PATTERNS OF LARVAL DRIFT IN SOUTHERN CALIFORNIA MARINE SHORE FISHES INFERRED FROM ALLOZYME DATA

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ABSTRACT

A multispecies analysis of allozyme data for 10 marine shore fishes was undertaken to identify patterns of genetic differentiation resulting from larval drift. Previous studies suggest that allele frequencies in these fishes are sensitive primarily to the effects of migration, rather than to natural selection or historical factors. The following patterns recur in most species: 1) Two northern populations (La Jolla, California, and the California Channel Islands) share a relatively high genetic affinity with all other populations, while the two southern populations (Isla de Guadalupe and Punta Eugenia, Baja California, Mexico) are relatively divergent; 2) the two southern populations apparently exchange genes much more frequently with northern populations than with each other; 3) anomalous results for the ocean whitefish, *Caulolatilus princeps*, can be understood on the basis of known patterns of larval distribution in this species. The consistency of these large-scale patterns among species with markedly different life history features and dispersal capabilities suggests that the results obtained here may provide insight into the population structure of other species (invertebrates as well as fish) with pelagic larvae.

Two characteristics of shallow-water marine organisms make the analysis of their population structure interesting and challenging. First, adults of these species are restricted to relatively shallow, inshore waters, so adult populations can be isolated from other populations by expanses of deep water or areas of otherwise unsuitable habitat. On the other hand, many marine species have a pelagic larval stage lasting several weeks or months and thus at least the potential for long-distance transport by ocean currents. Indeed, such long-distance dispersal events are generally invoked to explain the presence of shallow-water marine organisms on oceanic islands isolated by up to several thousand kilometers from possible sources of propagules.

However, very little is actually known concerning the complex process of larval drift, and several questions remain largely unanswered. For example, by what pathways do larvae traverse oceanic barriers separating different populations? Furthermore, do recruits arrive at remote areas on a more-or-less continuous basis, or is long-distance dispersal the result of rare or unique "sweepstakes" events? The answers to these questions are relevant not only to evolutionary biologists seeking to understand the processes of differentiation and speciation, but also to those who, in order to formulate management policies for marine fishery resources, must determine the degree to which geographic stocks correspond to independent reproductive units.

Several approaches have been used to address the problem of pelagic dispersal. In some cases, sufficient data regarding oceanic currents are available to construct models capable of predicting patterns of larval distribution if time and place of spawning are known. However, as such models are generally based on long-term mean current patterns, they may be misleading if successful dispersal is actually due to anomalous conditions that occur infrequently. Furthermore, few data are available regarding the inshore currents intimately involved in the initial dispersion (or retention) of larvae spawned in shallow water. Marked drifters (e.g., Schwartzlose 1963; Tegner and Butler 1985) can provide biologically relevant data regarding current patterns, but such studies rely on retrieval by the human population at large and thus provide little information about dispersal to remote (and typically poorly inhabited) localities. Tagging studies, although very resource intensive, can provide valuable, direct information regarding oceanic migrations but are not well-suited to the study of larval drift.

For the above reasons, indirect methods must often be used to estimate the incidence of gene flow in marine organisms. The electrophoretic analysis of protein polymorphisms is one such approach that has seen extensive use in both terrestrial and aquatic

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systems. Electrophoretically detectable allele frequencies can be used to estimate levels of migration if it can be assumed that these frequencies reflect a balance between the opposing forces of migration (gene flow) and random divergence of allele frequencies (genetic drift). The main difficulty with this approach is that other forces, notably natural selection and historical contact, can influence allele frequencies, and the relative importance of these forces in natural populations has proved extremely difficult to evaluate directly.

The present study differs from most previous ones in an important way: rather than concentrate on one or two species, we sampled 10 marine shore fishes from the same suite of island and mainland localities in southern California and Baja California, Mexico. Substantial differences between species in fecundity, length of larval life, and other life history features allowed us to test the hypothesis that species with low dispersal capability should show greater genetic differences between populations than do species that are better dispersers. As discussed by Waples (in press), the statistically significant negative correlation between dispersal capability and levels of genetic differentiation in these shore fishes is consistent with expectations based on an equilibrium model involving gene flow and genetic drift. Scenarios invoking natural selection and/or historical (nonequilibrium) perturbations of migration patterns could be hypothesized to explain these results, but there is no a priori reason to expect the observed correlation to result from selection or historical factors. The test discussed by Waples (in press) does not exclude the possibility of selection at individual gene loci, but does suggest that such forces have not been strong enough to disturb the overall patterns of genetic differentiation due to gene flow that are of interest here.

In this paper we extend the analysis of these data to address two questions regarding larval dispersal that can only be understood by considering data for a number of species simultaneously: 1) Are there consistent patterns (across species) of genetic similarity among localities that suggest common avenues of larval transport? 2) If such patterns do exist, can results for those species that are exceptions to the pattern be understood in terms of different behavioral or life history features that might cause their larvae to be affected differently by the current regime? The question of the frequency of successful long distance dispersal in these shore fishes and some of the problems associated with estimating this frequency will be discussed in a later paper.

MATERIALS AND METHODS

Experimental Design

Collections were made at six sites in four major areas: La Jolla, CA; the California Channel Islands (San Nicolas Island and Santa Catalina Island); Isla de Guadalupe, Mexico; and near Punta Eugenia, Mexico (Cabo Thurloe and Islas de San Benito; see Figure 1). Two sites were used in the Channel Islands and near Punta Eugenia because not all species could be collected at a single locality. The area of study describes a quadrilateral roughly 600 km long and 100-300 km wide that encompasses almost the entire area south of Point Conception governed by the California Current System. Furthermore, few of the species studied occur north of Point Conception in any numbers, and central Baja California, Mexico, is at or near the southern distributional limit for most of these species as well. The study areas thus cover a major portion of the normal range for these species, and this sampling pattern should have been able to detect significant population subdivision if it exists.

The study sites were also chosen in such a way that the genetic affinities of populations in certain areas could be evaluated. Mainland populations are represented by samples taken at La Jolla. The California Channel Islands harbor large populations of many marine organisms, and it is important to assess the degree to which these populations are independent of those from the mainland. Guadalupe is a small, oceanic island of volcanic origin surrounded by deep (>3,000 m) water. It is remote enough (275 km west of the central Baja California coast) that genetic differentiation of shore fishes might be expected. Collections in the vicinity of Punta Eugenia were made to serve as controls for evaluating the extent of differentiation at Guadalupe and to estimate the relative importance of east-west larval drift in this area.

Well-developed oceanic currents serve as potential transport mechanisms for pelagic larvae in the study area. The California Current brings relatively cold, low salinity water from high latitudes toward the Equator; its principal characteristics have been known for some time (Reid et al. 1958; Hickey 1979). The California Current is most strongly developed north of Point Conception; further south, nearshore flow becomes somewhat variable because of the eastward jut of the coastline and the complicating effects of the Channel Islands (Fig. 1). Between about lat. 30° and 33°N, the current shifts toward the east, and a portion of the water is deflected

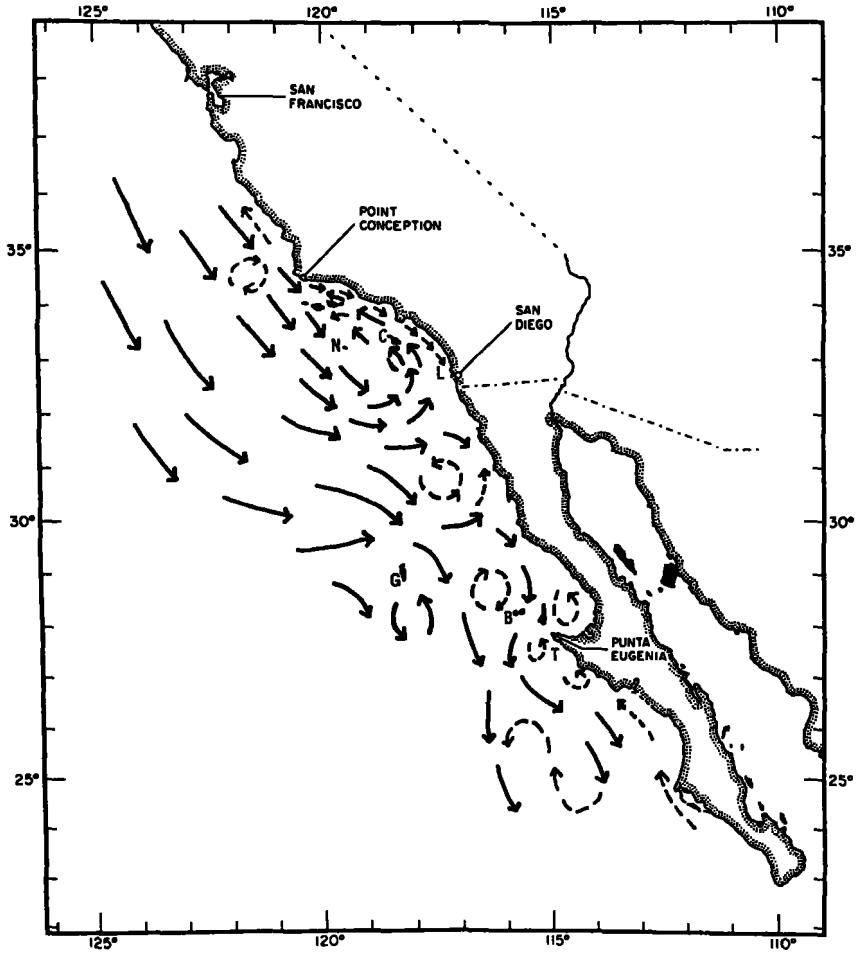

FIGURE 1.—Schematic representation of mean flow patterns in the study area, based on data from Wyllie (1966) and Hickey (1979) and modified from Cowen (1985). Consistent flow directions are shown with solid arrows; dashed arrows indicate more variable features. Study sites are also indicated: La Jolla (L); San Nicolas (N) and Catalina (C), California Channel Islands; Isla de Guadalupe (G); Islas de San Benito (B); Cabo Thurloe (T).

northward along the Southern California Bight, forming the Southern California Eddy (Schwartzlose 1963). This eddy can be found throughout the year except during periods of peak southward flow (generally January to May).

The 10 shore fish species used in the analysis (Table 1) were generally those that could be collected in adequate numbers during brief visits to remote localities. However, attempts were made to include species with widely varying life history strategies and, hence, different dispersal capabilities. The life history and larval capture data summarized in Table 1 were taken from personal observations, unpublished data from the California Cooperative Fisheries Investigations (CalCOFI) and the Ichthyoplankton Coastal and Harbor Studies (ICHS), and from the literature; see Waples (1986) for discussion and references. Sample sizes of about $N = 50$ individuals per species were collected at each of the four areas [ranges of mean sample sizes: for species, $\bar{N} = 36$ (blacksmith) to $\bar{N} = 63$ (sheephead); for localities, $\bar{N} = 46$ (Punta Eugenia) to $\bar{N} = 55$ (Guadalupe)].

Electrophoresis and Data Analysis

Whole fish or tissue samples were frozen in the field, transported to Scripps Institution of Oceanography, and stored at −25°C to −35°C. Procedures of horizontal starch gel electrophoresis and

TABLE 1.—Summary of life history information for the 10 shore fish species used in the analysis.

Family/species	Common name	Batch fecundity	Length of larval life	Larval catches	Dispersal capability
Embiotocidae					
Embiotoca jacksoni	black perch	10	none (viviparous)	—	nil
Cottidae					
Clinocottus analis	wooly sculpin	10^2-10^3	few weeks?	only near rocky shores	low
Clinidae					
Alloclinus holderi	island kelpfish	10^3	brief?	inshore?	limited
Gobiidae					
Lythrypnus dalli	bluebanded goby	10^2-10^3	two or more months	inshore	moderate
Malacanthidae					
Caulolatilus princeps	ocean whitefish	10^5	few months?	inshore/offshore	high
Pomacentridae					
Chromis punctipinnis	blacksmith	10^5	few months?	inshore/offshore	high
Kyphosidae					
Girella nigricans	opaleye	10^5	few months?	mostly inshore	high
Serranidae					
Paralabrax clathratus	kelp bass	10^5	few months?	mostly inshore	high
Labridae					
Semicossyphus pulcher	sheephead	10^5	2-4 months	inshore/offshore	high
Kyphosidae					
Medialuna californiensis	halfmoon	10^5	few months	offshore	very high

histochemical staining have been described elsewhere (Waples 1986). The 26 enzymes and proteins surveyed were acid phosphatase, aconitate hydratase, adenosine deaminase, adenylate kinase, alchohol dehydrogenase, aspartate aminotransferase, creatine kinase, esterase (α-naphthyl acetate), fumarate hydratase, glucose-6-phosphate dehydrogenase, glucosephosphate isomerase, glutamate dehydrogenase, glyceraldehyde-phosphate dehydrogenase, glycerol-3-phosphate dehydrogenase, L-iditol dehydrogenase, isocitrate dehydrogenase, lactate dehydrogenase, malate dehydrogenase, mannosephosphate isomerase, phosphoglucomutase, phosphogluconate dehydrogenase, peptidase (leucyltyrosine; leucylglycyl-glycine), superoxide dismutase, umbelliferyl esterase, xanthine dehydrogenase, and general muscle proteins. Presumptive gene loci for which any variant alleles were detected were surveyed in all individuals. Loci for which only a single allele had been identified after sampling at least 20 individuals in each population were considered to be monomorphic and were not surveyed further in that species.

Wright's F_{ST} was computed for each polymorphic locus in each species by the method of Weir and Cockerham (1984). F_{ST} values ($0 \leqslant F_{ST} \leqslant 1$) indicate the proportion of total variance in allele frequencies attributable to differences between (as opposed to within) populations. Workman and Niswander's (1970) test was used to identify F_{ST} values significantly larger than zero. Data for all presumptive gene loci resolved in each species were combined in an index of overall genetic differentiation (Nei's [1972] genetic distance (D)), which provides a direct means of comparing levels of genetic divergence between pairs of populations. D is the negative natural logarithm of genetic similarity (I), which is essentially the proportion of genes shared by two populations.

To determine whether similar patterns of population structure occur in several species, D values for each pair of localities (or the mean D values for each locality) were ranked within each species. The resulting matrix of rankings was evaluated for recurring patterns (departure from randomness) by Friedman's method for randomized blocks (Sokal and Rohlf 1981), which computes a statistic that is a chi-square variate with $b - 1$ degrees of freedom:

$$\chi^2_{(b-1)} = [(12/(ab[b+1])) \sum^{b} (\sum^{a} R_{ij})^2] - 3a(b+1) \quad (1)$$

where a = number of rows (species, in this case), b = number of columns (localities, or pairs of localities), and R_{ij} is the ranking of the i^{th} locality (or pair of localities) for the j^{th} species.

To identify species that exhibit anomalous patterns of genetic differentiation, a jackknife procedure was used, the rankings of localities (or pairs of localities) for each species being compared with the overall ranking computed for all the other species combined. Spearman's rank-order correlation coefficient (r_s) was used to determine the

strength of the agreement (or disagreement) between these two sets of rankings:

$$r_s = 1 - (6 \sum d_i^2/[n(n^2 - 1)]) \quad (2)$$

where n is the number of items ranked (in this case, 4 localities or 6 pairs of localities) and d_i is the difference in rankings of the i^{th} locality (or pair of localities).

RESULTS

The electrophoretic analysis provided information regarding variation at 32-42 presumptive gene loci in the 10 species. The genetic interpretation of banding patterns was guided by comparisons of observed and expected number of bands exhibited by presumed heterozygotes, by tissue specificity of isozyme expression, and by quality and consistency of resolution. A detailed discussion of results for each enzyme can be found in Waples (1986). Except for *Semicossyphus pulcher* (discussed below), no overall departures of heterozygote frequencies from those expected under conditions of Hardy-Weinberg equilibrium were found (Waples 1986, in press).

Table 2 summarizes the allozyme data. Average heterozygosities for the 10 species (mean H = 0.031; range = 0.009-0.087) are somewhat lower than the mean value of 0.055 reported for over 100 marine fishes by Smith and Fujio (1982), but at least 5 loci (*Embiotoca jacksoni*) and as many as 19 loci (*Lythrypnus dalli*) were found to be polymorphic in each species. Space does not permit reporting here the allele frequencies for all of these variable loci; these data appear in Waples (1986), or can be obtained from the first author.

Interpopulational genetic distance values (Table 2) were generally fairly small: for half of the species (*Alloclinus holderi*, *Chromis punctipinnis*, *Girella nigricans*, *Medialuna californiensis*, *Paralabrax clathratus*) all possible pairwise comparisons of populations yielded D values <0.001. Even the largest observed D value (0.029 for the Guadalupe-Punta Eugenia comparison in *E. jacksoni*) is well within the range of values typically found between conspecific populations of fish species (Shaklee et al. 1982; Thorpe 1983). Nevertheless, it is apparent that populations of most of these shore fishes do not behave as a single panmictic unit. For 8 of the 10 species, significantly nonzero single-locus F_{ST} values indicate heterogeneity of allele frequencies among populations (Table 2; see also Waples 1986). Furthermore, the statistically significant tendency for species that are better dispersers to have lower mean D values (Waples in press) suggests that the relatively small D values reported here for most species contain valid information relating to population structure.

Our interest here is primarily to identify recurring patterns (across species) of genetic similarity between areas. One way to approach this topic is to compute, for each species, a mean of all the pairwise D values involving each locality. In Table 3 these mean D values have been ranked within each species, thus providing an indication of which populations are most similar (or dissimilar) genetically to the other populations as a whole. Two species (*A. holderi*, *L. dalli*) that could be collected from only three of the four areas have been deleted from this analysis.

The two southern populations, Guadalupe and Punta Eugenia (total of rankings for each = 15), are consistently more divergent than are La Jolla (24.5) and San Nicolas (25.5). Substitution of these totals and values for a (8 species) and b (4 localities) into Equation (1) yields a χ^2 value of 7.54 with 3 df. This

TABLE 2.—Summary of electrophoretic results. Number of loci surveyed (T), number polymorphic (P), and number with significantly nonzero F_{ST} values (F) are indicated. H = average heterozygosity; L = La Jolla; C = Channel Islands; E = Punta Eugenia; G = Isla de Guadalupe.

	Number of loci				Genetic distance (× 10^2)					
Species	T	P	F	H	L-C	L-G	L-E	C-G	C-E	G-E
A. holderi	32	10	1	0.009	—	—	—	0.063	0.042	0.023
Ca. princeps	35	14	1	0.049	0.183	0.146	0.205	0.062	0.144	0.050
Ch. punctipinnis	40	10	1	0.009	0.007	0.021	[1]0.009	0.023	[1]0.012	[1]0.027
Cl. analis	36	17	10	0.046	0.158	0.293	0.237	0.269	0.158	0.362
E. jacksoni	40	5	4	0.015	0.665	0.457	1.55	1.45	0.338	2.87
G. nigricans	42	17	1	0.025	0.043	0.022	0.021	0.046	0.073	0.052
L. dalli	35	19	3	0.087	0.094	0.218	—	0.171	—	—
M. californiensis	38	18	—	0.025	0.022	0.019	0.024	0.018	0.037	0.054
P. clathratus	41	12	—	0.012	0.011	0.020	0.015	0.007	0.028	0.032
S. pulcher	38	14	3	0.033	0.009	0.178	[1]0.098	0.155	[1]0.070	[1]0.083

[1]Mean of comparisons involving Cabo Thurloe and Islas de San Benitos.

TABLE 3.—Chi-square test of homogeneity of ranking of areas by decreasing mean *D* values and correlation of ranking of areas in each species with overall ranking of all other species. Statistics computed for 8 species collected at all four areas and for the remaining 7 species after data for *Ca. princeps* were omitted. L = La Jolla; C = Channel Islands; E = Punta Eugenia; G = Isla de Guadalupe.

	Rankings by area				Correlation (r_s) with other species	
Species	L	C	E	G	8 spp	7 spp
Ca. princeps	1	3	2	4	−0.80	—
Ch. punctipinnis	4	3	2	1	0.60	1.0
Cl. analis	3	4	2	1	0.75	0.80
E. jacksoni	3	4	2	1	0.75	0.80
G. nigricans	4	1	2	3	−0.23	0.20
M. californiensis	4	3	1	2	0.60	0.80
P. clathratus	3.5	3.5	1	2	0.75	0.75
S. pulcher	2	4	3	1	0	0.40
	Totals				CSQ (3 df)	Signif. level
8 spp	24.5	25.5	15	15	7.54	NS
7 spp	23.5	22.5	13	11	10.59	$P < 0.05$

value is not quite significant ($0.1 > P > 0.05$; critical value 7.81). Although the pattern of differentiation over all eight species cannot be shown to depart significantly from randomness by this nonparametric test, it is instructive to continue the analysis to see whether anomalous results in one or two species may be obscuring an underlying pattern in the others. Aberrant species can be identified by measuring the correlation (r_s) of rankings for each species with the overall rankings for all other species combined. To do this, rankings for the localities were computed as each species in turn was deleted from the analysis. These rankings were then compared with those for the species deleted. The r_s values for this analysis clearly indicate a core group of five species (*Chromis punctipinnis, Clinocottus analis, E. jacksoni, M. californiensis, P. clathratus*), rankings for each of which are highly correlated with those of all other species (Table 3). At the other extreme, rankings of *Caulolatilus princeps* are essentially the opposite of those of the other species ($r_s = -0.80$). Thus *C. princeps* is the only species for which La Jolla was ranked the most divergent locality, as it is the only species for which Guadalupe is the locality with the highest overall genetic similarity to the other populations.

In order to evaluate the influence of *Caulolatilus princeps* on the overall analysis, Friedman's test was repeated after data for *C. princeps* had been deleted. The resulting chi-square value for seven species (10.59; 3 df) is significant at the 0.05 level. After omitting *C. princeps*, the correlation (r_s) for each species with all other species was again computed (Table 3). It is apparent that the remaining species form a more coherent group with *C. princeps* omitted, values for each species being positively correlated with those from all other species.

More detail regarding possible pathways of larval drift can be obtained by considering the relative degree of divergence of each pair of populations. *D* values for the six possible pairwise comparisons of the four study areas have been ranked within each species in Table 4. An analysis similar to the preceding indicates that the two northern populations (La Jolla and the Channel Islands) are consistently the most similar genetically, and the two southern populations (Punta Eugenia and Guadalupe) are the most divergent. There are no consistent differences in rankings of the four other comparisons, each of

TABLE 4.—Chi-square test of homogeneity of ranking of pairs of localities by decreasing mean *D* values and correlation of ranking in each species with overall ranking of all other species. Statistics computed for 8 species collected at all four localities and for the remaining 7 species after data for *Ca. princeps* were omitted. Abbreviations as in Table 3.

	Rankings of pairs of localities						Correlation (r_s) with other species	
Species	L-C	L-E	L-G	C-E	C-G	E-G	8 spp	7 spp
Ca. princeps	2	1	3	4	5	6	−0.77	—
Ch. punctipinnis	6	5	3	4	2	1	0.49	0.94
Cl. analis	5.5	4	2	5.5	3	1	0.46	0.93
E. jacksoni	4	2	5	6	3	1	0.14	0.26
G. nigricans	4	6	5	1	3	2	−0.16	0.31
M. californiensis	4	3	5	2	6	1	0.09	0.14
P. clathratus	5	4	3	2	6	1	0.43	0.54
S. pulcher	6	3	1	5	2	4	−0.03	0.54
	Totals						CSQ (5 df)	Signif. level
8 spp	36.5	28	27	29.5	30	17	7.09	NS
7 spp	34.5	27	24	25.5	25	11	11.84	$P < 0.05$

which involves one northern and one southern population. The same five species identified in the previous analysis (*Chromis punctipinnis, Clinocottus analis, P. clathratus, E. jacksoni, M. californiensis*) have the highest correlation with rankings of the other species, although only for the former three is $r_s > 0.40$. Again, results for *Caulolatilus princeps* ($r_s = -0.77$) are strongly negatively correlated with those of the other species. The chi-square value testing the equality of rankings for pairs of localities (7.09; 5 df) is not statistically significant (critical value = 11.07).

In light of the results obtained above, the analysis was repeated after deletion of *Caulolatilus princeps*. When this was done, the r_s values for each of the other species increased, to as high as 0.93 and 0.94 for *Clinocottus analis* and *Chromis punctipinnis*, respectively. The chi-square value (11.84) indicates that for the remaining species the rankings of pairs of localities are significantly heterogeneous. With data for *Caulolatilus princeps* omitted, it is even more apparent that the Guadalupe-Punta Eugenia comparison is the most divergent, and La Jolla-Channel Islands remains the most similar pair of localities (Table 4).

DISCUSSION

Two major points emerge from the analysis of patterns of genetic similarity between areas. First, large-scale patterns of larval dispersal for most species appear to be affected in a similar way by the local current regime. The recurrent patterns can be summarized as follows: 1) La Jolla and the Channel Islands are the two areas with the greatest (and Punta Eugenia and Guadalupe the two areas with the lowest) overall genetic affinity with other populations; 2) the two northern populations share similar allele frequencies, while the two southern populations have much stronger genetic affinities with the northern populations than with each other.

That the southern populations are relatively isolated genetically is not surprising, since they are at the periphery of the distributional range for most of the species. However, it was not expected that the Punta Eugenia populations would show nearly the same degree of genetic isolation as do those from Guadalupe, an oceanic island with a substantial endemic component in its marine flora and fauna (Briggs 1974). The nature of genetic differentiation of Guadalupe shore fishes is discussed more fully in Waples (1986). That many marine species with northern affinities are found along the coast of Baja California, Mexico only in localized upwelling areas (Dawson 1945; Hubbs 1960) may be responsible for the observed divergence of Punta Eugenia populations. These upwelling populations, isolated from other shore fish populations by areas with water temperatures up to 10°C warmer, may represent largely independent reproductive units. One aspect of the population structure that seems clear from the results of this study is that the southern populations studied exchange genes much more frequently with northern populations than with each other. Such a finding would be difficult to predict on the basis of known current patterns, which are quite variable and complex off the coast of Baja California (Fig. 1).

Because the southerly flowing California Current is the dominant hydrological feature in the study area, it is of interest to examine the possibility that the link between northern and southern populations is due primarily to one-way gene flow from the north. This possibility can be evaluated in terms of the presence or absence of rare alleles. If gene flow were unidirectional (north to south), one would expect most alleles present in the northern populations also to appear in samples from the south. Alleles originating in the southern populations, on the other hand, would have no tendency to spread to the north. For the 10 species combined, 50 alleles are found in one or more northern populations but are absent from all southern populations, while only 36 alleles are restricted to southern populations (Waples 1986).

These data thus do not provide evidence for gene flow only from the north, as such a model would predict more alleles restricted to southern populations. Furthermore, the average frequency of alleles restricted to the southern populations (0.0098) is slightly higher than the frequency of those restricted to the north (0.0092); this is the opposite of the result expected if unidirectional migration were "swamping" alleles restricted to the south. It is possible that the episodic northward advection of water from the south is an important source of genetic exchange among populations. Such movement is known to occur even in years not associated with El Niño events, and organisms with southern affinities that apparently have been transported into southern and central California are reported on a fairly regular basis (Hubbs and Schultz 1929; Hubbs 1948; Radovich 1961; Brinton 1981). The data for restricted alleles are consistent with the hypothesis that such processes may be important in the overall genetic structure of these shore fishes. Two factors, however, argue for caution regarding this conclusion: 1) the pattern of occurrence of restricted alleles is

quite variable among species, and four species have more alleles restricted to southern localities; 2) relatively few restricted alleles are found in these shore fishes, further increasing the already large sampling variation in the number and frequency of restricted alleles (Waples 1986, in press; M. Slatkin[3]).

That the Channel Islands populations are no more genetically isolated than those at La Jolla was somewhat unexpected, as La Jolla is part of the major mainland metapopulation that includes much of the distributional range of these shore fishes. It was therefore thought that La Jolla samples would show the greatest overall genetic affinity with other localities. Such a pattern was reported by Haldorson (1980), who found allele frequencies in the surfperch *Damalichthys vacca* to be similar in a series of mainland populations but distinctive at Catalina. Furthermore, Tegner and Butler's (1985) study of drift bottles released at the Channel Islands indicated at most 5-10% reach the mainland, suggesting that the amount of genetic exchange may likewise be low.

However, these findings are not inconsistent with the results of the present study when two factors are considered. First, Tegner and Butler's (1985) study was designed to estimate the numerical impact on local green abalone, *Haliotis fulgens*, populations of larvae derived from the Channel Islands. Because relatively few *H. fulgens* larvae appear likely to cross from the Channel Islands to the mainland, it was concluded that the Channel Islands populations cannot be expected to reseed those on the mainland that are locally depleted through overfishing, pollution, destruction of habitat, etc. Although a small percentage (say 5%) of larval exchange may not exert a significant numerical impact on a population, migration at that rate is very high from the perspective of maintaining similar frequencies of neutral alleles. In fact, the exchange of only a few breeding individuals per generation is sufficient to prevent substantial genetic divergence between populations (Spieth 1974).

Second, the Channel Islands populations might well have proved to be relatively more divergent in the present study if additional mainland populations had been included, as was the case in Haldorson's study. Nevertheless, it is noteworthy that Channel Islands populations do not appear to be genetically isolated to any substantial degree. They may thus play a more significant role in the population structure of marine species in this area than had been believed. The consistently strong affinity between Channel Islands and La Jolla populations suggests that the Southern California Eddy may be effective as a means of larval transport between mainland and island localities.

The second major point to emerge from this study is that the population genetic structure of *Caulolatilus princeps* is very different from that of any of the other species. In fact, the pattern of genetic affinity between populations of the ocean whitefish is almost exactly the opposite of the pattern typical of the remaining shore fishes. This result was puzzling at first, as the life history features of this species are not particularly unusual. However, through the aid of H. Geoffrey Moser (National Marine Fisheries Service, La Jolla, CA), we obtained unpublished larval capture data that shed considerable light on this problem. Figure 2 is a plot of these data, collected by CalCOFI sampling programs during 1955-59. In this 5-yr period no *C. princeps* larvae were collected north of central Baja California, Mexico (lat. 30°N). In this respect, the larval distribution of the ocean whitefish is similar to that observed by Kramer and Smith (1973) for the California yellowtail, *Seriola dorsalis* (= *S. lalandi*). In contrast, larvae of the other species in this study for which data are available were frequently taken in the Southern California Bight during 1955-59 (percentage of positive collection localities north of lat. 30°N: *Chromis punctipinnis*, 28%; *G. nigricans*, 44%; *M. californiensis*, 54%; *S. pulcher*, 39%; Waples 1986). In a more extensive survey of larval catches, Moser et al. (1986) confirmed the unusual pattern for the ocean whitefish for years 1954-81 (only 4 of 163 larvae taken north of 30°N, and none taken in the Southern California Bight), and suggested some possible explanations for the southward shift observed in this species. Thus while the southern populations are near the periphery of the range for most study species, it is the northern populations that are far removed from the apparent sources of ocean whitefish larvae.

As we have seen, a significantly nonrandom pattern of genetic affinity among areas or pairs of areas was found when data for *Caulolatilus princeps* were omitted. This result is not entirely unexpected, as removing the most aberrant data in an analysis of this nature will generally result in an improved significance level of the test statistic. On the other hand, such an approach seems justified in this case, as the objectives of this study were to search for generalized patterns of genetic differentiation and to attempt to explain data for anomalous species in

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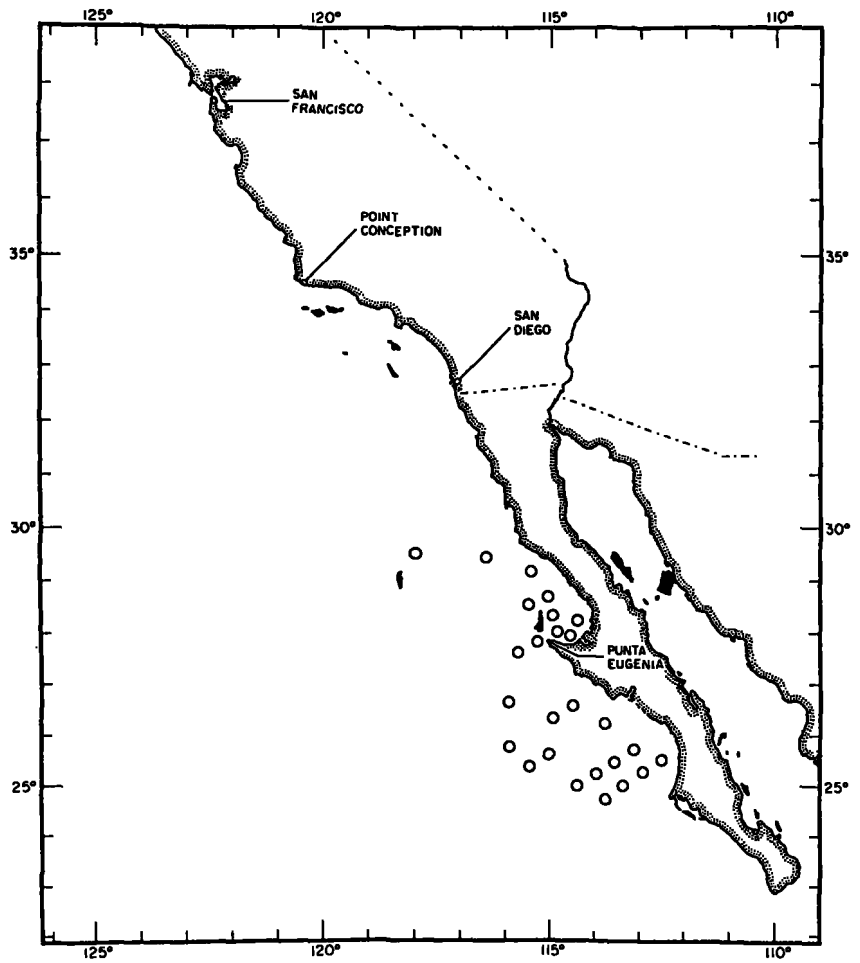

FIGURE 2.—Location of positive collections of *Caulolatilus princeps* larvae taken in CalCOFI sampling program, 1955-59.

terms of life history features. Given the larval capture data discussed above, it is not difficult to understand why the inclusion of data for *C. princeps* tends to obscure patterns of genetic differentiation shared by the other species.

Two other species are exceptions (albeit not as dramatic exceptions as *C. princeps*) to the recurring patterns discussed above. *Girella nigricans* is the only species for which the Channel Islands was found to be the most genetically divergent locality (Table 3), and *S. pulcher* is the only species apart from *C. princeps* for which a strong Punta Eugenia-Guadalupe connection was observed (Table 4). The pattern in *S. pulcher* is due to loci for which consistent heterozygote deficiencies were found (Waples 1986) and thus may provide information that is unrelated to actual levels of gene flow. *Girella nigricans* was the only species to be collected primarily as juveniles; these samples largely comprise a single year class, the allele frequencies for which might be prone to short-term variations. Sampling of juveniles might thus have been expected to yield relatively high levels of genetic divergence, but there was no a priori reason to expect the particular pattern of D values found in this species.

Whether the results for *G. nigricans* are due to as-yet-undetected processes of larval transport or merely random noise in our analysis is thus unclear at present. We face a similar difficulty in explaining the heterogeneity (even among the "core" species) in patterns of genetic affinities between the two northern and two southern populations (Table 4). The decision to include a large number of species in this study mandated a geographically restricted

sampling program, and the resulting analysis provides only a basic outline of these species' population genetic structure. More extensive sampling would no doubt reveal more variations on the patterns identified here. It is likely that such variations would be significantly affected by differences between species in location and timing of spawning. At present, there are neither sufficient inshore hydrographic data nor extensive life history information over the geographic range of most of these species to allow more specific predictions concerning the dynamics of larval drift. Our understanding of the process of larval transport in shallow-water marine organisms can thus be enhanced by more comprehensive sampling programs, involving both genetic and life history analyses.

Nevertheless, it is significant that no major differences in patterns of genetic differentiation could be attributed to dispersal capability per se. Thus of the five "core" species with the most strongly correlated sets of rankings, *E. jacksoni* is a livebearer; *Clinocottus analis* spawns intertidally and has a brief larval life; *P. clathratus and Chromis punctipinnis* have high fecundity and a lengthy larval life; and *M. californiensis* has pelagic juveniles, commonly occurs far offshore with drifting kelp, and thus has the highest dispersal capability of all. This result suggests that the multispecies approach used here may provide information of general use for studying the population biology of other marine organisms (fishes and invertebrates) with pelagic larvae.

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