p. 26-54. In: The Ecology of Marine Fishes: California and Adjacent Waters. 2006.
L.G. Allen, D.J. Pondella, and M. H. Horn (eds.). University of California Press, Berkeley, 670 pp.

CHAPTER 2

Phylogeography

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Introduction

Comparative Phylogeography

Phylogeography seeks to explain the geographic distribution of genetic lineages. To the extent that organisms are products of their DNA, phylogeography also seeks to explain the distribution of organisms, including variation within and, less commonly, between species. Because genetic variation may take thousands or millions of years to accrue, phylogeography has a strong historical component. Thus, phylogeography is closely allied with biogeography, particularly historical and cladistic biogeography, and can be thought of as opening a window in time through which we can observe the influence of historical factors on modern patterns of biodiversity.

Since its inception (Avise et al., 1987), phylogeography has grown exponentially (Avise, 2000), reflecting its intuitive appeal and perceived success. Although the vast majority of phylogeographic studies still explore patterns within single species, greater access to larger amounts of molecular data is making comparative phylogeography, which compares the genealogies of two or more species with overlapping geographic ranges, increasingly popular and powerful (Avise, 1992, 1994; Riddle et al., 2000a, b, c). Comparative phylogeography has proven particularly useful in revealing common patterns and causes of genetic heterogeneities within species as well as suggesting links between life history and genetic structure. The goal of this chapter is to employ the comparative phylogeographic approach to elucidate the factors that have most influenced geographic patterns of genetic variation in California fishes.

Phylogeographic hypotheses fall into two categories: those that focus on (intrinsic) properties of the organism and those that focus on (extrinsic) properties of the environment. They map, to an extent, onto the juxtaposed issues of dispersal and vicariance, often focusing on issues regarding (1) life-history, particularly the duration and dispersal potential of larval stages, and (2) the degree of geographic isolation, respectively.

1. Dispersal potential, gene flow, phylogeographic structure, and the case of planktonic larval duration. As formulated above, a larva may move between populations if the distance between them is shorter than the distance over which it can disperse; the closer they are together, the more likely it will move between them (assuming there is not some minimum time to competence that precludes early settlement). Gene flow measures the actual dispersal and mixing that occurs between populations. Because mixing cannot occur without dispersal and more dispersal should foster more mixing, gene flow is expected to reflect dispersal potential. Hypothetically, the larger the disposal potential, the greater the gene flow, the less the phylogeographic structure (fig. 2-1). Typically, in coastal marine fishes that exhibit a benthic sedentary adult phase and a pelagic larval phase, dispersal potential has been framed in the context of planktonic larval duration (PLD). A number of studies have now examined whether PLD is a good estimator of gene flow in a wide range of fishes and areas as diverse as coastal California, the Sea of Cortez, the Caribbean, and the Great Barrier Reef (Waples, 1987; Doherty et al., 1995; Shulman and Bermingham, 1995; Riginos and Victor, 2001). Few have found conclusive evidence that the degree of population or phylogeographic structure is simply correlated with PLD. The vast majority suggests that a complex of interacting factors, including PLD but also historical geography, hydrography, ecology, chance events, extirpations, habitat, and other life-history attributes (e.g., fecundity), influence modern phylogeographic structure. In addition, many coastal marine fishes can be highly vagile as adults (Chapter 20) and this needs to be taken into account. Hypotheses based on PLD may have little relevance to fishes that are strongly nektonic throughout much of the potentially dispersive life stages, such as anadromous fishes. Thus, the relationship between dispersal potential and realized gene flow remains something of an enigma.

2. Deep phylogenetic gaps usually arise from long-term zoogeographic barriers to gene flow. Zoogeographic barriers are environmental discontinuities that demonstrably have limited the distribution of a large number of species. Such discontinuities are expected to have a similar effect within some species, leading to divergent populations on different sides of the barrier. The special value of phylogeography in this context is that phylogeny can indicate the mode of divergence (fig. 2-2). Moreover, in this context, phylogeography explicitly integrates microevolution and macroevolution, relating ecology to evolution and patterns of variation within species to patterns of variation among species. These relationships were proposed, in the phylogeographic context, in the original phylogeographic paper

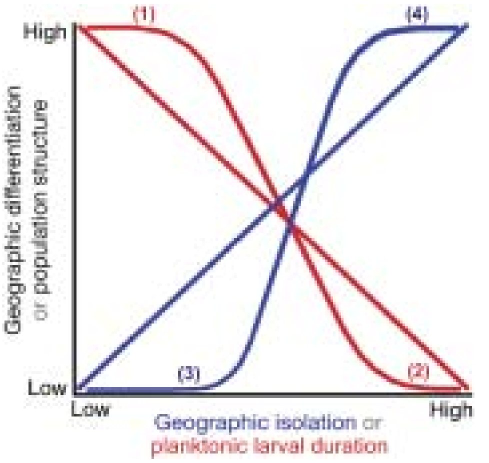

FIGURE 2-1 Schematic of possible relationships of genetic differentiation to planktonic larval duration (PLD; red) and geographic isolation (blue). The shapes of the curves (initially drawn as straight lines) may vary depending on, for example, habitat structure (e.g. stepping stone model) and, notably, may be sigmoidal if certain levels of PLD (1) are required to establish any gene flow or (2) flood the system, or if certain levels of geographic isolation (3) do not inhibit gene flow or (4) prevent gene flow. Realized gene flow is likely to be a complex of these and possibly other functions, such as fecundity. Please note that the shapes and positions of lines (straight and curved) are extremely generalized and are likely to vary among species, places, and possibly times.

(Avise et al. 1987) and subsequently tested in coastal California (e.g. Burton and Lee, 1994; Edmands et al., 1996; Burton, 1998; Bernardi, 2000; Dawson et al., 2001). Like hypotheses relating PLD to genetic structure, the phylogeographic hypotheses were found wanting (Burton, 1998), although a solution has since been offered (Dawson, 2001). Data describing additional taxa in California and adjacent Pacific North American coastal areas are now available, so we will revisit these issues here and examine the implications for our understanding of genetic variation in coastal marine fishes.

RECOGNIZING SUBREGIONS

Coastal Pacific North America can be subdivided geographically on the basis of species distributions (e.g., Chapter 1). These biogeographic divisions are important in phylogeography because, along with environmental data, they suggest extrinsic biotic and abiotic factors that have influenced the distributions of organisms at the species level and, according to the phylogeographic hypotheses, may have had similar effects within species. The geographic relationship between intraspecific phylogenetic structure and supraspecific biotic and abiotic divisions is key in understanding modes of evolution (fig. 2-2). As such, in this chapter, we consider phylogeography in the context of five regions in which different processes probably played greater or lesser roles in structuring coastal fishes (fig. 2-3): (1) the *Cordilleran*, northwest North America, where the effects of glacial cycles have been most immediate and most intense; (2) *California* state, where debate has focused on the presence of a biogeographic break at Point Conception yet its apparent lack of influence on phylogeographic structure; (3) *Pacific Baja California*, which includes another proposed biogeographic and phylogeographic boundary at Punta Eugenia; (4) the *Gulf of California*, where populations of circa 20 species of California fishes are thought to be disjunct in the northern Sea of Cortez; and (5) *California's Islands* which, although they lie relatively short distances from the mainland California and Baja California coastlines, are inhabited by populations that are apparently somewhat isolated from the mainland and from each other by deep-water channels. On the basis of life-history characteristics, we recognize a sixth category, *anadromous fishes*, that illustrates another set of processes leading to quite different evolutionary patterns. By discussing these subgroups, we hope to elucidate certain processes by describing specific local examples. This has the added benefit of further simplifying discussions that naturally cover a large region, numerous species, and complex histories. At the end of the chapter, we briefly synthesize the regional studies to provide a more holistic perspective and highlight areas that require further research.

Some Technical Background Comments

A number of landmark papers provide historical context for this chapter. Large-scale phylogenetics, as practiced in phylogeography (although the field did not exist at the time), made a giant leap forward with the advent of PCR and sequencing. Phylogeography was conceived and christened less than 10 years later (Avise et al., 1987). A momentous paper from Allan Wilson's laboratory at the University of California Berkeley that described "universal" vertebrate oligonucleotide PCR primers (Kocher et al., 1992) provided tools that promoted the rapid growth and diversification of the new discipline. Primers described in that paper included mitochondrial cytochrome b primers that were proven well matched to diverse fish DNAs by the ensuing deluge of data. Although cytochrome b was used more often for interspecific studies than intraspecific studies, the trend of generating vast amounts of data was set and provided the stepping stone for more involved studies on fish populations. Wide access to the rapidly evolving noncoding mitochondrial control region (mtCR; also referred to as the "D-loop") of fishes was promoted by Lee et al. (1995) and mtCR is now the workhorse of intra-specific phylogeography. MtCR tends to evolve more rapidly than most markers accessed via DNA sequencing technology due to its noncoding nature, the lack of a mitochondrial DNA repair mechanism in fishes, very low levels of recombination, usually uniparental inheritance, and the haploid state of mtDNA (Avise, 1994). Thus, mtCR is particularly well suited for studies that require resolution of genetic variation among populations using gene trees. Throughout this period, advances in statistical phylogenetics have been central to the reconstruction of the reliable gene trees that are central to phylogeography (Avise, 2000).

In recent years, critics of mitochondrial-based studies have championed the use of nuclear molecular markers such as RAPDs, "EPIC" amplification of intron sequences, microsatellites, AFLPs, and SNPs which, notably, generate types of information similar to that of allozymes—the first molecular markers widely used to quantify connectivity between populations by determining levels of genetic similarity or gene flow. One consequence has been an increase in the number of non-tree-based analyses often co-opted from the already very well developed field of population genetics. Gene flow is usually estimated using traditional *F*-statistics or their molecular equivalents, Φ_{ST} and Φ_{CT}, derived by analysis of molecular variance (AMOVA; Excoffier et al., 1992). Though there are a number of important differences in the use of these various

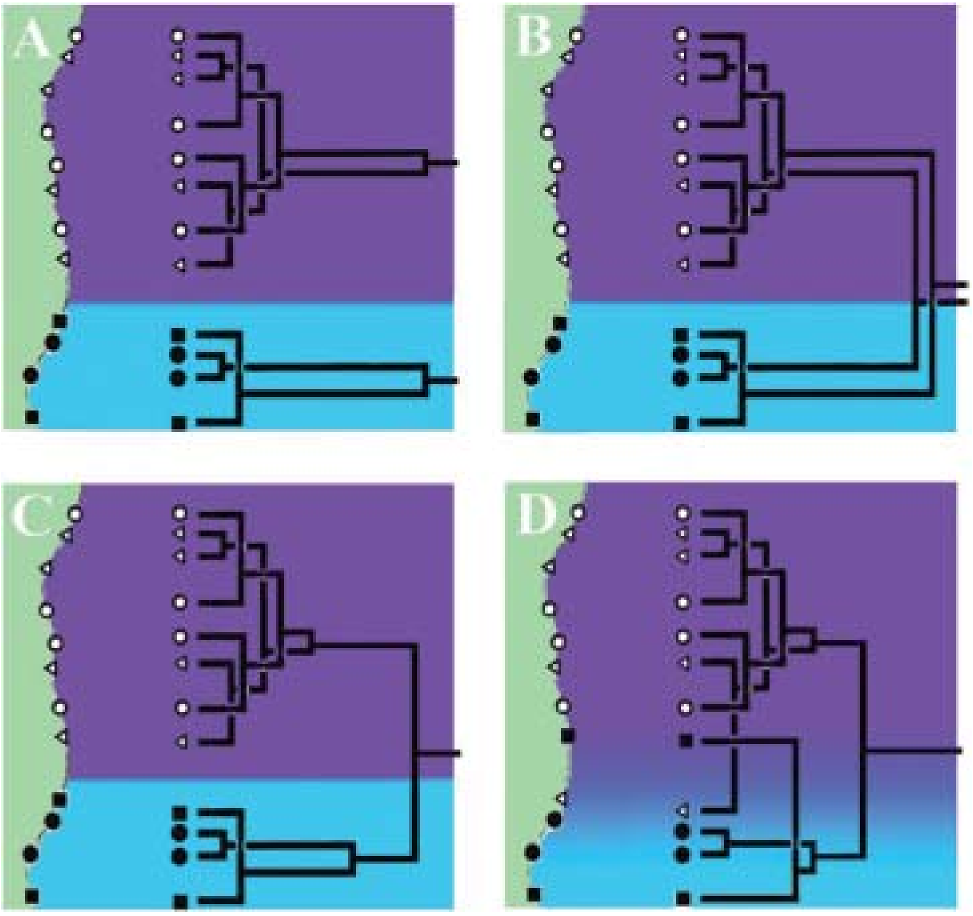

FIGURE 2-2 Schematic of patterns of biogeography, phylogeography, and speciation. In each fig. (A–D), the map shows 12 coastal populations that lie in two biogeographic provinces (purple or blue; green is land). The four symbols (triangles, squares, filled circles, and open circles) represent four distinct evolutionary groups (e.g., intraspecific clades or species). The trees in panels A–C show that the same biogeographic pattern can result from at least three phylogenetic patterns representing three modes of divergence: (A) sympatry, (B) allopatry [or peripatry], (C) mixed allopatry and sympatry. An alternative biogeographic pattern, which is inconsistent with a firm barrier to gene flow is (D) parapatric speciation. However, the biogeographic pattern illustrated in panel D also could result from allopatric or sympatric speciation that subsequently was modified by postspeciation dispersal. The probability that dispersal has modified the pattern of differentiation increases with time since divergence. Extirpation also might modify phylogeographic and biogeographic patterns. For example, extirpation of the fourth or fifth populations from the bottom in D might lead one to infer that speciation was not parapatric. A fifth pattern, not shown, is no phylogeographic structure, which might result from high gene flow. Finally, it is possible that such patterns could result from chance or lineage sorting, although these are considered unlikely—particularly if phylogenies for multiple species show concordant structure. The figures show generalized patterns along an anonymous coastline; to generate patterns specific to California, simply place a mirror along the left-hand side of the figure and look at the reflection.

markers, our goal here is not to evaluate the relative advantages of one method over another. We will rarely mention allozymes in favor of focusing, for simplicity and because of their explicit historical component, on tree-based approaches, although the strongest analyses undoubtedly will use a multitude of markers and analyses and the current emphasis on mtDNA sequence data will probably diminish in the future.

Using different markers raises the issue of how to reconcile analyses that indicate different results. This issue cannot be avoided because many DNA sequence-based studies have been inspired by and directly benefited from prior analyses using allozymes (e.g., Waples, 1987) or employ multiple markers (e.g. Burton, 1998; Huang and Bernardi, 2001). In some cases, differences may be random (e.g., due to genetic drift). In others, they may reflect more orderly, deterministic processes. For example, molecular markers that evolve at different rates may provide additional information on the timing of divergence using molecular clocks. Notably, if a marker does not show any phylogeographic structure, it could be for one of two reasons. There may really be no population structure due to gene flow, or the method may be too insensitive (e.g., the marker evolves too slowly). In either case, the comparative approach is key to maximizing information, for example, about a species' life history (e.g., Dawson et al., 2002) or about the rate of evolution.

Studies of evolutionary rates often employ molecular clocks. Molecular clocks have a largely chaotic mechanism (mutation) with epigenetic modifiers (e.g., drift, selection). Their rates may vary between very closely related taxa and even within lineages (Hillis et al., 1996b). Calibration is therefore essential—ideally against a series of clear-cut, well-dated geological events each of which left indisputable molecular signatures. However, calibration can be tricky because similar geological events may

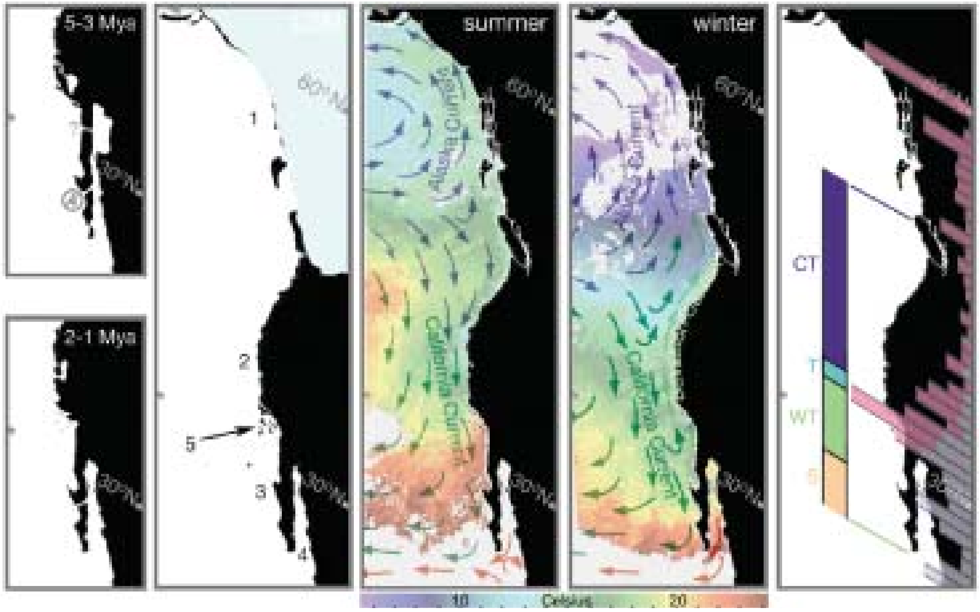

FIGURE 2-3 Summary of some factors hypothesized to influence or be related to phylogeographic structure in coastal California fishes. Reconstructions of coastal topography during the early-to-mid Pliocene (5–3 My BP; Riddle et al., 2000; Carreño and Helenes, 2002; Hall, 2002; Murphy and Aguirre-Léon, 2002), the early Pleistocene (2–1 My BP; Riddle et al., 2000; Dawson, 2001; Carreño and Helenes, 2002), and last glacial maximum (LGM; ice cover shown in light blue; based on Jennings et al., 1977; Vedder and Howell, 1980; USGS 1991; Álvarez-Borrego, 2002; Durazo and Baumgartner, 2002; Williams et al., 2004). The numbers 1–5 (LGM) indicate the regions discussed in this chapter: 1 Cordilleran, 2 California, 3 Pacific Baja California, 4 Gulf of California, and 5 the California Islands. Schematics of major coastal currents in the northeastern Pacific Ocean during spring and summer (summer) or fall and winter (winter; Lyle et al., 2000) overlaid on 9-km weekly composite NOAA/NASA Pathfinder Advanced Very High Resolution Radiometer (AVHRR) sea-surface temperature images for August and February, 1996, respectively (gray, no data; http://coho.coas.oregonstate.edu/Pathfinder/comp/9698.html). Finally, a histogram showing the modern-day frequency distribution of northern (pink) and southern (blue) end points of the ranges of California fishes (see Chapter 1) compared with nearshore biogeography during Pleistocene glaciation (CT, cold temperate; T, temperate; WT, warm temperate “Verdean Province”; S, subtropical-to-tropical; Addicott, 1966).

have occurred multiple times in the same place, for example, glaciation, sea-level rise, opening of the Bering Strait, or take many millions of years to complete, as for the emergence of the Isthmus of Panama, and have different effects at different stages (Lyle et al., 2000). In addition, different species may not respond in the same way to the same event. For example, geminate species pairs across the Isthmus of Panama diverged between 12 million years ago (My BP) and 3 My BP depending, in large part, on whether they occupied offshore or coastal habitats (Knowlton et al., 1993; Bermingham et al., 1997; Lessios, 1998; Donaldson and Wilson, 1999). Another is raised by the results of Craig et al. (2004), who showed that transisthmian species pairs were not sister taxa.

The immense value of a well-calibrated molecular clock, however, has generated a vast literature on the subject and a number of rules of thumb (e.g., Li and Graur, 1996). For example, protein-coding regions generally evolve more slowly than noncoding regions; nDNA generally evolves more slowly than mtDNA. Thus noncoding mtDNA—the mtCR of vertebrates—is among the fastest evolving regions of DNA. Within the mtCR, the region adjacent to tRNA^{Pro} generally evolves faster than the region adjacent to tRNA^{Phe}, and there is a highly conserved region in the middle (Lee et al., 1995). The rules of thumb also extend to absolute rates of evolution. For example, the evolutionary rate of cytochrome b (cyt b), the most sequenced marker in fishes, is generally between 1.5% and 2.5% per million years (My), but in some rare cases may be as much as 8 to 20% per My (Bowen and Grant, 1997). In extreme cases, several factors may be invoked to explain the unusual behavior of cyt b, including errors in species identification. In general, cyt b sequence data offers a better gauge of divergence times than mtCR and thus can be used to corroborate mtCR calibrations (McMillan and Palumbi, 1995). Thus, molecular clocks can provide an indication of the relative merits of different evolutionary scenarios and might then be recalibrated to causally related events.

Case Studies

Anadromous Fishes

A variety of native (e.g., salmonids, sturgeons) and nonnative (e.g., American shad, striped bass) anadromous fishes occur in California. Here we focus on salmonids (table 2-1), in part due to their high conservation profile and relatively rich literature. Populations of Pacific salmon and anadromous trout (*Oncorhynchus* spp.) are distributed in temperate to cold waters around the Pacific Rim, where they play major roles in both marine and freshwater ecosystems. The state of California represents the current and/or historical southern limit of the range of these species and presents significant ecological challenges to species with limited thermal tolerance. Although pink (*O. gorbuscha*), chum (*O. keta*), and sockeye salmon (*O. nerka*) are only sporadically found in California and anadromous cutthroat trout (*O. clarkii*) are found only in streams from the Eel River to

TABLE 2-1

Phylogeographic Characteristics of Some California Salmonids

Species	*Range of Species*	*Range Sampled*	*Life History*	*Marker*	*Phylogeographic Structure*	*Reference*
Oncorhynchus kisutch (coho salmon)	Central California to Russia	Central California to British Columbia	Anadromous	50+ allozymes	Populations south of Punta Gorda are most distinctive group	Weitkamp et al. (1995)
O. mykiss (steelhead)	Southern California to Kamchatka (all California populations are in coastal subspecies)	California	Anadromous	mtCR	Gualala River/Russian River, Pt. Sur/San Simeon	Nielsen (1999)
		Southern California to Washington		50+ allozymes	Central Valley distinct from coastal populations; coastal populations distinct south vs. north of Klamath	Busby et al. (1996)
		California range		18 microsatellites	Isolation by distance; three regions: (1) Klamath River to the north, (2) Russian River to the south, and (3) those in between.	Garza et al. (2004)
O. tshawytscha (chinook salmon)	Central California to Russia	Central California to northern British Columbia	Anadromous	33 allozymes	Central Valley and Upper Klamath distinct from coastal populations and each other; coastal populations distinct south vs. north of Klamath; multiple parallel evolution of run time in coastal and upper Klamath populations	Waples et al. (2004)
		Central Valley		10 microsatellites	Distinct winter-run populations in upper Sacramento River	Banks et al. (2000b)

the north, chinook salmon (*O. tshawytscha*), coho salmon (*O. kisutch*), and steelhead (anadromous *O. mykiss*) all were historically abundant and well distributed geographically in California.

Human interventions have strongly affected the abundance and, in some cases, the population structure of salmon and steelhead in California (Moyle, 1994). For example, a century and a half ago, hydraulic mining transformed most of the streams in the Central Valley. During the middle of the twentieth century, the construction of high dams on major tributaries of the San Joaquin and Sacramento blocked access to historic spawning areas for spring-run chinook salmon, which historically was the dominant life-history form in the Central Valley. Smaller dams and water withdrawals have restricted access by steelhead to the lower reaches of many streams in central and southern California. Large hatchery programs, particularly in the Klamath River basin and the Central Valley, have altered population structure as a result of stock transfers and, in some cases, widespread straying of hatchery fish.

In spite of these anthropogenic effects, which have led to listing the majority of California's anadromous salmonid populations under the federal Endangered Species Act, California salmon and steelhead populations are genetically diverse, and empirical data illustrate several interesting phylogenetic and biogeographic patterns. First, coho salmon and steelhead show high levels of genetic diversity among California populations compared to similar areas in the Pacific Northwest. For example, Waples et al. (2001) reviewed extensive allozyme data for Pacific salmon and steelhead from California to southern British Columbia and, using standardized criteria, identified major genetic groups of populations in each species. Just two major genetic groups of coho salmon were identified over this large geographic area; one group included only coastal populations south of Punta Gorda (see Bartley et al., 1992). Similarly, five of the seven major genetic groups of steelhead populations identified by Waples et al. (2001) occur only in California.

These results are consistent with, and provide a broader geographic context for, studies of mtDNA in California steelhead (Nielsen, 1994, 1999; Nielsen et al., 1997) that have demonstrated a high level of genetic diversity among populations. Notably, both allozyme and mtDNA diversity among steelhead populations is highest in the southern half of the state (Busby et al., 1996; Nielsen, 1999). These results refute two common perceptions regarding the origin of steelhead in southern California. First, they show that steelhead are *not* merely the offspring of hatchery rainbow trout. Nielsen et al. (1997) and Busby et al. (1996) showed that southern steelhead are not genetically similar to any hatchery populations of rainbow trout that have been sampled. Second, they show that these populations are *not* part of a large, relatively homogeneous metapopulation that opportunistically invades streams with ocean access in years when environmental conditions are favorable and numbers are abundant. Genetic divergence among populations in both mtDNA and nuclear DNA is much too large to be consistent with this hypothesis.

In addition to the high degree of divergence among California steelhead populations, Nielsen (1994) also reported high mtDNA haplotype diversity within populations. This was particularly true in the area south of Point Conception, where many haplotypes occur that have not been found in populations to the north. Nielsen (1999) believes this pattern is not consistent with the hypothesis that southern steelhead are a result of simple range extension by northern populations following the last glaciation; instead, she has argued that the data support Behnke's (1992) hypothesis for a separate Pleistocene refuge for *O. mykiss*, perhaps in the Gulf of California, and that the current population structure reflects secondary contact by two divergent lineages. Low genetic diversity and derived haplotypes in northern, glaciated areas relative to more southerly areas, as reported for several salmonids (Danzman et al., 1998; Turgeon and Bernatchez, 2001; Brunner et al., 2001), has been interpreted as support for this type of scenario. However, preliminary data on microsatellite variation in California steelhead (Garza et al., 2004) indicate that levels of nuclear gene diversity increase with latitude, and stronger evidence for recent bottlenecks is found in populations from the southern part of the state. Additional analyses and perhaps additional sampling will be required to disentangle the apparently complex history of anadromous *O. mykiss* in the southern part of the species' range.

Genetic data also provide important insights into the evolution of life-history diversity in California chinook salmon. Salmon populations are typically characterized by the time of year at which adults enter freshwater (e.g., spring-run fish enter freshwater in the spring, whereas fall-run fish remain in the ocean until later in the year). Table 2-2, which summarizes data for a gene diversity analysis of chinook salmon (Waples et al., 2004), illustrates a pattern described earlier by Utter et al. (1989) and Myers et al. (1998): in coastal areas and in the lower Columbia River, the majority of the genetic differences are explained by geography (differences among areas within geographic provinces or among samples within areas) rather than run timing. As a result, spring-run and fall-run populations from the same coastal river typically are more similar genetically to each other than either is to populations of similar run timing from other river basins. In these areas, therefore, spring- and fall-run populations do not form discrete, monophyletic lineages; instead, the two life-history forms appear to have evolved independently many times through a process of parallel evolution (Waples et al., 2004). In contrast, in the interior Columbia River, spring- and fall-run chinook salmon form two very divergent genetic lineages, and in these regions (mid Columbia, Upper Columbia, Snake River), run-timing differences explain most (74–94%) of the total gene diversity (G_{SP}) within each province (table 2-2). In the interior Columbia River, therefore, run-timing differences have a much more ancient origin, perhaps predating the last episode of glaciation. A possible explanation for the contrasting coastal and interior patterns is that coastal basins are not large enough to provide strong and persistent reproductive isolation between run types, whereas the extensive Columbia-Snake basin does provide opportunities for geographic isolation of run types. For example, in the Snake River basin, the spring chinook salmon spawn and rear in high-elevation (up to 2000 m) upper tributaries, well isolated from the mainstream spawning fall-run populations.

In California, joint analysis of geographic and run-time variation for chinook salmon is possible in the Klamath and Sacramento basins. Both allozyme (Myers et al. 1998; Waples et al. 2004) and nuclear DNA (Banks et al. 2000a,b) data show that chinook salmon from the Klamath River basin follow the "coastal" pattern above, and that geography is a stronger determinant of genetic differences than run timing (table 2-2; $<4\%$ of G_{SP} is due to differences in run timing). In the California Central Valley, the pattern of genetic variation does not perfectly follow either the coastal or inland template. The overall level of genetic differentiation is modest compared to other regions ($G_{SP} = 0.018$ for the Central Valley compared to $G_{SP} = 0.09–0.16$ in the interior Columbia), but a substantial fraction (39%; table 2-2) is attributable to differences among

TABLE 2-2

Hierarchical Gene Diversity Analysis of Chinook Salmon in the Western United States

Region	G_{SP}	*Run/ Province*	*Area/ Run*	*Sample/ Area*
California Central Valley	0.018	38.9	5.6	55.6
Klamath Mts.	0.055	3.6	85.5	10.9
Oregon/Wash. Coastal	0.038	10.5	31.6	57.9
Lower Columbia	0.050	32.0	42.0	26.0
Mid-Columbia	0.131	76.5	9.8	13.6
Upper Columbia	0.164	93.9	2.4	3.6
Snake River	0.091	73.9	7.6	18.5
Georgia Basin	0.064	12.3	41.5	46.2

NOTE: Values in hierarchy columns are the percent of the total within-province gene diversity (G_{SP}) that is explained by that hierarchical level. Modified from Waples et al. (2004).

populations with different run times. Furthermore, all of the fall- and late-fall run populations from both the Sacramento and San Joaquin basins form a single genetic lineage that is well differentiated from all the native spring-run populations and the single remaining winter-run population (Winans et al., 2001; Banks et al., 2000a,b; Hedgecock et al., 2001). Thus, the Central Valley is the only area in the United States outside the interior Columbia where there is evidence for the monophyletic origin of different run types. However, the absolute level of divergence among run types is small, suggesting either a relatively recent origin or incomplete isolation. A monophyletic origin of the spring-run populations is not well established. It is also possible that sampling current populations in this area does not accurately assess historical evolutionary relationships. Prior to about 1850, spring-run chinook salmon were very abundant in the upper tributaries of the San Joaquin system, but they were decimated by placer mining in the latter half of the nineteenth century. Subsequently, the construction of dams on the lower reaches of all major San Joaquin streams blocked access to historical spawning and rearing areas of spring chinook salmon. Therefore, it is possible that genetically divergent spring-run chinook salmon evolved in high-elevation tributaries of the San Joaquin system but were extirpated before modern genetic sampling commenced. It may be possible to test this hypothesis in the future if scales or other archived material that will yield DNA from these populations exists and can be analyzed.

Finally, analysis of ocean harvest of tagged fish shows that California populations of coho and chinook salmon tend to remain in the productive waters south of Cape Blanco, southern Oregon, rather than migrating along the continental shelf northward to British Columbia and Alaska, as do most populations originating north of Cape Blanco (Myers et al., 1998; Weitkamp et al., 1995; Weitkamp and Neely, 2002). Not surprisingly, genetic data for most anadromous Pacific salmonids also show strong genetic differentiation across Cape Blanco (summarized by Waples et al., 2001). Thus, in addition to occupying distinctive freshwater habitats, California salmon populations also have a distinctive marine ecology.

In summary, the current population structure of California salmon and steelhead reflects a balance of several forces. Whereas many areas of the Pacific Northwest became habitable only after the Wisconsin glaciation, i.e., within the last 15,000 years, salmon and steelhead have had a continuous presence over a much longer time in California habitats, thus providing ample opportunities for divergence. On the other hand, high temperatures and seasonally low and variable flow rates in California streams present extreme environmental challenges to anadromous salmonids in the southern extent of their ranges. Environmental conditions have become even more challenging in the last century as a result of human pressures. These considerations suggest two hypotheses regarding population structure of anadromous salmonids in California. (1) Genetic and demographic linkages among salmonid populations in California may be fundamentally different than in areas to the north. California populations may have evolved the ability to persist in relatively strong isolation at relatively low numbers, perhaps by developing ways to dampen natural fluctuations in abundance. (2) The current population genetic structure may not reflect historical, equilibrium conditions; instead, it may reflect a relatively recent and rapid genetic drift caused by habitat fragmentation and population bottlenecks. Under this scenario, the population structure may be in a state of decay. These hypotheses should be testable in the near future through careful design of experiments that use highly polymorphic molecular markers in conjunction with field observations.

Coastal Marine and Estuarine Fishes

CORDILLERAN REGION

Influence of Glaciations

Northern hemisphere glaciation initiated during the Pliocene, approximately 2.6 My BP (Lyle et al., 2000). The Pleistocene (1.8 My BP–10 Ky BP) was characterized by over a dozen glacial episodes (Dawson, 1992). During the last glacial maximum (LGM; fig. 2-3), the Cordilleran ice sheet extended south to Puget Sound and sea surface temperatures (SSTs) off northwestern North America were substantially cooler—estimates range from −3.3°C (± 1.5°C) to −6°C off Oregon depending on the source (Lyle et al., 2000)—than at present. In general, the impression of glacial cycles is one of unremitting cold forcing organisms further and further south during glacial advance, contrasted by uncovering of a denuded landscape ripe for colonization by species advancing northward during glacial retreat. Then the cycle repeats, erasing what went before. Such a monolithic scenario is expected to have left behind genetic signatures—derived haplotypes and low genetic diversity—that differentiate recently established northern populations from their ancestors to the south (fig. 2-3A).

As mentioned above, some evidence of these patterns exists in several salmonids in Canada and the northern United States (Danzman et al., 1998; Turgeon and Bernatchez, 2001; Brunner et al., 2001). However, the intensity and likely effects of different glacial, interglacial, and interstadial periods varied (Dawson, 1992; Lyle et al., 2000), as did the regional effects. For example, the Younger Dryas (~11–10 Ky BP) was almost as cold as but much shorter than the LGM, the Cordilleran ice sheet displaced organisms westward as well as southward, and some places within the limits of the ice sheet remained relatively unscathed (Williams et al., 2004; fig. 2-3 *LGM*). The same studies of the salmonids also indicated the occurrence of glacial intrusions and refugia (Danzman et al., 1998; Turgeon and Bernatchez, 2001; Brunner et al., 2001).

Studies of marine fishes (table 2-3) have revealed similarly mixed evolutionary histories consistent with a complex history in the north. For example, northern clingfish, *Gobiesox maeandricus*, which occur from Baja California to Alaska, occur in two distinct mitochondrial clades: one is characterized by low haplotype diversity and includes only individuals from the Strait of Georgia, the other has high haplotype diversity and representatives in all populations. These genetic patterns indicate an unglaciated refugium in the Strait of Georgia where fish survived and maintained ancient haplotypes while surrounded by areas of unsuitable habitat (Hickerson and Ross, 2001; figs. 2-4A, 5A). Two distinct mtCR clades are also evident in painted greenling, *Oxylebius pictus*, and occur at significantly different frequencies in populations along a north–south axis, consistent with ancient glacial vicariance (fig. 2-6).

The painted greenling data set, however, also demonstrates that episodic glaciations periodically expose the population structure they generate, if any, to other influences that may maintain or erode it. The two mitochondrial clades in painted greenling, for example, are equally represented in all populations bar the most northerly and most southerly populations (in which they occur in significantly different proportions (1.0/0.0 and 0.25/0.75, respectively), indicating high levels of gene flow following secondary contact. In this case, glaciation appears to have had a long-lasting effect on molecular diversity but a somewhat transient effect on population structure.

Oceanographic Influence and Pelagic Larval Duration (PLD)

Population differentiation in rosethorn rockfish, *Sebastes helvomaculatus*, also indicates restricted gene flow in the northeastern Pacific (Rocha-Olivares and Vetter, 1999). Given this coastal species' deep-water habitat, the structure seems unlikely to be attributable to vicariance caused by glaciation, although this cannot be ruled out during colder climes they may have inhabited shallower water and reduced genetic diversity in Alaskan populations is consistent with postglacial northward expansion (Rocha-Olivares and Vetter, 1999). Rather, the genetic heterogeneity between populations of rosethorn rockfish from Alaska (Fairweather and Sitka,) and those from further south (Vancouver Island, Oregon, California; $\Phi_{CT} = 0.22$, $p << .001$) has been attributed primarily to patterns of larval dispersal, particularly with reference to the divergence of the North Pacific Gyre into the northward flowing Alaskan Current and southward flowing California Current in the vicinity of the Aleutian–Oregonian provincial boundary (fig. 2-3). Similar genetic structure has been reported in algae (Lindstrom et al., 1997) and mtDNA of moon jellyfish (Dawson and Jacobs, 2001), but this is by no means a ubiquitous pattern (e.g., Debenham et al., 2000). Dover sole (*Microstomus pacificus*) and shortspine thornyhead (*Sebastolobus alascanus*) show no population structure in the region. Although the absence of structure could indicate recent postglacial colonization, the associated high haplotype and nucleotide diversity in this case are more likely to indicate a long history of high gene flow (Stepien, 1995, 1999; Stepien et al., 2000; see also Hedgecock, 1994 for an analysis of barnacles). The extremely long, >1 year, PLD of Dover sole and shortspine thornyhead may explain why these species also do not show genetic heterogeneity across the proposed biogeographic boundary between Aleutian and Oregonian provinces (Rocha-Olivares and Vetter, 1999).

Plurality of Influences and Commonality of Effects

Comparison of these studies raises several issues. First, the same geographic area has been affected by glaciation and by divergent ocean currents, probably for over 2 My. Second, both of these factors are expected to lead to population differentiation north and south of the region. Third, northward range extension, a bottleneck (in a refugium), and high PLD are all expected to result in low population structure, although the genetic signatures of each should vary. Fourth, evolutionary changes are contingent on those changes that preceded them. Thus, multiple influences can have common effects on phylogeographic structure and it may be difficult to distinguish among them. The same influence may also vary through time, such as in glacial cycles, but also in the weakening and strengthening of the North Pacific Gyre (Maruyama, 2000) and its changing latitude (on seasonal and other timescales; e.g., Lyle et al., 2000). Of course, a multiplicity of variable influences with a common effect and others that maintain or erode that effect, or even generate a different effect, probably does reflect the true evolutionary history of species in this region (Rocha-Olivares and Vetter, 1999). Thus, an evolutionary tension is established among various factors with a suite of possible outcomes, depending on the chain and intensity of events, and it is these things we are interested in deciphering. In these cases from the *Cordilleran* region, however, it is still difficult to distinguish among most of the probable causes.

CALIFORNIA

Tectonism and Its Influence on Oceanographic Patterns

"Pacific" coastlines are tectonic coastlines. Tectonism, with its many consequences including orogenesis (mountain formation), erosion, changing catchment areas, and coastal uplift, has been the single most important factor shaping California's coastline; it has also influenced climate, ocean currents, and the distribution of habitat. The entire coast of California has been affected by tectonism with potentially important biotic consequences—for example, Tomales Bay, where the San Andreas Fault flooded, may form a warm-water refuge for some species (McCormick et al., 1994). Here, we will focus our attention on southern California where the suite of factors in which we are interested is best documented.

For the last several millions of years, coastal southern California has been uplifted approximately 1 km My^{-1} (Vedder and Howell, 1980; Sorlien, 1994). Uplift radically changed the structure of the coast (fig. 2-3). For example, the California Channel Islands probably emerged less than 5 My BP as a result of changing tectonic movements (Atwater, 1998) forming a channel off Ventura; the Palos Verdes peninsula became a

TABLE 2-3

Phylogeographic Characteristics of Some Pacific Coastal California Fishes

Species: Fishes	*Habitat and Depth*	*Life History**	*Range Sampled*	*Marker*	*Phylogeographic Structure*	*Reference*
Paralichthys californicus (California halibut)	Nearshore: to 183 m, within 6 km of shore	3 to 6 wks planktonic larvae, juveniles estuarine, coastal adults, longevity 30 yrs, fecundity 10^5–10^6	LA and San Diego	15 allozyme loci	Significant at 2 loci	Hedgecock and Bartley (1988)
			Monterey to Bahia Magdalena	mtCR	Weak (Punta Eugenia?)	Dawson (2001)
Clevelandia ios (arrow goby)	Estuaries	Planktonic larvae in estuaries and nearshore waters, fecundity 300–1200, longevity 1–3 yrs	Central and southern California	mtCR	None	Dawson et al. (2002)
Sebastes atrovirens (kelp rockfish)	Kelp beds and rock reefs to 50 m	Planktonic larvae, fecundity 10^5, longevity 20 yrs	Monterey to San Diego	Morphology (tympanic spines)	Sta. Barbara/San Diego	Love and Larson (1978)
Microstomus pacificus (Dover sole)	Deep ocean slopes	Planktonic larvae	Bering Sea to San Diego	mtCR	None	Stepien (1999)
Sebastolobus spp. (thornyheads)	Deep ocean slopes	1 to 2 months planktonic larvae, fecundity 10^4–10^5	Bering Sea to San Diego	mtCR	None	Stepien et al. (2000)
Gobiesox maeandricus (northern clingfish)	Rocky intertidal	Planktonic larvae,	Alaska to Monterey	mtCR	Two clades: Strait of Georgia / other pops	Hickerson and Ross (2001)
Oxylebius pictus (painted greenling)	Shallow rock reefs	Territorial, demersal eggs, 1–3 mo planktonic larvae	British Columbia to Pta. San Carlos	9 allozyme loci	Monterey Bay/Sta. Barbara	Davis et al. (1981)
Embiotoca jacksoni (black perch)	Subtidal rocky shore surface to 50 m	Live bearing, phylopatric, fecundity 8–60, longevity 4–10 yrs	Fort Bragg to south of Punta Eugenia	Allozyme loci mtDNA (CR)	Yes across Punta Eugenia LAR > Pta. Eugenia ≈ BigSur/MB	Waples (1987) Bernardi (2000)
Eucyclogobius newberryi (tidewater goby)	Estuaries and coastal lagoons (no marine phase)	Eggs brooded in burrows, ~3 d planktonic larvae, later stages are benthic, fecundity 10^2–10^3, longevity 1–3 years	California	mtCR, cytochrome b nDNA (CK6)	mtDNA: LAR > MB/PtB > Big Sur ≈ SC/PtA > Seacliff; nDNA none.	Dawson et al. (2001)
Embiotoca lateralis (striped seaperch)	Subtidal rocky shore surface to 40 m	Live bearing, phylopatric, fecundity 18–92, longevity 6–10 years	Alaska to Punta Banda	mtCR	LAR	Bernardi (2005)
Fundulus parvipinnis (California killifish)	Estuaries	Planktonic larvae	Santa Barbara to south of Punta Eugenia	mtCR	Pta. Eugenia	Bernardi and Talley (2000)

TABLE 2-3 (continued)

Species: Fishes	*Habitat and Depth*	*Life History**	*Range Sampled*	*Marker*	*Phylogeographic Structure*	*Reference*
Girella nigricans (opaleye)	Nearshore, shallow reefs	Several months-long planktonic larvae, fecundity 10^5	LA Region to south of Pta. Eugenia	26 allozyme loci	None	Waples (1987)
			San Luis Obispo to Bahia Ascuncion	mtCR	Pta. Eugenia	Terry et al. (2000)
Gillichthys mirabilis (longjaw mudsucker)	Estuaries, lagoons	Planktonic larvae, estuaries and nearshore waters,	Monterey Bay to south of Pta. Eugenia	cytochrome b	mtDNA: Break at or between LAR and/or Pta. Eugenia	Huang and Bernardi (2001)
				nDNA (CK7)	nDNA - none.	
Anoplarchus purpurescens (high cockscomb)	Intertidal to 30 m	Benthic egg mass, larvae in shallow water for few days	Puget Sound to San Luis Obispo	2 allozyme loci morphology	Weak break at Monterey Bay	Sassaman and Yoshiyama (1979)
Clinocottus analis (wooly sculpin)	Rocky inter-/sub-tidal to 20 m	Benthic eggs; nearshore, few wks planktonic larvae, fecundity 10^2–10^3	Monterey Bay to south of Pta. Eugenia	10 allozyme loci	San Simeon/Pt. Conception	Swank (1979) [weak]
				26 allozyme loci	Significant with distance	Waples (1987)
Alloclinus holderi (island kelpfish)	To depth 50 m larvae inshore?	Brief larval stage, fecundity 10^3	LA Region to south of Pta. Eugenia	26 allozyme loci	None 1 locus significant, $F_{ST} < 0.2$	Waples (1987)
Caulolatilus princeps (ocean whitefish)	Shallow water to 136 m, larvae inshore-offshore	Few months in plankton? Fecundity 10^5, longevity 13 years	LA Region to south of Pta. Eugenia	26 allozyme loci	None	Waples (1987)
Chromis punctipinnis (blacksmith)	Shallow water to 61 m, larvae inshore-offshore	Few months in plankton? fecundity 10^5	LA Region to south of Pta. Eugenia	26 allozyme loci	None	Waples (1987)
Paralabrax clathratus (kelp bass)	Larvae mostly inshore	4 weeks in plankton? Fecundity 10^5, longevity 30–34 years	LA Region to south of Pta. Eugenia	26 allozyme loci	None	Waples (1987)
Semicossyphus pulcher (California sheephead)	Larvae in/offshore; Rocky reef, kelp, intertidal to 85 m	37 to 78 days planktonic larvae, fecundity $3*10^4$ to $3*10^5$, longevity 20–29 yrs	LA Region to south of Pta. Eugenia	26 allozyme loci	None	Waples (1987)
			Pacific/Gulf	mtCR	None	Bernardi et al. (2003)
Medialuna californiensis (halfmoon)	Larvae inshore/offshore	Few months in plankton? fecundity 10^5	LA Region to south of Pta. Eugenia	26 allozyme loci	None	Waples (1987)
Gibbonsia spp (kelpfishes)	Neashore to 50 m	>2mo. larvae inshore fecundity 10^2–10^3	Monterey Bay to Guadalupe Is.	40 allozyme loci	Evidence of divergent forms on Guadalupe Is.	Stepien and Rosenblatt (1991)

NOTE: mtCR, mitochondrial control region; nDNA (CK) nuclear Creatine Kinase intron.

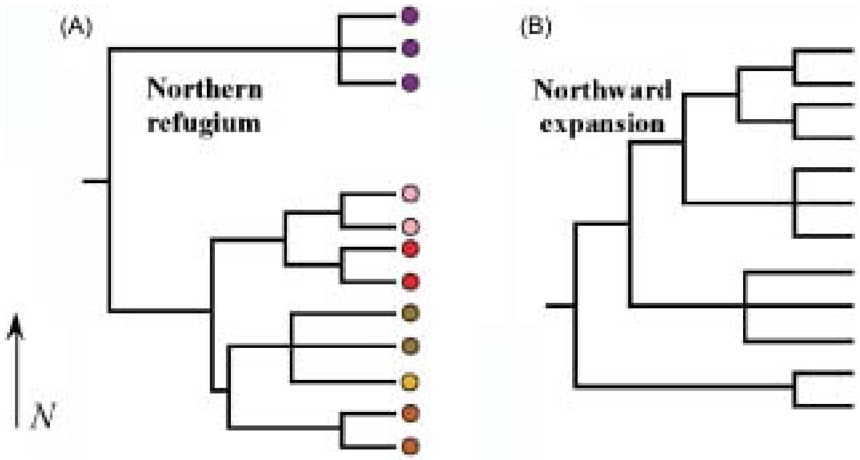

FIGURE 2-4 Phylogenetic trees expected to result from two different evolutionary histories. A. Vicariance, in this case involving a northern glacial refugium, although similar patterns could result from isolation of warm-water species in a refugium in, say, Tomales and Monterey Bays. Colored circles show the mitochondrial haplotypes used to reconstruct the phylogeny; note that they represent only a small portion of the evolutionary history of the species (see fig. 2-5A) and that some extant haplotypes may remain unsampled. B. Northward expansion resulting from, for example, climate warming that might result from deglaciation at high latitudes or northward movement of isotherms at lower latitudes. These patterns might also be reversed, indicating southward expansion or a cold-water refugium in the south, or occur on an east–west axis, consistent with colonization or isolation involving, for example, the Sea of Cortez.

permanent terrestrial feature only approximately 1 My BP (Nardin and Henyey, 1978; Ward and Valensise, 1994); the Los Angeles Region (LAR) remained fully or partially submerged; and Redondo Canyon did not exist until approximately 0.7 My BP (Nardin and Henyey, 1978; Vedder and Howell, 1980; Davis et al., 1989).

These changes inevitably affected the distribution of habitat and local environmental conditions. For example, uplift of the California Channel Islands and numerous submerged banks reduced exchange between the Southern California Bight and surrounding oceanic and coastal waters (Owen, 1980) increasing the mean residence time (currently about 3±14 days; Hickey, 1992) and facilitating a warming of surface waters in the Bight (e.g., Caldeira and Marchesiello, 2002). Reduced flow along the mainland coast likely was effected largely by constriction of a narrow seaway between the Northern Channel Islands and Point Hueneme but was also contributed to by the Palos Verdes peninsula which now interrupts longshore drift, causes eddies and localized upwelling, and modifies wind and wave patterns. The emergence of LAR during the Late Pleistocene eradicated much coastal habitat such as estuaries at the feet of the hills that now surround Los Angeles (fig. 2-6 of Vedder and Howell, 1980) although, at the same time, some replacement estuaries developed along the new coastline (as indicated by the currently submerged canyons at Redondo, Santa Monica, and Point Heuneme). Uplift of LAR also probably opened shortened migratory routes or allowed secondary contact between previously isolated shallow-water coastal fish populations north and south of LAR.

Tectonism also influenced weather patterns in California with effects recorded in coastal waters (Lyle et al., 2000). For example, a low deposition event, indicating low productivity, in the California Borderlands during the late Miocene to early Pliocene may be linked to the initiation of San Andreas fault motion around 6 My BP. Uplift of the Sierra Nevada mountains, from 2km elevation 3 My BP to 3 km elevation now, apparently trapped additional precipitation over western California contributing to increased sediment load out of the mountain range from the Pliocene to the Holocene. Interestingly, these sediments accumulated in the Central Valley "Lake Clyde" (Sarna-Wojcicki, 1995) until approximately 0.5 My BP when the lake emptied, as indicated by an increase in predominant particle size and rate of sedimentation (Lyle et al., 2000). Analogous changes likely accompanied building of the Santa Ynez and other mountain ranges in southern California.

Climate Change, Sea Level, and Coastal Conditions

Periods of glaciation likely exacerbated many of the effects of tectonism. Glacially lowered sea level would have rapidly increased the mass of islands in the Southern California Bight, further constricting seaways such as those between the Northern Channel Islands and Point Hueneme, inevitably altering coastal hydrography (Lindberg and Lipps, 1996) and possibly isolating some basins (e.g. Lyle et al., 2000). Lowered sea level also led to increased coastal erosion (Lyle et al., 2000). Although trends across the region are similar, signals also differ considerably between locales, indicating variation within the region, for example, in erosion and deposition (e.g., Lyle et al., 2000).

As in the *Cordilleran* region, glacial cycles affected more southerly regions, as is evident in, for example, records of depressed SSTs. Some floral and faunal planktonic assemblages suggest that sea surface and air temperatures of southern California were considerably cooler (e.g., 6–10°C) during some Pliocene and Pleistocene glaciations than at present (Powell, 1994; Mortyn et al., 1996; Davis, 1999). Abundances of the left-coiling foram *Neogloboquadrina pachyderma* have been posited to indicate SST in the California Borderlands as much as 8°C cooler than present (i.e. about 7–8°C SST at LGM, approximately the same as off Oregon now; Kennett and Venz, 1995; Thunell and Mortyn, 1995). However, these extreme temperatures have been disputed because these plankters also occur in

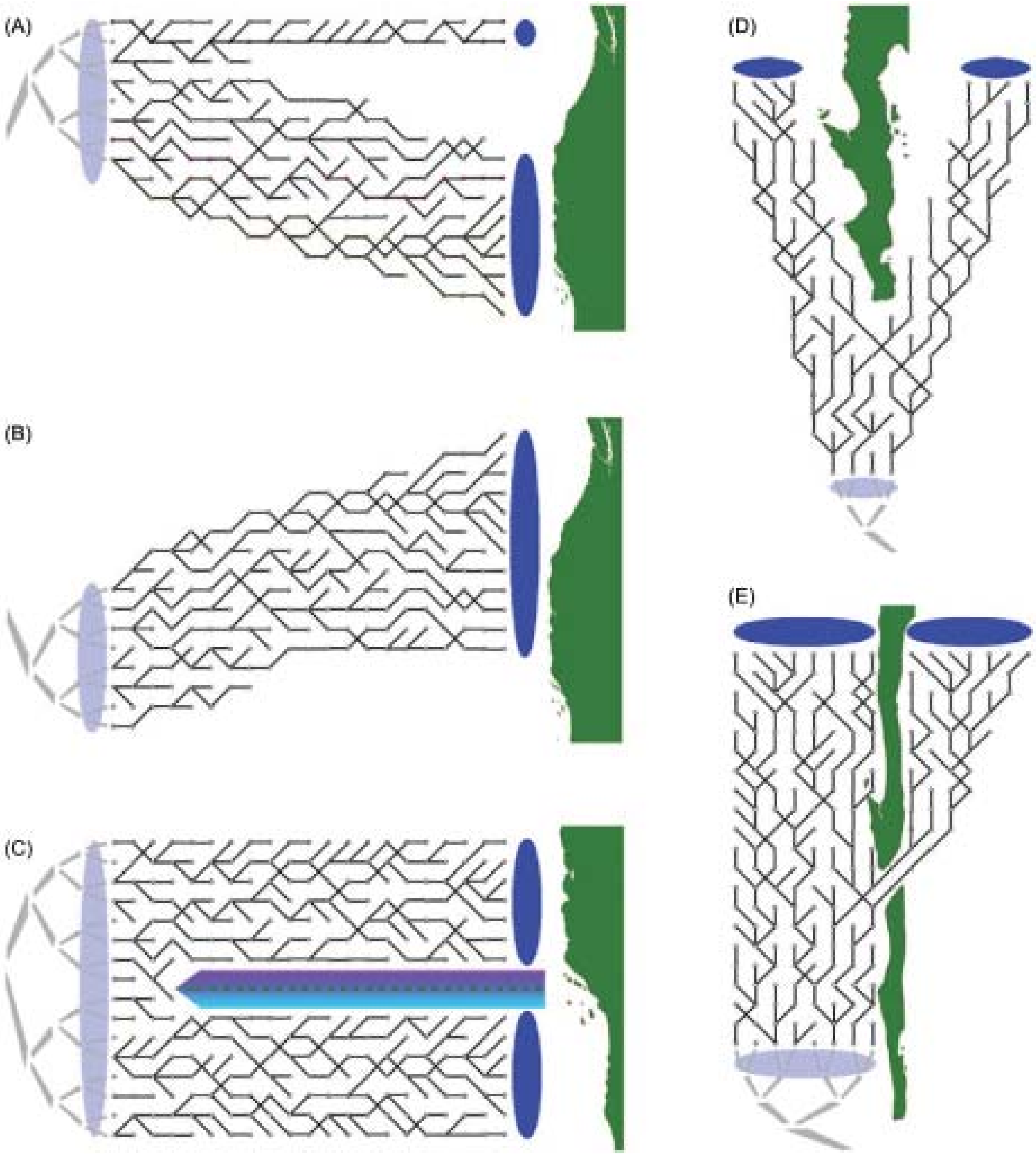

FIGURE 2-5 Schematic representations of the matrilineal inheritance and sorting of mitochondrial DNA, a complicated demographic, ecological, and evolutionary process of which we see only a small fraction in reconstructed phylogenies (compare panel A with fig. 2-4A). Five hypothetical patterns are shown; large gray branches represent prior evolutionary history, faint blue shading indicates the original range, black lines represent matrilineal inheritance, and circles are haplotypes. A. Southward shift of range accompanying incomplete glaciation which also leaves a northern refugium;a change of color in inherited haplotypes indicates mutation. B. Northward range shift and expansion accompanying deglaciation. C. Vicariance of existing wide range due, for example, to tectonic uplift or sea level lowering. D. Shift of range from the tip of a peninsula northward along opposing coastlines leading to disjunct populations, possibly associated with deglaciation. E. Dispersal through a temporary seaway followed by vicariance due, for example, to tectonic uplift, leads to disjunct populations. Note that similar patterns may also result from other processes in different regions. Modified from Grant and Waples (2000) and Avise (2000).

abundance associated with SSTs of 12°C (Lyle et al., 2000 and references therein) and other reconstructions of SST concomitantly estimate less extreme conditions, only 2–3°C cooler than present (Herbert et al., 1995; Yamamoto et al. 2000; Ostertag-Henning and Stax, 2000). It is possible that the extreme estimates from plankton represent relatively short excursions that influenced highly vagile organisms or extralimital observations (Muhs et al., 2002), as El Niño events influence extralimital observations today, but were not matched by redistribution of other less vagile organisms such as the vast majority of coastal invertebrates. It is also possible that changes were moderated considerably in nearshore waters, such as those

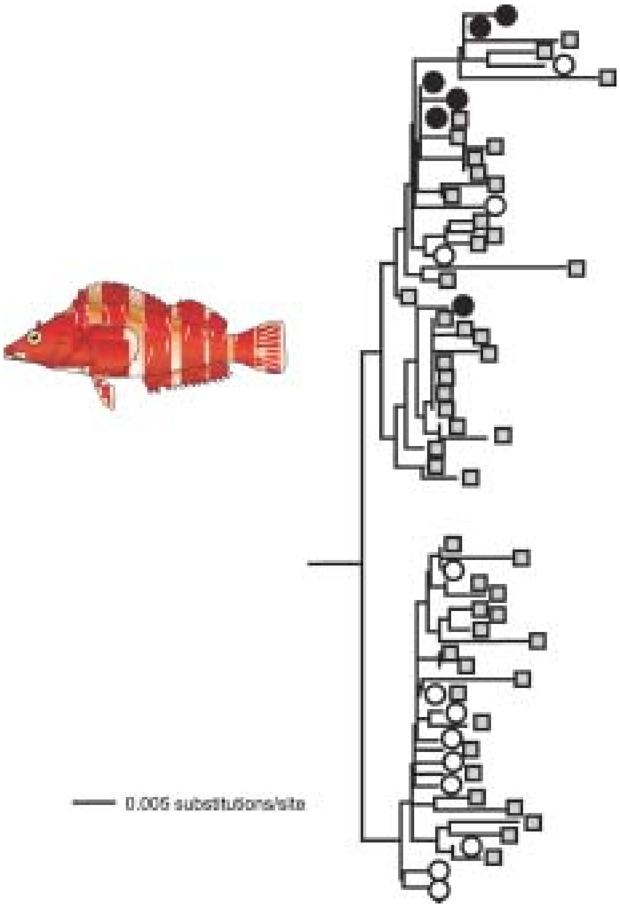

FIGURE 2-6 Molecular phylogeny of *Oxylebius pictus* (Bernardi, unpubl.) based on mitochondrial control region sequences from southern (La Bufadora, Baja California, Mexico; white circles) and northern (Kelvin Grove, British Columbia, and Queen Charlotte Island; black circles) individuals. Gray squares represent individuals from intermediate locations: Bodega Bay, Monterey Bay, Anacapa Island, Palos Verdes, and Point Loma).

protected by the Borderlands within the Southern California Bight (fig. 2-3); embayments contained consistently warmer water faunas than open coastal regions during cooling trends (Jacobs et al., 2004). However, the controversy over how extreme the changes were in SSTs off California during the glaciations remains far from settled.

Glaciation did lead to a cooler wetter climate in southern California, increasing the flow through coastal canyons and their impact on longshore transport and local habitat and likely increasing the frequencies of catastrophic floods (e.g. Schimmelmann et al., 1998). Conversely, during drier periods, as some in the Holocene (Stine, 1990; Davis, 1999), droughts may have had equally severe impacts on coastal lagoons and wetlands. Thus, climate change presumably shifted conditions suitable for habitation to more southerly latitudes, only for them to expand northward again during interglacials. The fossil record shows that climate change did affect the distribution of coastal organisms, generally pushing faunas southward during glaciation and allowing them to expand northward during deglaciation, and that these effects were probably less extreme at lower latitudes in the eastern Pacific Ocean (Valentine, 1958; Addicott, 1966; Valentine, 1966; Johnson, 1977; Graham and Grimm, 1990; Fields et al., 1993; Mortyn et al., 1996; Davis, 1999). However, modern oceanographic conditions appear to have persisted in the area for at least the last 3.5 My BP, although conditions were not constant. (The disparity in SST between Oregon and central California, for example, suggests that the California Current flow weakens during glacial maxima, decreasing to ~60% of its strongest flow compared to strong interglacials [Lyle et al., 2000]). Therefore, at least during a few of the cool Pleistocene highstands, the Oregonian-San Diegan faunal boundary occurred in the vicinity of LAR (Valentine, 1958; Addicott, 1966), and faunal distributions were also similar during some periods of warmer climate (Gobalet, 2000).

Preliminary analyses of a number of California fishes reveal genetic patterns that are consistent with different aspects of these historical scenarios. For example, the phylogeographic structures of the tidewater goby, *Eucyclogobius newberryi,* and black perch, *Embiotoca jacksoni,* suggest derived haplotypes and shallower evolutionary history in the north of their ranges (fig. 2-7; Bernardi, 2000; Dawson et al., 2001; see also figs. 2-4B, 2-5B). In the next section, we focus on phylogeographic patterns associated with the climatically more stable, but physically more variable, region in southern California.

Phylogeography and Biogeography

The long-term stability of the position of departure of the massive cold California Current from the coast at Point Conception has been posited as a major factor influencing California coastal biogeography (Briggs, 1974) and phylogeography (Burton and Lee, 1994). Environmental discontinuities (ecotones) at biogeographic 'boundaries' are expected to inhibit movement physically, tax the physiologies of species beyond their limits, or put them at selective disadvantages resulting in limited, or in the extreme, zero realized migration across the "boundary." Thus, much of the early work in the region focused on determining whether the Point Conception biogeographic break and genetic discontinuities of fish populations coincided. Morphological work on kelp rockfish, *Sebastes atrovirens*, and midshipman, *Porichthys notatus* (Love and Larson, 1978; Thompson and Tsuji, 1989), and early genetic work using allozymes in painted greenling, *Oxylebius pictus* (Davis et al., 1981), were consistent with Point Conception as a zone of genetic transition. The other major work indicating a phylogeographic break at Point Conception is a study of the invertebrate intertidal copepod *Tigriopus californicus* (Burton and Lee, 1994). However, further investigations of *T. californicus* with additional sites and markers and a review of existing data on invertebrates indicated that, although there was a small break, Point Conception was not a major region of genetic discontinuity for populations of marine species (Burton, 1998). This result has been supported by analysis of painted greenling using mtCR (Bernardi, unpubl.).

In recent years, two phylogeographic studies of fish populations have focused on this region (Bernardi, 2000; Dawson et al., 2001), providing an opportunity to compare patterns between species with overlapping ranges. The first described the black surfperch, *Embiotoca jacksoni*, which like other species of surfperches (Embiotocidae) broods its young and displays very little dispersal potential (Bernardi, 2000). The second focused on a small estuarine gobiid, the tidewater goby, *Eucyclogobius newberryi* (Dawson et al., 2001), which also displays minimal dispersal potential. The patterns found in the two species were remarkably similar to each other (fig. 2-7) and with that of *T. californicus* (Burton, 1998). All three species showed a major phylogeographic break in the Los Angeles

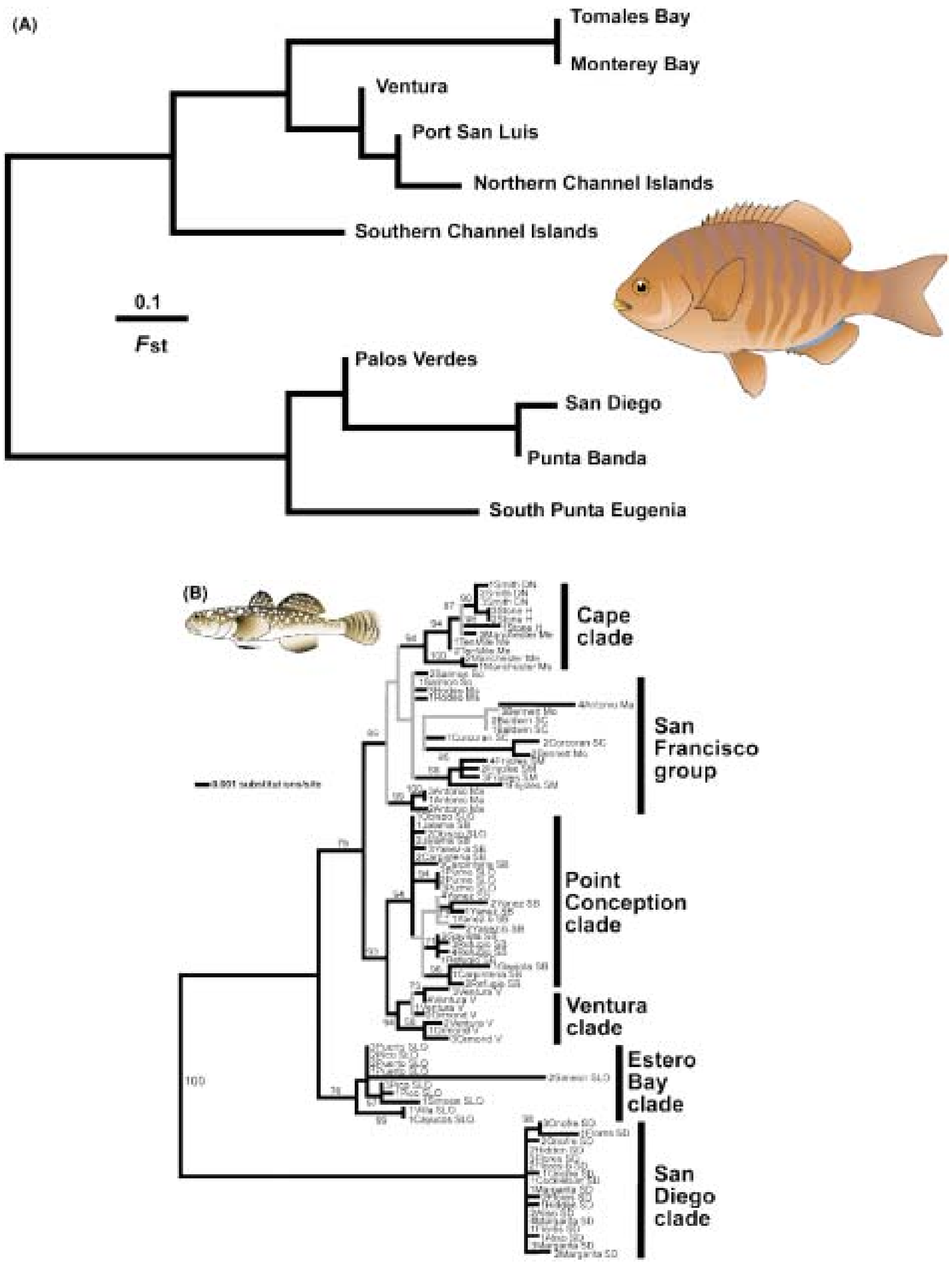

FIGURE 2-7 Phylogeographic structure of California fishes showing discontinuities in the Los Angeles Region. A. Relationships among populations of black perch, *Embiotoca jacksoni*, reconstructed by neighbor-joining analyses of pairwise population F_{st} values (scale bar indicates F_{st} of 0.1; from Bernardi, 2000). B. Phylogeographic structure in the tidewater goby, *E. newberryi*, as indicated by maximum likelihood analyses of combined mitochondrial cytochrome b and control region (redrawn from Dawson et al., 2001). Dashed branches were not present in all reconstructions. Numbers above branches indicate percent support calculated by quartet puzzling.

Region (LAR). Black perch populations sampled extensively in that region indicated that Santa Monica Bay was the precise area of the genetic break (see also Edmands et al., 1996). Recent extirpation of key populations of tidewater gobies in the region prevented similarly fine-scale conclusions based on genetic data, but subsequent analysis of the sensory canal system of tidewater goby in museum specimens shows an abrupt change in morphology in the vicinity of Palos Verdes (Ahnelt et al., 2004). Thus, there is strong evidence that a relatively short stretch of coastline in the LAR is the site of processes that have severely restricted gene flow in multiple coastal marine species. A review of molecular data for over 30 species reinforced the idea that this region was an important zone of genetic transition (Dawson, 2001) and, most recently, new molecular data on the striped seaperch, *Embiotoca lateralis*, have again revealed a pattern almost identical to that of its sister species, the black surfperch (Bernardi, 2005). Thus, at present, three species of fishes, and an invertebrate, have geographically concordant phylogeographic gaps in the LAR. Variation in the depths of these breaks suggests somewhat different evolutionary histories in these taxa. This is perhaps related to ease of extirpation, timing of original divergence, and disposition to erode breaks by subsequent gene flow, but also reinforces the view that clustering of phylogenetic gaps in this region results from long-term processes.

This has left an apparent discrepancy between the placement of the traditional biogeographic boundary (at Point Conception) and phylogeographic breaks (at LAR). Such a discrepancy might conceivably result from a number of factors, including decoupling of factors influencing biogeographic and phylogeographic patterns (Burton, 1998) and the migration of boundaries with changing climate (Addicott, 1966). However, reconsideration of biogeographic data suggests that, in this case, it most probably is a misconception (Dawson, 2001). Although Point Conception is often cited as the principal biogeographic boundary in California, none of the three related measures that are often used to estimate the position of biogeographic boundaries, (1) concentrations of range termini of many widely distributed species, (2) peaks in edge-effect species, and (3) regions of high species richness (e.g., Newell, 1948; Valentine, 1966; Seapy and Littler, 1980; Longhurst, 1998; Briggs, 1974; Hayden and Dolan, 1976; Doyle, 1985) support that assignment. Rather, LAR is indicated as the site of the predominant biogeographic boundary. The range termini of fishes peaks at 33° N (Horn and Allen, 1978; and Chapter 1, this volume), and the highest densities of range termini, of "edge-effect" species, and of the most species-rich assemblages of marine algae and mollusks occur between 33° and 34° North (fig. 2-3; Murray et al., 1980; Newell, 1948; Valentine, 1966; Murray and Littler, 1980). The number of 1° species, species-richness, and the number of range terminations are fewer, and usually considerably fewer, between 34° and 35°N, the degree of latitude that encompasses Point Conception (Newell, 1948; Valentine, 1966; Horn and Allen, 1978; Murray and Littler, 1980).

In retrospect, the implication of LAR, rather than Point Conception, as the site of long-term barriers to gene flow makes some sense. Though Point Conception has been a relatively stable coastal feature associated with the California Current and changes in dominant plankton for millions of years (Maruyama, 2000), which might reflect suitable conditions for stable long-term differences to arise, it is also associated with features that could inhibit or break down such patterns. Point Conception is part of an open coastline along which relatively quick currents flow in opposite directions at different times of year and from which eddies are frequently shed into the Santa Barbara Channel, i.e., it is a point that would seem to foster relatively high gene flow. In contrast, during the last several millions of years—the timescale we are dealing with in the evolution of structure in surfperches and tidewater goby—coastal southern California has undergone dramatic metamorphoses that likely would limit genetic exchange in coastal marine taxa.

Other Areas in California

Lesser genetic heterogeneities occur elsewhere in California, most notably in the Monterey Bay Region (e.g. Bernardi, 2000; Dawson et al., 2001) consistent with distributional evidence of a secondary biogeographic discontinuity also linked to physical discontinuities attributable to tectonism, oceanography, and habitat distribution (Dawson, 2001). As such, we suggest that these lesser breaks result from a subset or suite of processes similar to those in the LAR, but perhaps less severe, and therefore do not discuss them in detail here.

BAJA CALIFORNIA

Geological, Geographic, and Oceanographic Setting

The eastern Pacific coastline at approximately the modern latitudes of Baja California, circa 30 My BP, had features reconcilable with the modern geography of the peninsula (Helenes and Carreño, 1999). The late Oligocene also saw the tectonic movements that presaged the formation of peninsular California which had begun to separate from mainland Mexico by the middle Miocene, as indicated by the establishment of a protogulf. The peninsula has resembled its current configuration for over 5 My (Helenes and Carreño, 1999: Carreño and Helenes, 2002; fig. 2-3). Modern eastern North Pacific oceanographic conditions were probably established by the middle Miocene and certainly by the late Miocene (Helenes and Carreño, 1999, and references therein). This is indicated by Pacific coast deposits and biogenic sediments from an inland sea east of the forming peninsula characterized by mixed temperate and tropical flora and fauna that may have entered via a central transisthmian seaway (Helenes and Carreño, 1999, and references therein).

The Pacific coast of Baja California is characterized by long stretches of sandy coastline occasionally fragmented by rocky outcrops. One of the major geographic features of the region is Punta Eugenia (~28°N; fig. 2-3), approximately halfway between the peninsula's northern and southern ends, like a large barb on an otherwise straight hook. At Punta Eugenia, the California Current from the north meets a warmer current from the south which, in association with the San Benito islands just off shore from Punta Eugenia, creates a complex oceanography in the region. A massive estuary complex (Ojo de Liebre) lies just north of Punta Eugenia, and a very long stretch of sandy shore lies to the north of Ojo de Liebre. The southern portion of the Baja California Peninsula has very large bays and estuaries, Bahía San Ignacio and Bahía Magdalena. The latter corresponds to the transition zone between the San Diegan biogeographic province and the Panamic biogeographic province (Chapter 1). Thus, we will not discuss the features of Bahía Magdalena and its southern Panamic fauna beyond noting that this probably has been the site of this boundary, approximately, on and off for quite some time.

Climate Change

Current evidence indicates that climatic excursions associated with glacial cycles may not have been large in Baja California. The distributions of fossil fauna indicate that the warm-temperate Verdean Province probably occupied much the same range as its Holocene analog, the San Diegan Province (Addicott, 1966; Fields et al., 1993; fig. 2-3). Thus, the northern extent of the Magdalenan region—the region of overlap between San Diegan and Panamic provincial faunas—may have been relatively stable, perhaps in the vicinity of Punta Eugenia, 28°N (Addicott, 1966; fig. 2-3). Analyses of fossil molluscan assemblages, which are most strongly indicative of distributions during interglacials, show peaks in the number of end points and 1° endemics at 27–28°N (also at 30°N and 25°N; Valentine, 1966). Although there was also an accumulation of end points at 23°N, there was no concomitant peak in 1° endemics (Valentine, 1966). This fits with arguments that the southern extent of the Magdalenan region, where the Verdean Province is supercsded by the northern limit of the tropical Panamic fauna, may have migrated from its currently recognized position at Magdalena Bay southward past the tip of Baja California Sur and then north again with each glacial cycle. On the whole, however, biogeographic zones along the Pacific coast of Baja California probably changed little, at least compared to regions further north (Fields et al., 1993).

Part of this stability was likely due to the reduced influence of the California Current this far south, whose weakening during the latest Miocene and Pliocene did have considerable effects on SST, recorded in diatom assemblages, north of Point Conception and evident at least as far south as 30–31°N (Maruyama, 2000). Analogous events probably also occurred more recently (Pisias, 1978). For example, the weakening of the California Current occurred during high latitude warming (Barron, 1981; Muhs et al., 2002), conditions resembling modern El Niño patterns [including reduced upwelling] (Maruyama, 2000). Consequently, an idea of the potential effects in more southerly parts of Baja California during this period can be gleaned by examining oceanographic changes from the 1980s and 1990s (Hernandez-Trujillo, 1999; Durazo and Baumgartner, 2002; see also Schwing et al., 2002).

PHYLOGEOGRAPHY

Conceptually, the area of Punta Eugenia is similar to Point Conception and the LAR. For example, it is an obvious geographic feature that strongly influences local oceanography, and adjacent regions are physiographically quite distinct. Punta Eugenia also has been proposed as the site of an important biogeographic break. The obvious question then, is whether phylogenetic gaps are concordant with a biogeographic break at Punta Eugenia. DNA sequence data pertinent to this question are available from six species of fish: the California killifish (*Fundulus parvipinnis)*, opaleye (*Girella nigricans*), black perch (*Embiotoca jacksoni*), longjaw mudsucker (*Gillichthys mirabilis*), spotted sand bass (*Paralabrax maculatofasciatus*), and sargo (*Anisotremus davidsonii*). In all cases, genetic discontinuities were found across Punta Eugenia (figs. 2-8 and 2-9; but see Tranah and Allen, 1999). Due to sometimes limited geographic sampling, however, it is difficult to determine precisely where discontinuities occur (or even to exclude the alternative of isolation by distance) and, therefore, which factors may have been the dominant influence. Though the lack of habitat in itself could contribute to the separation, as has been hypothesized for biogeographic discontinuities in other regions (Hastings, 2000; see Chapter 1), it is not yet possible to distinguish its contribution from that of ocean currents in the region, although coastal fishes show lower gene flow than offshore fishes (Waples, 1987; Waples and Rosenblatt, 1987), suggesting a role for nearshore processes. Only samples of the estuarine California killifish were obtained at Ojo de Liebre and, in this case, the genetic discontinuity was found between the Ojo de Liebre population and the one south of Punta Eugenia at La Bocana (fig. 2-8; Bernardi and Talley, 2000). Though this implicates Punta Eugenia as a potentially important factor in generating phylogeographic structure, it does not exclude other influences within that ~200 km stretch of coastline. More work is obviously needed in the region.

GULF OF CALIFORNIA

Evolutionary Setting

Much of the pertinent information regarding the geography, climate, and sea level of Baja California was discussed in the previous section. These include a hypothesized, relatively stable biogeographic structure on the Pacific coast of the Peninsula for the last several millions of years, with the exception of the southern limit of San Diegan taxa, which may have extended well south of Cabo San Lucas during periods of glaciation. To interpret genetic patterns in the region, a few additional details are necessary, specifically those pertaining to the opening of the Gulf of California, and possible routes of communication with the Gulf from the eastern Pacific (fig. 2-3).

The rift valley that became the Gulf of California is first evident in the middle Miocene, approximately 12 My BP (Helenes and Carreño, 1999). Marine deposits with mixed tropical and temperate floras and faunas in a central protogulf sea suggest similar oceanographic conditions in the Pacific Ocean and a transisthmus seaway in the vicinity of San Ignacio by the late Miocene, ~8 My BP (Carreño and Helenes, 2002). By this time, the protogulf had extended and reached depths of at least 150 m (Helenes and Carreño, 1999). A separate marine embayment also formed south of the protogulf (Helenes and Carreño, 1999). The Gulf of California in its modern configuration was probably largely established around 5–4 My BP when the protogulf and southern embayment merged, opening the mouth of the Gulf (Helenes and Carreño, 1999; Carreño and Helenes, 2002).

More than 40 fish species have been described as disjunct across the Baja California peninsula, in the northern Sea of Cortez versus Pacific Baja California and/or California (Present, 1987). However, only 19 species, representing a highly variable assemblage of taxonomic and ecological groups encompassing 14 families, are unequivocally disjunct. Each of the disjunct species is absent or rare in the warmer southern waters of the Cape region (Cabo San Lucas), and the majority exhibit morphological differences between Gulf and Pacific coast populations (Walker, 1960), although differences are usually small and often limited to color variations. Questions of the origin, relationships, and divergence among the disjunct species have stimulated molecular investigations into levels of genetic isolation (Crabtree, 1983; Orton and Buth, 1984; Present, 1987; Terry et al., 2000; Huang and Bernardi, 2001) and can be framed in the context of specific dispersal/vicariance hypotheses (Avise, 2000; Grismer, 2000). The restriction of disjunct species to the northern colder waters of

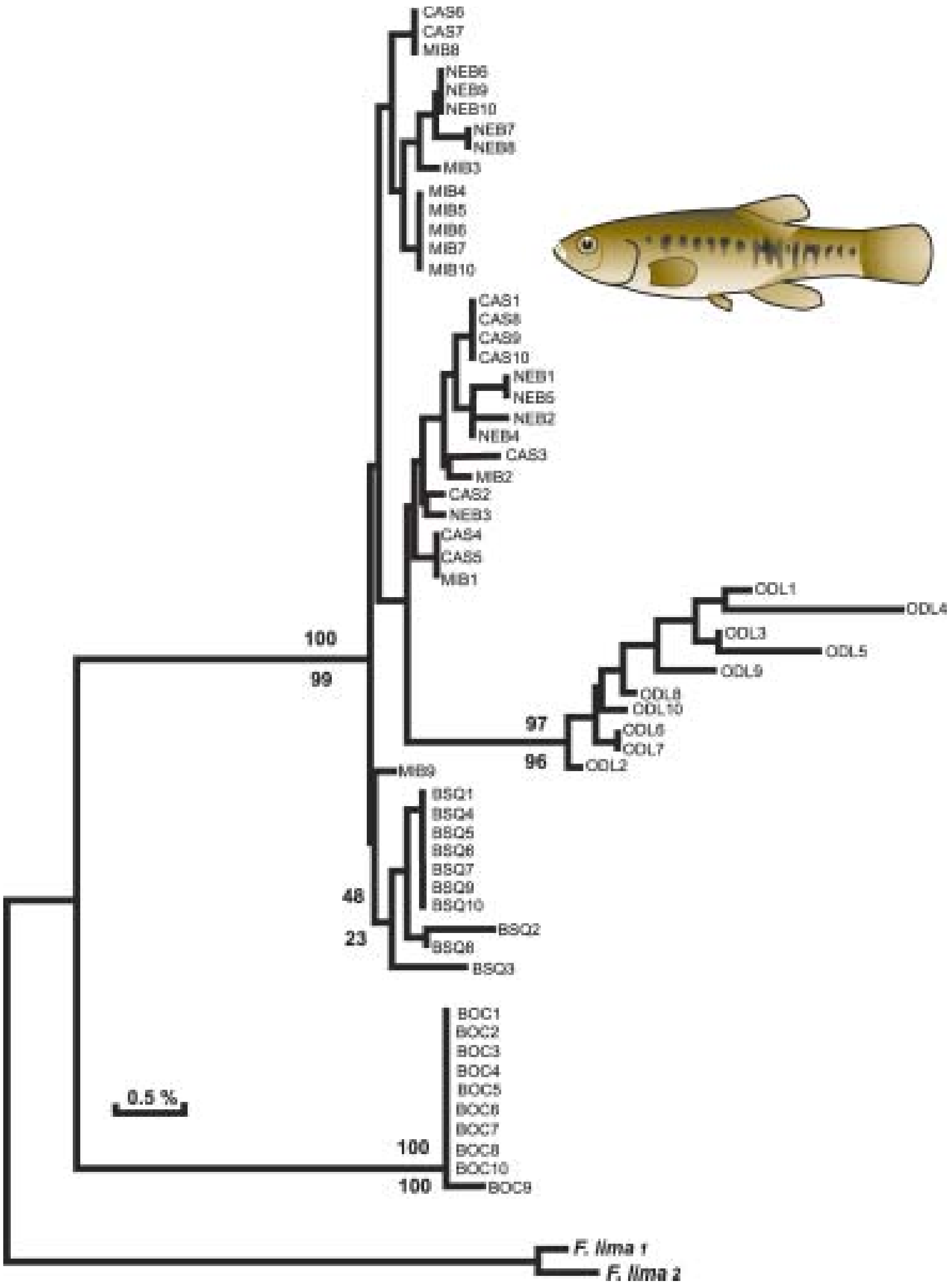

FIGURE 2-8 Mitochondrial control region (D-loop) gene tree for *Fundulus parvipinnis* (from Bernardi and Talley, 2000). Labels correspond to sampling localities as follows (from north to south): north of Punta Eugenia: Carpinteria Slough (CAS), Newport Bay (NEB), Mission Bay (MIS), Bahia San Quintin (BSQ), Ojo de Liebre lagoon (ODL), and south of Punta Eugenia: La Bocana (BOC). The tree is rooted using *Fundulus lima* as an outgroup. Bootstrap support higher than 70% is shown above the nodes (for the neighbor-joining method) and below the nodes (for the maximum parsimony method).

the Gulf of California may have resulted from two different processes: (1) dispersal during periods of oceanic cooling associated with glacial events (between 1 My BP and 10,000 BP; Brusca, 1973) or (2) vicariance with the closing of Neogene transisthmus waterways connecting the Gulf of California to the Pacific (>1 My BP; Riddle et al., 2000a,b,c). Furthermore, on the basis of geological, biogeographic, and molecular analyses of terrestrial fauna (Walker, 1960; Murphy, 1983; Grismer, 1994; Upton and Murphy, 1997; Carreño and Helenes, 2002; Murphy and Aguirre-Léon, 2002), three scenarios for dispersal via Neogene waterways have been posited. One, a Pliocene (~5-3 My BP) seaway connecting the northern Gulf of Mexico to the Pacific Ocean around Ensenada. Two, a Pliocene (~4-3 My BP) seaway connecting the southern Gulf of Mexico to the Pacific Ocean around La Paz. Three, a Pliocene (5 or 3 [but not 4] My BP) or middle Pleistocene (ca. 1 My BP) seaway connecting the central Gulf of Mexico to the Pacific Ocean south of Punta Eugenia and north of Santa Rosalia (fig. 2-3). These scenarios generate specific hypotheses regarding the evolutionary histories of fishes in this region that can be tested using the phylogeographic approach (e.g., fig. 2-5C,D).

Phylogeography

Molecular analyses of 12 disjunct species (table 2-4), using allozyme, RFLP, and DNA-sequence data, revealed two distinct patterns of phylogenetic relationships. The first pattern, evident in eight species, was of distinct Gulf and Pacific clades (fig. 2-9A) between which there were many fixed differences ($0.97 \geq F_{st} \geq 0.51$; $0.01 \leq \mathrm{Nm} \leq 0.48$); sequence divergences between Gulf and Pacific populations varied from 1.06% to 11.6% in mtCR and from 1.34% to 2.21% in cytochrome b (table 2-5). The second pattern, evident in the remaining four species, was of indistinct Pacific and Gulf populations ($0.00 \leq F_{st} \leq 0.02$; Fig. 2-9B; table 2-5). These two major patterns between Gulf and Pacific populations may reflect, respectively, vicariant events (fig. 2-7A) or high levels of gene flow (fig.-7B). However, questions remain as to the timing of vicariant events and whether apparent gene flow reflects recent massive dispersal or ongoing dispersal at lower levels.

Of the eight species showing fixed differences between the Gulf and Pacific, populations of three—blue-banded goby, spotted bass, and orangethroat pikeblenny—were separated by relatively small genetic distances. Using rule of thumb molecular clocks, genetic divergence (table 2-5) between Gulf and Pacific populations were estimated to have occurred between 120,000 and 600,000 years ago in spotted bass (Stepien et al., 2001; but see Tranah and Allen, 1999), 200,000 to 900,000 years ago in orangethroat pikeblenny, and 200,000 to 400,000 years ago in blue-banded goby. The similarity of both pattern and estimated times of divergence suggests that these three species were affected by common extrinsic mechanisms compatible with a Pleistocene separation of disjunct populations (Stepien et al., 2001). But the actual divergence time of Pacific and Gulf populations (which will be smaller than molecular estimates of divergence times [e.g. Knowles, 2004]) may postdate even the most recent transisthmian seaway, making expansion around the cape during glacial periods then separation as populations shift northward during subsequent warming the more likely cause of disjunction (Tranah and Allen, 1999).

Populations of the five species that showed higher levels of sequence divergence (opaleye, grunion, sargo, mussel blenny, and longjaw mudsucker) including many fixed differences, are likely to have separated much earlier (Bernardi et al., 2003). Using molecular clocks, the times of divergence between Gulf and Pacific populations have been estimated at 0.76–2.3 My BP (longjaw mudsucker, *Gillichthys mirabilis*; Huang and Bernardi, 2001), 0.3–2.2 My BP (opaleye, *Girella nigricans*; Terry et al., 2000), 1.3–2.6 My BP for sargo, 0.3–2.0 My BP for mussel blenny, and 0.4–3 My BP for grunion (Bernardi et al., 2003). While the lower end of the potential divergence times is again consistent with Pleistocene separation of disjunct populations after dispersal around the cape, the upper limits are more compatible with vicariance due to closure of more ancient northern transpeninsular seaways 3–1 My BP (e.g., Upton and Murphy, 1997; Riddle et al., 2000a; fig. 2-3). Thus, although geological evidence may leave room for interpretation (Carreño and Helenes, 2002; Jacobs et al. 2004), biological data on terrestrial (Murphy and Aguirre-Léon, 2002) and marine faunas strongly indicate a midpeninsular, Pliocene–Pleistocene, transpeninsular seaway and, interestingly, as has happened before (Rudwick, 1985), may prove to be the decisive evidence. The issue could be further elucidated by comparing the genetic affinities of fishes from north of Punta Eugenia, central Baja (say, between Natividad and Laguna San Ignacio), the southernmost Pacific populations, and their Gulf counterparts. A suite of alternate hypotheses can be tested, including (1) if fish dispersed around the cape, the southernmost Pacific and Gulf populations should be most similar and genetic distances small; (2) if populations were connected via a recent midpeninsular seaway, then central Pacific Baja and Gulf populations should be most similar and genetic distances intermediate; and (3) if populations were connected via an older northern (or alternatively southern) seaway, Gulf and northern (or alternatively southern) Pacific Baja populations should be most similar and genetic distances large. No species studied to date clearly distinguish among these hypotheses. For example, considering *G. mirabilis*, Gulf populations are more similar to populations north of Punta Eugenia (1.9%) than south of Punta Eugenia (2.3%; Huang and Bernardi, 2001), but genetic distances between central Pacific and Gulf populations are consistent with the timing of the midpeninsular seaway (see above); yet, this population south of Punta Eugenia also shares haplotypes with Gulf populations consistent with recent dispersal around the cape (fig. 2-9a); moreover, human introduction also cannot be discounted (Huang and Bernardi, 2001). Irrespective of the route, the similarity of phylogeographic patterns among opaleye, longjaw mudsucker, sargo, mussel blenny, and grunion, together with similar times of divergence among disjunct populations (1.3–2.6 My BP for sargo, 0.3–2.0 My BP for Mussel blenny, 0.4–3 My BP for grunion) suggest that broadly similar historical processes shaped the population structures of these species (Bernardi et al., 2003).

CALIFORNIA ISLANDS

Studies of islands have been central to the growth of ecological and evolutionary sciences for almost 150 years (Darwin, 1859; Wallace, 1880; MacArthur and Wilson, 1967; Grant, 1998). The patterns and processes of evolution by natural selection and genetic drift continue to be elucidated by seminal ecological and evolutionary studies of insular faunas inhabiting oceanic islands, freshwater lakes, headwaters and tributaries, and mountaintops and forests (e.g., Grant, 1998). *The Theory of Island Biogeography* (MacArthur and Wilson, 1967) contributed to and stimulated major advances in ecology, evolution, biodiversity, and conservation biology (Hubbell, 2001) and is merging with other key areas such as metapopulation dynamics (Matter et al., 2002). However, studies of marine taxa that are heavily invested in island biogeographic theory are rare (e.g. Thomson and Gilligan, 2002). In part, this may be because the recent paradigm of marine dispersal did not foster an "island" perspective. For several decades, the oceans were typically thought to be large, essentially well-mixed, interrelated units with few barriers to gene flow and few discrete islands of habitat (Palumbi, 1992, 1994). However, this perspective is changing, and reports of structure in marine organisms, particularly coastal animals, are becoming increasingly common, as in this chapter. It is therefore reasonable to ask whether studies of islands can also make large contributions to the knowledge of patterns of evolution in marine taxa.

There are several series of islands off Pacific North America, including the Farallon Islands, California Channel Islands, San Benito Islands, and Guadalupe Island (plus the islands of

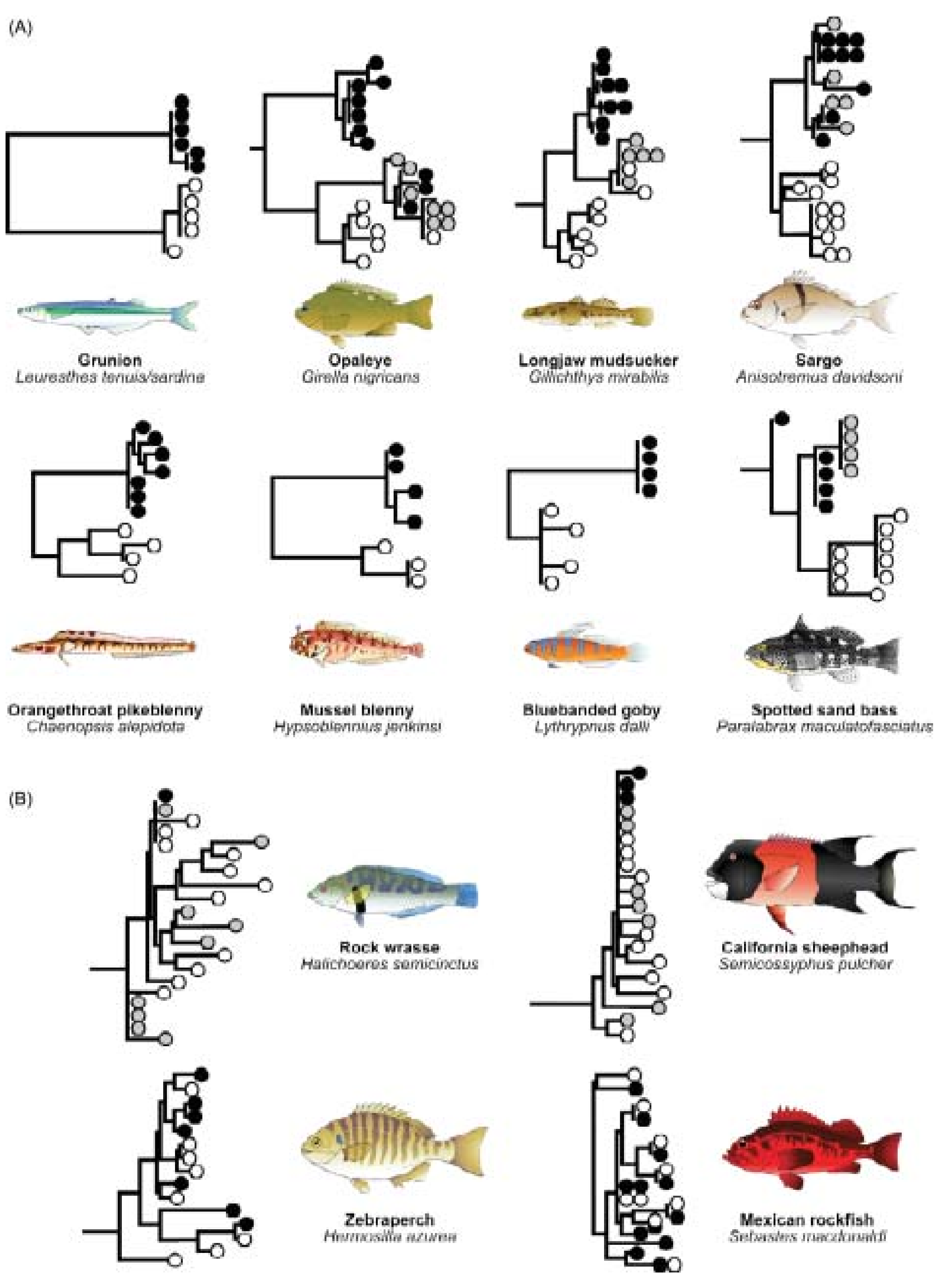

FIGURE 2-9 Parts a and b. Phylogenetic relationships of populations of fishes disjunct across the Baja California peninsula. Phylogenetic relationships were based on a portion of the mitochondrial cytochrome b gene for *Lythrypnus dalli*, *Gillichthys mirabilis*, and *Anisotremus davidsonii* and on a portion of the mitochondrial control region for all remaining species. Each individual is represented by a circle, white if collected in the Sea of Cortez, black if collected on the Pacific coast north of Punta Eugenia, and gray if collected on the Pacific coast south of Punta Eugenia. Trees with large numbers of individuals were pruned to facilitate presentation but retain their principal elements (*Gillichthys mirabilis, Girella nigricans, Paralabrax maculatofasciatus, and Sebastes macdonaldi*).

TABLE 2-4

Phylogeographic Characteristics of Some Coastal Fishes Disjunct Across the Baja Peninsula

Species	*Habitat and Depth*	*Life History**	*Range Sampled*	*Marker*	*Phylogeographic Structure*	*Reference*
Paralabrax maculatofasciatus (spotted sand bass)	Sand/rocky reef	18 to 31 days planktonic larvae, fecundity $5*10^4$, longevity 9–15 years	Pacific/Gulf	RFLP mtCR	Pacific/Gulf	Tranah and Allen (1999) Stepien et al. (2001)
Anisotremus davidsonii (sargo)	Rocky reef, intertidal to 60 m	Planktonic larvae, longevity 12–15 yrs	Pacific/Gulf	cytochrome b	Pacific/Gulf	Bernardi et al. (2003)
Gillichthys mirabilis (longjaw mudsucker)	Estuaries, lagoons	Planktonic larvae, estuaries and nearshore waters,	Pacific/Gulf	cytochrome b	Pacific/Gulf	Bernardi et al. (2003)
Girella nigricans (opaleye)	Rocky reef, intertidal to 30 m	2–4 months planktonic larvae, longevity > 10 yrs	Pacific/Gulf	mtCR	Pacific/Gulf	Bernardi et al. (2003)
Leuresthes tenuis/sardina (grunion/gulf grunion)	Eggs buried in sandy beaches; rocky reef to 18 m	30 to 40 days planktonic larvae, fecundity 1000–3000, longevity 3–4 yrs	Pacific/Gulf	mtCR	Pacific/Gulf	Bernardi et al. (2003)
Lythrypnus dalli (bluebanded goby)	Intertidal to 70 m	2 to 3 months planktonic larvae, fecundity 10^2–10^3, longevity 19–24 months	LA Region to south of Pta. Eugenia Pacific/Gulf	26 allozyme loci cytochrome b	2 of 3 polymorphic loci significant, $F_{ST} > 0.2$ Pacific/Gulf	Waples (1987) Bernardi et al. (2003)
Halichoeres semicinctus (rock wrasse)	Rocky reef, kelp, intertidal to 40 m	Planktonic larvae, longevity 9–14 yrs	Pacific/Gulf	mtCR	None	Bernardi et al. (2003)
Sebastes macdonaldi (Mexican rockfish)	Rocky reef	Planktonic larvae	Pacific/Gulf	mtCR	None	Bernardi et al. (2003)
Hermosilla azurea (zebraperch)	Rocky reef, intertidal to −27 m	Planktonic larvae	Pacific/Gulf	mtCR	None	Bernardi et al. (2003)
Semicossyphus pulcher (California sheephead)	Larvae in/offshore; Rocky reef, kelp, intertidal to 85 m	37 to 78 days planktonic larvae, fecundity $3*10^4$ to $3*10^5$, longevity 20–29 yrs	Pacific/Gulf	mtCR	None	Bernardi et al. (2003)
Chaenopsis alepidota (orangethroat pikeblenny)	Rocky reef	Planktonic larvae	Pacific/Gulf	mtCR	Pacific/Gulf	Bernardi et al. (2003)
Hypsoblennius jenkinsi (mussel blenny)	Rocky reef	Planktonic larvae	Pacific/Gulf	allozymes mtCR	Pacific/Gulf	Present (1987) Bernardi et al. (2003)

TABLE 2-5

Genetic Characteristics of Coastal Fishes Disjunct Across the Baja Peninsula

Family	*Species*	*Common Name*	*Method*	*n*	*D*	*Fst*	*Nm*	*%div Pac/Gulf*	*%div Pacific*	*%div Gulf*
Atherinopsidae	*Leuresthes tenuis, L. sardina*	Grunion	ALLO/mtCR	NA/11	0.28	0.97	<0.1	11.60 (0.39)	0.29 (0.25)	0.31 (0.26)
Kyphosidae	*Girella nigricans*	Opaleye	ALLO/mtCR	24/119	0.99	0.51	0.5	8.49 (1.70)	5.77 (4.58)	2.58 (1.43)
Blenniidae	*Hypsoblennius jenkinsi*	Mussel blenny	ALLO/mtCR	200/7	0.04	0.84	0.1	7.87 (0.61)	0.44 (0.38)	0.20 (0.00)
Chaenopsidae	*Chaenopsis alepidota*	Orangethroat pikeblenny	mtCR	11		0.67	0.3	1.87 (0.14)	0.04 (0.10)	1.16 (0.28)
Serranidae	*Paralabrax maculatofasciatus*	Spotted sand bass	ITS, mtCR	180/63		0.81	0.1	1.06 (0.26)	0.15 (0.14)	0.25 (0.30)
Gobiidae	*Gillichthys mirabilis*	Longjaw mudsucker	CYTB	63		0.67	0.2	2.21 (0.51)	0.69 (0.48)	0.72 (0.60)
Haemulidae	*Anisotremus davidsonii*	Sargo	CYTB	26		0.65	0.3	1.34 (0.17)	0.30 (0.31)	0.65 (0.48)
Gobiidae	*Lythrypnus dalli*	Bluebanded goby	ALLO/CYTB	254/10	0.003	0.71	0.2	0.20 (0.07)	0.00 (0.00)	0.11 (0.09)
Kyphosidae	*Hermosilla azurea*	Zebraperch	mtCR	15		0.02	28	2.30 (1.28)	2.33 (1.50)	2.32 (1.34)
Labridae	*Halichoeres semicinctus*	Rock wrasse	mtCR	21		0.01	38	0.79 (0.41)	0.68 (0.44)	0.89 (0.38)
Labridae	*Semicossyphus pulcher*	California sheephead	mtCR	20		<0.01	115	0.84 (0.59)	0.76 (0.61)	0.91 (0.50)
Scorpaenidae	*Sebastes macdonaldi*	Mexican rockfish	mtCR	95		<0.01	602	0.64 (0.25)	0.55 (0.29)	0.53 (0.26)

NOTE: Methods are ALLO = allozymes, mtCR = mitochondrial control region sequences, ITS = ITS RFLPs, CYTB = cytochrome b sequences. n is sample number (if more than one method is used, sample number refers to each method). D is Nei's genetic distance. Divergences are given as percentage sequence divergence; the standard deviations are in parentheses. Seven of the unequivocally disjunct taxa have not yet been studied: *Hypsoblennius gentilis* (Blenniidae, bay blenny), *Pleuronichthys verticalis* (Pleuronectidae, hornyhead turbot) *Zalembius rosaceus* (Embiotocidae, pink seaperch), *Scorpaena guttata* (Scorpaenidae, scorpionfish), *Stereolepis gigas* (Polyprionidae, giant seabass), *Xeneretmus ritteri* (Agonidae, stripefin poacher), and *Hypsopsetta guttulata* (Pleuronectidae, diamond turbot). Citations to studies are given in table 4.

the Gulf of California). The intraspecific evolution of fishes of the California Channel Islands and San Benito Islands has been investigated with genetic tools in the last two decades. In both cases, early work indicated that offshore islands harbored divergent populations. The original study of the San Benito Islands indicated that island populations were more genetically divergent from populations on the adjacent mainland, the Baja California peninsula, than were other populations along the Pacific coast of the Baja California peninsula separated by much greater geographic distances (Waples, 1987). The indication is that something about islands (biological and/or physical) can lead to isolation in coastal marine fishes, as in terrestrial and freshwater organisms, and therefore that island biogeographic theory might also be relevant. Below, we elucidate processes influencing islands as well as possible by reviewing and exploring the data set describing black perch in the California Channel Islands (Bernardi, 2000).

Geologic, Geographic, and Oceanographic Context for California Channel Islands

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 currently separated from each other by narrow channels generally shallower than 50 meters. 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, deep-water channels; the shallowest point is approximately 800 meters deep. The third group comprises several small islets and rocks generically referred to as Santa Barbara Island. It is centrally located halfway between the two previous groups and is separated from them by deep water.

During the last several millions of years, the California Borderlands have been uplifted approximately 1 m per millennium (Vedder and Howell, 1980; Sorlien, 1994). The California Channel Islands emerged within the last 5 My and have generally increased in area since. The islands are thus relatively new structures that have changed within the evolutionary timescale of many of the lineages discussed above. Climate change also has been considerable during this period, and lowered sea level rapidly increased island mass in the Southern California Bight with several results (see section on *California*) of which two are of particular interest here. First, the seaway between Anacapa Islands and the mainland was reduced to approximately one-sixth of its current (6 km) breadth (Johnson, 1977). Second, the shallow shelf between the four northern Channel Islands—Anacapa, Santa Cruz, Santa Rosa, and San Miguel—was exposed thus generating the superisland Santarosea (Johnson, 1978).

These changes almost certainly influenced the hydrography of the Southern California Bight, likely reducing connectivity with the California Current to the west and diminishing northward flux in the California Counter Current. Increased island mass would also have affected mesoscale patterns within the Bight. Depending on their area, shape, elevation, and orientation to prevailing winds, currents, and swell, islands modify local circulation, including the formation of boundary layers, mesoscale eddies, and modification of vertical water-column structure (e.g. Wolanski and Hamner, 1988; Wolanski et al., 1996), which can influence local productivity (Caldeira and Marchesiello, 2002), have knock-on effects through the food web (Lasker, 1975), and might entrain larvae near discrete habitat patches in the vicinity of their natal area for up to several weeks (e.g. Owen, 1980; Black et al., 1990; Hickey, 1992; Scheltema et al., 1996; Pinca and Huntley, 2000; Strub and James, 2000).

Relationships Between Mainland and Island Populations

As a group, Channel Island black surfperch individuals cluster with samples collected north of Santa Monica Bay (fig. 2-7A). This is consistent with prevailing southward currents in the region. More specifically, however, fish from the northern Channel Islands clustered with fish from Ventura-Port Hueneme-Point Dume, i.e., the geographically closest region of the mainland. This genetic connection probably was greater during periods of lower sea level when Santarosae was separated from the mainland only by a much reduced seaway (Vedder and Howell, 1980; Junger and Johnson, 1980), thus explaining the observed high genetic similarity between northern Channel Islands and the Ventura region. These observations are consistent with island biogeographic theory regarding mainland and connectedness along island series.

In contrast, in general, individuals from the southern channel islands did not cluster with individuals from the mainland closest to them (Palos Verdes-San Diego region) but, like the northern Channel Islands, with areas to the north. Only one individual from the southern islands, from Santa Catalina Island the island closest to the mainland, showed a strong affinity with fish from the adjacent "southern" mainland clade. Another single individual from Ventura showed close affinity with Catalina haplotypes. The closer genetic affinity of the southern Channel Islands with the northern Channel Islands, rather than nearest mainland, is largely consistent with prevailing currents in the region (fig. 2-3). The California Current washes over and through the northern islands, presumably picking up potential migrants as it heads toward the southern islands. In contrast, the southern California Countercurrent runs northward out of the open ocean or along the mainland coast and therefore tends not to carry potential migrants or, at least, not to the islands.

Relationships among the California Channel Islands

Within the Channel Islands, mitochondrial control region sequences of fish from the northern Channel Islands (San Miguel, Santa Cruz, and Anacapa) were all very closely related (mean pairwise divergence = 0.3%, haplotype diversity = 0.58), even on north- and south-facing shores that show striking differences in habitat conditions, forming a monophyletic clade (figs. 2-5A and 2-8). One dominant haplotype was shared by 65% of individuals from all northern islands. Gene flow between islands within the northern group was therefore high (average $F_{st} = 0.05$, Nm = 39.1).

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, distinct from all individuals from the inshore Santa Catalina Island. 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 San Clemente Islands were remarkably homogeneous (genetic diversity was 0.38 and 0.00, respectively), Santa Catalina Island showed the highest diversity of all island populations (0.80). The population on the smallest of the Channel

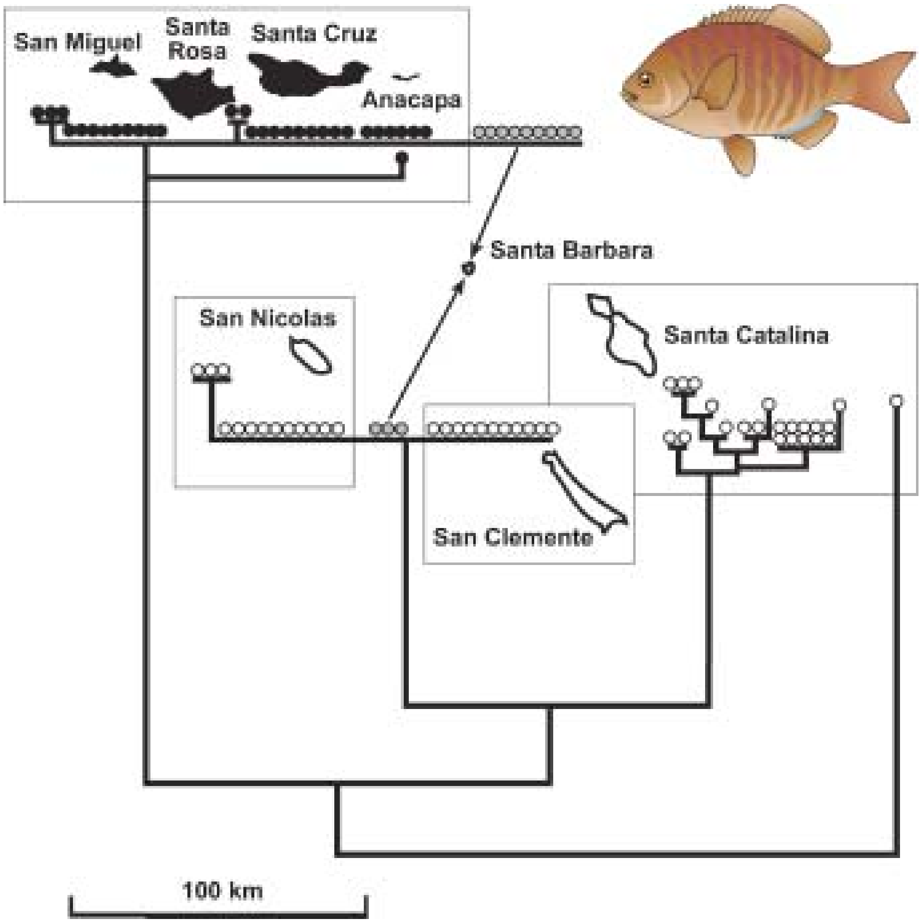

FIGURE 2-10 *Embiotoca jacksoni*. Superimposed map of the California Channel Islands and a simplified (polymorphisms were removed) neighbor-joining phylogenetic tree of the corresponding island populations of black surfperch. Each sample is represented by a circle. Black circles represent individuals 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 (9 individuals) and with San Nicolas/San Clemente Island individuals (3 individuals). One individual from Santa Catalina Island clustered with mainland individuals. Santa Rosa Island was not sampled (Bernardi, 2000)

Islands, Santa Barbara Island, which lies between the northern and the southern group, did not show any unique haplotypes, it was composed of northern Channel Islands (75%) and southern Channel Islands (25%) haplotypes (fig. 2-10). 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 southward current pattern between the islands (Hickey, 1992). Moreover, because the island is very small, the local population of black perch may be prone to replacement. The absence of unique haplotypes on Santa Barbara Island may be due to high rates of extirpation and recolonization due, for example, to environmental stochasticity, consistent with island biogeographic theory (Matter et al., 2002). The dynamics of *E. jacksoni* may therefore be amenable to modeling using metapopulation models and population genetic expectations of island biogeographic theory (Johnson et al., 2000).

Deep and Wide: Water as an Effective Barrier to Gene Flow

The high genetic similarity of all northern Channel Island individuals, their close association with haplotypes from the adjacent mainland, and their high degree of separation from southern Channel Island individuals suggests that deep water is an effective barrier to gene flow for black perches. The bimodal distribution of F_{ST} values (<0.2 or >0.4) with respect to geographic distance (fig. 2-11) bears hallmarks of the sigmoidal relationship proposed between genetic differentiation and geographic isolation, assuming that dispersal over a certain distance is a particularly rare event (fig. 2-1; blue curve), of which fishes on Santa Barbara Island may constitute particularly recent examples (Bernardi, 2000) leading to anomalously low genetic differentiation at high geographic distances (and vice versa). Though black perch are probably able to migrate between the different northern islands, their access to the southern islands is most likely via rafting in association with floating debris or kelp patties that provides cover against predation. The frequency of rafting is very low, as indicated by fish collection efforts that failed to detect the presence of black perch in rafts of giant kelp, *Macrocystis pyrifera* (Mitchell and Hunter, 1970; Kingsford, 1995 [for a genetic study of kelp that shows interisland and ecological differences, see Miller et al., 2000]). That occasional dispersal events do occur, however, is indicated by the capture of one southern mainland haplotype at Catalina Island, one Catalina haplotype at Ventura, and the occurrence of only shared haplotypes at Santa Barbara Island (Bernardi, 2000). Thus, the pattern of predominantly different clades on different islands suggests that, though dispersal potential and physical environment are likely to play a role in population structure, the incumbent biota and subsequent demographic effects also influence successful establishment. The indication that deep marine water can act as a barrier to dispersal by shallow water marine fish such as the black surfperch, can be added to its list of isolating effects on organisms already including animals restricted to freshwater, such as Hawaiian gobies (Chubb et al., 1998) and many terrestrial animals, including the miniature California Islands mammoth (e.g. Johnson, 1977; Gilbert et al., 1990; Edwards, 1993; Thorpe et al., 1993; Clarke et al., 1996; Grant and Grant, 1996; Juan et al., 1998; see also Lessios et al., 1998).

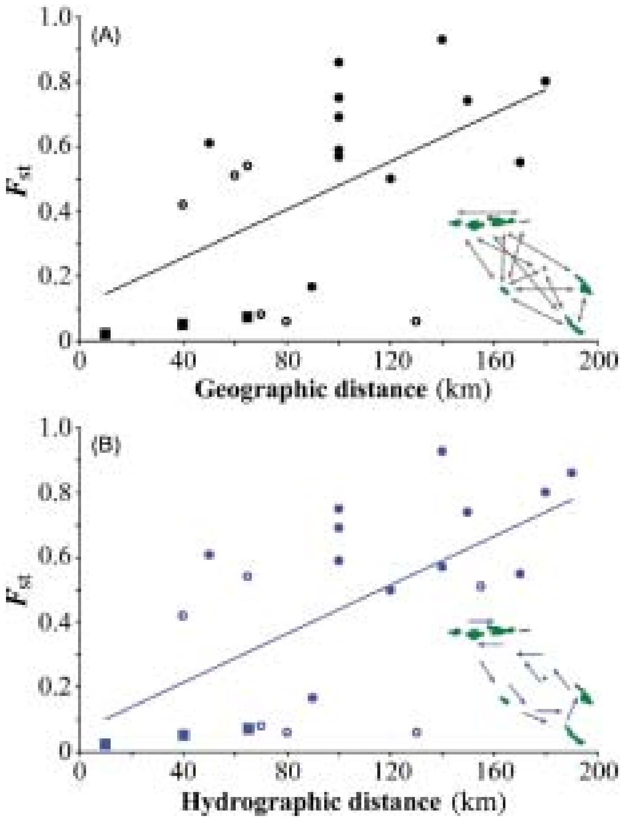

FIGURE 2-11 Genetic differences among California Channel Island populations of black surfperch, *Embiotoca jacksoni*, in relation to A, the shortest geographic distance between populations ($y = 0.0037x + 0.1095$, $r^2 = 0.29$), and B, the shortest distance in line with predominant circulation in the Southern California Bight ($y = 0.0038x + 0.0643$, $r^2 = 0.39$). The lines of best fit differ significantly in their intercepts ($F = 67.54$, $p < .001$) but not slope ($F = 2.06$, $p = .218$). Solid squares, comparisons between Northern Channel Islands only; hollow circles, comparisons with Santa Barbara Island; solid circles, all other comparisons.

Rare Migrations and Founder Effects—Distant Islands

The absence of shared haplotypes among the southern islands indicates very low levels of migration (Edwards, 1993). However, migration among southern islands has occurred more recently than migration between the northern and southern islands because individuals from the southern islands are phylogenetically more closely related to each other than they are to northern island individuals (figs. 2-5, 2-8). Overall, rates of migration among the islands are negatively correlated with their geographic separation, a relationship that is improved slightly by taking into account likely routes of dispersal via currents (fig. 2-11; see also Michels et al., 2001; Muñoz et al., 2004) even though such generalized currents (inset, fig.-11B) dramatically over-simplify both the complexity of modern flow and changes in flow on evolutionary timescales.

Assuming a molecular clock for mtCR of 20%/MY to 8%/MY (Bowen and Grant, 1997), populations on the southern islands have been isolated for 30,000 to 110,000 years (0.6% to 0.9% sequence divergence). If such rare migratory events reflect the main mechanism for island colonization, founder effects should dominate the early genetic structure on islands and their signal be retained subsequently. One would expect to find single or very few very closely related haplotypes on recently colonized islands, and more numerous, more divergent, haplotypes within monophyletic clades on islands colonized for longer periods of time. This expectation is consistent with patterns observed in the southern islands but, given the low heterogeneity and highly derived nature of San Nicolas and San Clemente populations (0.38 and 0.00, respectively [Bernardi, 2000]) also suggests a role for founder effects and local bottlenecks. In this case, the higher diversity of Santa Catalina populations (0.94) indicates that the island historically has had a larger more stable population allowing endemic diversification. As well as the stochastic extinction/recolonization dynamics of small islands, as indicated by Santa Barbara and San Nicolas, changes in temperature may have led to repeated, severe, selective bottlenecks in black perch populations (Holbrook et al., 1997).

In some ways, the widespread occurrence of marine taxa with limited dispersal ability on isolated islands initially seems paradoxical (Johannesson, 1988) because it is not obvious how they got there. However, it is consistent with patterns seen in the terrestrial faunas and floras of oceanic and coastal islands (Wallace, 1880; Cody and Overton, 1996) and can be explained by the fact that reduced dispersal ability favors establishment of populations after rare accidental colonization events (Johannesson, 1988). Given its viviparous birth, phylopatry, and low dispersal ability, it is no surprise, therefore, that the black perch is relatively common among the California Channel Islands.

Synthesis

Dispersal

Genetic studies investigating the relationship between dispersal potential and gene flow in phylogenetically disparate species with variable pelagic larval durations (PLDs) have not reached definitive conclusions (Waples, 1987; Doherty et al., 1995; Shulman and Bermingham, 1995; Grosberg and Cunningham, 2001; Riginos and Victor, 2001). Comparisons of California taxa suggested relationships between phylogeographic structure and PLD, habitat structure, and fecundity (Dawson, 2001). A comparative study of sympatric sister species in California demonstrated that the species with higher dispersal also had less phylogeographic structure (Dawson et al., 2002). This suggests that, though gene flow is related to dispersal potential, phylogeographic structure is also influenced by numerous other factors. The results reported here generally support this perspective. For example, opaleye which display a strong phylogeographic break, have a pelagic larval stage of 2 to 4 months (Waples, 1987). Spotted sand bass and blue-banded goby (*Lythrypnus dalli*), which display a shallow phylogeographic break, have a pelagic larval stage of approximately 1 month and ≥2 months, respectively (Waples, 1987). Sheephead (*Semicossyphus pulcher*) and rock wrasse (*Halichoeres semicinctus*), which show no phylogeographic break, have a pelagic larval stage of 37 days and 30 days, respectively (Victor, 1986). Thus, understanding geographic structure demands a more holistic approach, which may begin by looking in more detail at deviations from hypothesized relationships between dispersal potential and gene flow (e.g., fig. 2-1).

Vicariance

Deviations from the relationship between dispersal potential and realized gene flow indicate the influence of other factors. One obvious factor is the traditionally juxtaposed phenomenon of vicariance. Sigmoid relationships (e.g. fig. 2-1; consider also fig. 2-11) would be consistent with a certain intensity of a barrier to gene flow below which structure is unlikely to form and above which structure is likely to form. The critical intensity is unlikely to be the same for different species and is probably affected by the many factors previously discussed. The idea that modifiers of gene flow are not all-or-nothing is more consistent with the idea of zootic filters (Carlquist, 1965) that inhibit the movement of individuals of different species, and therefore their genes, to different extents depending in part on the strength and nature of the filter, and in part on the attributes of the entity being filtered (see also Mayr, 1942:243). Undoubtedly, the strongest filters, which are functional barriers for marine organisms, are land bridges, isthmuses, and long peninsulas such as Baja California, but other significant filters clearly exist and are likely to operate in concert. The influence of reduced gene flow linked to vicariant events is evident in Gulf and Pacific fish population disjunctions, across the LAR, in the north due to currents and glaciation, and to a lesser extent among the California Channel Islands. Sometimes the mechanism of the filter may be difficult to identify because physical and ecological factors may often be superimposed.

Sympatry

Ecological effects are probably easiest to investigate in sympatric species or in geographically proximate but ecologically separated con-specific populations between which there is no obvious physical reason for a lack of gene flow. Since the early development of the idea (Bush, 1969), evolution in sympatry has become more widely considered as a possible component of speciation and is currently the subject of much theoretical and empirical work (Bush, 1994; Kondrashov and Kondrashov, 1999; Dieckmann and Doebeli, 1999; Schilthuizen, 2001). In this context, the most interesting species discussed in this chapter are the chinook salmon in coastal streams, the lower Columbia River, and Klamath River basin, in which spring- and fall-run populations appear to have evolved independently multiple times in close geographic proximity (Myers et al., 1998; Banks et al., 2000a,b).

Evolutionary Consequences—Speciation

Recent evidence based on molecular phylogenetics and distributional data, following the arguments of Lynch (1989) and others, suggests that some species of California fishes may have evolved sympatrically, possibly in relation to microhabitat colonization, i.e., via ecological speciation (Dawson et al., 2002; Bilton et al., 2002; McKinnon et al., 2004). Though divergence in sympatry is now generally accepted as a real mode of speciation, it is likely that allopatric speciation has an essential role and is probably the most common mechanism for incipient speciation in disjunct species (Endler, 1977). However, there are still relatively few studies that have evaluated the role of population disjunctions in the speciation of marine organisms (Stepien and Rosenblatt, 1991; Palumbi, 1992, 1994; Hellberg, 1998; Burton, 1998).

Future Directions

We have attempted to summarize the phylogeographic patterns that have been described for California fishes and to elucidate the principal factors that influence them. In the light of the apparent complexity of factors influencing the modern genetic structure of organisms, what we find remarkable about these patterns is that they are so similar for many different species, suggesting that the comparative approach can be informative of predominant patterns and processes. However, it is also clear from this review that, for the most part, studies to date lack the necessary resolution and experimental design to distinguish among the many potential influences that often overlap geographically. Distinguishing among these factors will require more thorough geographic sampling and choices of species that will maximize information retrieval (e.g., groups of closely related species within monophyletic clades that are broadly sympatric and possess a variety of life-history traits, with replication). Such study systems may be few and far between, but they are one possible way that we may learn more about the generalities of the processes influencing evolution in coastal marine fishes. This endeavor will also depend on greater knowledge of the geological and climatic history of the region, as well as better oceanographic information and models. The theoretical and analytical foundations, often based on such information, must also continue to be developed. For example, despite advances in statistical phylogeography (see Knowles, 2004) and quantification of coastal complexity methods for statistically integrating molecular with biogeographic and environmental information are still relatively poorly developed and would be helpful in this field.

Acknowledgments

This publication would have been impossible without the Editors' vision that a synthesis of the ecology of California marine fishes was necessary and without the unusually rich history of coastal research in California indicated by the many diverse publications we were able to cite. This collaboration/review was made possible by the organizations and people who have contributed financially, intellectually, and otherwise to our prior researches on this topic. MND was supported by a Vice-Chancellor's Post-doctoral Research Fellowship at the University of New South Wales. GB was funded by UC Mexus, the Committee on Research at UCSC, and the David and Lucille Packard Foundation's PISCO program. We would like to thank Pete Raimondi, Nicole Crane, David Huang, Astrid Terry, Stian Alesandrini, Karen Crow, and Marina Ramon for their contributions to this research.

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