Genes, Diversity, and Geologic Process on the Pacific Coast

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■ **Abstract** We examine the genetics of marine diversification along the West Coast of North America in relation to the Late Neogene geology and climate of the region. Trophically important components of the diverse West Coast fauna, including kelp, alcid birds (e.g., auks, puffins), salmon, rockfish, abalone, and *Cancer* crabs, appear to have radiated during peaks of upwelling primarily in the Late Miocene and in some cases secondarily in the Pleistocene. Phylogeographic barriers associated with Mio-Pliocene estuaries of the mid-California coast, the Pliocene opening of the Gulf of California, tectonic and eustatic evolution of the California Bight, as well as the influence of Pleistocene and Holocene climate change on genetic structure are assessed in a geologic context. Comparisons to East Coast and western freshwater systems, as well as upwelling systems around the globe, provide perspective for the survey.

INTRODUCTION

The southwestern region of North America is distinct from the East Coast in terms of biotic diversity and apparently in the relationship between phylogeography[1] and biogeography. A diverse freshwater fauna (Mayden 1992) as well as a coincidence of phylogeography and biogeography of coastal faunas (Avise 1992) characterize the Southeast. In contrast, depauperate freshwater faunas (e.g., Smith et al. 2002), diverse marine faunas (e.g., Briggs 2003), as well as an apparent discordance

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[1]Phylogeography is the genetic structure internal to a species usually based on molecular data, and often represented as a phylogenetic tree placed in a geographic context (see Avise 2000). It is distinct from biogeography in that biogeographic boundaries are geographically coincident range termini of multiple species. Geographically coincident breaks in gene flow in multiple species, which if deeply historic develop into separate clades in gene trees, constitute phylogeographic boundaries. Similar studies of geographically coordinated within-taxon genetic change have also been referred to recently as "community genetics" (Wares 2002). The detailed analysis of how variable geography influences gene flow on a fine scale within species, often involving correlation of genetics with distance, has been referred to as "landscape genetics" (e.g., Manel et al. 2003).

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between phylogeographic and biogeographic boundaries characterize the western coast of North America, hereafter referred to as the West Coast (Burton 1998, Dawson 2001). We present a historical synthesis of West Coast diversity and phylogeography. At issue are the timing and origin of coastal marine diversity and the geography of population differentiation. In this examination of coastal marine taxa, we secondarily consider terrestrial issues along the coast and the impacts on the freshwater ecosystem. We treat a series of geologic and climatic processes that appear to have influenced the unusually high marine, and low freshwater, diversity of the region in temporal order from older to more recent events. We then assess the consistency of the available genetic data with each of these transitions in physical process. Our approach of discussing the hydrography and geologic history of a region followed by biologic aspects is one of long standing. Ekman (1935, 1967) took a similar approach in touching on many of the same themes, such as the difference between North Atlantic and North Pacific marine diversity, albeit without recourse to genetic data or detailed climate reconstruction.

The geologic/climatic transitions that appear to have strongly influenced West Coast marine diversity and phylogeography include: 1. Transition to an upwelling regime that began roughly 15–12 million years ago (mya), late in the Middle Miocene. This transition appears to have been critical in establishing the high productivity and high mid-latitude diversity of the West Coast biotic regime that we know today. Upwelling is also associated with a contemporaneous Miocene transition to a summer-dry regime that affected terrestrial flora and likely eliminated much western freshwater diversity. Late Miocene tectonics led to a complex heterogeneous coastline, which may also have facilitated diversification. 2. Rapid uplift of the mountains proximal to the West Coast, and a transition to a more active, more southern, polar front bringing intensified winter storms occurred during the Late Pliocene and Pleistocene. Together, uplift and winter precipitation provided snowmelt that sustained large perennial river systems, such as the Colorado and the San Joaquin. Uplift, greater sediment flux owing to winter precipitation, and glacio-eustatic fluctuations reduced bay/estuarine habitat and faunas along the California coast. Some taxa appear to exhibit a genetic structure that reflects the Miocene to mid-Pliocene estuarine geography. Uplift and glacioeustatic fluctuation increased the prevalence of rocky shores through the Plio-Pleistocene. Combined with a return to upwelling conditions in the Pleistocene, this allowed some additional evolution of the diverse rocky shore fauna. 3. The tectonics of the opening of the Gulf of California, which began approximately 6 mya, are well understood. Nevertheless, the biotic consequences on land and in the sea appear complex. Issues include (*a*) potential relict fauna from pre-drift rift basins; (*b*) population differentiation and speciation of taxa in the Gulf of California owing to isolation from outer coast populations; (*c*) isolation of the northern and southern Gulf in the area of the Midriff Islands; and (*d*) a terrestrial phylogeographic boundary across the Baja California Peninsula (BCP) in the vicinity of the Vizcaino Desert is taken as an indication of a Pleistocene transpeninsular seaway, although geologic evidence for a seaway is equivocal and other factors likely contributed to the biotic patterns. 4. By approximately 300 thousand years ago (kya), current transport and

wave action typical of the open coast were considerably reduced in the California Bight, leading to the development of a regional phylogeographic barrier in the Bight itself, rather than one coincident with the biogeographic barrier near Point Conception. 5. Genetic structure of individual coastal species documents the effects of the last glacio-eustatic cycle, including evidence of northward post-glacial expansion of ranges, expansion from coastal glacial refugia in the North, and patterns of recolonization of estuaries following Pleistocene/Holocene sea-level rise. Inland, drier Holocene climate isolated relicts of larger Pleistocene freshwater systems, especially in the Great Basin Region.

We first express some caveats about the study and the general structure of the argument. We then discuss each of the transitions enumerated above, treating geologic process and timing followed by an examination of biological response in terms of diversity and/or phylogeographic structure.

CONTEXT AND CAVEATS

We compare the western and eastern coasts of North America to illuminate West Coast marine diversity; however, multiple factors complicate the comparison. Differences between the Atlantic and Pacific margins include the amount of rocky shore, climatic history, and interplay between tropical and temperate diversity. Tropical-temperate interaction of the East Coast marine fauna has been subject to complex interpretation (e.g., Petuch 1982, Allmon 2001). Climate stability may have contributed to the diversity of eastern freshwater systems over a range of timescales (e.g., Mayden 1992) rather than just in the Neogene as discussed here. However, comparison to other mid-latitude coasts, besides that of the western Atlantic, suggests high West Coast diversity (Ekman 1967, Briggs 2003). We focus on the physical transitions responsible for the geographic component of genetic structure and the relatively high West Coast biodiversity. The eastern context is discussed as it applies to these West Coast arguments.

We apply a broad brush in correlation of genetic data and geologic process. In our view, the ability to resolve time points with genetic data is limited (e.g., Jacobs 2002). Thus, we make broad consistency arguments when it comes to the use of molecular data in timing events. Our phylogeographic focus is on older events that can be related to geologic process. Thus, we examine taxa with limited dispersal ability rather than examining gene flow in taxa that are thought to disperse well; as a consequence, we primarily treat sequence-based, rather than allozyme or microsatellite, studies. Many taxa showing discrete genetic separation could be considered cryptic species. Formal taxonomic treatment of these species is an important endeavor beyond the scope of this work.

A trend toward lower global temperature and sea level has long been recognized through the Tertiary. However, this trend is not monotonic; an initial Oligocene phase of Antarctic glaciation and associated upwelling was followed by Miocene warming and a subsequent phase of cooling later in the Miocene (e.g., Zachos et al. 2001). We focus on Miocene and later (Neogene) geologic events, including later

episodes of upwelling, both because they have had strong impacts on the modern fuana and because the genetic data can be more effectively interpreted in this time frame.

Our initial focus on the California Coast ultimately led to an examination extending from southern Alaska to the Gulf of California. The history of marine connections to other regions, such as between the Arctic and the North Pacific that occurred off and on again since the Late Miocene (Marincovich & Gladenkov 1999) and the gradational closure of the Panamic Portal (ca. 4 mya), are also considered as they likely impacted West Coast diversity.

LATE MIOCENE SHIFT TO UPWELLING AND DIVERSIFICATION OF NORTH PACIFIC FAUNA

Global Process and Geologic Setting

The duration of the Miocene (23.8 to 5.3 mya) is long relative to the subsequent Pliocene and Pleistocene. The Middle Miocene was a time of warm or "optimal" climate, followed by the expansion of glacial conditions on Antarctica for the second time in the Tertiary. This southern continental glaciation has persisted until today. Cooling of the Southern Ocean adjacent to Antarctica caused a surface-to-bottom flux of dense cold waters that migrate northward at depth, ultimately refrigerating much of the water mass below the thermocline. Polar cold deep-water production and cooling below the thermocline were contemporaneous with later Miocene (15–12 mya) initiation of upwelling along north-south trending mid-latitude west coasts. Upwelling in the regions of the modern California, Humboldt, and Benguela currents off the coasts of North America, South America and southern Africa became prominent late in the Middle Miocene.

Upwelling Mechanism

One might anticipate that the production of colder water below the thermocline would lead to greater stability of the water column and less upwelling, and this might well be the case if not for feedback from the atmosphere. Cold upwelled water, especially relative to warmer adjacent continents, generates cool descending air and a stable high-pressure regime. In the classic conception of mid-latitude western margin upwelling, this stable high pressure and the atmospheric pressure difference between land and sea generate shore-parallel winds blowing toward low latitudes. These winds generate offshore water flow and the upwelling of cool, nutrient-rich deeper waters through the Coriolis Effect and Ekman Transport. Along the West Coast, this high-pressure system is most intense and localized off California in the summer when the Intertropical Convergence Zone (ITCZ) moves further north with the locus of greatest solar heating in the Northern Hemisphere. In principle, the intensity of shore-parallel winds that generate upwelling can be influenced by regional factors that affect the temperature difference between the continent and ocean, as well as more distant components

of the ocean-atmosphere system that effect the intensity of the Hadley Circulation.

In the marine-dominated Southern Hemisphere, there is less seasonal variation in the land-sea temperature regime and the larger components of the atmospheric circulation, such as the polar-front-related storm track and Westerly Circulation. They are more stable in their seasonal intensity and position. Consequently, the position and intensity of the high-pressure cell and the upwelling regime in the Southern Hemisphere, such as off South America, are less seasonal (e.g., Ekman 1967). Regional features such as topography and orientation of the coast and adjacent highlands can accentuate land-sea contrasts in atmospheric pressure and help localize the descending limb of the Hadley Circulation and high pressure over the ocean adjacent to the continent. Again, features such as the Andes and the relatively continuous north-south trending South American coast extend upwelling to lower latitudes than occurs in other upwelling regions. In addition to regional and more distant causal factors that may modulate upwelling intensity through atmospheric feedback, water depth and stability must also be conducive to upwelling, and the biotic consequences of upwelling are likely to be critically influenced by the nutrient content of the upwelled waters. In this last regard, recent work documents that most subthermocline waters in the world's oceans are produced in the Southern Ocean and are largely depleted in silica, a critical nutrient for diatoms. This is not the case in the North Pacific where there is independent vertical mixing in the Northwest Pacific that supplies silica-rich waters to the subthermocline waters across the Pacific (Sarmiento et al. 2004).

Stability and Change of the Upwelling Regime

Despite the higher wind regime characteristic of maximum glacial conditions, productivity associated with upwelling was commonly reduced during glacial times. Regional and more distant factors that influence upwelling intensity (e.g., Palmer & Pearson 2003) as well as the variable nutrient content of feedstock waters (e.g., Berger & Lange 1998, Berger & Wefer 2002, Loubere 2002) have been implicated as the causes of this difference between glacial and interglacial times. Arguments invoked to explain this phenomenon provide a set of plausible mechanisms that modulate upwelling, and can be used to infer causes of changes in the upwelling regime at other times in the Neogene. It seems reasonable that the high-pressure regime and upwelling intensity along the West Coast would be influenced by the glacial conditions on the North American continent. Ice sheets extended as far south as southern Washington and Idaho, displacing the track of the polar front southward and extending its activity through more of the year (e.g., Kutzbach 1988). Glaciers were present in the Sierra Nevada, and there was substantial lake area in the West during the Pleistocene. All of these factors would have limited the summertime differences in temperature between land and sea, and/or the placement and stability of the summertime high pressure.

In addition, the strength of the Hadley Circulation appears to influence the intensity of upwelling in the Peru-Galapagos region (Palmer & Pearson 2003), suggesting that an El Niño-like reduced Hadley Circulation at the glacial maximum

may have reduced upwelling (Loubere 2002, Stott et al. 2002). Finally, production of "Northern Component Waters (NCW)," deep and intermediate water generated in the North Atlantic, provides a source of water below the thermocline that is initially nutrient poor. Its rate of production and proximity to the surface varies with glacial cycles. Increased production of NCW after the closure of the Isthmus of Panama in the Pliocene is thought to have decreased the nutrient richness of upwelled waters as far away as Peru (Loubere 2002) and California (Berger & Lange 1998, Barron et al. 2002). These arguments have yet to be integrated with recent observations (Sarmiento et al. 2004) that show critical differences in sources and silica concentration of subthermocline waters, with the North Pacific having silica-rich intermediate waters beneath the thermocline that are produced within the region. Other oceanic regions have subthermocline silica-poor waters derived from the surface waters of the Southern Ocean (Subantarctic Mode Water). It is tempting to speculate that the expansion in influence of North Pacific silica-rich subthermocline waters might have produced the widespread and intense upwelling and diatom-based productivity in the late Miocene. Conversely, expansion of sub-thermocline waters of sub-Antarctic or North Atlantic origin may have confined the influence of silica productivity to the northern-most Pacific, potentially explaining the mid-Pliocene pattern of minimal diatom-based productivity localized to the North Pacific (see details below). Wind stress and depth to the thermocline can also vary with the precession cycles as documented in the Benguela system (Donner et al. 2003). It should be noted that other factors control the iron-limited portions of the Southern Ocean and North Pacific that are more remote from shoreline and benthic sources of iron (e.g., Berger & Wefer 1991). The iron content of dust storms can trigger blooms in the North Pacific (Tsuda et al. 2003), and glacial-age dust is thought to have been an important variable influencing productivity in northern and southern oceans (Latimer & Filippelli 2001), albeit in different locations and times from the mid-latitude coastal upwelling regimes of primary interest here. In addition, on shorter timescales El Niño clearly perturbs upwelling systems. Thus, a variety of factors modulate the upwelling regime and its biotic consequences between Pleistocene interstadial and glacial conditions.

Neogene Record of Upwelling

Fine stratigraphic resolution provided by offshore cores reveals a series of transitions in the onshore-offshore location of West Coast upwelling (Barron et al. 2002), as well as the latitudinal position of the upwelling regime in the late Middle and Late Miocene through the base of the Pliocene (14–4.8 mya) (Barron & Baldauf 1990, Barron 1998). Global factors appear to have modulated this upwelling regime and/or its diatom productivity through the latter half of the Miocene. Mechanisms similar to those proposed for the distinction between glacial and interglacial upwelling regimes, including processes that affect upwelling intensity and the nutrient content of upwelled waters, as discussed above, appear to have modulated upwelling regimes earlier in the Neogene.

The North Pacific is oceanographically far removed from the North Atlantic sources of Northern Component Water thought to limit the nutrient content of

upwelled waters (e.g., Venz & Hodel 2002), and when West Coast upwelling decreased in the Pliocene, there was a compensatory increase in productivity in the Aleutian region (Barron 1998), consistent with the local source of subthermocline nutrient-rich waters through vertical mixing (Sarmiento et al. 2004). These factors appear to have buffered the North Pacific from the biotic effects of a widespread decline in upwelling-related productivity in the mid-Pliocene.

Tectonic influences on bathymetry and coastal orography also contributed to the local and regional lithologic changes observed in cores and sections along the West Coast (Barron 1992). However, much of this variation is too fine-scale to compare to the genetic data. Four aspects of upwelling history appear appropriate for comparison: (*a*) upwelling began worldwide on mid-latitude west coasts roughly at 14 mya as a consequence of global process; (*b*) upwelling was at its peak in intensity and area from 8 to 5 mya (e.g., Dickens & Owen 1999, Deister-Haass et al. 2002); (*c*) upwelling ceased for approximately a million years in the mid-Pliocene, perhaps with a limited refuge in the extreme North Pacific; and (*d*) in the Late Pliocene and Pleistocene, upwelling conditions returned (e.g., Marlow et al. 2000), albeit with fluctuations associated with the glacial cycles (e.g., Berger & Lange 1998).

Effects on Coasts and Continents

The physical consequences of an upwelling regime extend beyond the area of upwelling water. Cool upwelled coastal waters confer atmospheric stability precluding convective activity and the passage of frontal systems onto the adjacent continent, generating "summer-dry" conditions profoundly limiting growth of many types of plants (e.g., Axelrod 1986a,b). In addition, small estuaries along the coast of California are closed in the summer because there is insufficient stream runoff to maintain an opening to the sea in the face of wave action that builds a berm across the mouth of such estuaries. This summer-closed condition resulting from the dry summer, "Mediterranean," climate likely began with the initiation of the upwelling regime late in the Miocene. Also, in the Late Miocene the mountains of the West were less pronounced, and the polar front was far less active than it became subsequently (see below). Thus, both winter and summer rainfall must have been relatively low (Axelrod 1986a). In the absence of winter storms and the high elevations that store winter snows today, large perennial river systems would have been difficult to sustain in the Southwest in the Late Miocene and early Pliocene.

BIOLOGICAL CONSEQUENCES AND CONTEXT OF MIOCENE UPWELLING

Primary productivity is thought critical to the evolution of biologically diverse marine systems (Vermeij 1989, Vermeij 1993, Leigh & Vermeij 2002). This need not always be the case; coral reefs occupy nutrient-poor seas yet are diverse

relative to other tropical settings. Nevertheless, upwelling appears correlated with the mid-latitude regional diversity of coastal fish and invertebrate faunas. A direct link exists between upwelling and nutrition of the coastal fauna. Upwelling-induced diatom blooms are the primary resource for the filter-feeding communities of invertebrates along the rocky coast, as well as the primary source of organic material in estuaries such as Tomales Bay (Smith & Hollibaugh 1997). West Coast estuaries differ from East Coast estuaries in that both inorganic nutrients and living plankton from upwelled ocean waters enter the system. Additionally, low stream flow, especially in the warmer months, limits the input of terrestrial nutrients. Kelp, sustained by upwelled nutrients, also contributes nutrition to the nearshore fauna, as discussed below.

Other factors besides the instantaneous strength of upwelling must also be important in sustaining diversity. Upwelling along the Peru-Chile Margin is usually stronger than along California, yet its coastal species diversity is lower (e.g., Ekman 1967, Lindberg 1991, Briggs 2003). In any case, the mid-latitude western coast of North America has a high diversity of fishes and coastal invertebrates relative to other mid-latitude settings and even relative to other upwelling regions (Briggs 2003). Explanations for the high marine diversity present on the West Coast, include (*a*) geographic barriers to gene flow enhanced speciation, (*b*) seasonal and long-term temporal stability sustained high equilibrium diversity, (*c*) connectivity to other regions permitted faunal interchange providing a flow of new taxa to the region, and (*d*) regional ecologic interaction sustained a complex trophic structure maintaining high diversity. These are discussed below.

Geography, Tectonics, and the Speciation Process

Most speciation is allopatric, proceeding through geographic isolation (e.g., Futuyma 1998). The apparent homogeneity of the marine environment has led to the assumption that speciation in the sea is more difficult, limited, or occurs on a different scale than terrestrial speciation (Scheltema & Williams 1983, Palumbi 1992). Recent work on abalone suggests that evolution of molecules involved in sperm-egg interaction could provide a mechanism for assortative mating that might be critical for speciation in these sessile invertebrates (e.g., Swanson & Vacquier 1998). Similar evolution of sperm-egg interaction is correlated with recent speciation in Indo-West Pacific urchins (Landry et al. 2003). Nevertheless, there is general agreement that geographic isolation enhances the frequency and rate of speciation, but it is not clear that geographic isolation is essential to all marine speciation.

Several pairs of sister species are isolated in the Gulf of California and on the Pacific Coast by the Baja California Peninsula, suggesting that geographic isolation in the Gulf produced modest numbers of species since its initial opening 6 mya. In the Miocene, large West-Coast embayments may have similarly isolated populations. Thus, the tectonic complexity and the large semi-isolated embayments present along the coast of California (see Hall 2002 for recent reconstructions) may

have contributed to the evolution of species during the Miocene and early Pliocene. The California coast continues to be more complex than that of the western coast of South America and southern Africa. However, the eastern coast of Asia is yet more complex, suggesting that geomorphologic complexity alone is insufficient to sustain high levels of diversity.

Seasonal Stability

In comparison to the mid-latitude Atlantic Coast of North America or comparable latitudes in East Asia, the temperature regime of the West Coast is remarkably stable (see Ekman 1967). Dramatic seasonal change in water temperatures characterizes the mid- to high-latitude eastern coasts of Northern Hemisphere continents. For example, sea ice covers much of the Sea of Ohkutsk each winter, at latitudes comparable to Vancouver Island, negatively impacting much of the intertidal and nearshore fauna (http://www.ssd.noaa.gov/PS/SNOW/).

One of the most dramatic differences in East and West Coast intertidal invertebrates is the difference in reproductive cycle. On the Atlantic Coast, nearly all marine invertebrate reproduction occurs in the spring. On the West Coast, reproduction is highly variable between taxa and much less seasonal overall; many taxa have a prolonged intermittent or cyclic period of reproduction extending over 6 to 12 months (Strathmann 1987). These differences are likely a product of the seasonality of nutrient regimes. The spring nutrient peak and phytoplankton bloom are characteristic of temperate oceans, such as the North Atlantic, which do not experience substantial coastal upwelling. With the reduction in mixing following the winter, photosynthetic plankton can accumulate in the photic zone resulting in a "bloom." However, this bloom is short-lived; without mixing, the ocean is more stratified, and nutrients are soon depleted in the surface layer. After the spring bloom the water becomes oligotrophic and cannot support the food chain that sustains the high energetic costs of egg production and larval development. Reproduction in West Coast taxa should be less constrained as the upwelling regime of this area provides a more continuous resource for planktonic growth. Thus, the more stable, less seasonal nutrient supply has critical implications for the resources available for reproduction in West Coast invertebrates and fishes. This distinction is important, but it primarily applies to the difference between eastern and western margins of northern continents. The southern continents have greater maritime influence and less mid-latitude seasonality than continents of the Northern Hemisphere; consequently, upwelling along west coasts of southern continents is more seasonally stable than that of the California margin (e.g., Ekman 1967). Thus, positive influence of seasonal stability cannot, by itself, account for the greater diversity of coastal California relative to, for example, the western coast of South America.

Connectivity and Emigration from North Pacific

Connectivity with adjacent biotic provinces could be a crucial factor in sustaining high diversity. The North Atlantic provides a modest ocean barrier between

Europe and North America. The southern continents, as well as the inhospitable Antarctic margin, are well separated from each other. Coastal connectivity to multiple adjacent provinces is largely unique to the North Pacific. Opportunities exist for exchange across the Bering Shelf to the Arctic and East Pacific margin. Additionally, the north-south trending western coastline of the Americas provides the opportunity for interaction with a tropical fauna to the south. The South American upwelling regime extends very close to the equator, potentially permitting exchange of temperate faunas between the hemispheres (Lindberg 1991). Since the Late Miocene, marine communication between the Pacific and the Arctic has been intermittently possible during periods of high sea level (Marincovich & Gladenkov 1999). Until the rising Isthmus of Panama gradually choked significant marine circulation (e.g., Beu 2001), a shallow marine connection to the Caribbean was available through the Panamic portal. Tropical groups (e.g., gobiid and labrid fishes) have contributed to the marine fauna of the West Coast. Contributions from the Arctic, include the bivalve genus *Astarte*, (Marincovich & Gladenkov 1999) and fossil and modern lines of data document connectivity with the South American margin (Lindberg 1991). Thus, a component of the North Pacific fauna is derived from Neogene faunas from outside of the area.

However, comparative study of fossil data suggests emigration from the northeastern Pacific through the Arctic into the Atlantic (Vermeij 1991, Briggs 2003), as well as to the western coast of South America (Lindberg 1991). This outward migration is especially dramatic across the Arctic with an eight to one bias in favor of movement from the Pacific to Atlantic (Vermeij 1991). This far exceeds the two-to-one difference in diversities of the faunas. The general model for these movements presumes that taxa are responding to ecologic vacancies produced by extinction (Vermeij 1991, Briggs 2003). Regional extinctions leave vacancies that are filled more rapidly by immigration than by in situ evolution, a concept derived from the theory of island biogeography (e.g., Rosenzweig & McCord 1991). One can argue that the North Pacific is a geographic crossroads between biotic regions; however, it is clear that extensive speciation occurs in the Pacific region, that export of lineages that evolved in the North Pacific dominates over immigrants, and that diversity accumulated in the North Pacific due to in situ evolution rather than a direct product of connectivity.

Long-Term Stability and Lack of Extinction

Coordinated extinctions are often thought of as the product of perturbation in the physical environment. Cold regimes beginning in the Pliocene appear to have affected the Atlantic margin more than that of the Pacific (Stanley 1986). Although the causal chain is less well understood, extinctions also seem to have influenced the South American coast (see Lindberg 1991). A substantial number of fish taxa similar to those of the West Coast of North America were present, at least intermittently, on the west coast of South America in the Late Pleistocene but are no longer present (Landini et al. 2002), testifying to an ongoing extinction phenomenon in

that region. Causes of extinction on the South American coast may relate to discontinuity of upwelling rather than temperature alone. Thus, the pattern that is forthcoming contains two parts. First, perturbations in the Pleistocene, Pliocene, and perhaps also earlier in the Neogene were more extreme in other regions, such as the North Atlantic and the west coast of South America, and led to regional extinctions. Second, when conditions were suitable in these regions the Northeast Pacific served as a source of taxa, a scenario voiced previously (e.g., Ekman 1967) and recently put forward in greater synthetic detail (Lindberg 1991, Vermeij 1991, Briggs 2003). Thus, one can take the kinetic view that diversity is low in these areas in part because frequent disturbance precludes faunas from attaining the diversity that would be possible if oceanic conditions were constant over longer periods of time. The Pacific Coast may also sustain a higher standard equilibrium diversity owing to trophic factors, as discussed below.

Kelps and Trophic Stability

It has been argued that kelp plays an important role in sustaining a complex trophic structure (Estes & Steinberg 1988). Kelp beds retreat during low-upwelling El Niño years, as they require cold, nutrient-rich waters (e.g., Hernandez-Carmona et al. 2001). Multiple kelp lineages are thought to have originated in the North Pacific during the Late Miocene, roughly coincident with the initiation of the upwelling regime, and kelp lineages are more diverse in the North Pacific than elsewhere (Estes & Steinberg 1988, see Steneck et al. 2002 for review). An earlier origin of kelps seems likely (Domning 1989), but the radiation of kelp species during the Late Miocene of the North Pacific is also supported by the concurrent appearance of the sea cow lineage *Hydrodamalis*, a kelp specialist. Kelps do not fossilize well, and its historical association with upwelling is inferred from fossils of epiphytes, such as limpets. This record has been used to argue for a Pliocene origin of kelps (Vermeij 1992), but the database is minimal. Additionally, the nearshore record of rocky coasts is probably biased, as the record of rocky shore fauna is much better preserved for the Pleistocene and Pliocene than the Miocene. Rocky shores are normally eroding, consequently tend not to be preserved in the strata that make up the fossil record, and it is the uplift of terraces that has provided an unequaled record along the West Coast for the last million years. In addition, epiphytic barnacles associated with kelps have recently been recovered from Miocene rocks (Buckeridge & Finger 2001). Thus, the fossil data do not constrain the timing of the origin of kelps and are consistent with a Late Miocene radiation of kelps in the North Pacific. It has been argued that, as in many other taxa, kelps diversified in the North Pacific and dispersed to the Atlantic and Southern Hemisphere where these phaeophytes occur in far lower diversity (Estes & Steinberg 1988).

An argument involving trophic interactions has been developed to explain the high equilibrium diversity of the Northeast Pacific. Initially, a keystone predator, the sea otter (*Enhydra lutris*), was viewed as critical to sustaining higher coastal species diversity in the region than elsewhere. Sea otters are known to reduce

the densities of invertebrates that graze on kelps. In their absence, urchins (e.g., *Strongylocentrotus*) rise in abundance and decimate kelp beds primarily by severing the holdfasts (Estes & Steinberg 1988). Subsequently, this argument has been further developed with other predators, such as sheephead (family Labridae), contributing to the eastern Pacific trophic limitation on urchin density. Apparently, in Southern Hemisphere kelp forests, predators do not constrain the densities of destructive invertebrate grazers such as urchins to the same degree [Estes & Steinberg 1988, although see Shears & Babcock (2002) for conflicting data]. As a consequence, an evolutionary arms race has developed between the grazers and the kelps in the Southern Hemisphere, where the kelps have evolved high levels of phenolic substances and other defensive compounds (Steinberg 1995, Steinberg et al. 1995, see Steneck et al. 2002 for review). With greater phenolic content, Southern Hemisphere kelps provide a poorer resource for grazing invertebrates. Kelps are highly productive and can sustain large amounts of grazing, especially if it does not involve the critical holdfast. Drift kelp is also critical to sustaining many coastal invertebrates. A wide variety of herbivores, including decapod crustaceans, many molluscs such as abalone, and urchins, and an even wider variety of detritivores depend in whole or in part on kelp resources (Duggins et al. 1989). In the absence of otters or other comparable predators (Steinberg 1995, Steinberg et al. 1995), a higher concentration of defensive compounds reduces the nutritional value of the kelps to this broad array of consumers. Estes & Steinberg (1988) argue that the sea otter lineage in the North Pacific, as well as other kelp-dependent taxa such as Stellar's sea cow (*Hydrodamalis gigas*), was present and fulfilling its modern ecological role by the Late Miocene. This set of trophic interactions then permits a much more diverse set of primary consumers, a more complex food web, and a higher equilibrium value of diversity.

Summary and Prediction

Available evidence supports a more comprehensive elimination of the upwelling regime in the Pliocene outside of the North Pacific, as well as higher frequency of regional climatic perturbation over Plio-Pleistocene time and perhaps portions of the Miocene affected regions adjacent to the Northwest Pacific—the Arctic, North Atlantic, West Pacific, and western South America (Stanley 1986, Vermeij 1991, Lindberg 1991, Briggs 2003). The resulting extinctions in these regions have limited faunal diversity; rates of speciation are not rapid enough to supply new species locally, and a flux of migrants to the regions from the northeastern Pacific is observed.

Connectivity to other regions, such as across the North Pacific margin to the Asian coast, might have played some role in buffering the extinction frequency by providing temporary refugia and a modest source of new taxa, but connectivity mainly provides a means of export of the diverse North Pacific fauna to other regions. Thus, the high marine diversity of the northeastern Pacific appears to be largely a product of long-term relative stability, and protection of the system

from perturbations in the upwelling regime, combined with a trophic structure that facilitates this diversity. We argue that much of the marine diversity of the West Coast is nurtured in the Late Miocene and that diversity, or a sufficient part of it, was sustained through the less productive regimes of the mid-Pliocene and the varied productivity of the late-Pliocene and Pleistocene. Therefore, we predict that most of the fauna present in the upwelling region of the Pacific Coast should have originated in the Late Miocene during the glory days of upwelling (15–5 mya), and the Pliocene minimum in upwelling is expected to limit species production at that time. We also might expect some components of the rocky shore fauna to radiate in the Pleistocene owing to the return of upwelling and the increase in rocky shore habitat that occurred in that epoch. These predictions can be subject to test through the examination of divergence times of groups of taxa that appear to have undergone rapid speciation in the region.

Application of Genetic Data to the Question

Recently, a large number of molecular phylogenies have been generated for marine organisms, including several clades of fishes, crabs, molluscs, and birds. We examined these genetic data and applied rates of divergence of the relevant genes to determine the approximate time of divergence of each "West Coast clade." In our view (e.g., Jacobs 2002), molecular clocks are generally limited in their precision. In addition, we note that taxa can carry a portion of genetic diversity with them when they split into separate species or lineages. If the subdivided populations that generate species are large, significant genetic variation may exist within those populations. In such cases, the genetic differences in question may have started to evolve earlier than the actual reproductive isolation (e.g., Avise & Walker 1998). If these conditions pertain, the divergence times calculated will tend to be slightly older than actual reproductive isolation of the populations that subsequently evolve into separate species. Therefore, we make a consistency argument based on data from a range of taxa. The power of this argument is based on the multiplicity of examples rather than a high degree of precision for any one assessment. These examples are mainly based on information and calculations for genus- or family-level groups (Table 1). The evolutionary history of individual clades is discussed below.

SEBASTES This genus of rockfishes is speciose, with a long history of systematic revision at the subgeneric level. The genus currently consists of approximately 130 species occurring in cold and temperate waters in both hemispheres (Kendall 2000, Love et al. 2002). Diversity is concentrated in the North and especially in the northeastern Pacific; approximately 66 species occur along the North American Pacific Coast (Kendall 2000). These predatory, live-bearing fishes occupy a range of niches in kelp beds and on rocky shores. Given the number of species, the group would seem to be a candidate for rapid recent radiation. However, an analysis of cytochrome b gene sequences from 27 rockfish species in Monterey Bay showed

TABLE 1 Rates were calculated from the following sources: 16S rRNA, crustaceans (Strumbauer et al. 1996, Schubart et al. 1998, Stillman & Reeb 2001); 16S rRNA, fishes (Vences et al. 2001); COI, molluscs (Marko 2002); COI, crustaceans (Brower 1994, Knowlton & Weigt 1998, Buckley et al. 2001, Farrell et al. 2001); cyt b, fishes (Bermingham et al. 1997, Zardoya & Doadrio 1999, Machordom & Doadrio 2001); control region, fishes: (Donaldson & Wilson 1999, Falk et al. 2000); mtDNA, birds (Fleischer et al. 1998)

Taxon	Inferred time of divergence (mya)	Average divergence among West Coast Species	Rate estimate (%/my)	Genetic marker	Sequence length (bp)	References	Notes
Sebastes	4.5–3.0	0.045	1.00–1.52	cyt b		Johns & Avise (1998)	
Paralabrax	7.6	0.022	0.29	12S rRNA	424	Pondella (2001)	
Paralabrax	11.7	0.034	0.29	16S rRNA	570	Pondella (2001)	
Paralabrax	4.8	0.172	3.60	Control region	384	Stepien et al. (2001)	3 spp., inner and outer coast; distance = mean p-distance from *P. clathratus* to others
Embiotocidae	0.4	0.015	3.60	Control region	330	Bernardi (2000)	Intraspecific, 240 samples
Oncorhynchus	16.2–6.9	0.0571–0.135	0.833	ND3	351	McKay et al. (1996)	7 Pacific spp., pairwise Kimura 2-parameter (K2P)
Oncorhynchus	38.5–12.0	0.0136–0.0435	0.113	GH2	1406	McKay et al. (1996)	7 Pacific spp., pairwise K2P
Eucyclogobius	1.5	0.053	3.60	Control region	529	Dawson et al. (2002)	
Eastern Pacific gobies	8.7	0.314	3.60	Control region	651	Dawson et al. (2002)	
Alcidae	11.8–7.4	0.118	1.0–1.6	cyt b	1045	Friesen et al. (1996)	
West Coast *Ocinebrina* and *Nucella*	6.0–5.0	0.060	1.0–1.2	12S rRNA	290	Marko & Vermeij (1999)	(West Coast *Ocinebrina* and *Nucella*); *Acanthina, Ceratostoma, Mexacanthina, Nucella, Ocinebrina, Plicopurpura, Stramonita*
West Coast *Ocinebrina* and *Nucella*	11.0–6.4	0.077	0.7–1.2	COI	419	Marko & Vermeij (1999)	(West Coast *Ocinebrina* and *Nucella*)

California *Acanthina*	3.4–2.8	0.034	1.0–1.2	12S rRNA	290	Marko & Vermeij (1999)	(CA *Acanthina* only)
California *Acanthina*	6.7–3.9	0.047	0.7–1.2	COI	419	Marko & Vermeij (1999)	(CA *Acanthina* only)
Tegula	13.6–11.3	0.136	1.0–1.2	12S rRNA	480	Hellberg (1998)	24 spp. (0.080 CA only)
Tegula	12.7–5.9	0.089	0.7–1.5	COI	639	Hellberg (1998)	24 spp. (0.089 diverg. for CA only)
Haliotis	11.4–5.3	0.080	0.7–1.5	COI	528	Metz et al. (1998)	6 CA spp.; K2P divergences
Emerita	17.6	0.158	0.90	16S rRNA	322	Haye et al. (2002)	8 spp. including *Hippa pacifica*; not geographically limited to CA; divergence is between the 2 CA species.
Emerita	17.0–7.7	0.238	1.4–3.1	COI	419	Haye et al. (2002)	8 spp., including *Hippa pacifica*; not geographically limited to CA; divergence is between the 2 CA species.
Cancer	10.6–4.8	0.148	1.4–3.1	COI	1072	Harrison & Crespi (1999)	9 of 23 extant spp.
Tigriopus	12.1–5.5	0.170	1.4–3.1*	COI	177	Burton (1998)	1 sp.
Pacific porcelain crabs	18.9–7.35	0.100**	0.53–1.36	16S rRNA	479	Stillman & Reeb (2001)	37 spp.; mention divergence of California taxa during cool Miocene waters; *Allopetrolisthes* (3), *Liopetrolisthes* (1), *Pachycheles* (8), *Petrolisthes* (25); K2P divergences; estimated divergence for clade F, Figure 2
NE Pacific kelps	9.4	0.937	1.00	RuBisCo		Yoon et al. (2001)	44 taxa overall; rate data for RuBisco; only US West Coast taxa used; divergence range = 0.061–0.144.

a significant nonrandom peak in amount of molecular divergence among species, documenting an early radiation (Johns & Avise 1998). The authors suggest this peak in branching was at 5 mya, the very end of the Miocene and near the apex of upwelling. Subsequent work (Kai et al. 2003) provides a still more comprehensive survey of North Pacific Rockfish and suggests an earlier radiation, approximately 9 mya, clearly of Late Miocene age. The subsequent period of reduced speciation would then begin in the middle Pliocene, a time of reduced upwelling. Sequence data from the subgenus *Sebastomus* suggest a more recent Pleistocene radiation for this smaller subgroup as assessed by Rocha-Olivares et al. (1999a,b). Given that the rocky shore habitat for these taxa may have expanded in the Pleistocene (see below for discussion), it is surprising that Pleistocene divergences do not account for a greater proportion of the branching of the group overall. This strongly suggests that the stable upwelling regime of the Miocene was critical to generating a large fraction of rockfish diversity on the West Coast.

ONCHORHYNCHUS   The North Pacific salmonids include the rainbow and cutthroat trout lineages, which have some anadromous (seagoing) populations, but most populations remain in fresh water throughout their life-cycle, two East Asian anadromous salmon, and five species of Northeast Pacific anadromous salmon. Based on nuclear and mitochondrial sequences (McKay et al. 1996), the two Asian salmonids diverged in the Pliocene, and the two American trout diverged from each other in the latest Miocene to early Pliocene. The anadromous salmonids of the Northeast Pacific, the basal branches within the group, appear to be late Miocene in age (ca. 10 mya). The evolution of these salmonids in the Late Miocene is entirely consistent with their dependence on the richness of the marine waters of the North Pacific, where their populations are clearly susceptible to modulation of oceanic conditions. Anadromy in salmon facilitates reproductive isolation while retaining the capacity for subsequent dispersal, as salmon are known to colonize new streams (Milner et al. 2000). In the Miocene, sufficient stream flow for salmonids may have been restricted to regions north of California, owing to the drier climatic regime.

EMBIOTOCIDAE   Surfperches are nearshore, live-bearing fishes that have specific habitat requirements and lack a planktonic dispersal stage. They might reasonably be expected to experience reproductive isolation and speciation. However, the embiotocid family contains 14 genera and only 23 species (Bernardi 2000 and references therein). This low species-to-genus ratio suggests deep divergences between terminal taxa. The group is nearly exclusive to the northeastern Pacific, the exception being the presence of two species in Japan. A recent phylogenetic study reports an average divergence of 11.8% for cytochrome b, placing this radiation in the Late Miocene ballpark, or possibly a bit earlier (Bernardi 2000). These shoreline fishes might well have benefited from increased upwelling in the Miocene. Their speciation could also have been facilitated by the large Miocene and early Pliocene West Coast embayments.

ALCIDAE   The auk family is convergent on the penguins in that its members swim with their wings. Their mode of underwater pursuit of prey in marine conditions is well correlated with coldwater, nutrient-rich polar, or upwelling conditions. Penguins evolved in the initial phase of cooling in the Southern Hemisphere that occurred in the Eocene (Simpson 1976). Currently penguin ranges extend their Southern Hemisphere distribution to the equator in upwelling regimes as they are present in the Galapagos today (Akst et al. 2002). In general, birds that feed from the air can survey large regions and can persist in tropical settings with low-density resources. Cold water may give an advantage in muscle activity to "warm-blooded" pursuers over "cold-blooded" prey whose muscles necessarily operate at the ambient water temperature. In wing swimmers, airborne flight is increasingly impacted with size owing to the compromise of flying in two media, both air and water (Gabrielsen et al. 1991, Hodum et al. 1998). Thus, underwater pursuit via wing swimming might only be effective when a certain density of prey is available near breeding sites onshore, as will be the case in coastal upwelling regimes.[2] Three groups of wing swimmers, penguins, the recently extinct great auk of the Atlantic, and the extinct mancallid alcids of the Pacific, all evolved large size and lost the capacity for airborne flight altogether (e.g., Warheit 1992). Thus, wing swimming represents a tradeoff whereby efficiency of pursuit of prey underwater is increased at the cost of the reduction in efficiency and ultimate loss of the ability to survey prey from aloft. This strategy will be more effective where prey density is predictably high, as it is in cold, nutrient-rich upwelling regimes (Day & Nigro 2000). The alcid lineage precedes the Late Miocene, but alcids experienced an extremely rapid radiation in the Late Miocene of the Pacific from 13 to 7 mya (Warheit 1992). Eleven taxa are recorded in the fossil record of southern California alone during this period, including flightless members of the genus *Mancalla*, a lineage that went extinct in the Pleistocene. In the Pacific today, there are 17 alcid species, three of which are shared with the Atlantic. Three additional species are exclusive to the North Atlantic and adjacent regions of the Arctic Ocean. Sequence data from modern species (Friesen et al. 1996) again suggest a Late Miocene radiation that is no longer continuing and is entirely consistent with the rapid divergence observed in the fossil record. Modern alcid diversity is located much further north than the diversity observed during the Miocene in California, presumably because a far stronger and more continuous upwelling regime was present further south in the Late Miocene than occurs today.

CANCER   This classic crab genus is most diverse along the northern California coast where 9 of the 23 living species co-occur; consequently, this taxon has

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[2]Other birds that feed on fish, such as mergansers, loons, and cormorants, still fly effectively. Unlike alcids, these birds swim with their feet. They are not open-water pursuit predators, but lunging/ambush predators that feed via rapid extension of the neck rather than pursuit alone. They are not as "open marine" in their habitat preferences and spend a significant amount of time feeding in shallow water, near the bottom or around obstructions, and many species in these groups prefer freshwater.

also served as an icon of West Coast marine diversification (Ekman 1935, 1967). Fossil origins of the genus are tied to the Middle Miocene of the North Pacific, and seven of the nine species from the West Coast have fossil records extending well into the Late Miocene (Nations 1975). A Late Miocene radiation of now extinct taxa is also apparent in the fossil record, with 15 or more species co-occurring along the West Coast during the height of the upwelling regime in the region late in the Miocene. The appearance of the genus in the North Atlantic is consistent with current understanding of the potential for intermittent marine migration across the Bering region as early as 10 mya. Harrison & Crespi (1999) compared cytochrome oxidase subunit 1 (COI) gene sequences from 16 of 23 extant species of the genus *Cancer*, which are consistent with the Late Miocene radiation documented in the fossil record and our argument of the relationship of the radiation to upwelling. The data taken together suggest (*a*) the presence of two or three lineages prior to the inception of upwelling, (*b*) followed by a radiation that led to at least 15 species co-occuring on the West Coast for much of the Late Miocene, and (*c*) a subsequent reduction in diversity that conforms well to the more limited upwelling resources of the Pliocene. Thus, the modern species seem to be relics of the Miocene diversification. Along the West Coast, species of *Cancer* differ in substrate preference, feeding preference, and their ability to handle durophagous prey (Harrison & Crespi 1999 and references therein). Further study to elucidate the details of niche partitioning and the causal chain associating diversity and productivity in this group would be of interest.

KELP   Yoon et al. (2001) published a phylogeny of 44 species of kelp based on internal transcribed spacers 1 and 2 (ITS) between the nuclear ribosomal genes, and the chloroplast encoded spacer from RuBisCo, an enzyme involved in photosynthesis. These non-coding spacer sequences evolve rapidly and experience gain and/or loss of sequence through insertions and/or deletions, making them difficult to align. In such a situation, rate heterogeneity would be expected, and Yoon et al. (2001) did not discuss rates. In addition, there might be issues with the validity of some of the species [see recent study on Atlantic *Alaria*, (Kraan et al. 2001)]. Nevertheless, the tree topology and branch lengths (Yoon et al. 2001, figure 1) are intriguing and suggest the following regarding the evolution of kelps in the Neogene: (*a*) *Laminaria* of the West Coast and Atlantic diverged from Asian members of the genus *Laminaria* near the base of the tree, suggesting that a simple *Laminaria*-like form was ancestral to the radiation of living kelp;[3] (*b*) a relatively deep star phylogeny, suggesting the rapid radiation of 8 to 10 clades that are roughly 8% to 14% divergent and consistent with a 15 to 5 mya Miocene radiation assuming divergence rates of 1% to 2% per million years; and (*c*) within the genera where Yoon et al. (2001) sampled multiple species, including *Macrocystis*, Asian *Laminaria, Alaria,*

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[3]In Yoon et al. (2001) figure 1, *Egregia* is the basal ingroup taxon. However, this is likely a consequence of long-branch attraction to a distant outgroup. *Egregia* is a long branch owing to its singleton status; hence, the tree is difficult to root and *Egregia* may not be basal.

Undaria, "*Eklonia* clade," and *Lessonia*, divergences are often minimal, and consistently less than 2%. This suggests a second burst of Pleistocene speciation. These minimally divergent taxa include species of *Macrocystis* from North and South America as well as species of *Alaria* from the Pacific and Atlantic. Apparently, these oceanic transfers are a relatively recent Late Quaternary phenomenon. Divergences between the Atlantic and Eastern Pacific forms of *Laminaria* are on the order of 3%, possibly suggesting a Pliocene colonization event between these oceans. Interhemispheric movement within the dominantly Southern Hemisphere *Eklonia* and *Lessonia* are not assessed by these data. Thus, the major pattern suggested by the data is bimodal and potentially consistent with Late Miocene and Pleistocene components to the radiation separated by a Pliocene hiatus.

HALIOTIS   Abalones have a fossil record extending into the Mesozoic, and there is a significant diversity in the tropics today (Geiger & Groves 1999). However, reasonably high diversity of abalones exists in the North Pacific, with eight species, seven of which occur along the California coast. The North Pacific abalones form a monophyletic clade based on CO1 gene data and subsequent analyses (Metz et al. 1998). Sequence divergences of these North Pacific taxa are bimodal (Metz et al. 1998). Four of the taxa are closely related, with divergences from 1% to 3%. All other comparisons in the analysis range from 7.5% to 12.5%. When accepted divergence rates of roughly 1% to 1.5% are applied, this bimodality is consistent with a Late Miocene and a Pleistocene radiation, separated by a hiatus in the Pliocene. Thus, abalones appear to closely follow the kelps in their bimodal radiation. This is quite reasonable, as abalone depend on drift kelp as a food resource (Wood & Buxton 1996, Day & Branch 2002).

A number of gastropod genera such as *Tegula* and thaids appear to have somewhat greater diversity on the West Coast than elsewhere in their range (Hellberg 1998), but it is more difficult to consider them a species flock localized to the northeastern Pacific, as they do not represent single radiations exclusive to the region (Collins et al. 1996, Hellberg 1998, Marko & Vermeij 1999). It is also more difficult to link these taxa exclusively to a specific resource such as kelp that would be strongly controlled by upwelling. Nevertheless, there is a suggestion of heightened Late Miocene species production in the several lineages present on the eastern Pacific shoreline (see Table 1). A similar statement can made for the diverse but diminutive porcelain crabs of the intertidal eastern Pacific (Stillman & Reeb 2001).

DENDRASTER   Another taxon of considerable interest *vis a vis* a response to upwelling is the echinoid genus *Dendraster*. This sand dollar is a facultative filter feeder, as opposed to similar infaunal echinoids that are deposit feeders. Given their mode of feeding, members of this taxon can achieve high densities in sandy substrates where the individuals adapt a semi-infaunal posture, extending a large fraction of the test edgewise above the substrate when conditions are appropriate. It seems reasonable to infer that this filter-feeding behavior would be correlated with

planktonic resources and upwelling. The fossil record of *Dendraster* documents a California origin and radiation in the Late Miocene, approximately 7 mya (Mooi et al. 2000). No molecular data are available to corroborate this timing.

PLIO-PLEISTOCENE

Mid-Pliocene Upwelling/Nutrient Hiatus

The mid-Pliocene was a time of unusual global warmth (e.g., Knies et al. 2002) and reduced upwelling, or at least reduced production of biogenic opal on a very broad scale (Barron 1998, Barron et al. 2002, Berger & Wefer 2002, Loubere 2002). Interestingly, this warmth appears to be contemporaneous with significant ice accumulation in the Northern Hemisphere, especially on Greenland (Knies et al. 2002). One scenario relates this trend to the final closing of the Isthmus of Panama (e.g., Haug & Tiedeman 1998). This closure would limit the flow of water from the Pacific to the Atlantic, permitting an increase in salinity of Atlantic waters. This, in turn, facilitated the production of Northern Component Water—dense descending bottom- and mid-waters that form in the North Atlantic. This bottom water formation would accentuate the delivery of warmth and moisture to the North Atlantic and adjacent warming of Europe. This moisture may then have been critical to ice cap formation, ultimately accentuating the polar front (Knies et al. 2002).

Large-scale production of Northern Component Water is associated with the reduction of upwelling, and associated biological productivity, especially diatom growth, which specifically requires dissolved silica (see Berger & Lange 1998 for discussion). One possibility is that nutrient-poor subthermocline waters form in the North Atlantic and spread widely reducing the nutrient content of upwelled waters. Whatever the cause, the response varies with different consequences in the Atlantic and Pacific. Perhaps this distinction is due to local sources of nutrient-rich intermediate water in the Pacific (Sarmiento et al. 2004). In any case, there appears to be a high and reasonably globally coordinated peak in upwelling in the latest Miocene (Grimm et al. 1991, Barron 1998) with virtually complete shut down of temperate upwelling in the middle Pliocene with the exception of the northernmost Pacific (e.g., Barron 1998). In a simplified scenario, large-scale production of Northern Component Waters resulted in a decline in upwelling-related productivity in the middle Pliocene. This was followed by an increase in upwelling-related productivity as Northern Component Water production became more limited in the Late Pliocene and Pleistocene (see previous section for discussion).

Other critical factors besides the reinvigoration of the upwelling regime affected the California Coast in the late Pliocene and Pleistocene. They include (*a*) coastal and montane uplift, (*b*) the development of an active storm track generating winter precipitation, and (*c*) high-amplitude sea-level fluctuation. These factors operating in combination led to (*a*) the increase in storage of winter precipitation as snow to sustain larger river systems, (*b*) the elimination of extensive bay and estuarine systems, and (*c*) the generation of an increasingly rocky coastline.

Uplift

The timing of uplift of various features in the West, such as the Colorado Plateau, the Sierra Nevada, and the Coast and Transverse ranges of California,[4] has long been subject of discussion, and there has been a long tradition of emphasis on Miocene uplift across the West and resultant drying of the interior of the continent. However, recent data suggest that a very significant component of uplift of all these features is comparatively recent. Work on the Colorado Plateau suggests a far higher rate of uplift after the Miocene, and that rate appears to be increasing (Sahagian et al. 2002). Reconstructions of the path of the Snake River in the latest Miocene suggest that it crossed the northern Sierra Nevada rather than taking its current, more northerly course (Smith et al. 2002). This is consistent with much reduced Miocene topography, and, indeed, recent assessments suggest values in excess of 1 km of uplift in the Sierra Nevada occurred in the last three million years (Wakabayashi & Sawyer 2001). Reduction in the extent of pluvial lakes in the Great Basin with successive glaciation suggests an increasing rain shadow effect of the Sierra through the Late Pleistocene (Reheis 1999). Similarly, transverse ranges such as the San Bernardino and San Jacinto Mountains (Blythe et al. 2000, Kendrick et al. 2002) appear to have experienced Pleistocene uplift of 2 km. Uplift of 1 km or more in the Pleistocene is evident in the Santa Lucia Range (Ducea et al. 2003) and other topography of the mid-coast (Page et al. 1998, Perg et al. 2001), as well as the King Range (Dumitru 1991) of the northern California coast (Figure 1A). Terrace deposits provide strong documentation of uplift of 1 km in the past million years in the Palos Verdes Peninsula (Ward & Valensise 1994, 1996), San Clemente, and San Nicholas Island (Lindberg & Lipps 1996) (see Figures 1B, 2). Uplift is not uniform, but clearly there are dramatic increases in elevation and relief along coastal California and in the Sierra Nevada from the Late Pliocene throughout the Pleistocene.

The reasons for uplift in many cases relate to transpression between the Pacific and North American plates along the San Andreas and parallel systems. Increasing uplift rates through the Pleistocene may relate to increasing spreading rates in the Gulf of California (Antonelis et al. 1999). Thus, the dramatic features of the modern western landscape, especially those that extend above 2000 m, such as the crest of the Sierra Nevada and the Transverse Ranges, as well as much of the topography of the Coast Ranges (Figure 1A), appear to be a Pleistocene phenomenon and one that has been accentuated late in the Pleistocene.

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[4]Recent controversy has focused on the difficulty in discriminating the roles of climate and uplift in their effect on erosion (Molnar & England 1990), as well as controversy surrounding differences in interpretation of paleobotanical data (e.g., Wolfe et al. 1997). We focus on recent nonpaleobotanical studies, which provide strong support for substantial post-Miocene uplift in the western and coastal cordillera. This emphasis on Plio-Pleistocene uplift is reminiscent of early studies that used the term Cascadian Revolution for this late episode of orogenic activity (e.g., Schuchert & Dunbar 1937).
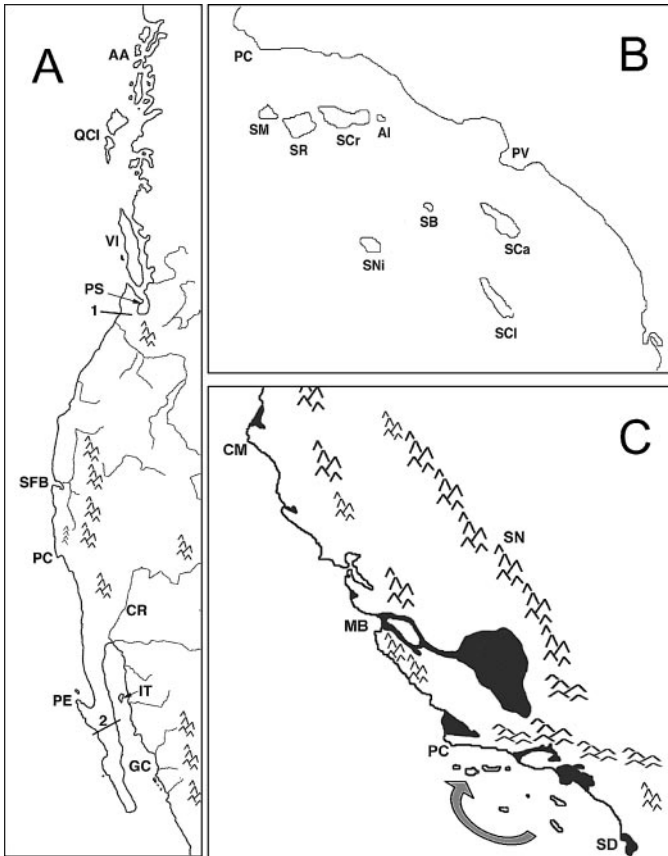
Figure 1 (*A*) Coastline of western North America, from the Alexander Archipelago
to the peninsula of Baja California Sur, Mexico: 1. southern limit of Continental Glacia-
tion on the coast; 2. location of postulated Transpeninsular Seaway; AA, Alexander
Archipeligo, QCI, Queen Charlotte Islands; VI Vancouver Island; PS, Puget Sound;
SFB, San Francisco Bay; PC, Point Conception; PE, Punto Eugenia; CR, Colorado
River; IT, Isla Tiburon; GC, Gulf of California. (*B*) Map of the Southern Califor-
nia Bight and Channel Islands: SM, San Miguel; SR, Santa Rosa; SCr, Santa Cruz,
AI, Anacapa; SNi, San Nicholas; SB, Santa Barbara, SCa, Santa Catalina, SCl, San
Clemente; PC, Point Conception; PV, Palos Verdes Peninsula. Pleistocene uplift of
1 km or more has been documented on many of the Islands and the Palos Verdes
Peninsula as discussed in the text. (*C*) Reconstruction of Early Pliocene estuaries 5–
2.5 mya (after Hall 2002) along the coast of California, from Cape Mendocino (CM)
to San Diego (SD): MB, Morro Bay; PC, Point Conception; SN, Sierra Nevada. Arrow
documents the sense of the Miocene rotation of the Northern Channel Islands away
from the coast. San Miguel Island would have been adjacent to San Diego 18 mya as
discussed in the text.

Winter Precipitation

Although there is some evidence for glacial ice reaching the sea in southern Greenland after 7 mya in the Latest Miocene (Larsen et al. 1994) and possibly even earlier (Winkler et al. 2002), it is generally agreed that a shift to a cooler regime, with more extensive ice and a far more active polar front, began approximately 3 mya. Since at least that time the average amount of area covered by ice has far exceeded the current interglacial coverage. When ice sheets are present on the North American continent, they displace the storm track to the south and maintain a stronger polar front that persists for a greater portion of the year, yielding greater precipitation, lower evapotranspiration and significant accumulation of moisture during glacial phases in regions well south of the glacial front; for instance, in California (e.g., Kutzbach 1988).

By the end of the Pleistocene, continental climatic conditions were much different than they were in the Late Miocene or Early Pliocene. In effect, winter precipitation was expanded and focused in rising mountains. During wet glacial phases of climate there was extensive mountain glaciation in the Sierra Nevada, and sufficient water to maintain expansive lakes and lush wetlands covering much of Great Basin of Nevada and Utah as well as portions of the Imperial, Mojave, and Central Valley regions of California. During glacial phases the meltwater from Sierra glaciers and high-altitude snows in the region would have dominated aquatic systems, with plentiful water reaching lowland riparian settings. Extensive, relatively moist conditions influenced the vegetation regime throughout the Southwest. Even in dry interglacial phases, such as the Holocene, focusing of precipitation in high elevation and the presence of mountain snows permitted significant flows in the region from the Sierra generating perennial streams in the San Joaquin River prior to damming of headwaters. Similarly, the Colorado River system has expanded greatly since the late Pliocene, with the development of the Grand Canyon and the capture of drainages both on the Colorado Plateau and to the north and east of the Plateau. These major systems of the Southwest are a product of the increasing accumulation of snow at high elevations that provides a source of runoff through the drier interglacial summers. Interestingly, although both winter and summer rain were limited in the Late Miocene, topography was more moderate, and the precipitation present was less focused on mountains. Therefore, although there was insufficient runoff to sustain river systems through dry summers, there were also less severe rain shadows in the interior southwest. More substantial rain shadows generate the extreme interglacial desert conditions observed today. The absence of the uplift that subsequently occurred allowed moisture penetration into the continent at moderate elevation in the Miocene (see Axelrod 1986a) without the extreme differences in precipitation imposed by the subsequently evolving topography and substantial wintertime precipitation.

Sea-Level Oscillation

An additional factor that also changed the physical context of the Pacific Coast in the Southwest is the increasing amplitude of sea-level oscillation. Climatic

processes that appear to be controlled in part by Milancovitch parameters of the Solar System led to fluctuations in the storage of ice in ice sheets. This, in combination with other factors, such as the storage of water in the Mediterranean basin when it was isolated during the Messinian Stage of the Late Miocene and in lakes and aquifers (Jacobs & Sahagian 1993, 1995), produces oscillations in sea level. Processes that sequester water in continental interiors and ice caps do so in an isotopically biased way. Water molecules containing the oxygen-16 isotope preferentially enter the vapor phase. As a consequence of the multiple evaporative and condensation and precipitation cycles (Rayleigh distillation) only light isotopes are left to precipitate in the center of continents or ice sheets, as the heavier isotopes are retained in or go into the liquid phase first. In the Late Miocene (11–7 mya), oscillations with frequencies less than 200,000 years have minimal amplitude of around 0.3 to 0.5 per mil (see Billups 2002, Diester-Haass 2002). From 5.5 to approximately 3 mya the amplitude was around 0.7 per mil with three or four larger excursions. From 3 to roughly 0.9 mya, oscillations occurred with frequencies in the 40,000 year range associated with the tilt of Earth's axis and amplitudes of approximately 1.0 to 1.5 per mil. Subsequently, 100,000-year obliquity cycles with amplitudes approaching 2.0 per mil or more predominate (see Zachos et al. 2001 for recent summary of isotopic fluctuations). Sea-level change since the last glacial maximum has been measured at around 140 m from submerged wave cuts in Australia. This change is associated with an approximately 2.0-per-mil change in oxygen isotopic values. Assuming a linear relationship, there has been at least a fivefold increase in amplitude of sea-level oscillations (with periods of less than 200,000 years) since the Late Miocene, most of it in the past 3 million years.

In combination, uplift, an active polar front, and sea-level oscillation have consequences for both freshwater and coastal marine systems including (*a*) reestablishment of perennial freshwater riverine and lake systems in the Southwest, (*b*) the elimination of a number of large estuarine habitats, and (*c*) the expansion of steep rocky shores. The nature and biological consequences of these changes and their implications for diversity and genetics are discussed in turn.

Freshwater Systems

One would assume that Miocene drying would have eliminated much of the primary or deeply historical freshwater fauna from the Southwest, a perspective supported by the relative absence of native "primary" or ancient freshwater fishes. Subsequent Plio-Pleistocene cooling and glaciation then appear to have eliminated much of the warm-adapted freshwater fauna from the Northwest (see Smith 1981, Smith et al. 2002, for limited fossil data), although a few primary fish taxa endemic to the East have subsequently colonized the Columbia drainage. The large perennial stream systems of the Southwest, the Colorado and San Joaquin, are inhabited by a depauperate primary native fish fauna, including a number of types of cyprinids (minnow) and the Sacramento perch, the only centrachid (bass, sunfish) native to the

Southwest. These fishes persisted through the Late Miocene/early Pliocene in the limited aquatic systems available at the time. They are supplemented by a "secondary" fauna that invaded from the sea. The freshwater salmonid species of the genus *Onchorhynchus*, cutthroat and rainbow trout, are Pliocene in age based on genetic divergences (see previous discussion). These undoubtedly marine-derived fishes expanded through the mountain West during the wet phases of the Plio-Pleistocene. Other marine-derived, "secondary" freshwater fishes of the West include sculpins (family Cottidae) and sticklebacks (family Gasterosteidae).

Estuarine Systems

From Miocene to middle Pliocene times, numerous large embayments extended in excess of 50 km inland from the present coast in the Los Angeles area, the Santa Clara Valley, Santa Ynez, Santa Maria, and Morro Bay regions of mid-coast California, and the Esteros/Alexander Valley region (Hall 2002) (see Figure 1*C*). An even larger system extended from the Monterey region for 250 km into the southern Central Valley. Marine sediments of Late Miocene age are present in the Imperial Valley region of southern California, although they may have connected to the sea to the south through an incipient Gulf of California. These embayments consistently have warmer, more tropical faunas than the outer coast during the cooling trend from the Middle Miocene to the Pleistocene (see Hall 2002 for detailed discussion of these estuaries). The large estuarine systems along the central California coast persisted for much of the Miocene and into the Pliocene, but they are gone today. The sedimentologic record exposed in uplifted features along the western boundary of the Central Valley are instructive, as they document the infill of the marine estuarine system via progradation of sediment derived from the uplift of the southern Sierra Nevada (Kern River Formation, Loomis 1990). This process appears to have initiated in the Late Pliocene from 2 to 3 mya. Subsequently, uplift combined with high erosion and sedimentation rates associated with increasing wintertime precipitation led to the infill of the more modest systems that penetrate the Coast Ranges (listed above). In addition, ice volume-driven oscillations in sea level increased from substantially less than 25 to over 125 m by the Late Pleistocene, subjecting shallower estuaries to frequent flooding and emptying cycles. For example, during the last glacial maximum, San Francisco Bay was entirely empty, and a large volume of glacial meltwater from the Sierra Nevada entered the sea at the shelf edge (see Lindberg & Lipps 1996). It is true that effects of sea-level change are global, but such change may be far less disruptive or isolating of estuarine habitats on shallower-sloping shelves that lack tectonic perturbation, such as the Atlantic margin. Thus, stable estuarine habitat was effectively eliminated from the California coast and much of the West Coast by some time in the Pleistocene.

Biotic Effects of Loss of Estuaries

The elimination of stable estuarine habitat on the West Coast has a number of biological implications. One would anticipate (*a*) extinction of the diverse faunas

that inhabited these estuarine settings in the Miocene and Pliocene; (*b*) invasion of recently formed, Holocene, estuaries owing to the absence of competing native fauna; (*c*) some relict diversity that evolved in the complex set of reentrants along the Mio-Pliocene coast and persisted until today; and (*d*) phylogeographic breaks persisting in such relictual taxa.

Clearly, there were diverse faunas in the Miocene and Pliocene embayments of southern California. They are generally representative of warmer water taxa than occur in the region today, and these were subject to Late Pliocene extinction (see Hall 2002). Apparently, a wide range of molluscs was eliminated through a series of transgressive-regressive cycles in the Pliocene (Stanton & Dodd 1997), a process finalized by the elimination the estuaries initially occupied by warm-water forms.

SUSCEPTIBILITY TO INVASION   One of the more obvious biotic phenomena on the West Coast is the human-mediated invasion of modern estuarine settings by taxa from around the world. An initial suite of taxa was derived from the transfer of oyster stock, first from the East Coast via rail in the nineteenth century and subsequently from Japan. Now, ballast water transfer appears to be one of the primary mechanisms of movement of new taxa to the area. By some accounts, these transfers make San Francisco Bay the most invaded estuary in the world (Bollens et al. 2002, Grosholz 2002). When one considers that prior to Holocene sea-level rise the Sacramento/San Joaquin/San Francisco Bay complex was a massive system delivering glacial meltwater almost directly to the shelf edge, and that the estuarine systems that exist along the coast today are spatially isolated from other systems, it is not surprising that the few large open estuarine systems along the coast are depauperate and vulnerable to invasion from estuarine taxa transported from elsewhere in the world.

RELICT DIVERSITY   Although much diversity associated with shallow water embayments was likely eliminated with those embayments as a consequence of the Plio-Pleistocene processes reviewed above, relict diversity in some groups may persist despite the absence of the primary estuarine habitat in which it evolved. Dawson et al. (2002) argued that loss of summer rainfall in the late Miocene associated with upwelling was responsible for generating the small summer-closed estuarine systems that predominate on the West Coast, an observation that is consistent with the genetic differences between the closed estuary specialist, the tidewater goby, and its closest relative. There are six estuarine or bay goby species in the California region, a seemingly large number given the relative absence of estuaries. These gobies are still more divergent than the tidewater and arrow gobies (Dawson et al. 2002), suggesting that they evolved in the West Coast estuarine setting earlier in the Miocene at a time when warm estuarine settings were extensive.

As mentioned previously, the nearshore surfperches (embiotocids) are diverse, varied in their habitat preference, live-bearing, and largely endemic to the northeastern Pacific. Given their nearshore character, it seems likely that the Mio-Pliocene embayments contributed to the diversification of this group. Members

of the group that persist along the coast today are likely the product of Miocene radiation, and diversity may have been more extensive in the past than it is today. Other taxa that appear anomalously speciose on the West Coast and use bays and estuaries in part of their life history include the flatfishes and rays. In the flatfish genus *Pleuronicthyes*, five of the seven species occur along the California coast and are often found inshore. Thus, some of the diversity of the warm-water, non-upwelling, bay-associated species from a range of fish families may have evolved in response to these earlier estuarine habitats.

PHYLOGEOGRAPHY AND MIO-PLIOCENE   In addition to the established species diversity discussed above, taxa with minimal vagility that lived in Pacific Coast estuaries may retain deep genetic divergences that reflect earlier estuarine structure. One such taxon is the small brooding bivalve *Nutricola tantilla*, where COI data (R. Kelly & D.K. Jacobs, unpublished data) are subdivided with approximately 10% regional sequence divergences that appear to reflect earlier estuarine settings of the Late Miocene or Pliocene. We would anticipate that more detailed study of other eastern Pacific estuarine- and bay-related taxa with very limited dispersal ability might reveal genetic structure reflecting these earlier systems. Wake (1997) argued that the embayment that crossed the Coast Ranges into the Central Valley from the Monterey region (Figure 1*C*) provided a barrier to gene flow and a source of deep phylogeographic structure for low-vagility terrestrial taxa, such as newts and ambystomid salamanders.

INCREASE IN ROCKY INTERTIDAL IN THE PLEISTOCENE   Although the West Coast has been tectonically active since the Mesozoic, the degree of uplift in the last two million years appears to have been particularly dramatic, and in the last three million years, the amplitude of 10-kiloyear to 200-kiloyear cycles in sea-level fluctuation has increased substantially. On the million year timescale, this combination of factors disperses the erosive power of the Pacific waves over a much larger area (set of elevations) of coastal rock. As documented by the Holocene sea-level stand, it takes roughly 10,000 years for shoreline erosion to cut a terrace surface of hundreds of meters in width. During the course of Pleistocene uplift many such terraces have been produced (e.g., Lindberg & Lipps 1996). Without sea-level oscillation and uplift, wave energy would have persisted at the same relative level over the long term. Under such a persistent erosive regime regions of softer sedimentary rocks form gently dipping coastal plains kilometers wide in a million years or less. Only coasts with harder granitic rocks could, for a time, resist this process.[5] For the Miocene and Early Pliocene one can envision some

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[5]In the absence of a significant polar front prior to 3 mya wave energy would have been limited, and there were other regional episodes of uplift along the Pacific Coast in the Tertiary. Nevertheless, the factors diffusing coastal erosion over multiple levels appear most extensive in the Pleistocene, leading to less sandy and more rocky shore than earlier in the Neogene.

rocky headlands, particularly in areas of tectonic activity, as well as more extensive
sandy shorelines—an intermediate condition between the extensive sandy barriers
of the Atlantic and Gulf coasts and the currently dramatic coastal topography of
California.

The increased rocky shoreline combined with the contemporaneous return of
upwelling conditions would have been conducive to the evolution of rocky-shore
specialists. As previously discussed, the genetic data concerning the recent Pleis-
tocene component in kelp and abalone diversification in the northeastern Pacific
are coincident with, and appear to be a consequence of, renewed upwelling and
the enhancement of the rocky shore setting.

THE BAJA CALIFORNIA PENNINSULA AND THE GULF OF CALIFORNIA

Formation and Isolation of the Gulf of California

The Baja California Peninsula (BCP) and the Gulf of California/Sea of Cortez
present a number of interesting challenges in interpreting the interplay between
geologic process and the resultant biological patterns. Much has been made of the
genetic isolation of terrestrial populations and species in the southern part of the
Peninsula, leading to the interpretation of a Pleistocene seaway across the BCP (see
Figure 1*A*). The Gulf is warmer than the outer coast yet is over 1000 km in length,
so it experiences its own latitudinal climatic variation as well as a cold upwelling
regime around Isla Tiburon (e.g., Soto-Mardonnes et al. 1999). Thus, it contains a
number of habitat types (Briggs 1974, Brusca 2004) and a diverse marine fauna.
However, the peninsula separates several species pairs between the outer coast and
the Gulf, a pattern that suggests mechanisms of allopatric speciation.

The tectonic opening of the Gulf began approximately 6 mya, with spreading
resolved to its current organization by 3.7 mya (e.g., Lonsdale 1989), albeit with
potential subsequent changes in rate (Antonelis et al. 1999). However, a previous
phase of extension may have followed cessation of subduction near the mid-BCP
at 12.9 mya and the southern BCP at 10.6 mya (e.g., Henry & Aranda-Gomez
2000). The earliest purported marine record in the Gulf is approximately 12 mya
from Isla Tiburón (Helenes & Carreño 1999). However, these dates have been
questioned, and a simple history of marine incursion from the south correlated with
the tectonic opening has been inferred, with flooding past the northern terminus
of the basin by 6.3–6.5 mya, near the end of the Miocene (Oskin & Stock 2003).
This interpretation is consistent with the biostratigraphy of the Imperial Formation,
a fossiliferous unit extending into Imperial and Riverside Counties in California
(McDougal et al. 1999).

In a number of taxa, closely related marine species occur on the Gulf and outer
coast of the BCP, and perhaps as many as 42 fish species have disjunct distribu-
tions with populations isolated in the more temperate regions of the northern Gulf

of California and the Pacific shoreline of the BCP (Present 1987). These disjunct distributions seem ideal for marine speciation to proceed in traditional allopatric mode. Most workers presume that disjunct Gulf and outer coast populations were established in colder epochs of the Pleistocene when more southerly ranges permitted movement around Cabo San Lucas, and that subsequent Holocene warming led to population isolation (e.g., Brusca 1980). Others invoke a seaway across the peninsula in the Pleistocene. The geologic evidence for a Late Pleistocene-age transpeninsular seaway is equivocal as discussed below. However, the severity of temperature changes during Pleistocene glacial phases is probably in excess of what most workers assume (as discussed below), making a climate-related mechanism involving southern range extension (Brusca 1980) particularly attractive for generating episodes of colonization and isolation between the Gulf and outer coast.

It should also be noted that there are some similarities between the warm-temperate to subtropical conditions of the Gulf today and the conditions that persisted in the Miocene in the substantial structural embayments present along the California coast from Miocene to Pliocene times. Some isolated species in the Gulf could have evolved in these more northern regions and retreated into the Gulf during the Pliocene, when similar warm-water habitats became available there and before complete loss of estuarine habitat and cooling eliminated comparable habitats from the outer coast (e.g., Hall 2002). Thus, one would predict that in genetic comparisons between the outer coast and the Gulf of California, disjunct populations might have evolved in response to relatively recent Pleistocene climate oscillations. Other possible scenarios include disjunctions now recognized as species that have been maintained since the time of formation of the Gulf, and those with longer histories that preceded the Gulf's formation.

Several recent works examining the genetics of fishes have begun to address some of these issues. In an intriguing study, Stepien et al. (2001) examined the population differences between the Gulf and outer coast populations of *Paralabrax maculofasciatus*, the spotted sand bass. The genus *Paralabrax* is most diverse in the eastern Pacific where it inhabits temperate to warm-tropical settings from California to Peru; there is but one Atlantic species. Stepien et al. (2001) examined the disjunct populations of *P. maculofasciatus* using mitochondrial control region sequence data. Two congeners, endemic to the outer coast of Baja and Alta California, were used as outgroups in the study. The data suggest that *P. nebullifer* and *P. maculofasciatus* diverged in the Pliocene, consistent with an allopatric mechanism following the opening of the Gulf. There is a slightly greater diversity of mitochondrial and allozyme alleles in the Gulf than in Pacific populations of *P. maculofasciatus*, leading one to speculate that the Pacific populations are a product of colonization from the Gulf, supporting an argument for an allopatric Gulf-of-California origin of *P. maculofasciatus*. In addition, given the cyclic nature of Pleistocene processes and the likely retention of genetic differences from ancestral populations, the few base pairs separating the Pacific and Gulf forms suggest the possibility that expansion to the Pacific Coast was comparatively recent, perhaps in the last one or two glacial cycles (see Avise & Walker 1998 for

discussion of the genetics of such Pleistocene speciation). More detailed studies, especially along the Pacific Coast, might clarify the history of this process.

A recent examination of the opaleye, *Girella nigricans*, between the Pacific Coast and the Gulf of California documents deeply divergent clades of haplotypes along the Pacific Coast (Terry et al. 2000). The degree of within-species variation along the Pacific (4.9% divergence) suggests separate clades, perhaps of late Pliocene or early Pleistocene age, that have subsequently been mixed by Pleistocene climatic process.[6] Taken at face value, their tree suggests a single emigration to the Gulf from the Pacific by the early Pleistocene followed by diversification in the Gulf. Clades are divergent, and there are no shared haplotypes; thus, there appears to be no late Pleistocene gene flow, suggesting an isolation process that has been going on for much of the history of the modern Gulf of California.

Huang & Bernardi (2001) examined the two members of the gobioid genus *Gillichthys*, the long-jawed *G. mirabilis* and the short-jawed *G. seta* mudsuckers. *G. mirabilis* has a disjunct distribution, but *G. seta* only occurs in the Gulf of California and is a high-intertidal tidepool fish adapted to high temperatures characteristic of this habitat. Pacific margin and Gulf clades of *G. mirabilia* are approximately 2% divergent, which, with the cytochrome b sequence used, suggests a Pleistocene isolation process. However, given the small number of widely spaced samples, isolation by distance may be at work here. In addition, two individuals in the Gulf have haplotypes typical of the southern Pacific clade. This suggests subsequent iterations of gene flow into the Gulf consistent with the climate model of iterative influxes of individuals during glacial phases, although human transport of *Gillichthys*, which is used as bait, is also possible (C. Swift, personal communication). In contrast, sequence divergence between *G. seta* and *G. mirabilis* measures 11%, suggesting a late Miocene divergence. This may precede the time of continuous marine habitat in the Gulf. Thus, the two mudsuckers likely speciated prior to the formation of the modern Gulf, and *G. seta* is now endemic. Perhaps *G. seta* first evolved in some other tectonic embayments of the California Miocene or colonized the Gulf and evolved its habitat specialty during an initial phase of opening.

Thus, in studies of spotted sand bass, opaleye, and mudsuckers, we have examples of speciation by isolation in the Gulf following its formation, and population isolation coincident with Pleistocene climatic processes. Also, the developing Gulf appears to have played a role as a refugium for warm temperate faunas that likely

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[6]In any case, the opaleye trees suggest very large populations without significant bottlenecking. They and other nearshore fishes have very different intrapopulational patterns of haplotype divergence than are evident in open marine taxa such as *Sardinops* (Bowen & Grant 1997). Sardines have little mitochondrial sequence variation within an oceanic gyre, suggesting population crashes or mechanisms that lead to dramatically different reproductive success operating such that these populations are effectively much smaller than they appear. This does not seem to be the case with coastal taxa. Even when species phylogenetic structure is not completely geographically coherent, populations are sufficiently subdivided as to prevent coalescence.

evolved in other similar settings prior to its formation. In addition, marine habitats are complexly distributed between the northern and southern Gulf, the Midriff Islands, and the eastern and western shores. Taxa with low vagility exhibit genetic structure within the Gulf that is geographically coherent in the case of blennioid fishes (Riginos & Victor 2001) and less coherent in the case of penaeid shrimps (Aubert and Lightner 2000).

Seaways Across the Peninsula

Clearly, the opening of the Gulf of California has had an isolating effect on the terrestrial biota of the BCP as well as on the islands of the Gulf. Tectonic data suggests that the cape region, a tectonic block, was initially separated from the rest of the BCP by a seaway and subsequently rejoined the BCP in the early Pliocene (e.g., Lonsdale 1989, Helenes & Carreño 1999, DeMets & Traylen 2000, Dixon et al. 2000). The Cape Block extends to the south of La Paz and is topographically high, providing areas isolated by altitudinal climatic features as well as the seaway in the vicinity of the Isthmus of La Paz during the initial phase of Gulf rifting (Miocene to early Pliocene). Its biota has also long been recognized as distinct from that of the rest of the BCP (see Nason et al. 2002 for recent analysis). For instance, populations of pocket mice studied across this boundary exhibit a 12.3% divergence for cytochrome oxidase subunit III (COIII) gene sequences (Riddle et al. 2000c). This would be consistent with isolation since the Miocene. Most other taxa examined to date do not suggest a phylogeographic boundary.

Rodents, including deer mice (*Peromyscus*), two groups of pocket gophers (*Chaetodipus*), a kangaroo rat (*Dipodomys*), and a ground squirrel (*Ammospermophilus*), as well as some data for lizards, show a shallow break in the mid-peninsular Vizcaino region (Upton & Murphy 1997; Riddle et al. 2000a,b). This coordination of genetic breaks suggests a significant "phylogeographic boundary." The species across the boundary are primarily distinct in terms of genetics rather than obvious morphology, showing differences ranging from 2% to 5% that have generally been inferred to be Pleistocene in age (ca. 1 mya). The phylogeographic differences in the region led to the invocation of a geologically recent seaway across the Peninsula (e.g., Upton & Murphy 1997). The seaway is generally viewed as a projection of Laguna San Ignacio across the Peninsula (see Figure 1*A*) and Pleistocene marine rocks have been reported from the Vizcaino region. The presence of significant Miocene volcanics might argue for a continuous exposure and against a Pleistocene seaway (Calmus et al. 2003). However, the relationships between these volcanics and sedimentary rocks deposited in a seaway are obscured by significant quantities of Pleistocene and even historic lava flows. Thus, the geologic data are unclear as to whether a seaway actually completely traversed the peninsula, and, if it did so, how long marine conditions persisted. Interestingly, there is no difference at this boundary in the toad *Bufo*, or the columnar cactus *Lophocereus* (Hartmann et al. 2001, Nason et al. 2002). That an amphibian such as *Bufo* does not show structure is inconsistent with an inferred marine boundary, as amphibians are not tolerant of salt water.

Whether or not a seaway existed earlier in the Pleistocene, it is clear from the series of Pleistocene volcanics in the region that no seaway has existed for several-hundred-thousand years. Consequently, it seems that other factors must have played and may still play a significant role in maintaining this boundary. A significant component of the biogeographic structure on the peninsula is localized in the Vizcaino region (Rojas-Soto et al. 2003). These desert lowlands of the western peninsula are dry, and the black recent volcanic flows of the San Ignacio area seem particularly uninviting. Furthermore, highlands to the south of Vizcaino receive significant summer rain, whereas more northerly regions primarily receive precipitation in the wintertime. Given these factors, it seems that the Vizcaino region might provide some of the lowest quality habitat for many lineages, and that it may serve as "tension zone"—a region where population densities and gene flows are minimal and where boundaries between lineages will tend to accumulate. Such boundaries can be accentuated by sexual or natural selection. Clearly, more study of biological processes and geologic history across this intriguing region are in order.

THE CALIFORNIA BIGHT

Neogene Tectonics of the Bight

The California Bight is the region extending from Point Conception southward past the Channel Islands to the vicinity of San Diego (see Figure 1*B*). It has a dramatic coastal morphology, a distinctive Neogene tectonic history, as well as a complex marine circulation. Prior to the opening of the Gulf of California and the contemporaneous development of the southern San Andreas system approximately 6 mya, transform motions were accommodated to the west of the modern San Andreas in Southern California (e.g., Ingersoll & Rumelhart 1999). This included substantial right-lateral movement near the edge of the continental shelf. This transform motion between the Pacific Plate and America was partially accommodated in the region of southern California by the rotation of a coastal block in a fashion akin to a windshield wiper around a pivot point near downtown Los Angeles. Currently, this block is bounded on the north by Point Conception and the Santa Ynez Mountains north of Santa Barbara, and on the south by the Northern Channel Islands (Anacapa, Santa Cruz, Santa Rosa, and San Miguel) and Santa Monica mountains (Ingersoll & Rumelhart 1999, Hall 2002). This rotation took place primarily between 18 and 12 mya and helped define the Mio-Pliocene bay/estuarine systems in the Los Angeles Basin and Santa Clara, Santa Ynez, and Santa Maria valleys discussed above.

Late Pleistocene Oceanographic Context of the Bight

The hydrodynamics of the Bight are commonly characterized as having an eddy generating a northward flow nearshore, inside of the southward flowing California

Current. This may be true on average, but flow rates are modest relative to the California Current, and subject to transitory modes of flow organization in each of the sub-basins of the region [e.g., Santa Monica Basin (DiGiacomo & Holt 2001) and Santa Barbara Channel (Harms & Winant 1998)]. As previously discussed, terraces on the Palos Verdes peninsula and San Nicholas Island document their first emergence from the sea approximately 1 mya; ongoing uplift has increased the area of numerous islands and raised a number of shoals that are barely submerged under the current high, Holocene, level of the sea (part of a more general transpressional uplift regime in the region). Through the Pleistocene island area and the number of emergent shoals has increased. This increase clearly reduces current velocities and wave energies in the Bight (see http://cdip.ucsd.edu/models/about_swell.shtml). Quaternary sea-level fluctuations are superimposed on ongoing tectonic uplift and geomorphologic development of the Bight. If one views uplift of the various blocks in the Bight as a continuous process, it appears that more islands and land area in the Bight have been exposed above sea-level with each successive glacial cycle. Thus, wave energy and current flow in the Bight must have been increasingly obstructed through the Late Pleistocene especially during lowstand conditions.

In addition to these effects of sea level and tectonics, large flows of fresh water would have entered the Bight through the rivers draining the highlands of the Transverse Ranges such as the Santa Ana, San Gabriel, and Santa Clara Rivers during glacial maximum conditions, and ocean conditions were likely substantially colder during glacial maximum conditions, as is discussed below. Overall rates of uplift suggest that sea levels began dropping off the edge of a coastal escarpment during low stand beginning approximately 500 kiloyears ago (kya), intermittently eliminating bay/estuarine conditions in the Los Angeles Basin. A sizable marine/estuarine incursion in the Los Angeles Basin occurred, presumably for the last time, during the stage 5 (ca. 100 kya) sea-level high stand.

Phylogeography of the Bight

The series of geologic and oceanographic phenomena very generally reconstructed above would be expected to lead to generate selective barriers to gene flow in taxa with limited fecundity, dispersal ability, or a high degree of habitat specificity (e.g., Dawson 2001). In addition, there is a change in temperature across the northwestern part of the Bight. Traditionally, a biogeographic boundary between the Oregonian cool-water fauna to the north and the warmer Californian fauna to the south was placed at Point Conception (e.g., Valentine 1966) near the steepest gradient in temperature, and a phylogeographic boundary was anticipated at Point Conception as well (see Figure 1*A*,*B*). However, Burton (1998) observed that there was no genetic data supporting a barrier to gene flow in any taxon with a range spanning Point Conception. Dawson (2001) summarized the data on genetic structure in relevant West Coast taxa and found a general pattern of coordinated phylogeographic and biogeographic structure, albeit in the middle of the Bight rather than at Point Conception.

Although there is a concordance of phylogeographic breaks in the Bight, this pattern may represent features with different times of origin and different causes. Here, we discuss the copepod *Tigriopus californicus* and the black surfperch *Embiotoca jacksoni*, which disperse along rocky shores, but are isolated by sand, and the tidewater goby *Eucyclogobius newberryi*, a closed estuary specialist that disperses over sand but not over rocky shores. We also comment on recent results from eelgrass-specific taxa that appear to show a concordant pattern of genetic divergence in the Bight.

Tigriopus californicus is isolated in, and broods its young in, high-intertidal tidepools on the rocky shore. Life history limits dispersal, which is especially low across water gaps and along sandy shores. *Tigriopus* shows a deep and complex sequence of divergences in the Bight (Burton 1998, Edmands 2001). Divergence between islands and rocky headlands and even different sides of islands approaches 15% for CO1. It may be that *Tigriopus* evolves at a high rate as a consequence of factors such as a rapid generation time and high UV exposure (Edmands 2001 suggested a rate in excess of 2%/million years for CO1). Nevertheless, the reported divergences are very deep and represent a minimum of several million years of reproductive isolation. Coadapted gene complexes (e.g., Willett & Burton 2001) may contribute to the pattern by limiting the viability of hybrids between populations. This could preclude effective reproduction of immigrants to populations once incumbents had evolved distinct complexes of gene interaction.

It seems plausible that *Tigriopus* divergences are not a consequence of "high rate" but record ancient tectonic events that separated populations during the organization of the Bight in the Late Miocene as well as initial colonization of the Channel Islands upon their emergence. It is intriguing that in the Burton (1998) analysis San Miguel Island populations at the end of the northern Channel Islands are sister to populations from the San Diego region. These regions were adjacent to each other prior to the rotational tectonics discussed above. They began to separate approximately 18 mya and are now approximately 250 km apart. The Torrey pine, *Pinus torreyanna*, is similarly distributed, with populations exclusively in La Jolla and Santa Rosa Island (e.g., Ledig & Conkle 1983). In addition, there are as many as 100 species of plants endemic to the Channel Islands. It appears that the islands in the Bight acted as a refuge for plant species that were eliminated on the continent owing to Late Neogene cooling and dessication.

Embiotoca jacksoni, the black surfperch, lacks dispersing larvae and is a rocky shore specialist. An analysis of mitochondrial control region sequence by Bernardi (2000) revealed a phylogeographic divergence on the order of 1% to 2% between sequences from samples in the Los Angeles region and southward along the coast, relative to a clade from the Channel Islands and locations along extending along the coast to the north. This second clade is further subdivided with sequences from the more remote Channel Islands (Santa Catalina, San Clemente, and San Nicholas) generally differentiated from sequences from the northern Channel Islands and coastal locations extending north beyond San Francisco. Patterns of sequence divergence in this taxon suggest processes that have operated from a few hundred

thousand to more than a million years. Multiple deeply divergent haplotypes in a clade largely exclusive to Catalina suggest that large populations persisted on Santa Catalina for multiple transgressive cycles of the Late Pleistocene. On the other hand, identical haplotypes are found on San Nicholas, San Clemente, and Santa Barbara islands, suggesting comparatively recent gene flow and possibly replacement of populations. The clade break between the coast south of the Los Angeles/Ventura region and the clade extending from the Channel Islands northward may be a product of expansion from two distinct Pleistocene refuges, one the Channel Islands and the other along the coast south of Los Angeles. Sandy, unsuitable, coastal habitat in the Long Beach, Santa Monica, and Ventura regions provides a modern barrier that continues to separate these groups as argued by Bernardi (2000). Thus, habitat preference for islands and rocky headlands and limited dispersal (as well as the reduced water movements nearshore in the Bight) seem likely contributors to the patterns observed and the phylogeographic break in the Los Angeles region.

Eucyclogobius newberryi, the tidewater goby, contrasts with the two taxa just discussed. This taxon lives along the Alta California coast primarily in summer-closed estuaries isolated from the sea as a consequence of the low summertime stream flow as previously discussed. Dispersal between stream-mouth estuaries is apparently limited to sandy shores, suggesting that dispersal, when it occurs, involves benthic adults evulsed from estuaries in winter floods. The larvae are largely sequestered in the estuaries during the summer reproductive season and don't disperse (Lafferty et al. 1999, Barlow 2002). Unlike taxa associated with rocky shores, this fish does not occur on the Channel Islands. Local and regional genetic subdivisions reflect the dispersal-barriers imposed by rocky headlands (Barlow 2002). A phylogeographic break of 4% is evident in the mitochondrial control region and cytochrome b across the Los Angeles region, and is suggestive of a barrier to gene flow operating for a million years or more (Dawson et al. 2002). This boundary in the Los Angeles region within the Bight is unique in its relative magnitude within the data set. This is distinct from the data for *Tigriopus* and *Embiotoca* where multiple genetic breaks of approximately the same magnitude are observed.

Assuming that the dispersal of tidewater gobies occurs as adults in the shallow nearshore environment, factors likely to lead to a boundary would involve the regional loss of appropriate closed estuary systems or factors that limit beach habitat and longshore processes that facilitate dispersal. As discussed above, in the Los Angeles region large rivers draining high ground meet the sea. These rivers likely sustained substantial year-round flow through all but the driest episodes in the Late Quaternary. In addition, during lower sea-level stands of the last few glacial cycles, the shoreline likely approached or even dropped off the shelf edge. Tidewater gobies are not known to inhabit large perennially flowing streams, and the combination with a narrow/steep shelf edge may have precluded the formation of good tidewater goby habitat across the Los Angeles region for much of the Late Pleistocene. In addition, the Palos Verdes peninsula, a rocky promontory, lacks

suitable habitat and will tend to generate divergent wave breaks and longshore current to the north and south of the promontory. This, combined with attenuated wave energy in the Bight during low stands of the sea, may have provided an effective barrier.

Tigriopus, the black surfperch, and the tidewater goby have all been densely sampled across the Bight region. Although there is rough geographic coordination, forming a phylogeographic boundary in the Bight, differences in timing of the genetic divergences, as well as difference in habitat preference and habitation of islands, suggest that heterogeneous causes are at work. Recent studies of specialist taxa that live on the blades of eelgrass, a limpet, *Tectura depicta*, and a small seahare, *Phyllaplysia taylori*, also suggest patterns of genetic differentiation in the Los Angeles region of the Bight (Louie 2003). Populations of these taxa from the northern shore of Santa Cruz Island are distinct from those south of Palos Verdes. Owing to the limited distribution of eelgrass habitat, the sampling of these taxa is not as dense as that for the three taxa described above, and the genetic differences involve the fixation of alleles but not substantial sequence divergence, suggesting that processes in the last glacial cycle, perhaps similar to those implicated in generating genetic breaks in the tidewater goby, including limited shelf area during low-stands, may also be operating here.

THE LAST GLACIAL CYCLE

Glaciers and West Coast Conditions

The Pleistocene terraces of the California coast, as well as the glacial-age lakes of the Great Basin (Figure 2), are classic subjects in the study of Pleistocene process and its effects on biology. Terrace deposits are formed primarily at high stands of the sea during interglacials, and the last high stand, Stage 5, has been studied in considerable detail, with the temperature tolerances of modern molluscs used to infer the temperatures of fossil assemblages deposited on terraces (see Lindberg & Lipps 1996 for review). These exercises yield temperatures for the stage 5, 100 kya high stand that are in places warmer than modern, and in others cooler than modern, by $1°C$ or $2°C$. The discrepancy has been resolved; Stage 5 is divisible into three substages each associated with highstands that formed terraces. Detailed dating (e.g., Muhs et al. 2002) reveals that cooler temperatures occur on open coast 80-kya-"5a" terraces, and warmer results are from 120-kya-"5e" terraces, consistent with the lower and higher sea level of these substages relative to modern sea-level, presumably caused by the cooler-than-modern/more continental ice condition of 5a and the warmer-than-modern/less polar ice condition of stage 5e. These climatic interpretations provide snapshots of time past, indicating that previous high stands were not identical to current conditions, but the approximately $3°C$ temperature range observed is not a useful indicator of the temperature departures experienced in the whole glacial cycle, as they reflect high-stand conditions more like
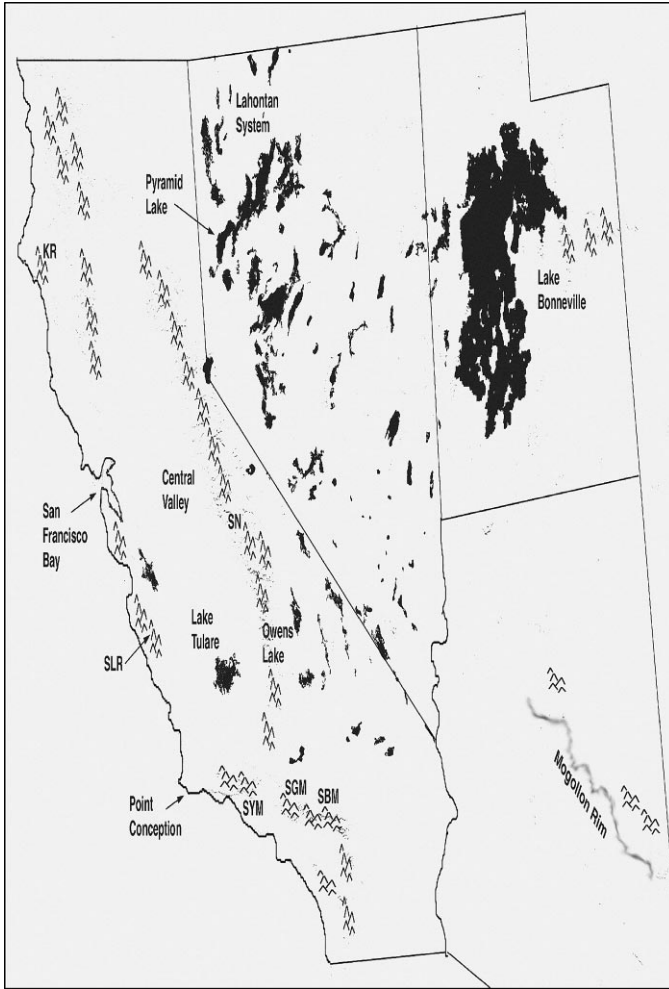
Figure 2 Map of glacial age pluvial lakes in the southwestern states. Significant Pleistocene uplift has been documented in the: KR, King Range; SN, Sierra Nevada; SLR, Santa Lucia Range; SYM, Santa Ynez Mountains; SGM, San Gabrial Mountains; SBM, San Bernardino Mountains.

the Holocene conditions than like glacial maximum times when glaciers reached the sea from Alaska to Washington State (see Figure 1*A*). These glaciers eliminated littoral fauna in this region, except that there appear to have been ice-free coastal refugia on the west side of Vancouver Island, the Queen Charlotte Islands of British Columbia, and the Alexander Archipelago of southeastern Alaska (Figure 1*A*).

Molluscs shells dredged from Monterey Bay, and dated to the last glacial maximum using carbon-14, include species that are currently restricted to much more northerly latitudes (Powell 1994). These include a species of *Astarte*, whose current southerly limit is the Pribilof Islands. These data indicate a glacial maximum sea temperature on the order of 8°C cooler than modern conditions in Monterey. Recent examinations of oxygen isotopes from foraminifera in cores in the Bight also indicate glacial maximum temperatures 8°C to 10°C colder than modern (Mortyn et al. 1996, Bemis et al. 2002). Thus, temperature conditions were far more extreme during glacial maximum than is implied by examination of terrace deposits alone. Presumably, the ranges of temperature-sensitive taxa were responding with significant range shifts to the south, followed by range expansions to the north during the transition to the Holocene.

Expected Genetic Patterns

Two kinds of biotic processes resulting in distinct genetic patterns are expected here. Taxa that can persist in the north may have occupied refugia within the glaciated region. In these taxa, expansions from northern refugia as well as northward along the coast from southern refugia is expected. Taxa that could not persist in limited ice-free coastline in a glacial habitat would expand exclusively from southern refugia during post-glacial warming. Work treating post-Pleistocene northward expansion of continental populations from glacial refugia is extensive and beyond the scope of this review (see Hewitt 1996, 2000). Assuming gene flow is modest and recruitment to new habitats does not involve large numbers of individuals, northward expansions from a southern West Coast refuge should lead to subset of southern haplotype diversity in the northern part of the range owing to founder effect, population "bottlenecks" in the expansion process. Conversely, if refugia permit the persistence of older populations of sufficient size in the northern region, a larger number of distinct haplotypes should be present there. In addition to these broader patterns, the rise in sea level at the end of the Pleistocene and its stabilization in the Holocene generated a suite of new estuarine habitats that were subject to colonization processes.

Range Expansion from Southern Refugia

Along the Alta California coast, a number of taxa show patterns suggesting post-Pleistocene range expansion, including the thaid predatory whelks *Nucella emarginata* (Marko 1998) and *Acanthinucella spirata* (Hellberg et al. 2001). Both taxa show reduced haplotype variation north of Point Conception, suggesting expansion around Point Conception from the south during the Holocene. Veliger larvae of these taxa are encased in egg capsules, somewhat limiting dispersal. A similar pattern of limited haplotype diversity is evident in the brooding bivalve *Nutricola tantilla* in the northern part of its range from Northern California to the San Juan Islands of Washington (R. Kelly & D.K. Jacobs, unpublished data). Further, exploration of taxa with limited dispersal potential would be expected to reveal more examples of this class of pattern.

Expansion from Northern Interglacial Refugia

A number of other taxa show haplotype diversity or structure that suggests they expanded from northern refugia as well as from regions to the south of the glacial front in Washington state. The refugia in question are thought to have occupied the outer coasts in the region of Vancouver Island (Clague 1989), and the Queen Charlotte Islands of British Columbia (Warner et al. 1982), as well as the Alexander Archipelago of southern Alaska (Heaton et al. 1996). For some taxa, especially salmonids, glacial age refugia in the Bering region may also be important (e.g., Taylor et al. 1996). Coastal marine taxa that show the same or higher haplotype diversity in the glaciated region from Puget Sound to southern Alaska include the clingfish *Gobiesox maendricus* (Hickerson & Ross 2001), the bay pipefish *Syngnathus leptorhynchus* (Louie 2003), and Taylor's seahare *Phyllaplysia taylori* (Louie 2003). *Gobiesox* and the seahare also show dominant unique haplotypes in the nearshore populations that may be a product of range expansion into the nearshore Georgia Straight/Puget Sound area following deglaciation from outer-coast refugia of Vancouver Island. Mitochondrial gene sequence from the high intertidal copepod *Tigriopus* shows cladistic subdivision, with two clades apparently expanding into new habitats following the glaciation. One clade is evident along the outer coast of Oregon and Washington. Samples from Vancouver Island and Puget Sound to southern Alaska form a second clade. Both clades show only modest internal subdivision and likely represent expansion from a southern and an intraglacial refugium, respectively. Divergent sequences in the most northern population may suggest an additional refugium in the Alexander Archipelago. In the case of *Tigriopus*, a clade apparently derived from one or more intraglacial refugea is evident in the data. However, the degree of divergence is much less than the very deep divergences evident in data from farther south in California (Burton 1998, Edmands 2001), suggesting that the intraglacial refugia maintained populations through at least the last glaciation, but were not effective for all glacial events. Apparently, populations were eliminated some time earlier in the Pleistocene. Similar arguments have been made for coho salmon (Smith et al. 2001) and steelhead (McCusker et al. 2000), where the range of haplotypes present suggest intraglacial refugia, but greater sequence divergence to the south in northern California suggests that refugia did not operate effectively at some earlier Pleistocene time. Alternatively, small population sizes in refugia may contribute to haplotype loss and limit the divergence of haplotypes found. Coastal taxa that show genetic structure consistent with isolation in, and expansion from, intraglacial refugia in the south Alaska British/Columbia region, include a wide range of taxa from red alga (Lindstrom et al. 1997) to yellow cedar (Ritland et al. 2001) and black bear (Byun et al. 1997), suggesting that these refugia have had a broad impact on the coastal biota.

Another attribute of this glaciated region is that freshwater systems appear de novo during glacial retreat, and were colonized in the Holocene by aquatic forms, such as anadromous fishes, that were able to disperse through the sea. Thus, sockeye salmon have evolved resident lake forms, referred to as kokonee, in parallel in

multiple lakes (e.g., Taylor et al. 1996). Three-spined stickleback, *Gasterosteus aculeatus*, also disperse through the sea and have colonized lake and river systems along the Pacific seaboard, including systems that are demonstrably postglacial. In some postglacial lakes, two resident ecologically distinct "species" of stickleback have evolved. Apparently, these are the product of successive invasions (Thompson et al. 1997). The first invasion of a lake results in benthic forager, and a subsequent invasion produce a planktivorous form. This evolutionary scenario appears to have played out independently in several lakes. A combination of sexual and natural selection limits gene flow and maintains these distinct forms in sympatry (e.g., Taylor & McPhail 1999).

Pleistocene/Holocene Transition Impacts on Lakes and Estuaries

Postglacial colonization of estuaries along the West Coast occurs on the same time frame as colonization of streams and coastal habitat following glacial retreat. As discussed previously, the tidewater goby preferentially occupies small, seasonally closed estuaries. It is limited in dispersal, especially where rocky shores intervene between estuaries, leading to population differentiation. At the end of the Pleistocene sea-level rise flooded small valleys, leading to many small, closely spaced estuaries along the California coast. It appears that close proximity of estuaries enhanced tidewater goby dispersal during this transgression phase. During the constant sea level of the past 9 ky, coastal erosion led to shoreline retreat and the formation the cliffs typical of picturesque stretches of the California outer-coast. This process eliminated small coastal estuaries, leaving the remaining systems isolated from each other, especially along the rough mid-coast from Monterey Bay to Bodega Head. In this region, many populations of gobies are isolated and are genetically distinct (Barlow 2002), presumably owing to absence of gene flow for much of the Holocene.

As mentioned previously, the invasion of freshwater systems from marine systems accounts for much of the freshwater diversity of the American West. South of the glacial front, invasions of Late Pliocene and Pleistocene age would be expected, owing to the focusing of precipitation associated with uplift and a southerly storm track that permitted development of large southwestern river systems. Genetic data suggest that rainbow and cutthroat trout lineages likely evolved in this time frame. It seems likely that many of the sculpins colonized the rivers and glacial lakes of the West as freshwater resources expanded in the Pliocene and Pleistocene. Dessication of the glacial-age lakes of the Great Basin and adjacent regions led to the isolation in streams of taxa that inhabit the two great lake systems, Lohantan and Bonneville, as well as extensive aquatic systems in the Owens Valley and Mojave (Reheis et al. 2002) (Figure 2). This process led isolation of aquatic fauna. Of particular interest are Pyramid and Bear lakes, which retained lake habitat from the vast Bonneville and Lohantan systems. There have been numerous studies of the genetics of the relict fish populations derived from the Bonneville and Lahontan systems, including the "primary" cyprinid fauna such as Gila chub and desert

pupfish, as well as the isolation of "secondary" marine-derived species such as cutthroat trout and sculpins (see Smith et al. 2002 for a recent review).

HOLOCENE PATTERNS

The Quaternary Period is well known for dramatic changes in climate. These include global changes at millennial timescales in the late Pleistocene and during the transition to the Holocene when a brief reversal to glacial conditions known as the Younger Dryas occurred. Core data from the Santa Barbara Channel document that these millennial scale global episodes have local impacts on climate (e.g., Hendy et al. 2002). However, genetic consequences of these events may be difficult to distinguish from the overall Pleistocene-Holocene transition. During the middle Holocene, from 8 kya to 3 kya, upwelling was more seasonally uniform (e.g., Barron et al. 2003, Roark et al. 2003), and the level of Owens's, Tahoe, and Pyramid lakes were lower (Benson et al. 2002). In addition, the frequency of fires was higher (Brunelle & Anderson 2003), documenting a warmer, dryer "hypsothermal" period. This dry period may have led to more profound isolation of aquatic and riparian taxa than current conditions merit, and according to Axelrod (1986a), led to the patchy modern distribution of giant sequoia in the Sierra Nevada foothills.

HISTORIC PROCESSES

As early as the railroad survey of 1869, it became apparent that numerous tropical species normally restricted to the Bight or further south temporarily extended their ranges to the Monterey region during what are now known as "El Niño" years. These years experience enhanced northward movement of water along the coast, as well as reduced upwelling and kelp productivity. Recent work has focused on molluscs, such as Kellet's whelk, *Kellettia kellettia*, which has recently recruited (apparently in El Niño years) from its historic range south of Point Conception to as far north as the Monterey Region (Zacherl et al. 2003). Similarly, the eelgrass limpet *Tectura depicta* has recently been found in Monterey Bay, well beyond its typical northern limit in the Bight. Recent genetic work documents identical cytochrome b haplotypes in the two regions supporting the viability of an El Niño northern expansion hypothesis for these populations (Louie 2003). Other extralimital northern populations in warmer bay settings, such as the occurrence of *Lottia limatula* in Tomales Bay far to the north of its contiguous range limit in Monterey, may be a product of similar processes, as they are identical in CO1 haplotype to limpets further south (Clabaugh 1997).

As mentioned previously, estuarine settings on the West Coast, especially San Francisco Bay, have been invaded by substantial numbers of taxa from overseas (e.g., Grosholtz 2002), including a substantial number that came from the East Coast in early shipments of oyster culture. Movement of oyster stock along the West Coast has been frequent and may be responsible for some unusual distribution patterns, as all of the larger estuaries have a history of oyster cultivation.

For example, a population of the brooding bivalve *N. tantilla* in Arcata Bay has haplotypes identical to more southerly populations in the Monterey and Morro Bay regions rather than those found in other north coast estuaries, suggesting an unusual mode of transport.

Although, studies of contemporary gene flow are not the primary subject of this review, numerous recent papers that have examined related topics of interest, such as the role of life history in genetic structure (e.g., Hellberg 1998) and the differential effects of current transport on planktonic and nonplanktonic taxa (Wares et al. 2001). Such studies that reflect current processes provide a basis of uniformitarian inference critical to understanding the gentic consequences of older events.

SUMMARY

West Coast coastal marine diversity may be a product of radiation of trophically important groups during the Late Miocene and, to a lesser extent, Pleistocene phases of upwelling. This diversity is also likely a consequence of greater continuity of biologically productive upwelling relative to other upwelling systems around the world. The presence of effective invertebrate predators in the trophic structure of the kelp ecosystem also may aid in sustaining high diversity. Relatively deep phylogeographic structure and cryptic speciation in taxa with limited dispersal appears to be a product of the Mio-Pliocene estuarine reentrants along the California coast, as well as the Pliocene evolution of the Gulf of California and the tectonically complex development of the California Bight. Less deeply divergent patterns in genetic structure are often attributable to range expansion associated with warming, deglaciation and sea-level rise at the end of the Pleistocene.

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