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Phylogeography in coastal marine animals: a solution from California?

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Abstract

Aim Recently discovered deep phylogenetic gaps in coastal California marine taxa are geographically discordant with the provincial biogeographic boundary at Point Conception. This discordance runs contrary to the phylogeographic hypotheses that were derived from studies of coastal marine taxa in south-eastern North America. Here, I investigate the nature of the discrepant phylogeographic and biogeographic patterns in coastal California.

Location Coastal south-western North America.

Methods The scientific literature describing the phylogeography and biogeography of coastal California taxa was reviewed. Data describing life-history characteristics, habitat, and degree of phylogeographic structure were extracted and compared. The geographical distribution of phylogenetic breaks was compared with regional biogeographic data.

Results All taxa were genetically variable. Those with greater dispersal ability generally had less phylogeographic structure. Although few taxa had very limited dispersal ability, many exhibited phylogeographic breaks within the California Transition Zone, a region of gradual species replacement between Oregonian and Californian biogeographic provinces. The most precisely resolved phylogeographic breaks were geographically concordant with peaks in the distribution of edge-effect species, which are strong indicators of environmental discontinuities, or ecotones. Moreover, these phylogeographic gaps, edge-effect species, and ecotones coincide geographically with Late Pleistocene faunal discontinuities and probable long-term physical barriers to gene flow.

Main conclusions Contrary to prior inference, phylogeographic patterns in coastal California marine taxa are consistent with the phylogeographic hypotheses. The concordance of phylogeographic and biogeographic patterns in the coastal marine faunas of south-eastern and south-western North America, and also the Indo-Pacific, suggests that the phylogeographic hypotheses are generally applicable to many coastal marine settings. As such, they provide a framework for investigating and comparing patterns of evolution in disparate coastal marine faunas.

Keywords
coastal biogeography, comparative phylogeography, dispersal, evolution, marine, North America, Pleistocene, Pliocene.

INTRODUCTION

The term ‘phylogeography’ was introduced by Avise *et al.* (1987) to describe geographically structured intraspecific genealogies (Avise, 2000, vii). Molecular analyses of mitochondrial DNA (mtDNA) from coastal maritime taxa had revealed intraspecific genealogies that were geographically coincident with each other and with biogeographic patterns in south-eastern North America (seNA; Avise *et al.*, 1987; Avise, 1992). These commonalities suggested that intraspecific phylogenies were shaped by biogeographic barriers

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Table 1 Intra-specific phylogeographic hypotheses (Avise *et al.*, 1987)

	Hypotheses
H_1	Most species are composed of geographical populations whose members occupy different branches of an intraspecific, phylogenetic tree
H_2	Species with limited phylogeographic population structure have life histories conducive to dispersal and have occupied ranges free of firm impediments to gene flow
H_3	Monophyletic groups distinguished by large phylogenetic gaps usually arise from long-term extrinsic (zoogeographic) barriers to gene flow
	Predictions of hypothesis H_3
	i. As time since isolation increases, the degree of phylogeographic concordance across separate gene genealogies increases
	ii. The geographical placements of phylogenetic gaps are concordant across species
	iii. Phylogenetic gaps within species are geographically concordant with boundaries between traditionally recognized zoogeographic bou[illegible]ies

to gene flow associated with Plio-Pleistocene hydrography, coastal topography, climate change, temperature discontinuities, and possibly other factors (Avise *et al.*, 1987; Avise, 1992). As a result, Avise *et al.* (1987) posited three phylogeographic hypotheses (Table 1), the generality of which, they suggested, should be tested by comparable studies of geographically distinct faunas.

The phylogeographic hypotheses have received support from studies in the Indo-Pacific where intraspecific phylogenies are also largely concordant with biogeographic provinces. Allozymes and mtDNA reveal distinct Indian Ocean and Pacific Ocean lineages in a coastal shrimp (Lindenfelser, 1984), two butterflyfish species-complexes (McMillan & Palumbi, 1995), four damselfishes (Lacson & Clark, 1995), the coconut crab (Lavery *et al.*, 1996), and two species of seastar (Williams & Benzie, 1998; Benzie, 1999), thus implicating processes proximate to Wallace's Line as the causes of both sub- and supra-specific biodiversity (Lindenfelser, 1984). As in south-eastern North America, genetic divergence within Indo-Pacific taxa has been attributed largely to reduced gene flow during Pleistocene low-stands (McMillan & Palumbi, 1995; Lavery *et al.*, 1996; Williams & Benzie, 1998).

In contrast, intraspecific phylogenies are discordant with biogeography in coastal California, south-western North America (swNA; Palumbi, 1995; Burton, 1998), despite marked changes in coastal hydrography, temperature, dissolved oxygen, salinity, and topography, in the vicinity of the biogeographic break at Point Conception (Briggs, 1974; Seapy & Littler, 1980; Browne, 1994). Thus, whilst studies of seNA and Indo-Pacific taxa suggest that phylogeography and biogeography are linked inextricably (Avise *et al.*, 1987), studies of swNA taxa suggest that phylogeography and biogeography are decoupled (Burton, 1998).

The discrepancy between seNA and swNA studies led Burton (1998) to conclude that the relationship between intraspecific phylogeography and biogeography is situation-specific. He suggested that, in this case, the discrepant results were caused by geological processes specific to seNA, although coastal marine processes also differ on western and eastern ocean boundaries (e.g. Hill *et al.*, 1998; Loder *et al.*, 1998). Burton (1998) also suggested that phylogeography will reflect biogeography only if the biogeographic boundary separates biotas that are phylogenetically closely related, and that this was not the case for the 'Oregonian' and 'Californian' provincial faunas separated at Point Conception. Others have suggested, more fundamentally, that intraspecific phylogeographic and biogeographic patterns should not be compared because they may result from different processes (see Palumbi, 1997). However, none of these three caveats is sufficient to explain the discrepancies between phylogeographic studies in seNA and swNA. First, intraspecific phylogeographic patterns and biogeographic patterns are concordant across the Indo-Pacific, which is geologically more similar to swNA than seNA, suggesting the geological differences between seNA and swNA may not have important phylogeographic consequences. Secondly, the Oregonian and Californian faunas actually are quite closely related. Approximately half of the 30% endemic Californian taxa are closely related to Oregonian taxa (Briggs, 1974, 228) and many of the 70% non-endemic species occur in both the Oregonian and Californian provinces. Moreover, the faunas of the Carolina and Caribbean provinces of seNA are no more closely related than those of the Californian and Oregonian provinces. Approximately, 30–40% of the Carolina Province fauna is endemic (Briggs, 1974, 224). Finally, the phylogeographic hypotheses assume that intraspecific phylogeography and biogeography are comparable (see also Eldredge & Gould, 1988; Palumbi, 1997) – as Avise and colleagues put it, 'macroevolution is ineluctably an extrapolation of microevolution' (Avise *et al.*, 1987, 490).

Thus, at this time, intraspecific phylogeographic patterns and biogeographic patterns in swNA appear discordant, the relationships of these patterns in seNA/Indo-Pacific and swNA are discrepant, and there is no satisfactory explanation for either result. Here, I review the patterns of intraspecific diversity in coastal California's marine animals, compare these phylogeographic patterns with local biogeography, and discuss local physical processes that may have influenced both intra- and interspecific diversity.

METHODS

Studies of the phylogeography of coastal California animals were reviewed and tabulated, noting the degree and location of phylogeographic structure (or lack thereof) reported by the original authors. Data describing the habitat and life-history of each species were gathered from the original phylogeographic publications and, when necessary, other relevant texts (e.g. Morris *et al.*, 1983). To facilitate assessment of the phylogeographic hypotheses, taxa were categorized in four ways. Firstly, as having zero, short (≤ 1 week), intermediate (2–4 weeks), or long (≥ 8 weeks) planktonic duration. Secondly, as having principally enclosed, intertidal, nearshore, or off-shore habitat. Thirdly, by the $\log_{10}$ of their fecundity. Fourthly, as having low or no (e.g. F_{st} principally $\ll 0.2$, shallow star-shaped gene trees), intermediate (e.g. regional allele-frequency differences), or high (e.g. F_{st} $\gg 0.2$, reciprocally monophyletic clades) phylogeographic structure. On a per taxon basis, the first three categories (i.e. factors affecting dispersal ability, e.g. see Waples, 1987), were then related in scatterplots to the last (which is commonly considered to be the result of dispersal ability, e.g. Palumbi, 1995). Deliberately few categories were used for each of the four attributes to minimize the problems of resolving differences between taxa and data sets; although boundaries between adjacent categories may be somewhat arbitrary, it is unlikely that non-adjacent categories contain taxa similar in that attribute.

In addition, a frequency distribution was made of the geographical position (accurate to one degree of latitude) of the deepest phylogeographic break in California (if any) found in each study, and the distribution compared using a χ^2 goodness-of-fit test (Steel & Torrie, 1980) against a null hypothesis of randomly (i.e. uniformly) distributed phylogeographic breaks. The geographical distribution of the deepest phylogeographic breaks, normalized for the number of taxa examined in each degree of latitude, was correlated (after verifying data were normally distributed, Lilliefors test, $P \geqslant 0.09$) with the distribution of edge-effect species (see definition in *Discussion*) using SYSTAT 6.0 for Windows 3.1.

RESULTS

Studies discussing the geographical structure of genetic variation in 40 coastal California taxa were examined (Table 2a–c). All studies bar one (a preliminary study of *L. gigantea*) found taxa to be genetically variable, whether or not the variation was structured geographically.

Plots of phylogeographic structure against planktonic duration, habitat, and fecundity showed similar patterns (Fig. 1). In each plot, datapoints were generally distributed from top-left (low dispersal potential and high phylogeographic structure) to bottom-right (high dispersal potential and low phylogeographic structure). Notably, in each case, both bottom-left and top-right corners of the distributions were empty, describing a lack of taxa with low-dispersal–low-phylogeographic-structure and a lack of taxa with high-dispersal–high-phylogeographic-structure, respectively.

Of the 41 taxa considered, 24 displayed intraspecific phylogeographic structure within the ranges investigated. Of these, eight were studied with sufficient geographical resolution that the major phylogeographic division could be placed within a single degree of latitude in California. The distribution of these phylogeographic breaks differed significantly from the null hypothesis of randomly distributed phylogeographic breaks ($\chi^2 = 11.5$, d.f. $= 5$, $P = 0.04$; Fig. 2). The distribution of phylogeographic breaks was highly correlated with the distribution of edge-effect species ($r = 0.93$, $P = 0.007$; Fig. 3).

DISCUSSION

The review of genetic diversity in coastal California marine taxa indicates that some degree of phylogeographic structure is relatively common (Table 2a–c) and that, within the traditional biogeographic framework, this structure is consistent with all but one of the phylogeographic hypotheses and predictions of Avise *et al.* (1987; see Table 1). First, all species studied in detail were found to be genetically variable, i.e. species were composed of geographical populations whose members occupied different branches of an intraspecific-phylogeny (H_1). Secondly, species with life histories conducive to dispersal generally had less phylogeographic population structure (H_2; Fig. 1; see also Waples, 1987; Hellberg, 1996; M.N. Dawson, K.D. Louie, M. Barlow, D.K. Jacobs & C.C. Swift, pers. commun.). Thirdly, phylogeographic patterns in *T. californicus* support the conclusion that, as time since isolation increases, the degree of phylogeographic concordance across separate gene genealogies also increases (H_3i) because more slowly evolving molecular markers revealed some, but not all, of the structure apparent in more quickly evolving markers (Burton, 1998). Finally, the geographical placements of phylogenetic gaps are concordant across species (H_3ii; Fig. 2). This concordance is most evident in the placement of the major phylogeographic breaks in *T. californicus*, *E. jacksoni* and *E. newberryi* in the Los Angeles region (LAR) but also is indicated by the co-occurrence of phylogeographic breaks in at least two other species in the vicinity of Los Angeles (*S. purpuratus* and *T. torosa torosa*), in shallower phylogeographic breaks in *E. jacksoni* and *E. newberryi* near Morro Bay, and in common phylogeographic breaks in ≥ 7 species near Monterey Bay (*A. purpurescens*, *Ensatina* spp., *E. newberryi*, *N. ostrina*, *O. pictus*, *O. mykiss*, *T. torosa torosa*). However, as others have found before (e.g. Burton, 1998), there apparently remains evidence against the last, and perhaps most prominent, prediction of phylogeographic theory (H_3iii) because intraspecific phylogenetic gaps are geographically discordant with the traditionally recognized biogeographic boundary between Oregonian and Californian provinces at Point Conception (Fig. 2).

Whether this discordance truly contradicts the hypothesis, however, rests on two assumptions. Firstly, that Point Conception is a strong biogeographic boundary that sharply demarcates Oregonian and Californian faunas and, secondly, that there is not a biogeographic boundary elsewhere

Table 2a Habitat, life-history, range and phylogeographic characteristics of coastal California invertebrates

Species: invertebrates	Habitat	Life history*	Range sampled	Marker†	Phylogeographic structure	Reference
Tigriopus californicus Baker [copepod]	Rocky supratidal pools	'Brooder' fecundity 10^4 per 100 days	Central and southern California	mtDNA (COI) nDNA (H1) 7 allozyme loci	Palos Verdes > Sta. Monica ≈ Sta. Cruz Is. > Sta. Rosa Is. ≈ Pt. Conception	Burton (1998)
Tetraclita squamosa rubescens Darwin (barnacle)	Rocky intertidal (10–15-year-old)	≤ 4-Week planktonic larvae fecundity = 10^3–10^5 pa	San Francisco to Port Hueneme	4 allozyme loci	None	Ford & Mitton (1993)
Pollicipes polymerus Sowerby [gooseneck barnacle]	Rocky intertidal	Planktonic larvae fecundity = 10^5–10^6	British Columbia (B.C.) to San Diego	mtDNA (COI)	None	Van Syoc (1994)
Strongylocentrotus purpuratus Stimpson [purple urchin]	Rocky inter/subtidal	Planktotrophic larvae 'broadcast'	SantaCruz-Baja	mtDNA (COI) 6 allozyme loci	Laguna/LaJolla supported by 1 locus	Edmands *et al.* (1996)‡
Strongylocentrotus franciscanus Agassiz [red urchin]	Rocky sub/intertidal	2–4 Month planktonic larvae 'broadcast'	Alaska to central Baja	6 allozyme loci nDNA sequences	Weak, no PC break None	Citations in Burton (1998)§
Mytilus galloprovincialis Lamarck [mussel]	Rocky inter/subtidal into bays	4-Week planktonic larvae 'broadcast'	SanFrancisco to Long Beach	15 allozyme loci	None	Sarver & Foltz (1993)¶
Mytilus trossulus Gould [mussel]	Rocky inter/subtidal into bays	4-Week planktonic larvae 'broadcast'	Alaska to central California	15 allozyme loci	None	Sarver & Foltz (1993)¶
Mytilus californianus Conrad [mussel]	Rocky inter/subtidal open shore	≥ 3-Week planktonic larvae 'broadcast'	Alaska to southern Baja California	2 allozyme loci	None	Levinton & Suchanek (1978)
Littorina plena Gould [prosobranch gastropod]	Upper intertidal bays & rocky shore	Planktonic eggs, fecundity not known	Oregon to Baja California	10 allozyme loci	No fixed differences Monterey Bay, Point Arena?	Mastro *et al.* (1982)
Littorina scutulata Gould [prosobranch gastropod]	Upper intertidal bays & rocky shore	Planktonic eggs, fecundity∼10^4	Alaska to Baja California	10 allozyme loci	No fixed differences Point Arena?	Mastro *et al.* (1982)
Nucella emarginata (Deshayes) [neogastropod]	Rocky intertidal	Benthic eggs, crawl-away larvae, fecundity∼10^2	Central California to northern Baja	9 allozyme loci mtDNA (COI,12S)	Gaviota-Sta.Barbara	Marko (1998)**
Nucella ostrina (Gould) [neogastropod]	Rocky intertidal	Benthic eggs, crawl-away larvae, fecundity∼10^2	Alaska to central California	9 allozyme loci mtDNA (COI,12S)	Monterey Bay	Marko (1998)
Lottia gigantea Sowerby [owl limpet]	Intertidal rocky shore	Planktonic larvae	Monterey Bay to San Diego	mtDNA (COI)	No variation in seven ∼650 bp sequences	M.N. Dawson & D.K. Jacobs (unpubl. data)
Colisella digitalis Rathke [limpet]	Rocky supra intertidal	≥ 3-Week planktonic larvae 'broadcast'	Alaska to southern Santa Barbara Co.	2 allozyme loci	None	Murphy (1978)††
Colisella austrodigitalis Murphy [limpet]	Rocky supra intertidal	≥ 3-Week planktonic larvae 'broadcast'	Monterey Bay to San Diego	2 allozyme loci	None	Murphy (1978) ††
Balanophyllia elegans Verrill [solitary coral]	Rocky subtidal	≥ 50 Crawl-away larvae pa (disperse ∼40 cm)	B.C. to N. Baja. California only	7 allozyme loci nDNA(ITS-1)	isol" by distance (allozymes) None (ITS-1)	Hellberg (1996) Beauchamp & Powers (1996)
Paracyathus stearnsii Verrill [solitary coral]	Rocky subtidal	≥ 10^5 Planktotrophic larvae 'broadcast'	B.C. to N. Baja. California only	6 allozyme loci nDNA(ITS-1)	None None	Hellberg (1996) Beauchamp & Powers (1996)
Aurelia Péron & Lesueur (moonjellyfish)	Bays & inlets, also open coastal waters	Perennial benthic polyp, shortlived larva/ephyra, 4–6-month planktonic medusae	British Columbia to San Diego	mtDNA (COI) nDNA (ITS-1)	Monterey-LA (COI, ITS-1); Vancouver Is.-Oregon (COI)	Dawson & Jacobs (2001) ‡‡

Table 2b Habitat, life-history, range and phylogeographic characteristics of coastal California fishes

Species: fishes	Habitat	Life history*	Range sampled	Marker	Phylogeographic structure	Reference
Eucyclogobius newberryi (Girard) [tidewater goby]	Estuaries and coastal lagoons (no marine phase)	Eggs brooded in burrows, ~ 3 days planktonic larvae, later stages are benthic	California	mtDNA (CR, cyt b) nDNA (CK)	mtDNA: LAR > MB/ PtB > Big Sur ≈ SC/ PtA > Seacliff; nDNA – None	Dawson *et al.* (in press)***
Paralichthys californicus (Ayres) [California halibut]	Coastal waters < 6 km offshore	Planktonic coastal larvae estuarine juveniles, coastal adults	Monterey-Magdalena Bay LA and San Diego	mtDNA (CR) 15 allozyme loci	Pta. Eugenia (weak) Significant at 2 loci	Dawson *et al.* (in press) Hedgecock & Bartley (1988)
Clevelandia ios (Jordan & Gilbert) [arrow goby]	Estuaries	Planktonic larvae estuaries and nearshore waters	Central and southern California	mtDNA (CR)	None	M.N. Dawson *et al.* (pers. commun.)
Gillichthyes mirabilis Cooper [longjaw mudsucker]	Estuaries, lagoons	Planktonic larvae, estuaries and nearshore waters	Monterey Bay to south of Punta Eugenia	mtDNA (cyt b) nDNA (CK)	mtDNA: Strong break at or between LAR and/or Pta. Eugenia nDNA – None	Huang and Bernardi (2001)
Girella nigricans (Ayres) [opaleye]	Nearshore, shallow reefs	Several months-long planktonic larvae	San Luis Obispo to Bahia Ascuncion	mtDNA (CR) 26 allozymes	Pta. Eugenia None	Terry *et al.* (2000) Waples (1987)
Sebastes atrovirens (Jordan & Gilbert) [kelp rockfish]	Kelp beds and rock reefs to 50 m	Planktonic larvae	Monterey to San Diego	Morphology (tympanic spines)	Sta. Barbara/San Diego	Love and Larson (1978)
Oxylebius pictus Gill [painted greenling]	Shallow rock reefs	Territorial, demersal eggs, 1–3 month planktonic larvae	British Columbia to Pta. San Carlos	9 allozyme loci	Monterey Bay/Sta. Barbara	Davis *et al.* (1981)
Oncorhynchus mykiss (Richardson) [steelhead salmon]	Rivers and ocean	Anadromous	California	mtDNA (CR)	Gualala River/Russian River, Pt. Sur/San Simeon	Nielsen (1996)
Anoplarchus purpurescens Gill	Intertidal to 30 m	Benthic egg-mass, larvae in shallow water for few days	Puget Sound to San Luis Obispo	2 allozyme loci morphology	Weak break at Monterey Bay	Sassaman & Yoshiyama (1979)
Embiotoca jacksonii Agassiz [black surfperch]	Subtidal rocky shore surface to 40 m	Live bearing, territorial, Phylopatric, low fecundity	Tomales Bay to south of Punta Eugenia	mtDNA (CR)	LAR > Pta. Eugenia ≈ BigSur/MB	Bernardi (2000)§§,***
Clinocottus analis (Girard) [woody sculpin]	Rocky inter/subtidal to 20 m	Benthic eggs; nearshore, few week planktonic larvae, fecundity 10^2–10^3	Monterey Bay to south of Pta. Eugenia	10 Allozyme loci 26 Allozyme loci	San Simeon/Pt. Conception Significant with distance	Swank (1979) Waples (1987)
Alloclinus holderi (Lauderbach) [island kelpfish]	To depth 50 m larvae inshore?	Brief larval stage, fecundity 10^3	LA Region to south of Pta. Eugenia	26 Allozyme loci	None 1 locus significant, FST < 0.2	Waples (1987)
Lythripnus dalli (Gilbert) (bluebanded goby)	Inter-/subtidal to 70 m	> 2 Month larvae inshore fecundity 10^2–10^3	LA Region to south of Pta. Eugenia	26 Allozyme loci	2 of 3 polymorphic loci significant, $F_{ST} > 0.2$	Waples (1987)
Five high dispersal fishes	Larvae inshore/ offshore	> 2 Month larval stage fecundity 10^6	LA Region to south of Pta. Eugenia	26 Allozyme loci	None	Waples (1987)¶¶
Gibbonsia spp. [kelpfishes]	Neashore to 50 m	> 2 Month larvae inshore fecundity 10^2–10^3	Monterey Bay to Guadalupe Is.	40 Allozyme loci	Evidence of divergent forms on Guadalupe Is.	Stepien & Rosenblatt (1991)†††

Table 2c Habitat, life-history, range and phylogeographic characteristics of other coastal California vertebrates

Species: other vertebrates	Habitat	Life history*	Range sampled	Marker	Phylogeographic structure	Reference
Taricha torosa torosa (Rathke) [California newt]	Streams, ponds, reservoirs, and forest floor	Aquatic for breeding, otherwise terrestrial fecundity 10^1	Coastal California	mtDNA (cyt b)	Monterey Bay LAR—Palos Verdes	Tan & Wake (1995)***
Ensatina spp. Gray [plethodontid salamander]	Fully terrestrial coniferous forest and oak woods	Damp earth for eggs, Fully terrestrial lifecycle	S. British Columbia to N. Baja California	mtDNA (cyt b)	Species boundaries: San Francisco Bay, Monterey Bay Hills of San Diego	Wake (1997)
Zalophus californianus Lesson [California sea lion]	Marine coastal	Live-bearing & parenting	San Miguel Is. To Bahia de Los Angeles	mtDNA (CR and cyt b)	Disjunct population in Sea of Cortez (mtDA CR only)	Maldonado *et al.* (1995)

* Additional life-history and range data for salamanders (Bishop, 1947; Stebbins, 1954; Hairston, 1987), fishes (Miller & Lea, 1972; Robins *et al.*, 1980; Capelli, 1997), invertebrates (Murray, 1979; Stimson, 1973; Morris *et al.*, 1983).

† mtDNA, mitochondrial DNA; COI, Cytochrome Oxidase c subunit I; CR, control region or 'D-loop'; cyt b, cytochrome b; 12S, 12 s ribosomal DNA; ITS-1, First Internal Transcribed Spacer region; nDNA, nuclear DNA; H1, Histone H1; CK, 6th intron and flanking regions of creatine kinase.

‡ No genetic subdivision found in *Strongylocentrotus purpuratus* between Washington and Ventura when mtDNA analysed with 13 restriction enzymes (Palumbi & Wilson, 1990) and COI sequenced (Palumbi, 1995).

§ Moberg and Burton (unpubl.) and Debenham (unpubl.), cited in Burton (1998).

¶ *Mytilus* species are parapatric around San Francisco (Sarver & Foltz, 1993).

** Break reported as Pt. Conception by Marko (1998).

†† Murphy (1978) separated *Colisella digitalis* into two species, *C. digitalis* and *C. austrodigitalis*, parapatric about the CTZ, on the basis of allozyme differences.

‡‡ Possible introduction into southern California? LA = Los Angeles.

§§ Using 26 allozyme loci, Waples (1987) found strong differentiation by distance between southern CTZ and south of Pta. Eugenia.

¶¶ High dispersal fish studied by Waples (1987) are *Caulolatilus princeps* (Jenyns) [ocean whitefish], *Chromis puntipinnis* (Cooper) [blacksmith], *Girella nigricans* (opaleye), *Paralabrax clathratus* (Girard) [kelp bass], *Medialuna californiensis* (Steindachner) [halfmoon], and *Semicossyphus pulcher* (Ayres) [sheephead].

*** LAR, Los Angeles Region; MB/PtB, Morro Bay/Point Buchon; SC/PtA, Salmon Creek/Point Arena.

††† *Gibbonsia* spp. = *G. metzi* Hubbs, *G. montereyensis* Hubbs, *G. elegans* (Cooper).

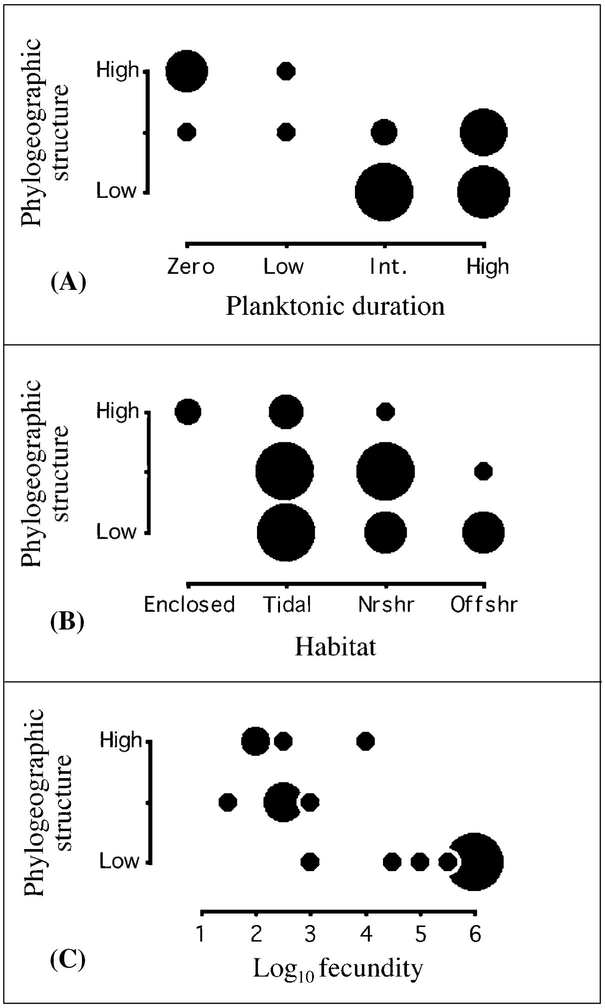

Figure 1 Relationships between factors affecting dispersal ability (x-axis) and phylogeographic structure (y-axis) in coastal California taxa. (a) Planktonic duration; Int. = intermediate. (b) Habitat; Tidal = intertidal and subtidal, Nrshr = nearshore, Offshr = offshore. (c) Fecundity. Aurelia was excluded from these analyses because of the possibility that it has been introduced into southern California.

that is concordant with the observed phylogeographic breaks. Re-evaluation of the biogeography of California marine taxa suggests that both of these assumptions are incorrect.

Biogeographic boundaries, transition zones and ecotones

There is no doubt that Point Conception demarcates the southern limit of some Oregonian species and the northern limit of some Californian species (Briggs, 1974, 227; Doyle, 1985; Gobalet, 2000). However, many more species ranges span Point Conception and end elsewhere (Briggs, 1974, 225; Hayden & Dolan, 1976; Horn & Allen, 1978; Newman, 1979; Murray *et al.*, 1980). Consequently, the biogeographic boundary between Oregonian and Californian provinces has, at times, been considered more akin to a transition zone (the 'California Transition Zone', Fig. 2), across which there is incremental replacement of Californian and Oregonian faunas, than to a sharp boundary at which one fauna ends and the other begins [e.g. Newell, 1948; Emerson, 1956 (cited in Briggs, 1974)]; (Newman, 1979; Seapy & Littler, 1980). However, the clustering of phylogeographic breaks in the vicinities of Los Angeles and Monterey Bay suggests that such a transition zone is an heterogeneous region that encompasses different areas that inhibit (or permit) gene flow to differing degrees. Of particular interest for further investigation in this context are regions strongly implicated as barriers to gene flow by the co-occurrence of many intraspecific phylogeographic breaks, i.e the LAR and Monterey Bay region (MBR; Fig. 2).

Traditionally, biogeographic boundaries have been recognized where the range termini of many widely distributed species coincide (e.g. Briggs, 1974; Hayden & Dolan, 1976; Doyle, 1985). Around the Americas, such biogeographic boundaries typically occur over several degrees of latitude (i.e. they are transition zones) and encompass regions of steep physical gradients, or ecotones (Hayden & Dolan, 1976; Seapy & Littler, 1980; Longhurst, 1998: 26). Ecotones are characterized by abundant 'edge-effect' species, which inhabit only the region of rapid physical change (Longhurst, 1998: 26) and, on the scales used in coastal biogeography, are endemic to one degree of latitude. Peaks in the distribution of these edge-effect species are highly correlated with the range termini of more widely distributed species ($r = 0.97$; Valentine, 1966) and edge-effect species therefore are relatively precise indicators of biogeographic boundaries (Newell, 1948; Valentine, 1966; Newman, 1979; Murray *et al.*, 1980). Ecotones are also characterized by high species richness [Odum, 1971 (cited in Longhurst, 1998)], presumably because of the co-occurrence of edge-effect species and the range termini of many more widely distributed taxa. In California, the two highest densities of 'edge-effect' marine algae occur between 33 and 34° North and between 36 and 37° North (Fig. 4; Murray *et al.*, 1980). Concomitantly, the two highest densities of 'edge-effect' molluscan species, the two most species-rich molluscan faunas, the two most species-rich marine algal floras, and peaks in the range termini of marine algae and molluscs in California also occur between 33 and 34° North and between 36 and 37° North (Newell, 1948; Valentine, 1966; Murray & Littler, 1980; Murray *et al.*, 1980). The range termini of fishes peak at 33° N (Horn & Allen, 1978). In contrast, the number of one-degree species, species-richness, and the number of range terminations are less, and usually considerably less, between 34 and 35° N, the degree of latitude that encompasses Point Conception (Newell, 1948; Valentine, 1966; Horn & Allen, 1978; Murray & Littler, 1980).

The close concordance between the distributions of edge-effect species and peaks in range termini and species diversity are strong evidence that LAR and MBR, but not Point Conception, are the sites of the principal ecotones within the CTZ. The concordance of these distributions with

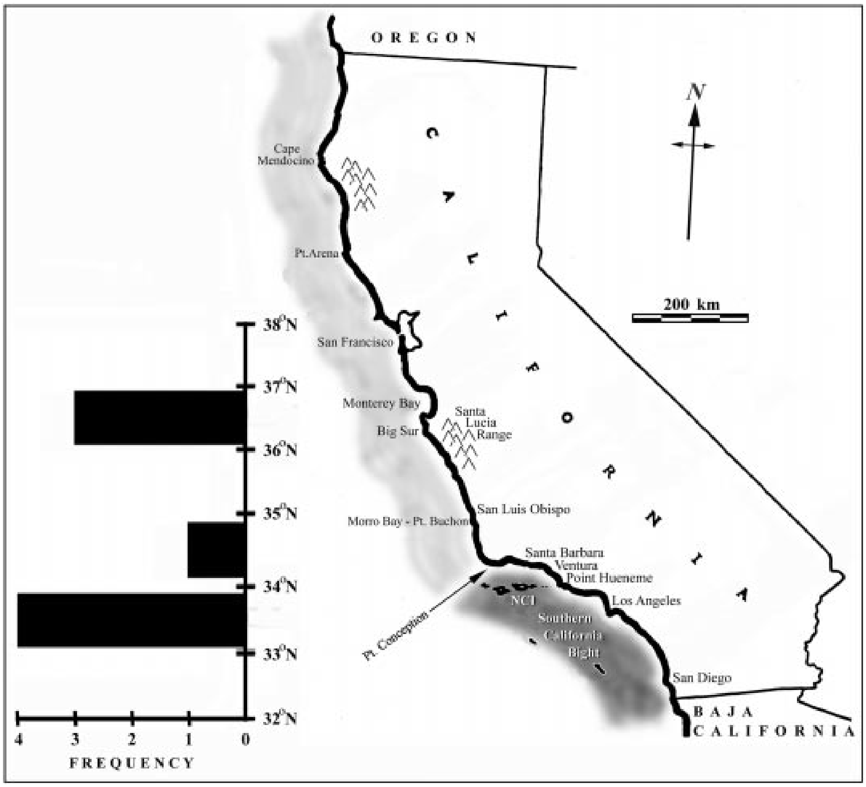

Figure 2 The distribution of the deepest phylogeographic breaks accurate to one degree of latitude in studies of coastal California marine taxa related to the geography of California. Locations shown on the map are those mentioned in the text. Light shading indicates the Oregonian Province and dark shading the Californian Province whose boundaries traditionally meet near Pt. Conception (e.g. Doyle, 1985), the approximate centre of the several hundred-kilometre long California Transition Zone that spans approximately five degrees of latitude from San Diego to Monterey Bay (e.g. Newman, 1979; Seapy & Littler, 1980). The northern channel islands (NCI; from West to East: San Miguel, Santa Rosa, Santa Cruz, and Anacapa islands), outer channel islands [San Nicolas (central), San Clemente (southern)], and submerged outer banks (see Fig. 5) delimit the Southern California Bight. The Palos Verdes peninsula is the prominent coastal feature adjacent to Los Angeles, and Long Beach lies immediately east of the peninsula.

intraspecific phylogeographic breaks (Fig. 3) is highly consistent with the correlative prediction that phylogenetic gaps within species are geographically concordant with biogeographic boundaries (H_3iii; Avise *et al.*, 1987).

Long-term physical processes and barriers to gene flow in the Los Angeles region

Support for the causative hypothesis that phylogenetic gaps usually arise from long-term extrinsic barriers to gene flow (H_3; Avise *et al.*, 1987), however, demands that modern physical discontinuities in LAR and MBR have ancient origins. Several physical discontinuities in LAR are likely to have ancient origins and to have affected the phylogeographic structure of coastal taxa by influencing gene flow within and between regions, changing the distributions of habitats and species, and facilitating the establishment and extirpation of populations.

Diastrophism

Southern California is tectonically active. Coastal southern California, including the submerged banks and island 'Borderlands', has been uplifted approximately 1 m per 1 Ka for the last several millions of years (Vedder & Howell, 1980; Sorlien, 1994). During this time, the Borderlands increasingly isolated the Southern California Bight ('the Bight') from surrounding oceanic and coastal waters (Owen, 1980) and since at least the Late Pliocene, the transfer of propagules into the Bight from northern and central California, via the California Current, has probably declined. Reciprocally, the mean residence time of water in the Bight must have increased, probably effected largely by constriction of a narrow seaway between the Northern Channel Islands and Point Hueneme, thus reducing the transfer of propagules from the Bight to more northerly regions. The modern residence time of water in the Bight is approximately 3–14 days (Hickey, 1992), a considerable period for some plankton (e.g. *E. newberryi* larvae are planktonic for only a few days; Capelli, 1997). Moreover, meso-scale circulation in the wake of islands or headlands or over canyons may entrain larvae and thus retain them in discrete habitat patches near their natal area for periods of several weeks (e.g. Owen, 1980; Black *et al.*, 1990; Hickey, 1992; Scheltema *et al.*, 1996; Pinca & Huntley, 2000; Strub & James, 2000). The Palos Verdes peninsula, for example, protrudes several kilometres from the adjacent LAR shoreline, influencing eddy formation, localized upwelling, and local sea-surface temperature and productivity (Dorman & Palmer, 1980; Owen, 1980; see also Lindberg & Lipps, 1996). It also interrupts long-shore flow, influences beach formation to the north and south of its own rocky headland, and can deflect the paths of onshore waves and currents, so creating divergent flow regimes (see Johnson, 1977; Owen, 1980; Hickey, 1992; Hayward *et al.*, 1996; Bray *et al.*, 1999). Such coastal heterogeneity inevitably occurred historically, albeit in modified forms, and probably contributed to genetic discontinuities (see Bucklin, 1991; Ruzzante *et al.*, 1998; Avise, 2000, 207) – Palos Verdes was an important

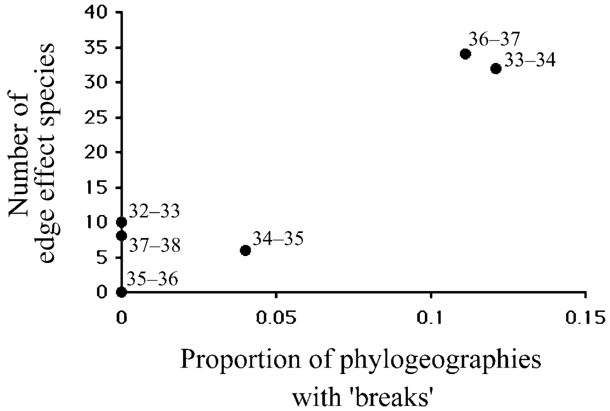

Figure 3 The frequency of phylogeographic breaks per degree latitude (see Fig. 3) vs. the number of edge-effect species of algae at that latitude (Murray *et al.*, 1980). The number of species included in phylogeographic studies, in order of increasing latitude, are $n = 34$, 34, 27, 28, 28 and 26. Numbers next to points indicate latitudinal range (°N).

submarine-cum-emergent structure 3–2 ma and the peninsula has been a permanent coastal feature since approximately 1 ma (Nardin & Henyey, 1978; Ward & Valensise, 1994).

North of the Palos Verdes peninsula, the submerged canyons at Redondo, Santa Monica, and Point Heuneme also indicate altered coastal topography (Johnson, 1977; Vedder & Howell, 1980). At lower sea-level, these canyons harboured rivers (e.g. Nardin & Henyey, 1978) that affected long-shore transport and gene flow by carrying suspended particles, including larvae, away from the shore. Such rivers also presented novel habitat that was unavailable outside the canyon or at times of higher sea-level or different coastal elevation. For example, prior to approximately 0.7 Myr BP, Redondo Canyon did not exist because prior to the Late Pleistocene LAR was variously, fully or partially submerged (Fig. 5a; Nardin & Henyey, 1978; Vedder & Howell, 1980; Davis *et al.*, 1989). However, while submerged, the LAR provided considerable additional coastal habitat with estuaries forming at the feet of the surrounding hills (Fig. 5a; also see Fig. 6 of Vedder & Howell, 1980). At the same time, the submerged LAR probably inhibited dispersal of both shallow-water and terrestrial coastal organisms between, for example, the Point Hueneme and San Diego regions. Subsequent emergence of LAR during the Late Pleistocene eradicated much coastal habitat, possibly extirpating coastal populations and creating or steepening clines or phylogeographic breaks. Emergence must have also opened new migratory routes or allowed secondary contact between shallow-water and terrestrial coastal populations north and south of LAR (e.g. Tan & Wake, 1995).

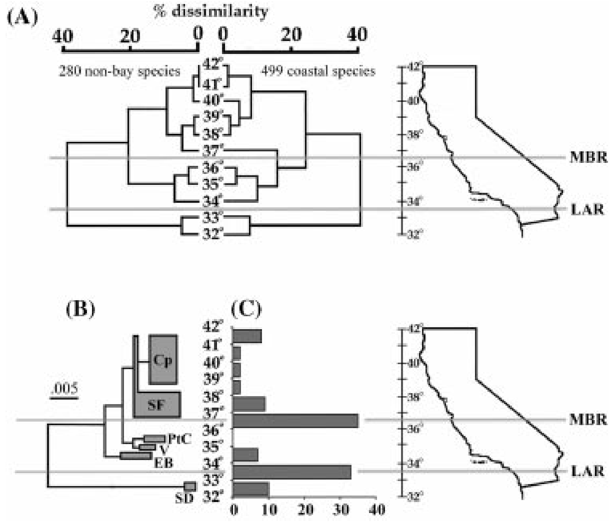

Figure 4 (a) The biogeography of coastal California marine fishes (Horn & Allen, 1978), (b) the maximum likelihood phylogeny of *Eucyclogobius newberryi* (Cp, Cape Mendocino clade; SF, San Francisco group; PtC, Point Conception clade; V, Ventura clade; EB, Estero Bay clade; SD, San Diego clade; Dawson *et al.*, in press), and (c) the distribution of 'edge effect' species of algae (Murray *et al.*, 1980). The coincidence of high dissimilarity between fish faunas, phylogeographic gaps, and peaks in the abundance of 'edge effect' species indicate that the principal biogeographic boundaries in the California Transition Zone occur in the vicinities of the Los Angeles region (LAR) and Monterey Bay (MBR). The regions identified by cluster analysis of coastal California marine fishes [based on one-degree divisions: 32.0–32.9, 33.0–33.9, … (Horn & Allen, 1978)] are similar to ichthyological provinces and regions of endemism in freshwater fishes (Moyle, 1976).

Climate change

Periods of glaciation accentuated many of the effects of tectonism by lowering sea-level and therefore increasing the mass of islands in the Southern California Bight, further constricting seaways. During the last glacial maximum, for example, the seaway between the Northern Channel Islands and Point Hueneme was less than half its present depth and width (Wenner & Johnson, 1980) and the seaway between Santa Catalina Island and Palos Verdes was also restricted considerably (Fig. 5b) inevitably altering coastal hydrography (Lindberg & Lipps, 1996). Glaciation also led to a cooler wetter climate in southern California, increasing the flow through coastal canyons and their impact on long-shore transport and local habitat.

Climate change also affected the distribution of faunas (Valentine, 1958; Addicott, 1966; Valentine, 1966; Johnson, 1977; Graham & Grimm, 1990; Fields *et al.*, 1993; Mortyn *et al.*, 1996; Davis, 1999). Sea-surface and air temperatures of southern California were as much as 6–10 °C cooler during Pleistocene glaciations than present day (Powell, 1994; Mortyn *et al.*, 1996; Davis, 1999), allowing 'subpolar' plankton to make southerly incursions into the outer basins of the Bight (Mortyn *et al.*, 1996). However, temperature minima and southern limits were not always so extreme (Mortyn *et al.*, 1996; Davis, 1999). During at least some cool Pleistocene high-stands, the Oregonian–Californian faunal boundary still occurred in the vicinity of LAR, at 34° N (Valentine, 1958; Addicott, 1966) and faunal distributions

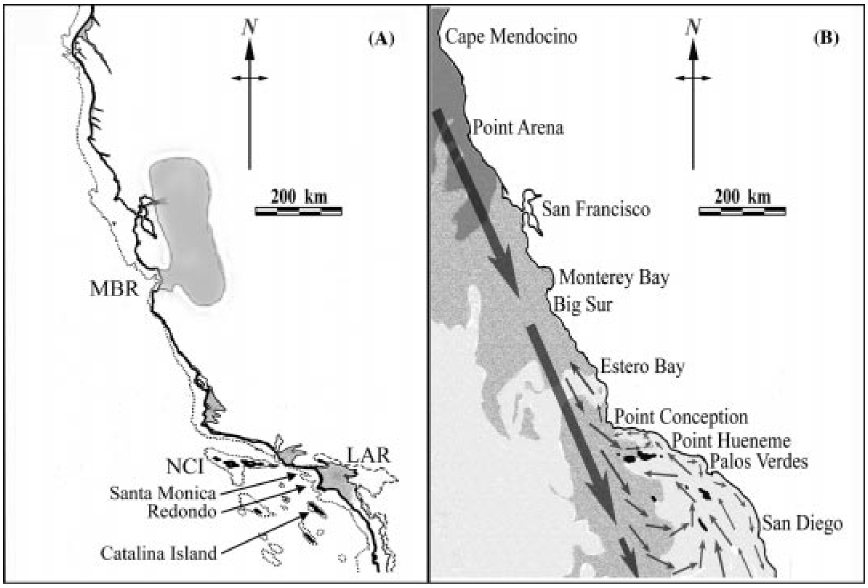

Figure 5 (a) Schematic diagram of California showing approximately the –100 m (dotted), +200 m (thin solid), and, in southern California, +500 m (dashed) contours relative to the present-day coastline (thick solid line), overlaid by the modern geographical extent of Pleistocene marine deposits, which suggest the approximate extent of Pleistocene seas (*sources*: Jennings *et al.*, 1977; Vedder & Howell, 1980). NCI, Northern Channel Islands. (b) Generalized hydrography of modern-day coastal California waters superimposed on a schematic representation of a SeaWiFs image from Spring (1999). Darker shading indicates cooler water. The California Current (cold, low salinity, well oxygenated, subarctic water) flows southward along much of northern and central California, departing the coastline in the vicinity of Point Conception. The Southern California Counter Current (or 'Davidson Current' north of the Southern Bight; warm, saline, low oxygen, equatorial Pacific water) flows northward near the coast in southern and central California. The Davidson Current is a stronger feature during Autumn and Winter, particularly north of San Francisco (Bray *et al.*, 1999; Strub & James, 2000). Interaction of the two currents, upwelling, wind, and coastal topography create many complex hydrographic features including eddies in the Monterey Bay, the Santa Barbara Channel, and the Southern California Bight. Other, smaller, eddies may exist adjacent to islands and the mainland, for example off San Luis Obispo, in Santa Monica Bay, south of Palos Verdes, and near San Diego. (*Sources*: Kanter, 1980; Owen, 1980; Seapy & Littler, 1980; Hickey, 1992; Browne, 1994; Hendershott & Winant, 1996; Bray *et al.*, 1999).

were also similar during periods of warmer climate (Gobalet, 2000). Thus, the geographical locations of temperature, oxygen, and salinity discontinuities and the boundary of the California Current may have changed little during much of the Pleistocene and Holocene. However, these patterns inevitably were variable and modified at times by small-scale, sometimes stochastic, events such as droughts (Stine, 1990; Davis, 1999), floods (Schimmelmann *et al.*, 1998), El Niño (Hubbs, 1948), and tsunami (Hauksson & Saldivar, 1989).

The Monterey Bay region

Similar features and events

Similar features and events probably affected the biota of Monterey Bay. Most obviously, MBR presents a habitat that differs from the open rocky shores and coastal upwelling regions to the north and south (Lindberg & Lipps, 1996) and populations may be maintained in this refuge by an eddy (Paduan & Rosenfeld, 1996) that also interrupts long-shore flow. In addition, the Monterey Bay Canyon, like canyons in LAR, probably inhibited gene flow by modifying currents and interrupting habitats. The Monterey Peninsula, at the south of the bay, similarly is the northernmost point of an 100 km-long steep, rocky, coastline that probably has been a barrier to estuarine and bay, but not rocky shore, faunas at both high and low sea-levels (Figs 4 & 5, e.g. Dawson *et al.* (in press); cf. Bernardi, 2000). In addition, Central California, like southern California, has undergone considerable topographic changes since the Miocene when an inland sea and coastal islands existed (Fig. 5; Yanev, 1980).

SUMMARY: LONG-TERM BARRIERS TO GENE FLOW AND PHYLOGEOGRAPHIC BREAKS

Long-term climate and topographical changes in coastal California have been proposed as important influences on the evolution of non-marine organisms such as salamanders (Yanev, 1980; Tan & Wake, 1995; Wake, 1997) and freshwater fishes (Moyle, 1976). The close geographical concordance of these environmental changes with phylogeographic and biogeographic patterns in marine invertebrates and fishes suggests that similar processes also influenced the evolution of coastal marine taxa. As such, phylogeographic and biogeographic patterns in coastal California marine taxa support the hypothesis that large phylogenetic gaps usually arise from long-term extrinsic barriers to gene flow (H_3).

CLOSING REMARKS

Phylogeographic and biogeographic patterns in coastal California marine taxa now are consistent with all of the phylogeographic hypotheses proposed by Avise *et al.* (1987; Table 1). Prior opinions of discordance arose syllogistically from the (supported) hypothesis that phylogenetic gaps will be concordant with biogeographic boundaries and the (incorrect) premise that Point Conception was a major biogeographic boundary. Rather, a review of the biogeographic and geological literature describing coastal California indicates that processes likely to cause phylogenetic gaps probably have been most severe in the LAR and MBR, at least during the Pliocene and Pleistocene. This is consistent with the clustering of modern phylogeographic breaks around Los Angeles and Monterey Bay.

The concordance of phylogeographic and biogeographic patterns in the coastal marine fauna of south-western North America, and similar patterns in south-eastern North America and the Indo-Pacific, suggest that the phylogeographic hypotheses will be applicable to many coastal marine settings. As such, they should provide a useful framework for investigating and comparing patterns of evolution in coastal marine faunas around the globe.

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BIOSKETCH

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