate oxalate transaminase* (GOT), *phosphoglucose isomerase* (PGI), *mannose phosphate isomerase* (MPI), and *esterase* (EST). Multiple loci for any assay are designated numerically, and multiple alleles at a locus are designated alphabetically, in order of decreasing anodal mobility. For example, LDH-1B would designate the second fastest allele at the fastest LDH locus.

Each fish was measured for twelve morphometric characters: total length, standard length, head length, maxillary length, snout length, gape, predorsal length, dorsal base length, anal base length, first dorsal spine to pelvic fin, last dorsal ray to anus, and length of ultimate dorsal spine. Measures are based on the descriptions in Lagler *et al.* (1962).

Eight meristic characters were counted on each fish: the numbers of dorsal fin spines, dorsal fin rays, anal fin rays, pectoral fin rays, scales on the lateral line, scales from anus to lateral line, and gill rakers.

Two multivariate techniques were used in analyses of both the morphometric and meristic data sets. Principal components analysis was done with SAS (Statistical Analysis Systems)

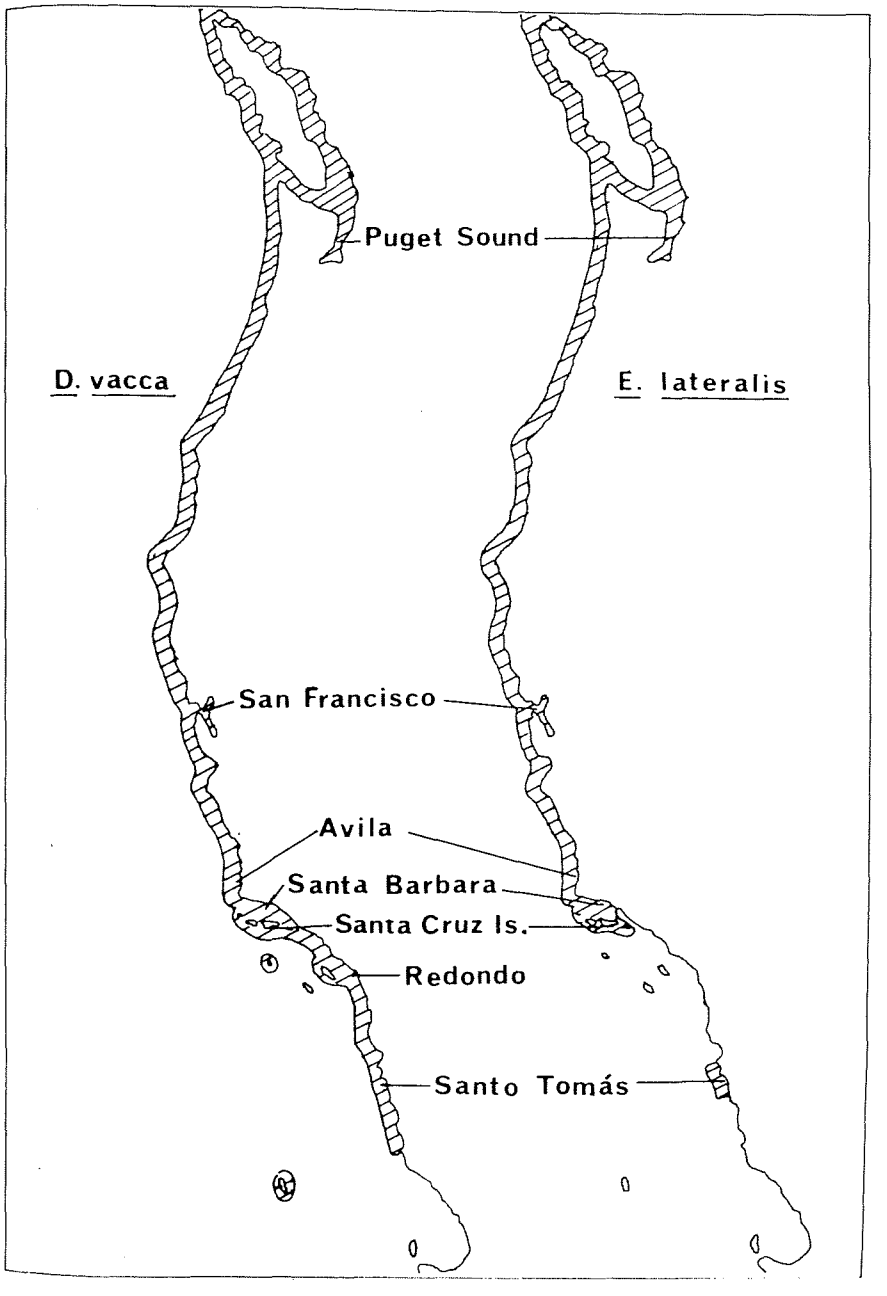

FIGURE 1. *Geographic ranges of* D. vacca *and* E. lateralis *with locations of sampling sites. Ranges extend north to Port Wrangell, Alaska.*

TABLE 2. Allele frequencies of all polymorphic loci in all population samples of *D. vacca* and *E. lateralis*.

	D. vacca						
Allele	PS	SF	AV	SCI	SB	RE	ST
TO 1A	.35	.32	.32	.72	.36	.25	.21
TO 1B	.65	.68	.68	.28	.64	.75	.79
PGI 1A	0	0	0	0	.01	.01	0
PGI 1B	1.0	1.0	1.0	1.0	.99	.99	1.0
PGI 2A	.26	.30	.25	0	.20	.22	.24
PGI 2B	.74	.70	.75	1.0	.80	.78	.76
	E. lateralis						
Allele	PS	SF	AV	SCI	SB	ST	
LDH 1A	1.0	1.0	1.0	.98	1.0	1.0	
LDH 1B	0	0	0	.02	0	0	
MDH 1A	0	0	0	.02	0	0	
MDH 1B	1.0	1.0	1.0	.98	1.0	1.0	
PGI 1A	1.0	1.0	1.0	.95	1.0	1.0	
PGI 1B	0	0	0	.05	0	0	

TABLE 3. Observed (and expected) genotype frequencies at all polymorphic loci in population samples of *D. vacca* and *E. lateralis*.

	D. vacca						
Genotype	PS	SF	AV	SCI	SB	RE	ST
TO 1AA	8(6)	6 (5)	5 (5)	20 (19)	5 (6)	3 (3)	1 (2)
TO 1AB	19(23)	20(22)	23(22)	13(15)	26(23)	16(16)	18(16)
TO 1BB	23(21)	24(23)	23(24)	4 (3)	19(21)	25(25)	29(30)
Chi-square	.86	.43	.09	.65	.75	0	.78
PGI 2AA	2 (3.5)	3 (4.5)	2 (3)	0 (0)	1 (2)	3 (2)	2 (3)
PGI 2AB	22(19)	24(21)	22(19)	0 (0)	18(16)	13(15)	20(18)
PGI 2BB	25(26.5)	22(24.5)	27(29)	38(38)	31(32)	28(27)	28(29)
Chi-square	1.20	1.18	.94	0	.78	.67	.37

E. lateralis (Santa Cruz Island)					
LDH 1AA	40(40)	PGI 1AA	38(38)	MDH 1AA	0 (0)
LDH 1AB	2 (2)	PGI 1AB	4 (4)	MDH 1AB	2 (2)
LDH 1BB	0 (0)	PGI 1BB	0 (0)	MDH 1BB	40(40)
Chi-square	0		0		0

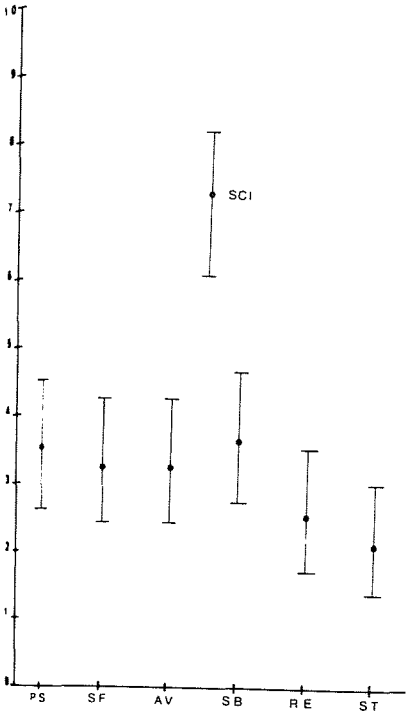

FIGURE 2. *Frequencies (P), with 95 per cent confidence limits, of allele TO-1A in population samples of* D. vacca.

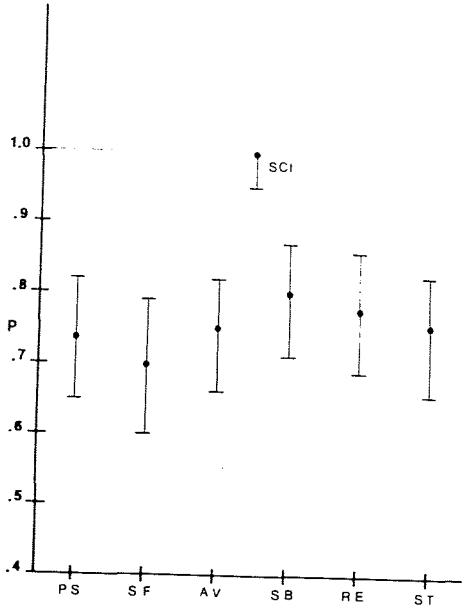

FIGURE 3. *Frequencies (P), with 95 per cent confidence limits, of allele PGI-2B in population samples of* D. vacca.

procedures FACTOR (using principal component and varimax options), SCORE, SCATTER, and MEANS (Barr *et al.* 1976). Canonical variates analysis was done through the use of a stepwise discriminant functions procedure, BMDP program BMDP7M (Dixon 1975).

RESULTS

Enzyme assays for both species produced very even patterns of allele frequencies in all mainland populations. In the striped surfperch all mainland populations were monomorphic for the same allele at all loci examined. In the pile surfperch two loci, TO and PGI-2, were polymorphic and had similar allele frequencies in all mainland populations. Table 2 gives allele frequencies for all observed polymorphic loci in all sampled populations. Table 3 gives genotype frequencies of polymorphic loci in each population. There were no significant deviations from expected Hardy-Weinberg equilibrium genotype frequencies. Figures 2 and 3 display the geographic distributions of allele frequencies at the TO and PGI-2 loci in the pile surfperch.

Both species show evidence of local differentiation in the Santa Cruz Island populations. The pile surfperch population has statistically highly significant ($P<.001$) differences in allele frequencies at the TO and PGI-2 loci. The striped surfperch has three polymorphic loci (MDH-1, LDH-1, and PGI-1) in the Santa Cruz Island population, those being the only

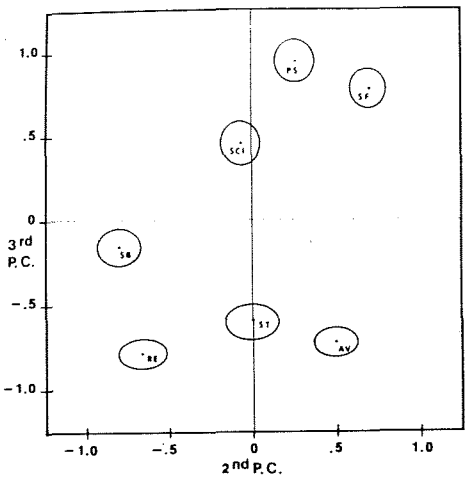

FIGURE 4. *Population samples of* D. vacca *ordinated by second and third principal components of variation of morphometric characters. Ellipses indicate one standard error on either side of sample means.*

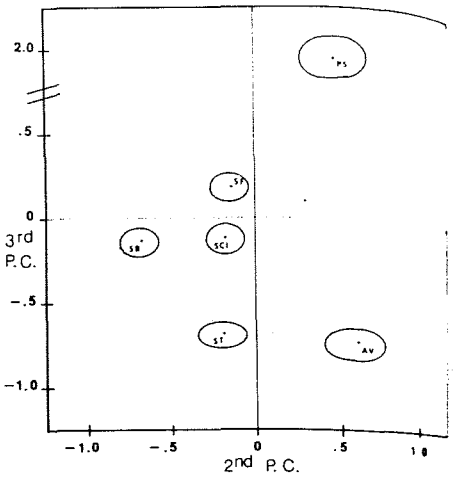

FIGURE 5. *Population samples of* E. lateralis *ordinated by second and third principal components of variation of morphometric characters. Ellipses represent one standard error on either side of sample means.*

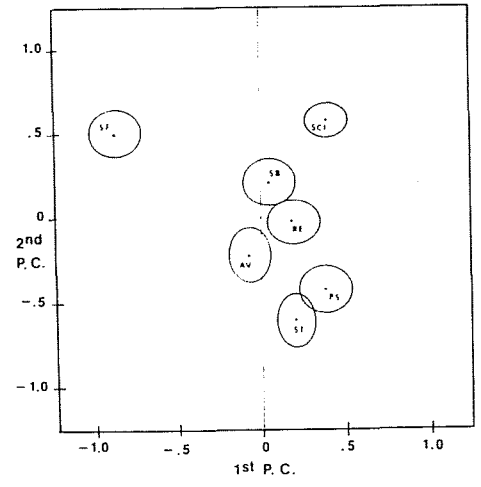

FIGURE 6. *Population samples of* D. vacca *ordinated by second and third principal components of variation of meristic characters.*

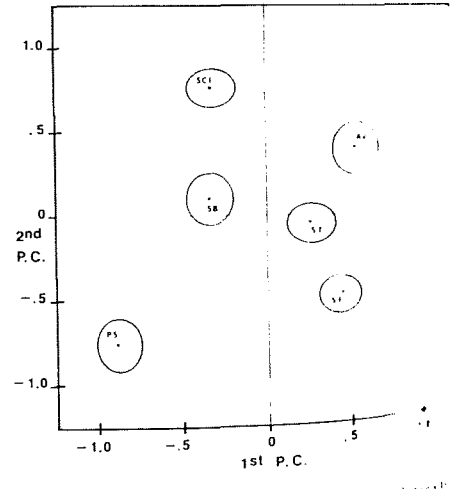

FIGURE 7. *Population samples of* E. lateralis *ordinated by second and third principal components of variation of meristic characters.*

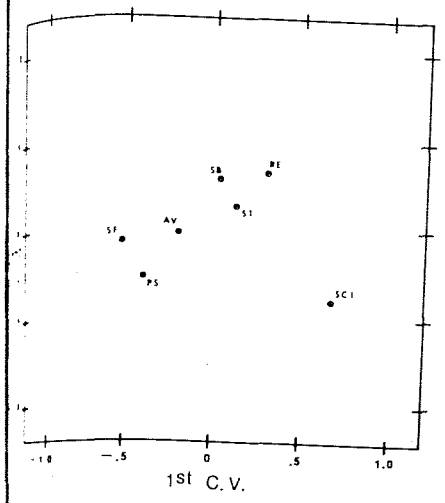

FIGURE 8. *Population samples of* D. vacca *ordinated by first and second canonical variates based on discriminant functions analysis of meristic characters.*

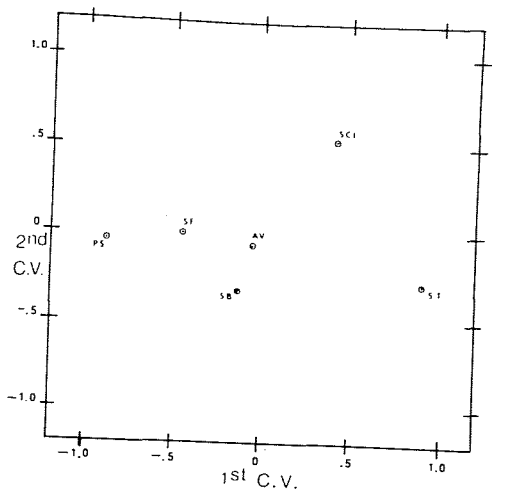

FIGURE 9. *Population samples of* E. lateralis *ordinated by first and second canonical variates based on discriminant functions analysis of meristic characters.*

observed polymorphisms in that species.

Principal components and discriminant functions analyses of the morphometric data produced very similar arrangements of the sampled populations of the two species. Only results of the principal components analyses are therefore shown; the mean values of the scores of each population in the two species on principal components 2 and 3 are plotted in Figures 4 and 5. When analyzing morphometric data, the first principal component represents size variation in the sampled individuals and is not used in determinations of shape differences (Blackith and Reyment 1971).

In *D. vacca* principal components analysis of meristic data produces a loose cluster of six populations with a seventh (San Francisco) well separated. In *E. lateralis* analysis produces a loose cluster of five populations with a sixth (Puget Sound) well separated (Figs. 6 and 7).

The results of discriminant functions analyses of meristic characters are displayed in plots of the populations, ordinated by the first and second canonical variates, in Figures 8 and 9 for *D. vacca* and *E. lateralis*, respectively. For *D. vacca* there is a loose cluster of samples with Santa Cruz Island relatively well separated. For *E. lateralis* the Santa Cruz Island and Santo Tomás populations are the most distinct.

DISCUSSION

The extreme geographic uniformity of allele frequencies in widely separated mainland populations of the study species is surprising, and it emphasizes the divergence of the Santa Cruz Island populations. Tagging studies of adult fish indicate low dispersion in embiotocid species (Morgan 1961, Beardsley 1969, Miller and Geibel 1973), and their reproductive biology almost certainly precludes a pre-adult dispersal stage. Low dispersal and a linear or one-dimensional population structure (the Pacific coastline) create a strong tendency toward local differentiation in theoretical models of population structure (Wright 1943, Kimura and Weiss

1964). Large effective population size is a characteristic that tends to promote geographic uniformity in the same models, and the results of reliable density studies of the two study species by Miller and Geibel (1973) and Ebeling *et al.* (1980) indicate that densities are high enough to produce very large effective population sizes—large enough, indeed, to result in the observed geographical uniformity of mainland populations (Haldorson 1978).

The divergence of the island populations of *D. vacca* and *E. lateralis* must be a result of a severe restriction in gene flow with mainland populations, unless prohibitively high selection coefficients are postulated for the individual gene loci (Haldorson 1973). It seems likely, therefore, that the Channel Islands provide an area of genetic isolation for all embiotocid species found there and that the observed morphologic divergence of *Cymatogaster gracilis* described by Tarp (1952) is a genetic effect.

The two procedures used to test concordance of morphologic and electrophoretic variation differ in their assumptions about the data and may provide different interpretations. Principal components analysis makes no *a priori* assumptions about data subgroups. From correlations among real variables, this procedure computes a new set of hypothetical variables that define the principal axes (components) of a multidimensional ellipse (see Blackith and Reyment 1971 for review). Discriminant functions analysis does make *a priori* identification of sample subgroups and investigates the relationship between them by maximizing between-group differences. Variables are added to this analysis in the order of their diminishing ability to distinguish between subgroups until the point at which the next variable does not significantly improve subgroup separation (Blackith and Reyment 1971).

The Santa Cruz Island populations were not in any way unique on the basis of principal components or discriminant functions analyses of morphometric data. There is strong evidence that the morphometric variation observed in this study is the result of some environmental effect, expressed either through some direct developmental phenotype modification or through local selective adaptation to environmental conditions (Haldorson 1978).

Unlike morphometric data, meristic data produced differing results when analyzed by principal components and discriminant functions procedures. In *D. vacca* the San Francisco sample had the highest mean count in six of the seven meristic characters, and diverged in principal components analysis. Discriminant functions analysis of *D. vacca* meristics produced another loose cluster of six populations with separation of a seventh, in this case the Santa Cruz Island population. This result corresponds closely to the electrophoretic results for *D. vacca*.

In *E. lateralis* the Puget Sound sample had the highest mean count in four of the seven meristic characters; in the other three it had the lowest mean count. The Puget Sound sample also clearly separated from the other samples in principal components analysis. Discriminant functions analysis of meristic data in *E. lateralis* produced a loose cluster of four populations and individual separation of two others, Santo Tomás and Santa Cruz Island. There is electrophoretic evidence that Santa Cruz Island is an isolate for *E. lateralis*, and there is observational evidence that the Santo Tomás population is isolated from the rest of the species distribution (Quast 1968). Thus, in both study species there is evidence that discriminant functions analysis of meristic characters is useful in identification of genetically isolated populations.

CONCLUSIONS

Even though the California Channel Islands lie in close proximity to the mainland, it apparently is not reasonable to assume that Channel Island populations of marine organisms are closely associated with mainland populations through migration and genetic similarity. The present study indicates that even species generally regarded as highly vagile, such as fishes, may be genetically differentiated in island waters. Such differentiation may ultimately result in

island endemic species. The likelihood of island population differentiation is related to the life history and habits of individual species; consequently, species with low dispersal characteristics, such as the embiotocid fishes studied here, are those where island differentiation may be more pronounced. The various fish species found in the waters of the Channel Islands possess a variety of life history characteristics and dispersal capabilities, and undoubtedly the level of genetic differentiation in those species varies accordingly. It would be valuable to obtain estimated levels of differentiation in island populations of species such as the ovoviviparous rockfishes *(Sebastes)*, as well as species with planktonic eggs and larvae.

SUMMARY

Populations of the pile surfperch and the striped surfperch from Santa Cruz Island waters are genetically differentiated from mainland populations at the biochemical level when analyzed by electrophoresis. In the pile surfperch two loci, tetrazolium oxidase and phosphoglucose isomerase, had highly significant differences in allele frequencies between island and mainland populations. The striped surfperch was monomorphic for all examined electrophoretic loci in all mainland populations, but was polymorphic at three loci in the Santa Cruz Island populations. It is unlikely that the observed allele frequency differences could be maintained unless migration from mainland populations is exceedingly low.

The populations were also examined for signs of morphological differentiation. Analyses of morphometric and meristic data provided disparate results. Principal components and discriminant functions analyses of morphometric data in both species produced very similar arrangements of populations and did not reflect the apparent genetic isolation of the Santa Cruz Island populations.

When the meristic data were analyzed by principal components there was no indication of island population differences; however, discriminant functions analyses of the meristic data showed the Santa Cruz Island populations to be the most distinct in each species. Apparently meristic characters may be useful as indicators of population isolation in these species.

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Distribution and Abundance of Seabirds Breeding on the California Channel Islands

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INTRODUCTION

The purpose of this paper is to provide an overview of the distribution, abundance, and history of the seabird populations that have bred or currently breed on the Channel Islands of California. Although adjacent to metropolitan Los Angeles and the subject of a large, albeit fragmentary, literature, the marine avifauna of southern California is surprisingly poorly known. Not only are accurate estimates of population size lacking, but often it is difficult to determine whether certain species were breeding or even present on the islands in the past. The recently completed baseline studies of marine birds and mammals of the Southern California Bight, sponsored by the Bureau of Land Management, have provided the first opportunity for a systematic assessment of marine bird populations in this area.

In this paper we (1) provide an update on the status of seabirds nesting in the Southern California Bight; (2) make comparisons of present-day populations with information on prior populations; (3) attempt to assess when and why populations have changed; and (4) discuss some of the interesting zoogeographical aspects of the southern California marine avifauna. It is not our intention that this paper provide the final or complete review of the literature on the history, ecology, or breeding biology of the species in question. Rather, we are providing a synthesis of the results of more detailed studies to be published in the future.

PAST AND PRESENT STATUS OF SEABIRD POPULATIONS

The breeding marine avifauna of the Southern California Bight is surprisingly diverse; 16 species have been recorded nesting there. Two of these species, the Common Murre (*Uria aalge*) and Tufted Puffin (*Lunda cirrhata*), no longer nest on the Channel Islands. Three other species, the Least Tern (*Sterna albifrons*), Elegant Tern (*Thallasseus elegans*), and possibly the Royal Tern (*T. maximus*), nest or have nested at mainland sites but not among the Channel Islands and will not be discussed here. Five families are represented among the marine birds that breed or have bred in recent historical times in the Bight: three storm petrels (Hydrobatidae), three cormorants (Phalacrocoracidae), one Pelican (Pelecanidae), one gull (Laridae), and five alcids (Alcidae).

As seabirds generally restrict their breeding activities to small, isolated islands, colonies are often crowded with thousands, sometimes millions, of birds. However, seabird populations in southern California are relatively small (Table 1); in total, only about 24,000 pairs of marine birds nest on the Channel Islands. Currently, the largest aggregation of nesting seabirds in southern California occurs on San Miguel Island and its two associated islets, Prince Island and Castle Rock (see Figure 1 for place names), where 14,000 to 15,000 pairs of nine species nest. Santa Barbara Island (3,400 pairs, ten species) and Anacapa Island (3,000 pairs, seven species) support the next largest colonies. Other islands support modest populations—San Nicolas (1,200 pairs), Santa Cruz (950 pairs), Santa Rosa (900 pairs)—or miniscule populations—San

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