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BARRIERS TO GENE FLOW IN *EMBIOTOCA JACKSONI*, A MARINE FISH LACKING A PELAGIC LARVAL STAGE

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Abstract.—Marine species generally show high dispersal capabilities, which should be accompanied by high levels of gene flow and low speciation rates. However, studies that focused on the relationship between dispersal and gene flow in marine fishes have been inconclusive. This study focuses on the black surfperch, *Embiotoca jacksoni*, a temperate reef fish that lacks a pelagic larval stage and lives on almost continuous reefs along the California and Baja California coasts. Mitochondrial control-region sequences from 240 individuals were obtained, and phylogeographic patterns were analyzed. A major phylogeographic break was found at Santa Monica Bay, a sandy expanse that prevents adult dispersal. Deep water separating the southern California Channel Islands was also found to be a major barrier to gene flow. Minor phylogeographic breaks were also detected in the Big Sur/Morro Bay and in the Punta Eugenia/Guerrero Negro regions, but none in the Point Conception region. Gene flow levels in *E. jacksoni* were found to be almost identical to those of another species with limited dispersal, *Acanthochromis polyacanthus*, thus indicating that the lack of a pelagic larval stage combined with barriers to adult dispersal may have had similar effects on these two species.

Key words.—Black surfperch, Embiotocidae, gene flow, larval dispersal, mtDNA.

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Reef fishes tend to live a sedentary life as adults and to be highly mobile as eggs, larvae, or juveniles. In theory, long pelagic larval stages should be associated with high levels of gene flow, thus preventing population structure and ultimately limiting the number of speciation events (Hansen 1980, 1982; Shaklee et al. 1982; Palumbi 1992, 1994). This contrasts with the large number of fish species found on reefs (Shulman 1998). In fact, studies that compared gene flow levels and dispersal capabilities have, for the most part, been inconclusive (Waples 1987; Waples and Rosenblatt 1987; Planes 1993a, 1993b; Doherty et al. 1995; McMillan and Palumbi 1995; Schulman and Bermingham 1995; reviewed in Shulman 1998). However, in *Acanthochromis polyacanthus*, a damselfish species that lacks pelagic larval stage, very strong population structure was found along its range on the Great Barrier Reef in Australia. Indeed, when comparing seven fish species, Doherty et al. (1995) found that the number of migrants per generation in *Acanthochromis* ($Nm = 0.06$) was one to two orders of magnitude less than for any other species studied.

To investigate the relationship between dispersal potential and gene flow in California fish species, we started a study on black surfperch, *Embiotoca jacksoni*, a fish that also lacks a pelagic larval life stage. Our goal was first to determine if results from *Acanthochromis* could apply to *E. jacksoni*. Then we tried to estimate the relative role of several factors that have been considered important in limiting gene flow for populations of marine species (Palumbi 1992, 1994).

The evolutionary mechanisms of gene flow in populations of marine species are influenced by several factors, which are not mutually exclusive: (1) historical factors, such as transient isolation due to tectonics or water level changes (e.g., Avise 1992, 1994; McMillan and Palumbi 1995); (2) dispersal capabilities at the larval or adult stage (e.g., Doherty et al. 1994; Schulman and Bermingham 1995); (3) natural selection (e.g., Bernardi et al. 1993; Powers et al. 1993); and (4) gamete recognition (Metz and Palumbi 1996). All these factors may play a role in allowing marine populations to diverge (Palumbi 1992, 1994).

Historical, oceanographic, and ecological barriers are found along the California and Baja California coasts. Historical breaks may have existed as a result of tectonic events, which considerably changed the shape of the California coast during the past 10 million years, by creating a succession of sea channels and land bridges (Yanev 1980). More recently, Pleistocene glaciating events, which were associated with low sea water levels (up to 200-m changes), may have connected or at least left shallow water between the northern Channel Islands and the mainland, thus making some islands accessible to coastal shallow-water species and possibly creating land bridges (Junger and Johnson 1980; Vedder and Howell 1980). The most salient oceanographic features of the coast are Point Conception and Punta Eugenia. Both these points have been considered regions of faunal breaks because they define many species distribution limits (Briggs 1974). Recently, however, Point Conception has been proposed to be a distribution break only at the species level, but not for populations (Burton 1998). Ecological features along the coast are represented by fragmented habitats characterized by long stretches of rocky shores occasionally separated by sandy habitat (e.g., Pismo Beach, Santa Monica Bay). The presence of submarine canyons such as the Monterey, Hueneme, Redondo, and Scripps Canyons may also have an influence on the dispersal of species restricted to shallow waters.

Genetic approaches, such as DNA sequencing followed by phylogeographic analyses, have proven useful in elucidating population patterns across biogeographic regions (e.g., Avise 1992, 1994; McMillan and Palumbi 1995; Bowen and Grant 1997). Phylogeography has been used in different regions of the world, but the southeastern coastal environment of the United States has, by far, been the most thoroughly studied over the years (reviewed in Avise 1992). In contrast, little has been done along the California coast, where only a few

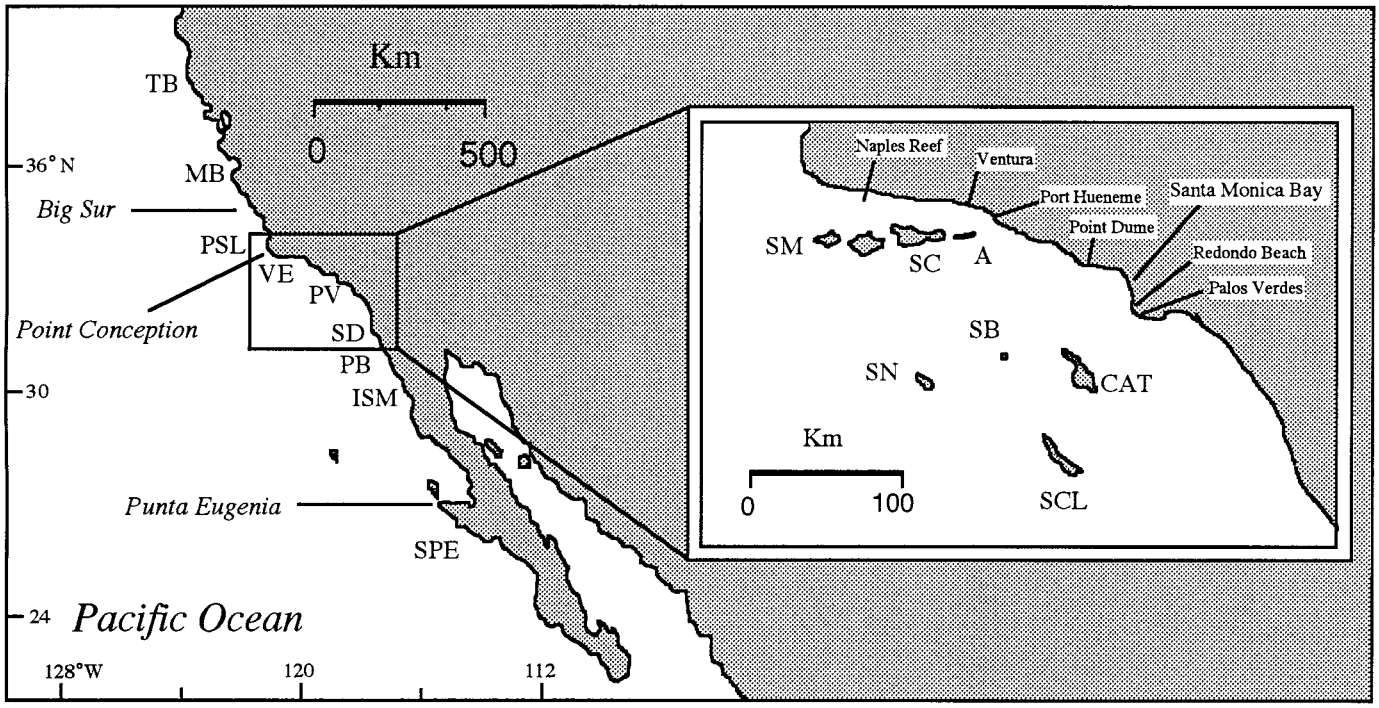

FIG. 1. *Embiotoca jacksoni* sampling locations. Sampling regions are shown on a map of the California and Baja California Coast. Within these regions, samples were collected at the following localities: Tomales Bay for the Tomales Bay region (TB); Santa Cruz, Capitola, and Monterey for the Monterey Bay region (MB); Diablo Canyon and Port San Luis for the Port San Luis region (PSL); Naples Reef, Ventura, Port Hueneme, and Point Dume for the Ventura region (VE); Redondo Beach, Palos Verdes, and Cabrillo Beach for the Palos Verdes region (PV); Point Loma, Mission Bay, and Shelter Island for the San Diego region (SD); Punta Banda, and Isla San Martin for the Punta Banda region (PB); and Bahia Tortuga, Isla San Roque, and Bahia Asuncion for the south of Punta Eugenia region (SPE). Samples were also collected in the Channel Islands as shown in the inset: San Miguel (SM), Santa Cruz (SC), Anacapa (A), San Nicolas (SN), Santa Barbara (SB), Santa Catalina (CAT), and San Clemente (SCL).

studies were done on fish (Davis et al. 1981; Waples 1987), snails (Marko 1998), corals (Hellberg 1996; Beauchamp and Powers 1997), urchins (Palumbi 1995), copepods (Burton and Lee 1994; Burton 1998), and mussels and barnacles (Ford and Mitton 1993; Sarver and Foltz 1993; Van Syoc 1994).

Here, we present a phylogeographic study of black surfperches, *E. jacksoni*, sampled along the California and Baja California coasts. Surfperches (Embiotocidae) possess unique life-history and speciation patterns (Bernardi and Bucciarelli 1999). They give birth to fully developed live young that stay close to their parents (Behrens 1977). Adult black surfperch have very limited dispersal capability and live in restricted territories (Hixon 1981). They live in shallow waters from Fort Bragg, California, to Punta Abreojos, Baja California, including offshore islands such as Guadalupe Island off the coast of Mexico, and the California Channel Islands (Miller and Lea 1972). The presence of black surfperch at these islands is probably due to infrequent drifting across deep-water channels of a few individuals associated with floating debris or drifting kelp mats.

MATERIALS AND METHODS

Samples and DNA Extraction

Two hundred forty individuals were collected by spear while free or scuba diving. Samples were taken from the mainland north to south at: Tomales Bay, Santa Cruz, Capitola, Monterey, Diablo Canyon, Port San Luis, Naples Reef (off Santa Barbara), Ventura, Port Hueneme, Point Dume, Redondo Beach, Palos Verdes, Cabrillo Beach, Mission Bay (San Diego), and Point Loma in the United States and Punta Banda, Isla San Martin, Bahia Tortuga, Bahia Asuncion, and Isla San Roque in Mexico (Fig. 1). Sample numbers per locality are given in Table 1. Sampling localities were grouped into regions, as described in the legend of Figure 1. Samples were also collected from all the Channel Islands except Santa Rosa Island, which lies between San Miguel and Santa Cruz Islands (Fig. 1). Both the north and south shores of Santa Cruz Island were sampled. The genus *Embiotoca* comprises only two species: the black surfperch, *E. jacksoni,* and the striped surfperch, *E. lateralis.* We used the striped surfperch as an outgroup.

Liver tissue was extracted immediately from collected specimens and preserved in 95% ethanol at ambient temperature in the field and then stored at 4°C in the laboratory. Tissues were digested overnight at 55°C in 500 μl of extraction buffer (400 mM NaCl, 10 mM Tris, 2 mM EDTA, 1% SDS). We purified the DNA by standard chloroform extraction and isopropanol precipitation (Sambrook et al. 1989).

PCR and Sequence Analysis

Amplification of the mitochondrial control region (also called the D-loop) was accomplished with universal primers

TABLE 1. Summary of sequence variation within and among populations of *Embiotoca jacksoni*. Number of haplotypes, number of variable sites, and mean sequence divergence were calculated using DNAsp (Rozas and Rozas 1997). Diversity was calculated according to the equation: $h = (1 - \Sigma x_i^2)n/(n - 1)$, where x_i is the frequency of the ith mtDNA type (Nei 1987).

Region name	Locality name	n	Number of mtDNA types	Diversity	No. of variable sites	Mean percent divergence
Mainland and Channel Islands		240	54	0.88	53	1.1
Mainland		152	31	0.81	35	1.1
Tomales Bay	Tomales Bay	10	0	0.00	0	0.0
Monterey Bay		26	5	0.29	6	0.1
	Santa Cruz Harbor	11	3	0.34	3	0.2
	Capitola	1	—	—	—	—
	Monterey	14	3	0.27	3	0.1
Port San Luis		17	6	0.69	9	0.5
	Diablo Canyon	1	—	—	—	—
	Port San Luis	16	6	0.72	9	0.5
Ventura		31	9	0.72	12	0.5
	Naples Reef	7	2	0.28	1	0.1
	Ventura	11	5	0.76	4	0.3
	Port Hueneme	2	—	—	—	—
	Point Dume	11	5	0.84	9	1.0
Palos Verdes		21	8	0.62	10	0.8
	Redondo Beach	11	5	0.62	7	0.8
	Palos Verdes	9	5	0.72	9	0.9
	Cabrillo Beach	1	—	—	—	—
San Diego		22	5	0.47	6	0.3
	Mission Bay	11	3	0.34	5	0.3
	Point Loma	5	3	0.70	3	0.4
	Shelter Island	6	1	0.00	0	0.0
Punta Banda		14	3	0.56	4	0.4
	Punta Banda	12	2	0.41	2	0.2
	Isla San Martin	2	—	—	—	—
South of Punta Eugenia		11	3	0.34	3	0.2
	Bahia Tortugas	1	—	—	—	—
	Bahia Asuncion	1	—	—	—	—
	Isla San Roque	9	2	0.22	1	0.1
Channel Islands		88	25	0.85	36	0.7
Northern Channel Islands		30	10	0.58	12	0.3
	San Miguel	12	5	0.66	4	0.3
	Santa Cruz	11	5	0.61	7	0.4
	Anacapa	7	2	0.28	1	0.1
Middle Islands	Santa Barbara	12	5	0.66	8	0.5
Southern Islands		46	15	0.86	19	0.9
	San Nicolas	13	2	0.38	1	0.1
	Santa Catalina	22	12	0.80	17	0.7
	San Clemente	11	1	0.00	0	0.0

PRO-L and D-Loop described in the literature (Meyer 1993). Each 100 μl reaction contained 10ng to 100 ng of DNA, 10 mM Tris HCL (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$, 2.5 units of *Taq* DNA Polymerase (Perkin-Elmer, Norwalk, CT), 150 μM of each dNTP, and 0.3 mM of each primer and was amplified with a cycling profile of 45 sec at 94°C, 45 sec at 48°C, 1 min at 72°C, for 35 cycles. After purification following the manufacturer's protocol (Applied Biosystems, Inc., Forter City, CA; Perkin-Elmer), sequencing was performed in both directions with the primers used in the PCR amplification on an ABI 373 automated sequencer (Applied Biosystems, Inc.).

We used the computer program Clustal V implemented by Sequence Navigator (Applied Biosystems, Inc.) to align the mitochondrial-control region sequences. Phylogenetic relationships were assessed using the neighbor-joining (uncorrected distances) method (Nei 1987) implemented by the Software package PAUP (vers. 4.0, Swofford 1998). Maximum-parsimony and robustness-of-trees (bootstrapping) methods could not be used on the complete dataset due to prohibitive computer time. Instead, we used the maximum-parsimony method on a subset of our data, which included all the individuals with differing haplotypes. Gene flow (F_{ST}) and haplotype diversity were calculated using the software package DNAsp (Rozas and Rozas 1997) following Hudson et al. (1992). Population structure was evaluated by an analysis of molecular variance (AMOVA; Excoffier et al. 1992) as implemented in Arlequin (vers. 1.1, Schneider et al. 1997). A phylogenetic tree relating populations was constructed using F_{ST} distances obtained with DNAsp (Rozas and Rozas 1997), with the neighbor-joining method (Nei 1987) using the software package PHYLIP (Felsenstein 1989). We used AMOVA to test for significant partitions of total genetic variance (Φ_{CT}) among previously defined regions. The signifi-

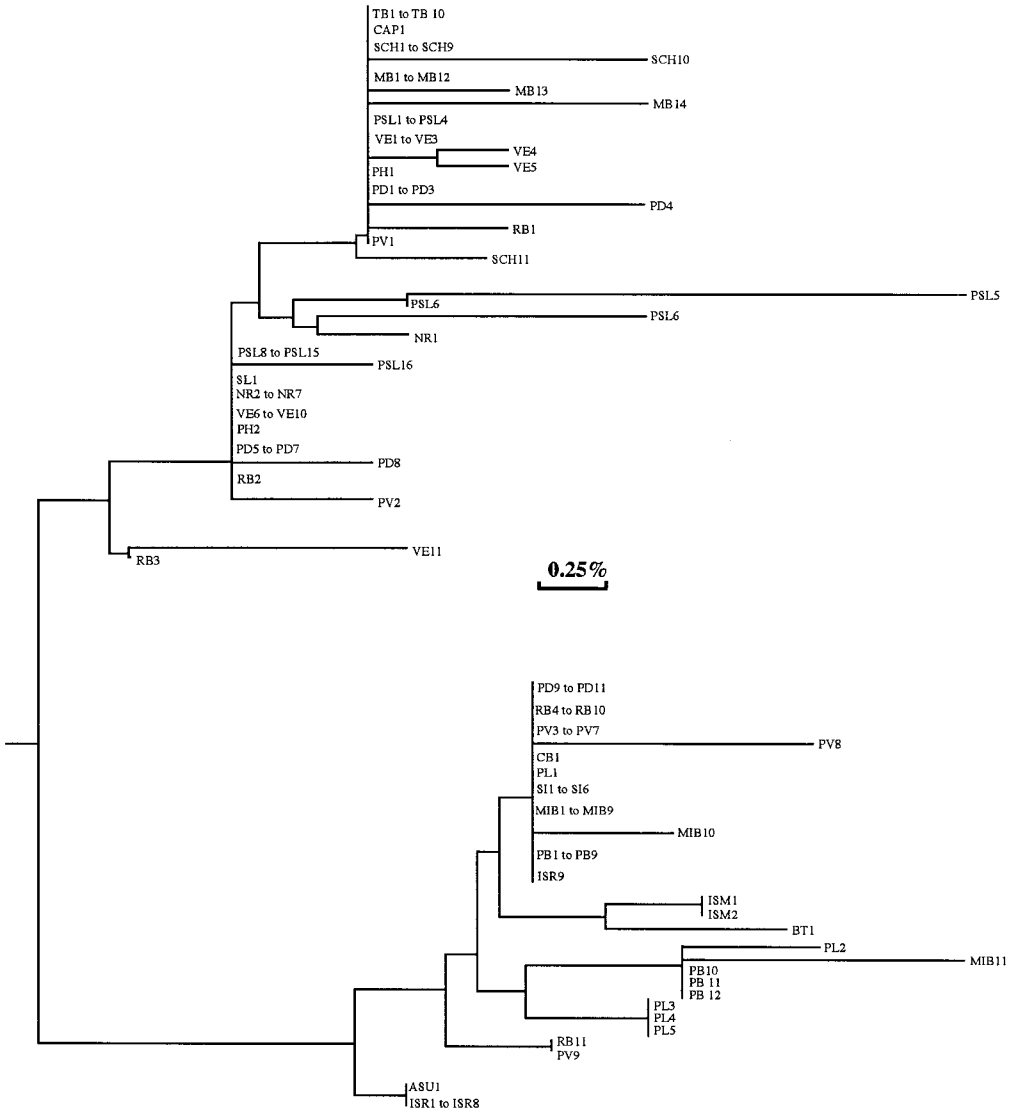

FIG. 2. Phylogenetic relationships between black surfperch samples collected on the mainland. The phylogenetic tree, based on mitochondrial control-region (D-loop) sequences, was obtained using the neighbor-joining method implemented by the software package PAUP (version 4.0). Labels correspond to sampling localities as follows (from north to south): Tomales Bay (TB), Santa Cruz Harbor (SCH), Capitola (CAP), Monterey (MB), Diablo Canyon (SL), Port San Luis (PSL), Naples Reef (off Santa Barbara, NR), Ventura (VE), Port Hueneme (PH), Point Dume (PD), Redondo Beach (RB), Palos Verdes (at Point Vicente, PV), Cabrillo Beach (CB), Point Loma (PL), Shelter Island (SI), Mission Bay (MB), Punta Banda (PB), Isla San Martin (ISM), Bahia Tortuga (BT), Bahia Asuncion (BA), and Isla San Roque (ISR). The length of each branch is proportional to the number of nucleotide substitutions. Scale bar indicates 0.25% sequence divergence. The tree is rooted using *Embiotoca lateralis* as an outgroup.

cance of individual Φ_{CT} statistics was tested by comparison to null distributions constructed from 1000 random permutations of the original data matrix.

RESULTS

Mitochondrial control-region sequences were obtained from all sampled individuals. Alignments included 330 positions, 53 of which were variable and 21 of which were phylogenetically informative. No evidence for size polymorphisms due to repeated sequences or heteroplasmy was found. All individuals from San Clemente Island and San Nicolas Island showed a one base-pair deletion (position 9). No other deletions or insertions were observed. Average pairwise sequence divergences, diversity indices, and haplotype diversity are shown in Table 1. Divergence between the ingroup (*Embiotoca jacksoni*) and the outgroup (*E. lateralis*) was 13.8%. Phylogenetic relationships based on the neighbor-joining and maximum-parsimony methods were very similar; however, the reconstruction based on the maximum-parsimony method yielded over 3000 trees. The analysis of these phylogenetic relationships is described below.

Mainland Individuals

Phylogenetic relationships, based on the neighbor-joining method between individuals sampled along the mainland are shown in Figure 2. Mainland samples partitioned into two

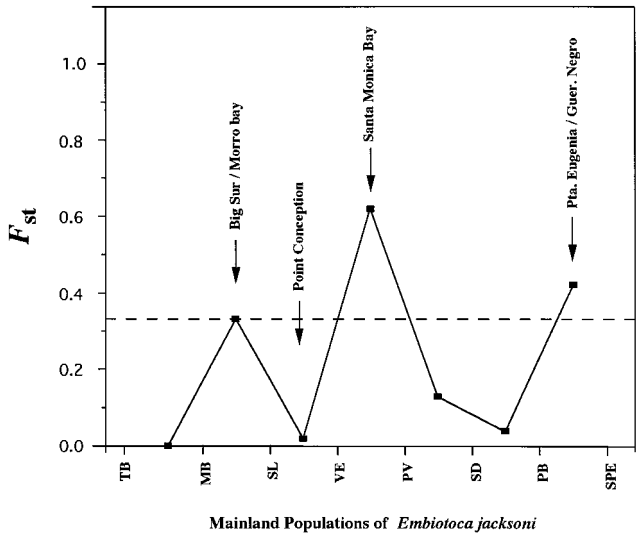

FIG. 3. Pairwise F_{ST} comparisons. F_{ST}-values (vertical axis) were calculated between successive pairs of adjacent populations along the mainland from north to south. Labels are defined in Figure 1. Important phylogeographic features are placed on the graph according to their geographic location. An F_{ST}-value of 0.33, which corresponds to $Nm = 1$ (migrant per generation), is shown as a dashed line.

major clades. This separation was also found in 85% of all the most parsimonious trees. Individuals from these two clades are geographically separated by Santa Monica Bay (Fig. 1). One clade, which we will call ''northern clade,'' comprised all individuals collected north of Point Dume. The second clade, which will be referred to as the ''southern clade,'' comprised all individuals collected south of Palos Verdes. Individuals collected at Point Dume were found predominantly in the northern clade (73%) and in a smaller proportion in the southern clade (27%). Conversely, 36% of Palos Verdes Peninsula individuals grouped in the northern clade and 63% in the southern clade. The northern and southern clades were separated by five fixed differences (1.5% sequence divergence). Population structure, as evidenced by an AMOVA, indicated that 70% of the variance of our samples derived from this separation ($\Phi_{CT} = 0.70$, $P < 0.01$). Gene flow between the regions north and south of Santa Monica Bay was therefore found to be minimal ($F_{ST} = 0.72$, $Nm = 0.2$). Although the sample size is limited, the higher proportion of southern individuals that group with the northern clade as opposed to northern individuals that group with the southern clade indicated a preferentially southbound gene flow (χ^2 test, $P < 0.05$).

Within the northern and the southern major clades, other groupings could be identified from the phylogenetic tree. A plot of F_{ST} and neighboring populations also evidenced these subclades as abrupt discontinuities in gene flow levels (Fig. 3). Within the northern clade, two subclades, geographically separated by the region of Big Sur/Morro Bay could be identified. Individuals from Tomales Bay and Monterey Bay were mostly (97% of individuals) found in one clade, whereas the other clade comprised 71% of individuals collected at Port San Luis, Naples Reef, Ventura, and Point Dume (Fig. 1). Gene flow between these two regions was also found to be limited ($F_{ST} = 0.32$, $Nm = 1.06$).

The southern clade was divided into two clades as well. Individuals from Palos Verdes, San Diego, and Punta Banda were all found in one clade, whereas individuals collected south of Punta Eugenia (Bahia Asuncion, Isla San Roque, and Bahia Tortuga) were all, except one, in the other clade. These two clades were also found in 84% of all the most parsimonious trees. The separation between these two clades was reflected by low levels of gene flow ($F_{ST} = 0.42$, $Nm = 0.68$; Table 2, Fig. 3).

The barriers to gene flow described above define phylogeographic provinces for black surfperch. Gene flow within these provinces was found to be high. While the average F_{ST} across phylogeographic boundaries was 0.42 ($Nm = 0.68$), the average F_{ST} within provinces was 0.05 ($Nm = 9.14$) (Fig. 3). These results are consistent with Waples's (1987) allozyme study on *E. jacksoni*, where no evidence for population structure was found. Doherty et al. (1995) interpreted this lack of population structure as evidence that adults and juveniles may be able to migrate along the California coast. In fact, *E. jacksoni* samples in Waples's study were mostly collected in the Southern California Bight (which is within our southern phylogeographic province), where we could also find little population structure. Our results show that gene flow and dispersal are mainly restricted across very definite barriers, but not within phylogeographic provinces.

Channel Island Individuals

Phylogenetic relationships between individuals sampled in the Channel Islands were superimposed with a map of the islands, as shown in Figure 4. Mitochondrial control-region sequences from individuals taken from the clustered northern Channel Islands (San Miguel, Santa Cruz, and Anacapa) showed a remarkable homogeneity (average pairwise divergence was 0.3%, haplotype diversity was 0.58; Table 1). The northern and southern shores of the northern Channel Islands show striking differences in habitat conditions. To determine if there were genetic differences between these sites, black surfperch samples were collected off the northern and southern shores of Santa Cruz Island. Burton (1998) has shown that copepods collected on the northern and southern sides of Santa Cruz Island presented genetic differences. Black surfperch samples did not reflect this separation (not shown). In fact, individuals from the northern islands were all included in a single clade (Fig. 4). One dominant haplotype was shared by 65% of individuals from all northern islands. Gene flow within the northern Channel Islands group was therefore found to be high (average $F_{ST} = 0.05$, $Nm = 39.1$, Table 2). In contrast, individuals collected from the more isolated southern islands (San Nicolas, Santa Catalina, and San Clemente) showed high levels of haplotype diversity (0.86) and grouped in two well-separated clades (average pairwise distance was 0.97%). Individuals from the offshore San Clemente and San Nicolas Islands grouped together, whereas individuals from the inshore Santa Catalina Island grouped in a distinct clade. No haplotypes were shared between these two clades, resulting in very low levels of gene flow ($F_{ST} = 0.59$; $Nm = 0.32$). Although San Nicolas and

TABLE 2. Gene flow among *Embiotoca jacksoni* populations. Pairwise comparisons of geographic regions are represented by values of F_{ST} (below diagonal) and *Nm* (above diagonal). Panel A corresponds to mainland regions, panel B corresponds to Channel Island populations. Region labels are described in Figure 1. Regions labeled NCI and SCI in panel A correspond to individuals from the northern Channel Islands (San Miguel, Santa Cruz, Anacapa) and the southern Channel Islands (Santa Catalina, San Nicolas, San Clemente), respectively. Values were calculated using DNAsp (Rozas and Rozas 1997).

(A)

	TB	MB	SL	VE	PV	SD	PB	SPE	NCI	SCI
TB		undef.	0.78	0.91	0.17	0.04	0.06	0.03	0.24	0.28
MB	0.00		1.00	1.16	0.20	0.06	0.06	0.06	0.36	0.33
SL	0.39	0.33		26.45	0.71	0.12	0.12	0.14	6.10	0.68
VE	0.35	0.30	0.02		0.30	0.09	0.08	0.19	5.31	0.86
PV	0.74	0.71	0.41	0.62		3.28	2.90	1.58	0.32	0.50
SD	0.93	0.89	0.80	0.85	0.13		12.03	0.59	0.10	0.22
PB	0.90	0.90	0.81	0.86	0.15	0.04		0.68	0.12	0.24
SPE	0.94	0.90	0.78	0.72	0.24	0.46	0.42		0.11	0.27
NCI	0.67	0.58	0.07	0.08	0.61	0.84	0.81	0.82		0.64
SCI	0.64	0.60	0.42	0.37	0.50	0.70	0.67	0.65	0.44	

(B)

	SM	SC	AN	SB	CAT	SCL	SN
SM		9.14	6.57	7.20	0.41	0.12	0.16
SC	0.05		23.43	7.42	0.49	0.18	0.22
AN	0.07	0.02		5.79	0.35	0.04	0.08
SB	0.06	0.06	0.08		0.68	0.42	0.49
CAT	0.55	0.50	0.59	0.42		0.32	0.38
SCL	0.80	0.74	0.93	0.54	0.61		2.50
SN	0.75	0.69	0.86	0.51	0.57	0.17	

San Clemente Islands were remarkably homogeneous (genetic diversity was 0.38 and 0.00, respectively), Santa Catalina Island showed the highest diversity of all sampled populations (0.80). In addition, one individual from Santa Catalina did not group with the other individuals sampled from this island (see discussion below).

The smallest of the Channel Islands, Santa Barbara Island, which lies between the northern and the southern group, did not show any unique haplotypes. Rather, it was a composite of northern Channel Islands (75%) and southern Channel Islands (25%) haplotypes, as shown in Figure 4.

Relationships between Mainland and Island Populations

Phylogenetic relationships of all individuals sampled are presented in Figure 5. Although the phylogenies of mainland and island individuals described separately above remained unchanged, relationships between mainland and island individuals were elucidated. As a whole, the Channel Islands individuals cluster with samples collected north of Santa Monica Bay (northern clade). The northern Channel Islands were found to cluster with individuals collected in the region that is geographically closest (Ventura–Port Huenem–Point Dume region). These islands have historically been in close contact, through a land bridge or through shallow water, with the adjacent mainland to the north, thus explaining the observed high level of gene flow between northern Channel Islands and the Ventura region (Junger and Johnson 1980; Vedder and Howell 1980).

Unexpectedly, individuals from the southern channel islands did not cluster with individuals from the mainland closest to them (Palos Verdes–San Diego region), but grouped with the northern clade as shown in Figure 5. Only one individual from Santa Catalina Island that does not cluster with the other Catalina individuals, CAT22, grouped with the southern clade.

DISCUSSION

Mainland Barriers to Gene Flow

Santa Monica Bay

The separation between the northern and southern clade at Santa Monica Bay was surprising, as it has never before been recognized as a phylogeographic barrier. To pinpoint the actual region of the break, we tried to collect samples as close to Santa Monica Bay as possible. Santa Monica Bay is an approximately 40-km long sandy beach that is flanked by rocky outcrops starting in Malibu to the north and Redondo Beach to the south. We were not able to find samples in Malibu, although black surfperch are occasionally caught there. The closest site to the north of the bay where black surfperch were collected was at Point Dume, which is approximately 30 km north of Malibu. For the southern end of the bay, samples were collected at the first rock/sand interface in Redondo Beach, which defines the southern end of Santa Monica Bay. Thus, Santa Monica Bay is likely to be the actual center of the phylogeographic break. Several factors may explain the phylogeographic break observed at Santa Monica Bay.

Historical.—The northern Channel Islands may have been connected to the mainland during the last glaciation. This land bridge may have been an effective barrier to gene flow, whose effects would still be observed today. Although possible, this explanation is weak because the very existence of the land bridge has been questioned (Junger and Johnson 1980; Vedder and Howell 1980). Furthermore, the connecting point between the land bridge and mainland is located north

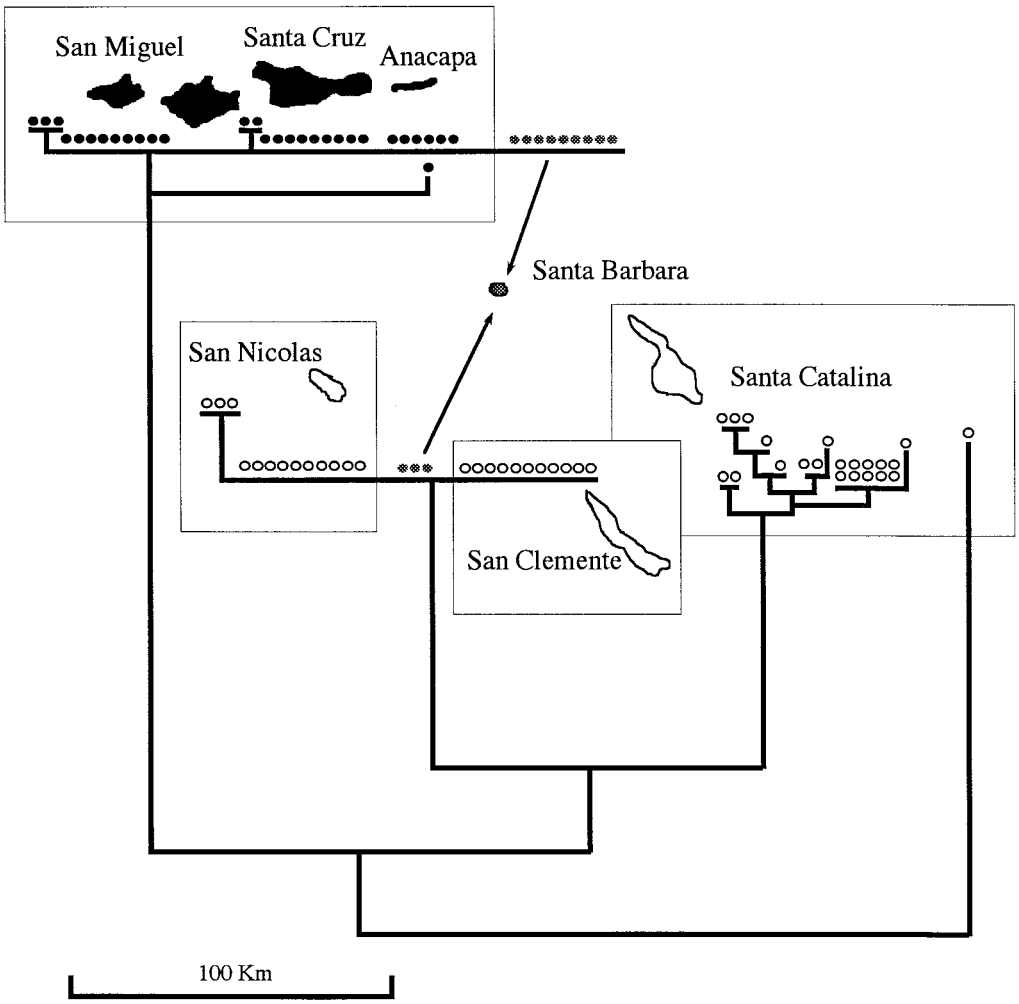

FIG. 4. Superimposed map of the California Channel Islands and a simplified (polymorphisms were removed) neighbor-joining phylogenetic tree of the corresponding island populations of black surfperch (*Embiotoca jacksoni*). Each sample is represented by a circle. Black circles represent individuals from the northern Channel Islands, open circles represent individuals from the southern islands, and gray circles represent individuals sampled in Santa Barbara Island. Samples from Santa Barbara Island were found clustered with northern Channel Islands (nine individuals) and with San Nicolas/San Clemente Island individuals (three individuals). One individual from Santa Catalina Island clustered with mainland individuals (see Results section). Santa Rosa Island (which is located between San Miguel and Santa Cruz) was not sampled.

of Santa Monica Bay (in the Port Hueneme area, Fig. 1). Finally, it is surprising that subsequent gene flow would not have obliterated this signal.

Natural selection.—Water temperature in the Southern California Bight is warmer than in central and northern California. This difference in temperature may result in selective pressure and eventually population divergence, which in turn is reflected in D-loop sequences. Although this explanation is possible, no sharp difference in temperature coincides with the Santa Monica Bay region, making this scenario very unlikely.

Geography and ecology.—Santa Monica Bay has a combination of two geographical features that are not compatible with black surfperch ecological requirements. Santa Monica Bay is a long expanse of sand, which is bordered to the south by an underwater deep canyon (Redondo Canyon). Black surfperch are tightly linked with rocky habitat and only live in shallow water (between 5 and 40 m in depth; Miller and Lea 1972). When crossing sandy habitats, black surfperch are exposed to predators and lack essential food resources. Thus, we think that Santa Monica Bay may be an effective ecological barrier to black surfperch dispersal. It is also important to note that this barrier may be reinforced by other sandy regions located north of Point Dume and south of the Palos Verdes Peninsula, which may explain the complete absence of northern and southern haplotypes in the San Diego and Ventura samples, respectively.

Point Conception

Phylogeographic studies of the Point Conception oceanographic break have focused on fish and invertebrate species primarily using allozymes (e.g., Davis et al. 1981; Rosenblatt and Waples 1986; Waples and Rosenblatt 1987; Hellberg 1995, 1996; Edmands et al. 1996) and more recently nuclear and mitochondrial DNA molecular markers (Burton and Lee

FIG. 5. Phylogenetic relationships between all black surfperch samples. Labels and methods are described in the caption of Figures 1 and 2. The length of each branch is proportional to the number of nucleotide substitutions. Scale bar indicates 0.25% sequence divergence. The tree is rooted using *Embiotoca lateralis.*

1994; Edmands et al. 1996). In a critical examination of all the data available, Burton (1998) concluded that Point Conception should not be regarded as a population phylogeographic break. Our data concur with this view because they show that Point Conception does not limit gene flow in black surfperch. In fact, gene flow between Port San Luis and Ventura, the two regions adjacent to Point Conception, is among the highest observed in this study (F_{ST} = 0.02, Nm = 26.4; Table 2, Fig. 3).

Big Sur/Morro Bay region

As presented above, the mainland northern clade was subdivided into two clades. One clade included samples collected in the Monterey Bay and Tomales Bay, whereas the other clade included samples collected south of Diablo Canyon. The rocky coast of Big Sur and the sandy Morro Bay are found between these two regions. Black surfperch are common along the Big Sur coast, but are absent from Morro Bay. Morro Bay is a fairly small area of approximately 15 km of sandy shoreline. More work is needed to determine if such a small ecological barrier is indeed responsible for the observed disruption of gene flow.

Punta Eugenia/Guerrero Negro region

Our data indicate that there is gene flow limitation between populations from Punta Banda and populations south of Punta Eugenia (F_{ST} = 0.42, Nm = 0.68; Table 2, Fig. 3). It is tempting to propose that this phylogeographic break coincides with the Punta Eugenia biogeographic boundary. Studies have shown that Punta Eugenia is a biogeographic barrier (Briggs 1974), but genetic studies have seldom been conducted there. Preliminary data on three other fish species, the California killifish *Fundulus parvipinnis* (G. Bernardi and D. Talley, unpubl. data), the opaleye *Girella nigricans* (Terry et al. 2000), and the longjaw mudsucker *Gillichthys mirabilis* (D. Huang and G. Bernardi, unpubl. data), also indicate that gene flow is restricted in regions neighboring Punta Eugenia. However, our black surfperch sampling was limited due to the rarity of the species in this region (southern distribution limit). It is possible that the phylogeographic break is elsewhere along the northern Baja California coast. For instance, the Guerrero Negro/San Quintin area, which is north of Punta Eugenia, is a region where no black surfperch habitat is available. It is possible that the real barrier to gene flow is not a region of transition in oceanographic patterns (Punta Eugenia), but rather a habitat barrier that is coincidentally adjacent to Punta Eugenia.

Islands Populations

Deep water as effective barriers to gene flow

Islands have been shown to be a source of population separation for terrestrial animals (e.g., Gilbert et al. 1990; Edwards 1993; Thorpe et al. 1993; Clarke et al. 1996; Grant and Grant 1996; Juan et al. 1998). In the case of fish species, islands may become the source of geographical isolation when the animals are either restricted to freshwater, as in Hawaiian gobies (Chubb et al. 1998), or restricted to shallow water and the islands are separated by deep water, as was observed in black surfperch.

The California Channel Islands comprise three groups of islands. The first group in the north includes four islands, San Miguel, Santa Rosa, Santa Cruz, and Anacapa, which are clustered and separated from each other by narrow, shallow-water channels. The second group in the south comprises three islands, San Nicolas, San Clemente, and Santa Catalina, which are separated from each other and from the northern group by wide and deep-water channels. The third group comprises several small islets and rocks generically called Santa Barbara Island. It is centrally located halfway between the two previous groups and is separated from them by deep water.

Northern Channel Islands are separated from each other by relatively shallow water with the majority of the shelf being shallower than 50 m and only a few points between the islands reaching 100 m in depth. In contrast, the shallowest point between any of the southern islands is approximately 800 m deep. Thus, the sharing of haplotypes among northern islands individuals, accompanied by the complete separation of haplotypes among southern island individuals, is consistent with the hypothesis that deep water is an effective barrier to gene flow for black surfperches. Indeed, black surfperch are probably able to migrate between the different northern islands, whereas the only way to access the southern islands is by rafting in association with floating debris while avoiding predation. Considering the geographic distance between the southern islands (Fig. 4), the frequency of migration events must be fairly low. This is consistent with previous fish collection efforts that have failed to detect the presence of black surfperch from rafting giant kelp (*Macrocystis pyrifera*) (Mitchell and Hunter 1970; Kingsford 1995). However, genetic indirect evidence of migration is given by one individual collected in Catalina Island (CAT22, Fig. 4), which shows a haplotype that is characteristic of the adjacent mainland, and by individuals collected in Santa Barbara Island, which share haplotypes with individuals from other Channel Islands.

Santa Barbara Island

Haplotypes from Santa Barbara Island individuals were related to the northern haplotypes in 75% of the cases and related to the southern (San Clemente Island) haplotypes in 25% of the cases. Although the small sample size may have an effect on these data, the higher proportion of haplotypes that originated from the northern group is consistent with the general current pattern of the region, which tend to flow southward between these islands (Hickey 1992). The absence of unique haplotypes on the island may be due to regular sweeping events that displace local populations. Because the island is very small, the local population of black surfperch may be prone to replacement.

Rare Migrations and Founder Effects

The complete separation of haplotypes between southern islands indicates very low levels of migration between them (Edwards 1993). However, migration must have occurred at a higher frequency within the southern islands group than

between northern and southern islands because individuals from the southern islands are phylogenetically more closely related to each other than they are to the northern island individuals (Fig. 4). On average, individuals from different southern islands showed a sequence divergence that ranged between 0.6% and 0.9%. When using the widest range of generally accepted mitochondrial control-region molecular clock rates (20%/million years to 8%/million years; Bowen and Grant 1997) to estimate the time of separation between these populations, we found that the isolation time of the southern islands ranges approximately between 30,000 to 110,000 years. If such rare migratory events reflect the main mechanism for island colonization, one would expect few haplotypes to be present in each island due to founder effects (Edwards 1993). This expectation correlates well with our observation in the southern islands of San Nicolas and San Clemente, which exhibit very small heterogeneity values (0.38 and 0.00, respectively, Table 1.). Yet, whereas San Nicolas and San Clemente exhibit such low diversity values, Santa Catalina has the highest diversity encountered (0.94). This puzzling result may be due to a difference in population size between islands, a higher frequency of colonization, or to a higher level of diversification on the island itself. It is also possible that some islands are subjected to wide fluctuations in population sizes. It has been suggested that surfperch populations experience repeated severe bottlenecks due to changes in water temperature, which would reduce their diversity (Holbrook et al. 1997). An alternative hypothesis is that migration did not occur from the mainland to the islands, but rather that gene flow is directed from the islands toward the mainland. Although this may seem unlikely, the high haplotype diversity found on Santa Catalina Island and the basal position of the Southern Channel Island individuals in the tree presented in Figure 5 are consistent with this hypothesis. Further work will be needed to separate these hypotheses.

Limited Dispersal and Restricted Gene Flow

Black surfperch, *E. jacksoni,* and *A. polyacanthus* have similar limited dispersal capabilities, as well as similar habitat ranges of approximately 2000 km of coastline. Unfortunately, data on population size for *A. polyacanthus* and *E. jacksoni* are scarce, and no realistic estimates are available at the moment. Yet, gene flow levels in these two species are strikingly similar. Doherty et al. (1995), using allozyme data, found that F_{ST}-values within groups in the north and in the south of the Great Barrier Reef averaged approximately 0.17. Black surfperch within-groups F_{ST} averaged 0.21. When comparing the northern and the southern group, *Acanthochromis* showed an F_{ST}-value of 0.79, which is very similar to the 0.70 value found in *E. jacksoni.*

The patchy nature of the Great Barrier Reef was shown to prevent adult migration in *Acanthochromis* (Doherty et al. 1994 1995; Planes and Doherty 1997a,b). The limited gene flow observed in *Acanthochromis* was proposed to be due to a conjunction of lack of adult migration and lack of larval dispersal (Doherty et al. 1995). In *E. jacksoni,* gene flow was found to be minimal in regions were adult migration was reduced, such as across Santa Monica Bay or across deep water between southern Channel Islands. Thus, restricted adult migration seems to be the common mechanism that reduces gene flow in both *Acanthochromis* and in *E. jacksoni.* Taken together, these results may indicate that similar ecological lifestyles may be accompanied by similar levels of gene flow.

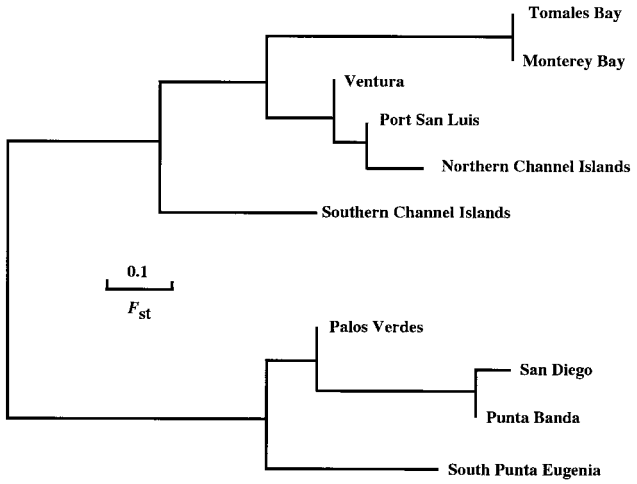

FIG. 6. Phylogenetic tree of *Embiotoca jacksoni* populations based on F_{ST}-distances calculated with DNAsp (Rozas and Rozas 1997) and shown in Table 2. The phylogenetic reconstruction was performed with the neighbor-joining method using PHYLIP (Felsenstein 1989). The bar indicates an F_{ST}-distance of 0.1.

Conclusion

Black surfperch, a live-bearing species that lacks a pelagic larval stage, was shown to exhibit limited levels of gene flow and strong population structure. Results on population structure are best summarized by deriving a tree from F_{ST}-distances as shown in Figure 6. This population tree underscores the main separation of *E. jacksoni* in two distinct northern and southern clades that are geographically divided by the Santa Monica Bay region. Recently, Avise and Walker (1999) have shown that 56% of all vertebrate species surveyed (252 species) also separated in two matrilineal phylogroups that, for the most part (96%), coincided with geographical partitioning as well. Thus, in a general context, our results can be seen as an example of deep (1.5% sequence divergence) phylogeographic separation of previously unrecognized populations. However, marine fish populations rarely follow the intuitive relationship between dispersal capability and gene flow levels. In our case, *E. jacksoni* follows the same pattern found in another fish that lacks pelagic larval stage, *A. polyacanthus.* Future work on species that share these same ecological characteristics will determine if these results can be generalized.

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Literature Cited

Avise, J. C. 1992. Molecular population structure and biogeographic history of a regional fauna: a case history with lessons for conservative biology. Oikos 63:62–76.

———. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York.

Avise, J. C., and D. E. Walker. 1999. Species realities and numbers in sexual vertebrates: Perspectives from an asexually transmitted genome. Proc. Natl. Acad. Sci. USA. 96:992–995.

Beauchamp, K. A., and D. A. Powers. 1997. Sequence variation of the first internal spacer (ITS-1) of ribosomal DNA in ahermatypic corals from California. Mol. Mar. Biol. Biotechnol. 5: 357–362.

Behrens, D. W. 1977. Fecundity and reproduction of the viviparous perches *Hypsurus caryi* (Agassiz) and *Embiotoca jacksoni* (Agassiz). Calif. Fish and Game. 63:234–252.

Bernardi, G., and G. Bucciarelli. 1999. Molecular phylogeny and speciation of the surfperches (Embiotocidae, Perciformes). Mol. Phyl. Evol. 13:77–81.

Bernardi, G., P. Sordino, and D. A. Powers. 1993. Concordant mitochondrial and nuclear DNA phylogenies for the populations of the teleost fish *Fundulus heteroclitus.* Proc. Natl. Acad. Sci. USA 90:9271–9274.

Bowen, B. W., and W. S. Grant. 1997. Phylogeography of the sardines (*Sardinops* spp.): assessing biogeographic models and population histories in temperate upwelling zones. Evolution 51: 1601–1610.

Briggs, J. C. 1974. Marine zoogeography. McGraw-Hill, New York.

Burton, R. S. 1998. Intraspecific phylogeography across the Point Conception biogeographic boundary. Evolution 52:734–745.

Burton, R. S., and B.-N. Lee. 1994. Nuclear and mitochondrial gene genealogies and allozyme polymorphism across a major phylogeographic break in the copepod *Tigriopus californicus.* Proc. Natl. Acad. Sci. USA 91:5197–5201.

Chubb, A. L., R. M. Zink, and J. M. Fitzsimmons. 1998. Patterns of mtDNA variation in Hawaiian freshwater fishes: the phylogeographic consequences of amphidromy. J. Hered. 89:8–16.

Clarke, B., M. S. Johnson, and J. Murray. 1996. Clines in the genetic distance of island land snails: how molecular leakage mislead us about speciation. Phil. Trans. R. Soc. Lond. Ser. B. 351: 773–784.

Davis, B. J., E. E. DeMartini, and K. McGee. 1981. Gene flow among populations of a teleost (painted greenling, *Oxylebius pictus*) from Puget Sound to Southern California. Mar. Biol. 65: 17–23.

Doherty, P. J., P. Mather, and S. Planes. 1994. *Acanthochromis polyacanthus,* a fish lacking larval dispersal has genetically differentiated populations at local and regional scales on the Great Barrier Reef. Mar. Biol. 121:11–21.

Doherty, P. J., S. Planes, and P. Mather. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier Reef. Ecology 76:2373–2391.

Edmands, S., P. E. Moberg, and R. S. Burton. 1996. Allozyme and mitochondrial DNA evidence of population subdivision in the purple sea urchin *Strongylocentrotus purpuratus.* Mar. Biol. 126: 443–450.

Edwards, S. V. 1993. Mitochondrial gene genealogy and gene flow among islands and mainland populations of a sedentary songbird, the grey-crowned babbler (*Pomatostomus temporalis*). Evolution 47:1118–1137.

Excoffier, L., P. E. Smouse, and J. M. Quattro. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491.

Felsenstein, J. 1989. PHYLIP. Vers. 3.4. University Herbarium, University of California, Berkeley, CA.

Ford, M. J., and J. B. Mitton. 1993. Population structure of the pink barnacle, *Tetraclita squamosa rubescens,* along the California coast. Mol. Mar. Biol. Biotechnol. 2:147–153.

Gilbert, D. A., N. Lehman, S. J. O'Brien, and R. K. Wayne. 1990. Genetic fingerprinting reflects population differentiation in the California Channel-Island fox. Nature 344:764–767.

Grant, P. R., and B. R. Grant. 1996. Speciation and hybridization in island birds. Phil. Trans. R. Soc. Lond. Series B. 351:765–772.

Hansen, T. A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. Paleobiology 6:193–207.

———. 1982. Modes of larval development in early Tertiary neogastropods. Paleobiology 8:367–377.

Hellberg, M. E. 1995. Stepping-stone gene flow in the solitary coral *Balanophyllia elegans*: equilibrium and nonequilibrium at different spatial scales. Mar. Biol. 123:573–581.

———. 1996. Dependence of gene flow on geographic distance in two solitary corals with different larval dispersal capabilities. Evolution 50:1167–1175.

Hickey, B. M. 1992. Circulation over the Santa Monica San Pedro Basin and Shelf. Prog. Oceanog. 30:37–115.

Hixon, M. 1981. An experimental analysis of territoriality in the California reef fish *Embiotoca jacksoni* Embiotocidae. Copeia 1981:653–665.

Holbrook, S. J., R. J. Schmitt, and J. S. Stephens. 1997. Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecol. Appl. 7:1299–1310.

Hudson, R. R., M. Slatkin, and W. P. Maddison. 1992. Estimation of levels of gene flow from DNA sequence data. Genetics 132: 583–589.

Juan, C., K. M. Ibrahim, P. Oromi, and G. M. Hewitt. 1998. The phylogeography of the darkling beetle, *Hegeter politus,* in eastern Canary Islands. Proc. R. Soc. Lond. B 265:135–140.

Junger, A., and D. L. Johnson. 1980. Was there a quaternary land bridge to the northern channel isalnds? Pp.33–39 *in* Dennis M. Power, ed. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Kingsford, M. J. 1995. Drift algae: a contribution to near-shore habitat complexity in the pelagic environment and an attractant for fish. Mar. Ecol. Prog. Ser. 116:297–301.

Marko, P. B. 1998. Historical allopatry and the biogeography of speciation in the prosobranch snail genus Nucella. Evolution 52: 757–774.

McMillan, W. O., and S. R. Palumbi. 1995. Concordant evolutionary patterns among Indo-West Pacific butterfly fishes. Proc. R. Soc. Lond. B. 260:229–236.

Metz, E. C., and S. R. Palumbi. 1996. Positive selection and sequence rearrangements generate extensive polymorphism in the gamete recognition protein bindin. Mol. Biol. Evol. 13:397–406.

Meyer, A. 1993. Evolution of mitochondrial DNA in fishes. Pp. 1–38 *in* P. W. Hochachka and T. P. Mommsen, eds. Biochemistry and molecular biology of fishes. Vol. 2. Molecular biology frontiers. Elsevier, Amsterdam, The Netherlands.

Miller, D. J., and R. N. Lea. 1972. Guide to coastal marine fishes of California. Fish Bulletin no. 157. Department of Fish and Game, Oakland, CA.

Mitchell, C. T., and J. R. Hunter. 1970. Fishes associated with drifting kelp, *Macrocystis pyrifera,* off the coast of southern California and northern Baja California. Calif. Fish Game 56: 288–297.

Nei, M. 1987. Molecular evolutionary genetics. Columbia Univ. Press, New York.

Palumbi, S. R. 1992. Marine speciation on a small planet. Trends. Ecol. Evol. 7:114–118.

———. 1994. Genetic divergence, reproductive isolation, and marine speciation. Annu. Rev. Ecol. Syst. 25:547–572.

———. 1995. Using genetics as an indirect estimator of larval dispersal. Pp. 369–387 *in* L. R. McEdward, ed. Ecology of marine invertebrate larvae. CRC Press, Boca Raton, FL.

Planes, S. 1993a. Genetic structure of *Dascyllus aruanus* populations in French Polynesia. Mar. Biol. 117:665–675.

———. 1993b. Genetic differentiation in relation to restricted larval dispersal of the convict surgeonfish *Acanthurus triostegus* in French Polynesia. Mar. Ecol.Pr. Ser. 98:237–246.

Planes, S., and P. J. Doherty. 1997a. Genetic relationships of the colour morphs of *Acanthochromis polyacanthus* (Pomacentridae) on the northern Great Barrier Reef. Mar. Biol. 130:109–117.

———. 1997b. Genetic and color interactions at a contact zone of *Acanthochromis polyacanthus*: a marine fish lacking pelagic larvae. Evolution 51:1232–1243.

Planes, S., R. Galzin, and F. Bonhomme. 1996. A genetic metapopulation model for reef fishes in oceanic islands: the case of the surgeonfish, *Acanthurus triostegus.* J. Evol. Biol. 9:103–117.

Powers, D. A., M. Smith., I. Gonzalez-Villasenor, L. DiMichele, D. Crawford, G. Bernardi, and T. Lauerman. 1993. A multidisciplinary approach to the selectionist/neutralist controversy using the model teleost *Fundulus heteroclitus.* Pp. 43–107 *in* D. Futuyma and J. Antonovics, eds. Oxford surveys in evolutionary biology. Vol. 9. Oxford University Press, New York.

Rosenblatt, R. H., and R. S. Waples. 1986. A genetic comparison of allopatric populations of shore fish species from the eastern and Central Pacific Ocean: dispersal or vicariance? Copeia 1986: 275–284.

Rozas, J., and R. Rozas. 1997. DnaSP version 2.0: a novel software package for extensive molecular population genetics analysis. CABIOS 13:307–311.

Sambrook, J., E. F. Fritsch, and T. Maniatis. 1989. Molecular cloning: a laboratory manual. 2d ed. Cold Spring Harbor Laboratory, Cold Spring Harbor, NY.

Sarver, S. K., and D. W. Foltz. 1993. Genetic population structure of a species' complex of blue mussels (*Mytilus* sp.). Mar. Biol. 117:105–112.

Schneider, S., J.-M. Kueffer, D. Roessli, and L. Excoffier. 1997. Arlequin version 1. 0: an exploratory population genetics software environment. Department of Anthropology, University of Geneva, Geneva, Switzwerland.

Shaklee, J. B., C. S. Tamaru, and R. S. Waples. 1982. Speciation and evolution of marine fishes studied by the electrophoretic analysis of proteins. Pac. Sci. 36:141–157.

Shulman, M. J. 1998. What can population genetics tell us about dispersal and biogeographic history of coral-reef fishes? Aust. J. Ecol. 23:216–225.

Shulman, M. J., and E. L. Bermingham. 1995. Early life histories, ocean currents, and the population genetics of Caribbean reef fishes. Evolution 49:897–910.

Swofford, D. L. 1998. PAUP: phylogenetic analysis using parsimony. Vers. 4.0. Sinauer, Sunderland, MA.

Terry, A., G. Bucciarelli, and G. Bernardi. 2000. Restricted gene flow and incipient speciation in disjunct Pacific Ocean and Sea of Cortez populations of a reef fish species, *Girells nigricans.* Evolution 54:*In press.*

Thorpe, R. S., D. P. McGregor, and A. M. Cummings. 1993. Molecular phylogeny of the Canary Island lacertids (Gallotia): mitochondrial DNA restriction fragment divergence in relation to sequence divergence and geological time. J. Evol. Biol. 6: 725–735.

Van Syoc, R. J. 1994. Molecular phylogenetics and population structure derived form mitochondrial DNA sequnece variation in the edible goose barnacle genus Pollicipes (Cirripedia, Crustacea). Ph.D. diss., Scripps Institution of Oceanography, La Jolla, CA.

Vedder, J. G., and D. G. Howell. 1980. Topographic evolution of the southern California borderland during late Cenozoic time. Pp. 7–31 *in* Dennis M. Power, ed. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Waples, R. S. 1987. A multispecies approach to the analysis of gene flow in marine shore fishes. Evolution 41:385–400.

Waples, R. S., and R. H. Rosenblatt. 1987. Patterns of larval drift in southern California marine shore fishes inferred from allozyme data. Fish. Bull. 85:1–11.

Yanev, K. P. 1980. Biogeography and distribution of three parapatric salamander species in coastal and borderland California. Pp. 40–47 *in* Dennis M. Power, ed. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

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