



## ORIGINAL ARTICLE

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# How sea level change mediates genetic divergence in coastal species across regions with varying tectonic and sediment processes

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## Abstract

Plate tectonics and sediment processes control regional continental shelf topography. We examine the genetic consequences of how glacial-associated sea level change interacted with variable nearshore topography since the last glaciation. We reconstructed the size and distribution of areas suitable for tidal estuary formation from the last glacial maximum, ~20 thousand years ago, to present from San Francisco, California, USA (~38°N) to Reforma, Sinaloa, Mexico (~25°N). We assessed range-wide genetic structure and diversity of three codistributed tidal estuarine fishes (California Killifish, Shadow Goby, Longjaw Mudsucker) along ~4,600 km using mitochondrial control region and cytB sequence, and 16–20 microsatellite loci from a total of 524 individuals. Results show that glacial-associated sea level change limited estuarine habitat to few, widely separated refugia at glacial lowstand, and present-day genetic clades were sourced from specific refugia. Habitat increased during postglacial sea level rise and refugial populations admixed in newly formed habitats. Continental shelves with active tectonics and/or low sediment supply were steep and hosted fewer, smaller refugia with more genetically differentiated populations than on broader shelves. Approximate Bayesian computation favoured the refuge–recolonization scenarios from habitat models over isolation by distance and seaway alternatives, indicating isolation at lowstand is a major diversification mechanism among these estuarine (and perhaps other) coastal species. Because sea level change is a global phenomenon, we suggest this top-down physical control of extirpation–isolation–recolonization may be an important driver of genetic diversification in coastal taxa inhabiting other topographically complex coasts globally during the Mid- to Late Pleistocene and deeper timescales.

## KEYWORDS

estuaries, fish, GIS, paleohabitat, population dynamics, refugia

## 1 | INTRODUCTION

Isolation and reconnection of populations through time can enhance genetic diversity (Briggs, 2006; Hewitt, 2000, 2004), alter species ranges (Kelly & Palumbi, 2010; Ludt & Rocha, 2014; Marko, 2004) and facilitate divergence or speciation (Briggs, 2006; Toms,

Compton, Smale, & von der Heyden, 2014). Previous work showed that glacially driven sea level change against heterogeneous continental shelf topography can alternately extirpate and re-form estuarine habitats, resulting in genetic signatures of isolation and mixing of coastal populations over millennia (Dolby et al., 2016). This work, however, was over a limited geographic range, which can bias

inferences (Slatkin, 2004; but see Beerli, 2004), particularly when using coalescent approaches; it also did not address the effect of differing shelf morphologies on those findings. This proposed sea level mechanism is important because the magnitude of sea level change is similar globally, whereas other proposed glacial-associated mechanisms act more locally or with varying magnitude. Examples include isolation in montane refugia (Knowles, 2001), in ice-free high-latitude refugia (Fraser, Nikula, Spencer, & Waters, 2009; Hewitt, 2004; Ilves, Huang, Wares, & Hickerson, 2010), by emergent land bridges (Benzie, 1999; De Bruyn & Mather, 2007) or by climatic effects (e.g., local aridity; Wüster et al., 2005; but see Rull, 2011). To determine the applicability of this sea level mechanism along coastlines with varying geomorphologies and geologic processes, we perform paleo-habitat modelling and genetic assessments of three fish species across widely varying physical settings. We test the ability of our sea level-based paleohabitat models to explain range-wide phylogeographic patterns compared to previously hypothesized mechanisms of isolation by distance and seaways (Riginos, 2005; Stepien, Rosenblatt, & Bargmeyer, 2001). Finally, we explore the top-down factors controlling shelf geomorphology to develop a framework that can be used to make and test predictions of sea level change and biotic evolution on other coasts, habitats and species.

### 1.1 | Regional tectonics and nearshore geomorphology

Tectonic and sediment processes shape the continental shelf, and these processes vary across our study area from San Francisco, CA (USA), to Reforma, Sinaloa (MX; Figure 1). A complex history of oblique tectonics caused faulting and rotation of rifted crustal blocks to form prominent headlands such as Punta Eugenia and Point Conception (Atwater & Stock, 1998; Hillhouse, 2010; Ingersoll & Rumelhart, 1999; Nicholson, Sorlien, Atwater, Crowell, & Luyendyk, 1994). These physical processes change the slope, width and orientation of the coastline. Estuaries occur in specific geomorphic settings (Bickel, 1978; Graham, Dayton, & Erlandson, 2003; Jacobs, Stein, & Longcore, 2011)—they require low-gradient slope to form and a relatively broad continental shelf to migrate with the coastline during sea level change. Physical processes that narrow or steepen the continental shelf render that coastline less permissive to estuary formation and persistence during such changes (Jacobs et al., 2011). Shelf-steepening processes include nearshore faults with vertical displacement, coastal uplift and limited sediment supply either from rivers and longshore transport, or through sediment bypassing the shelf via submarine canyons—a process particularly pertinent to southern and central California (Gorsline & Emery, 1959; Masters, 2006; Orange, 1999). Transform (strike-slip) faults typically do not directly contribute to shelf topography, but can delimit the width of the shelf, particularly if they accommodate some component of vertical movement (e.g., oblique normal fault; Spencer & Normack, 1979; Michaud et al., 2004, 2007). For example, the Tosco-Abreojos and San Clemente-San Isidro faults appear to delimit the shelf of the Pacific coast of the Baja California peninsula (Figure 1). In contrast,

processes conducive to forming broad, low-gradient continental shelves suitable for estuary formation include tectonically static or subsiding coastal areas, regions with high sediment supply from erodible sedimentary rocks subjected to wave attack, or riverine and/or longshore processes that contribute sediments to the shelf. The relative contribution of these factors varies across our study area (Figure 2), offering a good opportunity to examine how these processes affect the coastline and control the distribution of modern and historical estuaries, and the isolation and mixing of coastal populations in turn.

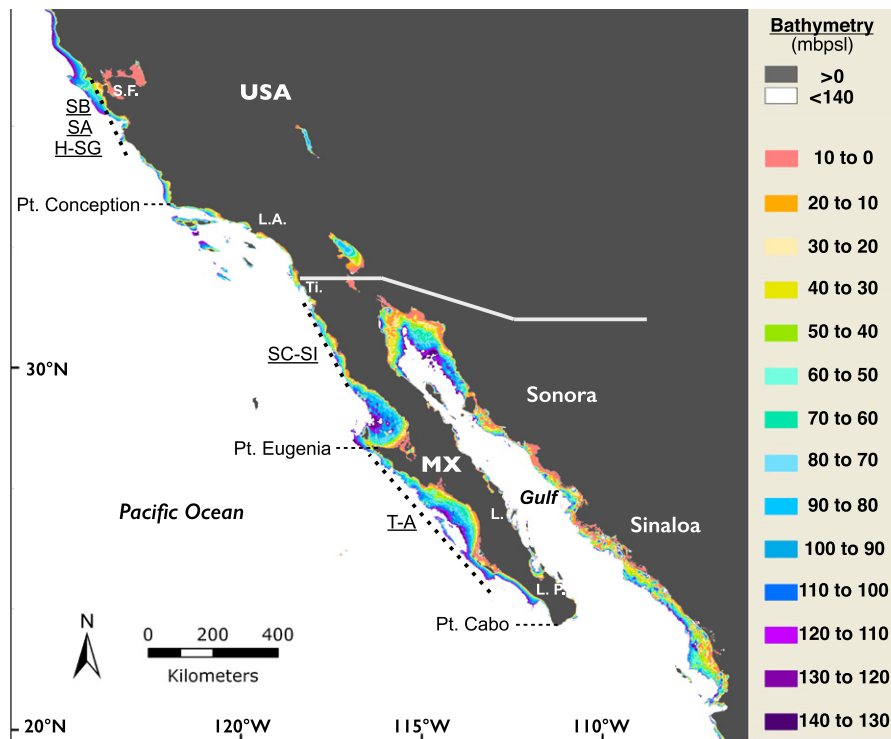
### 1.2 | Study system—tidal estuaries

Estuaries are semi-enclosed coastal bodies of water with marine influence and permanent, intermittent, or infrequent freshwater input. As discrete entities, estuaries resemble the island or stepping-stone models in population genetics that can promote genetically isolated groups (Bertness & Gaines, 1993; Bilton, Paula, & Bishop, 2002; Earl, Louie, Bardeleben, Swift, & Jacobs, 2010). The abundance and distribution of estuaries changes dynamically through time (Erlandson, 1985; Masters, 2006; Masters & Aiello, 2007), lending themselves to interesting isolation–recolonization metapopulation-type dynamics that are beyond the timescale of historical metapopulation biology (Dawson, Staton, & Jacobs, 2001; Dolby et al., 2016; Graham et al., 2003). For these reasons, they are excellent study systems to explore how physical processes mediate population connectivity through time.

Several classes of estuaries exist from small, closed bar-built lagoons to large, perpetually open tidal systems (Jacobs et al., 2011). We focus on tidal estuaries in a rainfall-limited climate where freshwater input is not a primary or uniform feature of these habitats (Jacobs et al., 2011; Kench, 1999; Ranasinghe, Pattiaratchi, & Maselink, 1998). They are distinct from the traditional freshwater-driven estuaries characteristic of the eastern U.S. Atlantic coast (Whitfield, Elliott, Basset, Blaber, & West, 2012). Our focal species: *Quietula y-cauda* (Shadow Goby), *Gillichthys mirabilis* (Longjaw Mudsucker) and *Fundulus parvipinnis* (California Killifish) are codistributed in these tidal estuaries, adapted to their abiotic variabilities, and therefore exhibit broad physiological tolerances (Collins & Melack, 2014; Courtois, 1976a; Feldmeth & Waggoner, 1972; Griffith, 1974; Jayasundara & Somero, 2013). Wide physiological tolerances suggest factors such as salinity and temperature, which fluctuate widely within tidal estuaries, are not major factors limiting these species' distributions (Earl et al., 2010), which simplifies our modelling approach. For tidal estuarine habitat, we used the geomorphic and sea level characteristics of modern tidal estuaries to predict the size and distribution through time of regions conducive to tidal estuary formation.

### 1.3 | Regional phylogeography

Previous research articulated geographic control of phylogeographic and biogeographic pattern across our study region. Promontories such as Pts. Eugenia and Conception (Figure 1) are thought to



**FIGURE 1** Bathymetric map showing present-day continental shelf across the study site. Areas meeting slope requirements for estuarine habitat shown for 10-m depth bins from 140 to 0 m below present sea level (mbpsl). Abbreviated localities in coastal order are: S.F.—San Francisco, L.A.—Los Angeles, Ti.—Tijuana, L.P.—La Paz, L.—Loreto. Thin dashed lines show biogeographic barriers (Pts. Conception, Eugenia, Cabo); thick dotted lines are shelf-bounding transform faults in coastal order—SB, San Bruno; SA, San Andreas; H-SG, Hosgri-San Gregorio; SC-SI, San Clemente-San Isidro; T-A, Tosco-Abrejos

control population subdivision on the Pacific coast (Bernardi & Talley, 2000; Dawson, 2001; Dawson, Louie, Barlow, Jacobs, & Swift, 2002; Jacobs, Haney, & Louie, 2004; Pelc, Warner, & Gaines, 2009; Swift, Spies, Ellingson, & Jacobs, 2016; Wares, Gaines, & Cunningham, 2001). Within the Gulf, north-south oceanographic gyres (Marinone, Ulloa, Parés-Sierra, Lavín, & Cudney-Bueno, 2008; Munguía-Vega et al., 2014; Soria et al., 2014), localized upwelling in the eastern and mid-Gulf (Santamaría-del-Ángel, Álvarez-Borrego, & Müller-Karger, 1994; Zeitzschel, 1969), currents (Jackson, Munguía-Vega, Beldade, Erisman, & Bernardi, 2015) and trans-peninsular seaways (Leaché, Crews, & Hickerson, 2007; Lindell, Ngo, & Murphy, 2006; Munguía-Vega, 2011; Riddle, Hafner, Alexander, & Jaeger, 2000; Riggins, 2005) may influence genetic structure. Meanwhile, Terry, Bucciarelli, and Bernardi (2000) and Bernardi, Findley, and Rocha-Olivares (2003) linked isolation during interglacial warm periods with species-level differentiation between Pacific and Gulf fish populations. Longer-timescale mechanisms proposed to generate high levels of endemism in the Gulf include the following: isolation in embayments before flooding of the Gulf (Dolby, Bennett, Lira-Noriega, Wilder, & Munguía-Vega, 2015; Hurtado, Lee, & Mateos, 2013; Hurtado, Mateos, & Santamaria, 2010), isolation in the Gulf after flooding 6.3 Mya (Dolby et al., 2015; Oskin & Stock, 2003) and adaptation to unique habitats such as the Colorado River Delta (Ellingson, Swift, Findley, & Jacobs, 2014; Jacobs et al., 2004; Lau & Jacobs, 2017; Swift, Findley, Ellingson, Flessa, & Jacobs, 2011). Here,

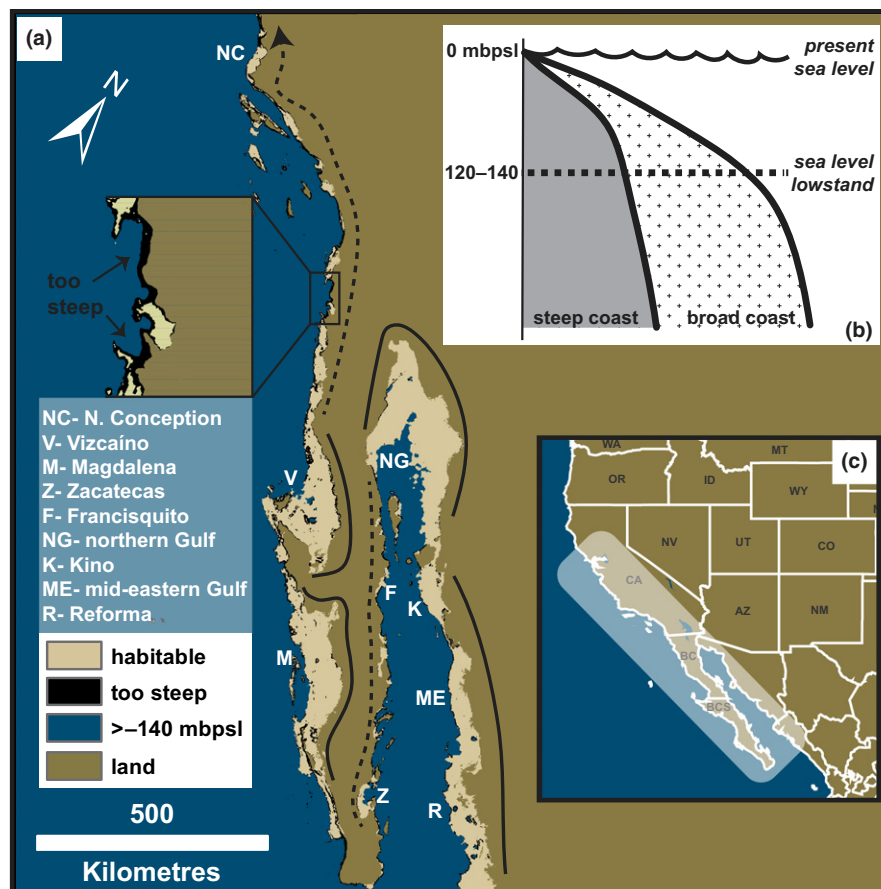
we assess the role of glacial-associated sea level change across regionally variable coastal topography as a mediator of diversification in three estuarine species. We consider the ability of these shorter-term subglacial or glacial-scale dynamics to produce longer-term phylogeographic or phylogenetic patterns when extrapolated over the 100-kyr to ~1-Myr period of repeated large-scale Northern Hemisphere glaciations.

We use a geographic information system (GIS) approach to reconstruct the distribution of tidal estuarine habitat 23–38°N since the last glacial maximum (LGM) at near millennial-scale resolution. We assess the population genetic structure of three codistributed, low-dispersing tidal estuarine fishes inhabiting these tidal estuaries to independently infer population history and range-wide intraspecific genetic patterns using mitochondrial DNA (mtDNA) and microsatellite data. We test refuge-recolonization scenarios against alternative hypotheses using approximate Bayesian computation (ABC) for each species and offer a general thesis of sea level driven isolation and recolonization.

## 2 | MATERIALS AND METHODS

### 2.1 | Paleohabitat modelling

To model estuarine habitat as a function of sea level, we developed a slope parameter that characterizes the modern estuaries in which



**FIGURE 2** Map showing present-day interplay of regional geology, refugia and continental shelf morphology. (a) Nearshore regions are classified as steep (dashed black lines) or broad (solid black lines). Steep continental shelves are dominated by recent tectonics including nearshore faults with vertical displacement and uplift and/or low sediment supply. Broad continental shelves have little or no proximal tectonism and/or higher sediment supply. Refugia from the best supported paleohabitat and ABC model are labelled. Refugia located along broad continental shelves tend to be larger, more genetically interconnected at lowstand than refugia on steep or narrow shelves, and have higher allelic richness. Habitable nearshore areas that meet slope and depth requirements are tan, and uninhabitable areas that are too steep are black. Central California coast is not shown for simplicity. (b) Conceptual hypsometric profile showing how wide continental shelves have more habitable area at sea level lowstand (Figure S1, Tables S8, S9). (c) Regional map denoting the study area (transparent box)

our three species occur today. We applied this slope parameter to a series of depth bins that reflect the position of sea level at different times from 20 thousand years ago (kya) to the present. This approach allowed us to identify regions along the coast conducive to forming tidal estuaries through time. Finally, we test whether areas meeting slope requirements during lowstand were similar in size to those producing tidal estuaries today and therefore likely to host our species of interest.

### 2.1.1 | Parameterization

To estimate the habitat characteristics of Pacific coast estuaries (south of Punta Eugenia, Baja California Sur (BCS) and north of Morro Bay, California; Figure 1), we used a slope range of 0.0%–1.3% as suitable habitat (Dolby et al., 2016). Due to different geomorphic landscapes between the Pacific and Gulf (Helenes & Carreno, 1999; Ingersoll & Rumelhart, 1999; Oskin & Stock, 2003), we

parameterized the slope limit separately for Gulf estuaries occupied by *G. mirabilis* and *Q. y-cauda* (*F. parvipinnis* does not occur in the Gulf). We measured within-estuary slope in GOOGLE EARTH® v5 (Google Inc., Mountain View, California) for the 23 present-day Gulf estuaries where the two species occur, calculating slope at five locations within each estuary to maximize intra-estuarine variability. We used the maximum observed slope value as an upper limit of tidal estuarine habitat formation. Islands and offshore features were excluded from analysis, as such habitat is minimal at present and was likely minimal and/or ephemeral in the past.

### 2.1.2 | Application

We partitioned bathymetry/topography into 10-metre depth bins from 0 to 140 m below present sea level (mbpsl) with the addition of a “modern” depth bin (0 kya, 0 mbpsl  $\pm$  5 m). In ARCMAP v10.2 (ESRI, Redlands, California), using the Raster Calculator tool, we

queried the 30-arc-second SRTM30\_PLUS Shuttle Radar Topography Mission (Becker et al., 2009) Digital Elevation Model for nearshore regions matching the slope criteria within each depth bin. These were converted to simplified polygon feature layers. Separately, we subdivided the coastline into regions based on shelf characteristics and modern distribution of estuarine habitat (Figure S1). We used the geometric intersection tool to summarize the polygon statistics of areas meeting slope requirements within each depth bin for each coastal region. We recorded number of polygons and calculated the minimum, maximum, total, mean and standard deviation for polygon areas in these coastal areas for each depth bin (a.k.a. “polygon attribute data”). We added a seventh attribute that normalized the polygon area by the coastal region area to provide a proxy for habitat density because coastal regions varied in size. There were 14 depth bins, 7 polygon attributes per bin and 9 Gulf coastal regions producing 882 size observations within the Gulf. New calculations for Pacific coastal regions not previously covered in Dolby et al. (2016) yielded 294 new observations. Finally, to correlate time with sea level position, we used a composite sea level curve (Chaytor et al., 2008), assigning age to the mid-point of each depth bin. Limitations of these models include the following: the absence of explicit environmental parameterization of temperature, salinity, etc. (Barron, Bukry, & Bischoff, 2004), using modern topography as a proxy for paleo-topography (Schwalbach & Gorsline, 1985), excluding species-species (ecological) effects and excluding the effect of local uplift rates which would slightly alter our depth–time correlations (Muhs, Rockwell, & Kennedy, 1992; Niemi, Oskin, & Rockwell, 2008; see Supporting Information).

### 2.1.3 | Assessment of Refugia

To assess whether lowstand areas meeting slope requirements were similar in size to present habitats and thus likely to support populations of the estuarine species studied here (Jacobs et al., 2011), we used discriminant function analysis (DFA) and generalized linear models (GLMs). This provides a cut-off for which regions are similar enough to present-day habitats to be considered refugia. The size variables we measured are proxies reflecting multiple coastal, fluvial and sediment processes that together control the shape and size of estuaries, but which cannot be accurately modelled as individual parameters over this timescale.

First, we used DFA to determine which among our seven measured polygon attributes predicted the modern distribution (presence/absence) of our three species. We performed DFA on the polygon attributes of modern coastal areas divided into two groups: those that host populations of these fishes today (“present” group;  $N = 6$ ; Reforma, Sinaloa, mid-eastern Gulf, Kino, northern Gulf, Francisquito, Zacatecas; Figure S3) and those that do not (“absent” group;  $N = 3$ : Isla Ángel de la Guarda/western Gulf, south of Francisquito and north of Zacatecas). We ran stepwise selection (SVSP), pseudo-inverses and quadratic (different) covariances, producing two models. Of these two models, the first had one significant variable (normalized habitat area,  $p = .04$ ) and one misclassification. To reduce

misclassifications, we added the next, nonsignificant variable (number of polygons) which produced  $p = .08$  with zero misclassifications. We chose this second, two-variable unequal covariance model (normalized habitat area and number of polygons) for further analyses. We applied this model in the lowstand (120–140 mbpsl) depth bin GLMs to test which lowstand areas were similar to the habitat characteristics of the modern “present” group. GLMs used a binomial distribution and logit-link function. For a given scenario, we classified regions as “yes” or “no,” for whether they were lowstand refugia and recorded the AICc and  $p$ -values for different scenarios (Table S3). Statistically significant models were rerun using Firth biased estimates and false discovery rates to correct for correlated variables.

For Pacific sites, we ran DFA using variables previously found to predict the distribution of these fishes (maximum polygon area and summed area; Dolby et al., 2016) applied to three new coastal regions (Bahía Magdalena, central California coast, San Francisco Bay). Comparing Pacific and Gulf models, normalized habitat area (i.e., “habitat density”) predicted occurrences for Gulf sites rather than total habitat area (as for Pacific sites), perhaps because the steep Gulf coastlines have small, isolated low-slope regions that are not actual estuaries where these fishes occur; the normalized area variable would better exclude such regions.

## 2.2 | Population genetic analyses

### 2.2.1 | Data generation

Specimens were collected via seine fishing in estuaries and deposited in 99% ethanol under permits DGOPA 14253.101005.6950 and CASCP No. 2679. We extracted DNA from lateral muscle tissue anterior to the caudal peduncle and amplified the mitochondrial control region (mtCR) for all three species and cytochrome B (*cyt B*) for *Q. y-cauda* and *G. mirabilis* using published primers (Iwata et al., 2000; Lee, Conroy, Howell, & Kocher, 1995) and standard protocols (Ellingson et al., 2014; Supporting Information). Individuals were genotyped at the UCLA GenoSeq Core (Dolby, 2015; Dolby et al., 2016). Total sample sizes and numbers of microsatellite loci were as follows: *F. parvipinnis* ( $N = 109$ , 20 loci), *Q. y-cauda* ( $N = 177$ , 17 loci), *G. mirabilis* ( $N = 238$ , 16 loci). Mean population sample sizes were 8 (range 5–14), 5 (range 1–12) and 8 (range 1–20), respectively (Tables S1, S4).

To assess population structure, microsatellite data sets per taxon were analysed as full data sets ( $K = 2–5$ ), Pacific-only samples ( $K = 2–4$ ) and Gulf-only samples ( $K = 2–4$ ) in STRUCTURE v2.3.4 (Pritchard, Stephens, & Donnelly, 2000). For *G. mirabilis*,  $K = 1$  was run for Gulf samples *post hoc* to assess the relative likelihood of a two-population versus one-population model using the  $\Delta K$  metric (Evanno et al., 2005). We ran three replicates per  $K$  and used correlated frequencies and admixture models; iterations included 1 million burn-in and 5 million post-burn-in generations each. We analysed all runs in STRUCTURE HARVESTER (Earl & vonHoldt, 2011) and combined replicates per species in CLUMPP v1.1.2 (Jakobsson & Rosenberg, 2007) using the GREEDY algorithm ( $M = 2$  with greedy option 1)



**TABLE 1** Summary of population groupings for ABC tests. Populations (three-letter codes, right) are listed per species in coastal order starting with San Francisco, California (ALB), and ending in Reforma, Sinaloa (REF). Populations were grouped geographically based on inferred group type according to paleohabitat models and STRUCTURE results

ABC grouping	Inferred type	<i>Fundulus parvipinnis</i>	<i>Gillichthys mirabilis</i>	<i>Quietula y-cauda</i>
San Francisco Bay	Admixed	n/a	ALB	n/a
North conception	NC refugium	MOR, CAR	MOR, DEV	MOR, GOL
Northern Baja California/ southern California	Admixed	ALA-QTN	USB-QTN	MDC-QTN
Vizcaíno	V refugium	MAN-OJO	MAN, GNG	MAN, GNG
Bahía Magdalena	M refugium	CUA-TAM	BOC-PUR	BOC-GAL
Zacatecas	Z refugium	n/a	n/a	ZAC
Western Gulf	Admixed	n/a	n/a	NOP-MRC
Francisquito	F refugium	n/a	MOJ	FRN
Northwest Gulf	Admixed	n/a	PAL-NWC	ANI-LGZ
Northern Gulf	NG refugium	n/a	ADR-REF	SGU-KIN
Mid-eastern Gulf	ME refugium	n/a	ADR-REF	YAV
Reforma	R refugium	n/a	ADR-REF	REF

and S of 1 (using G statistic). To infer phylogenetic history of these groups, we constructed neighbour-joining trees with the microsatellite data in POPULATIONS v1.2.3 (©Langella, [www.bioinformatics.org/populations](http://www.bioinformatics.org/populations)) with Nei minimum distance algorithm and 5,000 bootstrap replicates on loci per taxon. We reconstructed mtDNA trees using MRBAYES v3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) on the CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010); for parameterizations see Supporting Information.

## 2.2.2 | Testing refugia with ABC

To determine whether the refugia identified in the GIS paleohabitat models could be the driver of present-day population structure, we used approximate Bayesian computation (ABC). With ABC, we simulated data under different historical scenarios and compared these to our observed genetic data to evaluate which historical scenarios best explain the present-day genetic patterns. We ran separate Pacific and Gulf analyses per species in DIYABC v2 (Cornuet et al., 2014) using microsatellite data divided by geographic region (Table 1) and performed two sets of analyses (i.e., analysis sets) for each species (S9–S14). (i) Paleohabitat tests simulated genetic data under the GIS-predicted refugial scenario(s) and under scenarios where specific GIS-predicted refugia were removed (i.e., treated as admixed and not as refugia) to determine how consistent our genetic data were with the GIS-predicted refugia (scenarios P1a–c and G1a–c; Figures S9–S11). This can be thought of as way to biologically validate the paleohabitat results. These simulations were also done to assess the biological support among paleohabitat models in the Gulf, which produced more than one statistically supported scenario (Table S3). (ii) Phylogeographic tests compared genetic data simulated under the favoured per-species scenario (P2c, G2c) from analysis 1 above (the paleohabitat tests) with data generated under previously published

phylogeographic hypotheses of isolation by distance (Riginos & Nachman, 2001; Stepien et al., 2001) and trans-peninsular seaways (scenarios P2a–b and G2a–b, Figure S13; Riginos, 2005). This was done to determine whether there were alternative phylogeographic explanations for our present-day genetic patterns.

We simulated one million data sets per scenario (e.g., for four scenarios, we simulated four million data sets). We assumed a generation time of two years (Fritz, 1975; de Vlaming, 1972; Walker, Whitney, & Barlow, 1961), and timing of split (admix) and merge events based on inferred timing of habitat formation according to our habitat models (Figures S9–S13). We automatically grouped loci, used a uniform mutation rate prior with mean of 0.0005 bounded between  $1.00\text{E-}4$  and  $1.00\text{E-}3$  and a uniform prior on effective population size bounded between 10 and 10,000 individuals per population (default). We recorded summary sample statistics including number of alleles, genetic diversity, allelic size variance, Garza–Williamson,  $F_{ST}$  (Weir & Cockerham, 1984), classification index, shared allele distance and  $(\delta\mu)^2$  distance (Cornuet et al., 2014). We evaluated prior distributions, posterior distributions using 10% of simulations, and report logistic posterior predictive errors based on 1% of simulated data sets. For statistical power and simplicity, populations were grouped in coastal order (Tables 1, S1) according to genetic similarity inferred from STRUCTURE results.

## 2.2.3 | Assessing genetic diversity

We calculated diversity statistics per taxon using full microsatellite data sets with individuals grouped by collection site (i.e., population; Table S1). Fisher's exact test for population differentiation, pairwise  $F_{ST}$  (Weir & Cockerham, 1984) and Hardy–Weinberg tests for heterozygote deficit and excess were executed in GENEPOP v4.2 (10,000 dememorization steps, 20 batches, 5,000 iterations per batch). We calculated average gene diversity and mean observed

and expected heterozygosity in ARLEQUIN v3 (Excoffier, Laval, & Schneider, 2005). Using HIERFSTAT v0.04 (Goudet, 2005), we calculated allelic richness per locus per collection site in R v3.2 (the R Foundation for Statistical Computing, www.R-project.org) for each species and then calculated total mean and median allelic richness per population. Where applicable, we tested data for normality with the Shapiro–Wilk test (Shapiro & Wilk, 1965).

### 3 | RESULTS

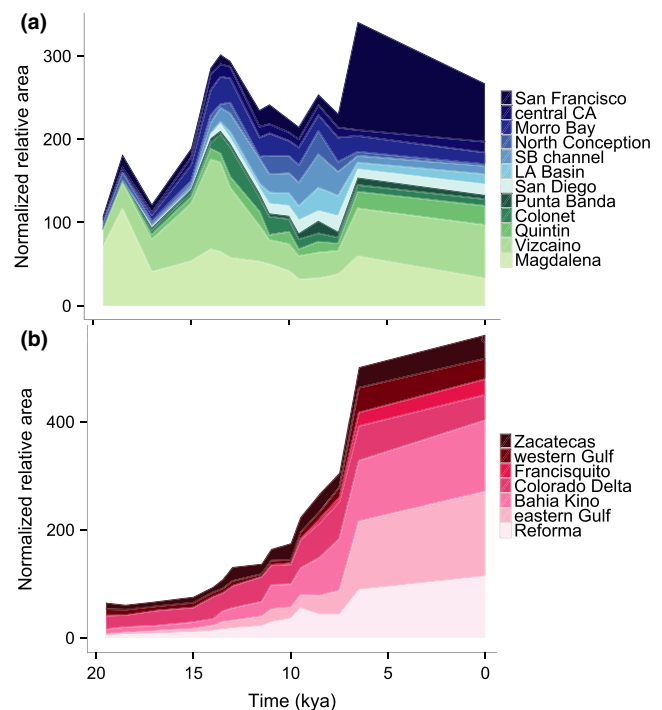
#### 3.1 | Paleohabitat modelling

##### 3.1.1 | Habitat patterns

The maximum slope observed for estuaries was higher in the Gulf ( $\leq 3.4\%$ ) than the Pacific ( $\leq 1.3\%$ )—Gulf habitats were significantly steeper ( $p = .0002$ , Mann–Whitney  $U$ -test), and Gulf habitats were steeper on the western side than eastern side ( $p = .0007$ ). The maximum habitat size of any depth bin in the Pacific was 2,390 km<sup>2</sup> (Bahía Magdalena refugium, 100–90 mbpsl) and 3,483 km<sup>2</sup> in the Gulf (Reforma refugium,  $0 \pm 5$  mbpsl; Figure S3). Despite different slope cut-offs, these maximum sizes are of comparable magnitude. Total lowstand habitat area was 1,006 km<sup>2</sup> in the Pacific and 1,557 km<sup>2</sup> in the Gulf. Habitat abundance through time showed distinctly different patterns between the Pacific and Gulf (Figure 3). Habitat area varied by region in the Pacific during postglacial sea level rise. For example, total habitat area in southern California (Morro Bay to San Diego) peaked 12–9 kya at ~436 km<sup>2</sup> (consistent with Masters, 2003, 2006), Bahía Vizcaíno peaked in size ~15 kya (2,815 km<sup>2</sup>) and San Francisco Bay peaked ~7 kya (3,242 km<sup>2</sup>; consistent with Atwater, 1979; Malamud-Roam, Lynn Ingram, Hughes, & Florsheim, 2006; Malamud-Roam, Dettinger, Ingram, Hughes, & Florsheim, 2007). By contrast, habitat area in the Gulf was simply reduced at lowstand and increased nearly exponentially between 15 and 5 kya. We estimate total change in Gulf estuarine habitat area from 20 kya to 0 kya was 1,557 to 10,331 km<sup>2</sup>.

##### 3.1.2 | Refugia

Generally, coastlines with broader shelves had larger refugia at lowstand (mean = 409 km<sup>2</sup>, range = 44–1228 km<sup>2</sup>) than areas with narrower shelves (mean = 35 km<sup>2</sup>, range = 25–53 km<sup>2</sup>; Figure S1, Tables S9, S10). Generalized linear models (GLMs) supported multiple refuge models ( $\alpha = 0.05$ ) in the Gulf. However, when we evaluated these significant models using genetic data in ABC (Table S3), it favoured a refuge model including Reforma, mid-eastern Gulf, Bahía Kino, northern Gulf, San Francisquito and Estero Zacatecas with all other populations recolonized (Figure S12; Table S7). The mid-eastern Gulf included three small, adjacent refugia that were grouped based on their proximity (“ME,” Figure 4). Of the Gulf refugia, two were large (Reforma: 147 km<sup>2</sup>, northern Gulf: 1228 km<sup>2</sup>) and four were small (mid-eastern Gulf: 44 km<sup>2</sup>, Kino: 57 km<sup>2</sup>, Francisquito: 28 km<sup>2</sup> and Zacatecas: 53 km<sup>2</sup>).



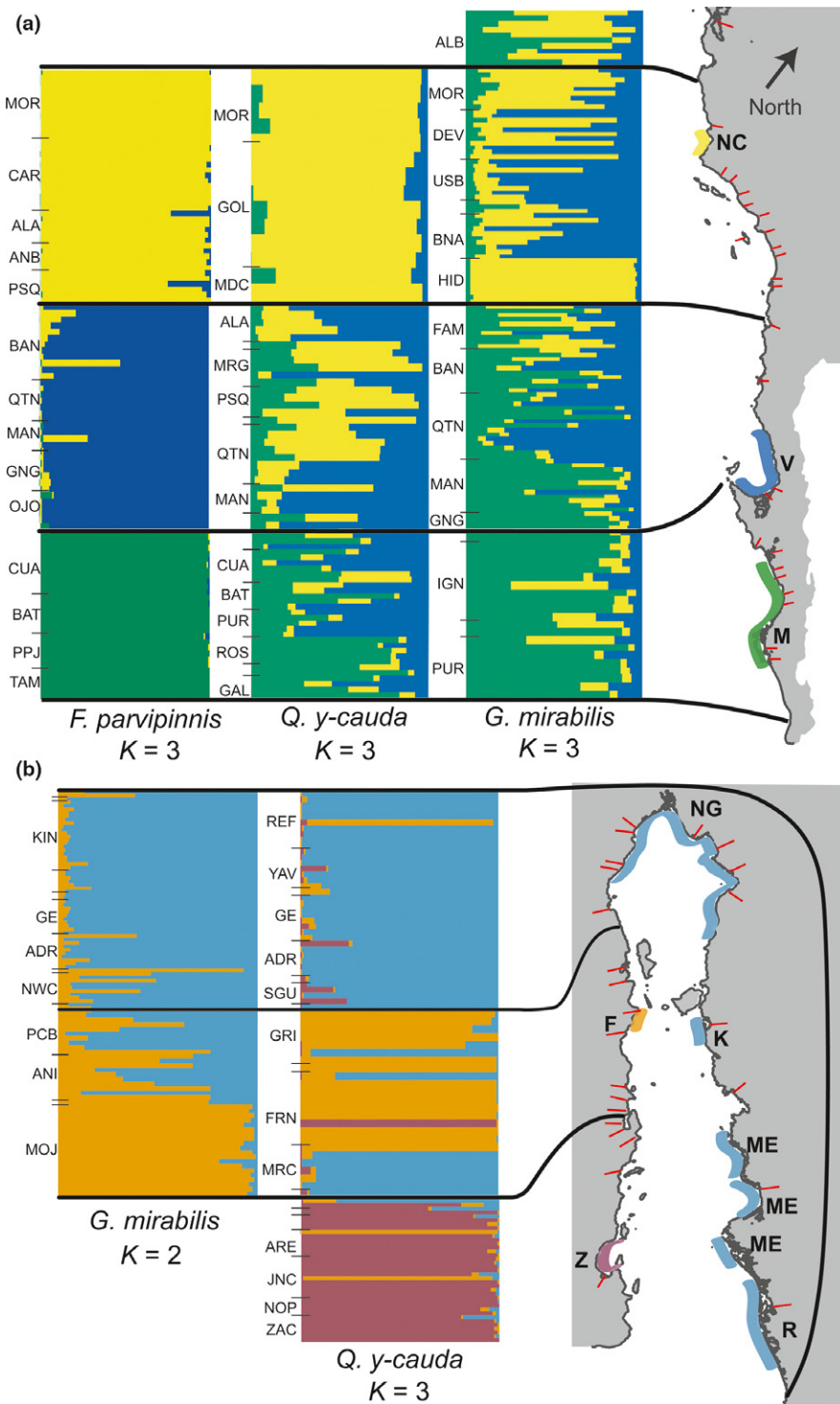
**FIGURE 3** Per-site habitat area, normalized by coastal region size for (a) Pacific sites and (b) Gulf sites. Sites are in coastal order (San Francisco Bay–Reforma) and area is in km<sup>2</sup>. This is a time series plot where habitat area is shown per time point, not a cumulative area plot. Time points are not evenly spaced because the rate of postglacial sea level rise was not uniform

In the Pacific, a GLM classified Bahía Magdalena (south of Punta Eugenia), Bahía Vizcaíno and North Conception as refugia ( $p = .04$ ), with all other regions classified as nonrefugia. Two of these three refugia were large (Bahía Magdalena refugium, 462 km<sup>2</sup>, and Vizcaíno refugium, 519 km<sup>2</sup>) and one was small (North Conception refugium, 25 km<sup>2</sup>). San Francisco Bay estuary (SFB) was not supported as a refugium ( $p = .07$ ). Also, meltwater draining the Sierra Nevada glaciers into SFB probably precluded inhabitants requiring warmer estuarine conditions because those high-volume meltwater flows would have been cold.

#### 3.2 | Genetic population structure and history

##### 3.2.1 | Regional patterns

Range-wide  $F_{ST}$  values from microsatellite data were lower between the Pacific and Gulf populations of *Q. γ-cauda* and *G. mirabilis* than intra-Pacific or intra-Gulf populations (Table S5). Reduced  $F_{ST}$  values were observed for *F. parvipinnis* populations across Punta Eugenia on the Pacific coast (Table S5), which was a previously identified biogeographic break (Bernardi & Talley, 2000) reflecting the subspecies designation (Miller & Hubbs, 1954) between *F. p. parvipinnis* (north) and *F. p. brevis* (south). Most pairwise  $F_{ST}$  values were statistically significant (despite being low values, Table S5), probably a



**FIGURE 4** Structure results with corresponding geographic refugia colour-coordinated. Red ticks mark collection locations for fish samples (Table S1). Thick black lines mark coastal locations, and thin black lines are population delimitations. Populations are labelled where possible; a full listing of populations is available in Figure S6. (a) Pacific individuals ordered north to south. (b) Gulf individuals ordered Z (bottom) to R (top). Refugia labelled are as follows: NC—North Conception, V—Vizcaíno, M—Magdalena, Z—Zacatecas, F—Francisquito, NG—northern Gulf, K—Kino, ME—mid-eastern Gulf, R—Reforma. Mean population sample sizes are 8 (range 5–14), 5 (range 1–12), 8 (range 1–20) for *F. parvipinnis*, *G. mirabilis* and *Q. y-cauda*, respectively

result of high allelic diversity, which biases  $F_{ST}$  values to be lower even when populations are completely differentiated (Jost, 2008; Meirmans & Hedrick, 2010)

Mean allelic richness for populations of the three species was as follows: *F. parvipinnis* (mean = 4.8), *Q. y-cauda* (mean = 2.5) and *G. mirabilis* (mean = 2.4), and was higher on broad coasts than steep coasts ( $p = .0034$ ) and higher south of Punta Eugenia than north of it ( $p = .001$ ), according to linear mixed models where the species was

treated as a random effect. In this model, inferred admixture history was not a significant variable. Based on Fisher's exact test (Table S6), *F. parvipinnis* appeared to be more differentiated than *Q. y-cauda* and *G. mirabilis*. All three species exhibited significant ( $p = .001$ ) isolation-by-distance patterns via Mantel tests. However, two-dimensional kernel density plots suggested the significant isolation-by-distance pattern was probably driven by geographically distant divergent populations rather than a steady cline in genetic mixing (Figure S15).



### 3.2.2 | Population structure

Pacific coast populations favoured  $K = 3$  for *F. parvipinnis* ( $\Delta K = 2,069$ ), *Q. y-cauda* ( $\Delta K = 28$ ) and *G. mirabilis* ( $\Delta K = 20$ ). In the Gulf,  $K = 3$  was favoured for *Q. y-cauda* ( $\Delta K = 707$ ), whereas  $K = 2$  was favoured for *G. mirabilis* ( $\Delta K = 357$ ). Favoured  $K$ s were identical to the number of refugia expected from the paleohabitat modelling for the Pacific (Figure 4), whereas the favoured  $K$ s in the Gulf were fewer than the number of refugia predicted by the paleohabitat models. Possible explanations include the following: (i) that the northern and eastern Gulf refugia were not isolated genetically at lowstand due to close proximity or large size, (ii) that there has been effective genetic mixing following isolation, or (iii) the habitat models overestimate the number of habitats in the Gulf and populations were similar because they were sourced from fewer refugia than predicted. This third scenario appears unlikely, as there is no cline in genetic diversity among populations as expected from postglacial expansion (Figure S8, Table S6). Scenarios one and two may both be a function of closer interestuarine distance, but are difficult to distinguish at this point. The expected number of Gulf refugia for *G. mirabilis* is one fewer than for *Q. y-cauda* because the present distribution of *G. mirabilis* does not extend south of Bahía Concepción on the western Gulf coast—this would eliminate its presence from the Zacatecas refugium (Figure 4B), which is consistent with the favouring of  $K = 2$  for *G. mirabilis* and  $K = 3$  for *Q. y-cauda*.

### 3.2.3 | Approximate Bayesian computation

To integrate the paleohabitat models with population genetic data, we performed ABC on competing historical scenarios for Gulf and Pacific populations separately. Nearly all tests favoured the paleohabitat-defined scenarios over alternatives (Figures 5, S9–S14; Table S7). For both the Pacific and Gulf analyses, ABC favoured the paleohabitat-supported scenarios over alternative paleohabitat scenarios (Figure 5B) or alternative phylogeographic scenarios such as isolation by distance and paleo-seaways (Figure 5C). This was true for Pacific analyses (posteriors = 0.94–1.00, PPE = 0.09–0.11) and Gulf analyses (posterior = 0.86–0.98, PPE = 0.08–0.28). The exception was for *G. mirabilis* Pacific analyses, which favoured a modified paleohabitat scenario where one of the GIS-predicted refugia (Vizcaíno) was postglacially admixed instead of being isolated. *Gillichthys mirabilis* may be more dispersive than the other species, particularly via the north-flowing Davidson current, and thus experienced mixing from southerly populations (Figure 4A), resulting in Vizcaíno presenting as a genetically mixed population. For *G. mirabilis*, we also tested whether San Francisco Bay was a refugium or postglacially recolonized—the latter was greatly favoured (posterior = 0.99, PPE = 0.17; Figure S10; Table S7).

Generally, the number of alleles, genetic diversity, allele size range and  $F_{ST}$  exhibited good model fit across runs. Mean Garza–Williamson's  $M$  was often lower in simulations than observed data; an excess of private or low-frequency alleles in our species due to isolation in individual estuaries could account for this. Classification

index (LIK) results varied between runs because favoured scenarios exhibited more congruent LIK values between observed and simulated data than did less supported scenarios. Model fit for Pacific scenarios of *G. mirabilis* and *F. parvipinnis* was worse than the others (Figure S14), suggesting that the true model may not have been among those tested or that those data were influenced by additional factors. Our study systems are complex and may be subject to additional evolutionary processes such as present-day gene flow and historical changes in population size that are not included in our models, but could affect model fit. We assumed constant and equal populations sizes, which could be unrealistic given the inferred postglacial habitat expansion, and we assume lowstand habitats are fully isolated, when some limited gene flow might have occurred.

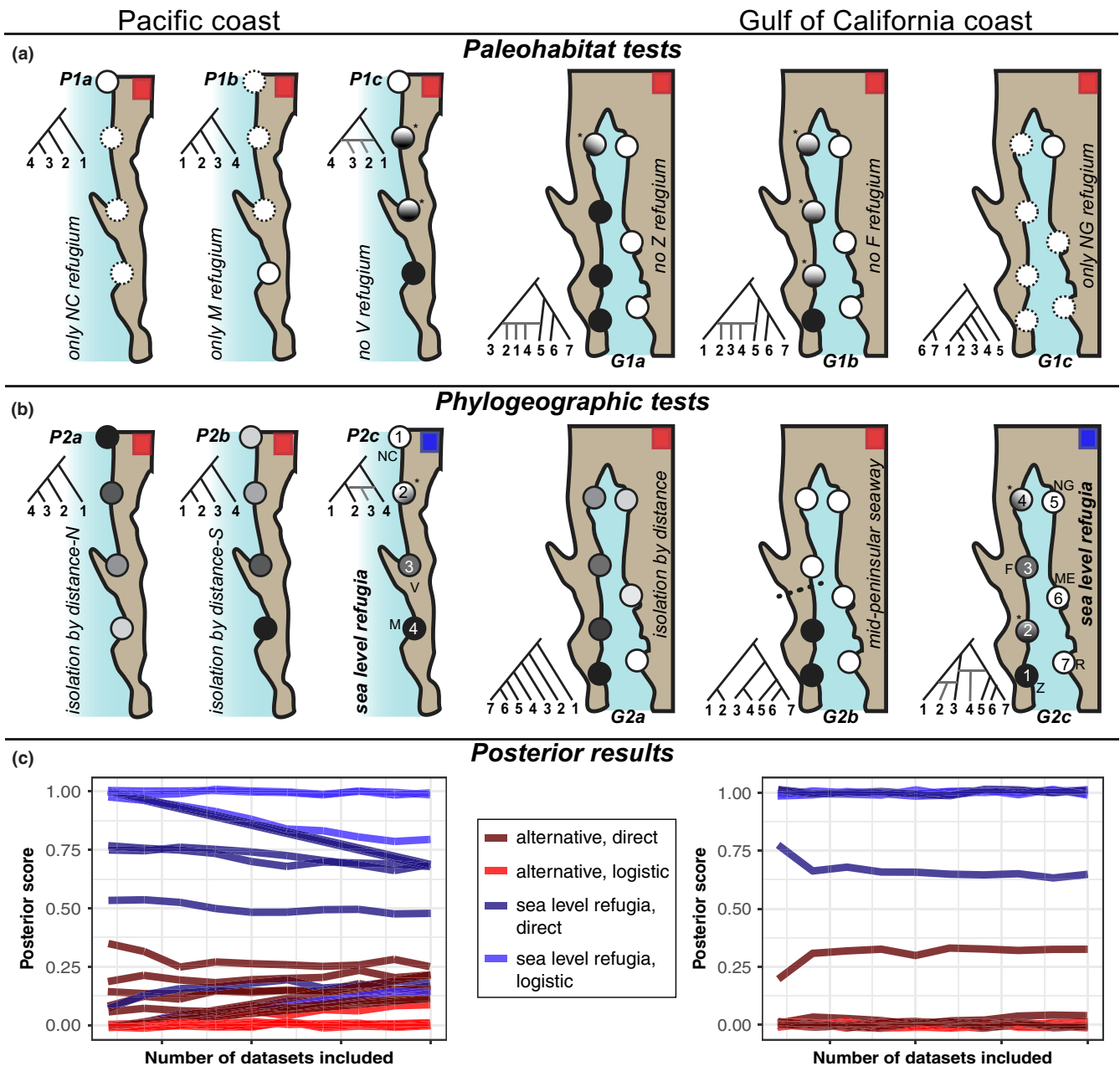
## 4 | DISCUSSION

We assessed the role of sea level driven refugia and postglacial sea level rise in generating population structure in coastal estuarine fishes. To do this, we employed range-wide paleohabitat modelling and genetic analyses of three tidal estuarine fishes from San Francisco Bay, California to Reforma, Sinaloa (Figure 1)—a coastal distance of ~4,600 km and 15 degrees of latitude (23–38°N). We evaluated how geologic processes shaped continental shelf topography (Figure 2) and tested how variable shelf morphologies affect the size and distribution of refugia (Figure 3) and genetic signatures of their inhabitants (Figure 4). Overall, we find statistically significant concordance between our habitat models and genetic analyses, which show a dramatic 83% reduction in estuarine habitat area at sea level lowstand relative to today (Figure 3). The number and location of modern-day genetic clades (Figure 4) geographically coincide with the refugia identified in the paleohabitat models, though not all inferred refugia produced genetically distinct populations. Paleohabitat models explain population genetic structure better than alternative refugial scenarios and better than previously suggested hypotheses of isolation by distance and seaways (Figure 5). Finally, we find that tectonically steepened (narrow) shelves host fewer, smaller and more genetically isolated refugia than broad shelves (Figures 2, 4, S1; Tables S8, S9) and populations along steep coasts have lower allelic richness, perhaps due to repeated extirpations and lower habitat availability. Because other types of coastal habitats are distributed discontinuously and form under certain geomorphic settings, as estuaries do, we suggest that this sea level model is applicable to a range of other coastal habitats (e.g., Papadopolou & Knowles, 2017; Waltari & Hickerson, 2013).

### 4.1 | Physical controls on nearshore geomorphology

#### 4.1.1 | Pacific coast

The subtropical eastern Pacific and Gulf have different tectonic histories leading to different continental shelf morphologies. Much of



**FIGURE 5** Schematic depicting (a) paleohabitat scenarios and (b) phylogeographic scenarios tested in ABC models. Scenarios P2c and G2c (favoured refugial scenarios) were also run in Panel a (paleohabitat tests) and were the favoured scenarios but they are not shown in Panel a due to space constraints. The colour of dots represents genetic identity. A gradient filled circle and asterisk represent admixture and a dotted circle represents recolonization from a single source (i.e., simple range expansion). Population trees symbolize the parameterized topology for each scenario; grey branches represent admixture events. Note some scenarios cannot be differentiated based on topology (e.g., P1a and P2a) because of the population configuration. The population numbers and refugium labels in P2c and G2c apply to each scenario, and the labels correspond to Figure 4. (c) The ABC results parameterized with our sea level refugia models are shown in blue, and alternative scenarios are in red. The “blue” result with low support in the Pacific graph is the paleohabitat-defined (i.e., unmodified) refuge scenarios for *G. mirabilis* (see results)

the Pacific coast has recent or active tectonic processes. Late Quaternary uplift rates up to 2 mm/year (Muhs et al., 1992; Niemi et al., 2008) have contributed to steepness locally in southern California, and nearshore transform faults delineate a narrow shelf along the Pacific coast in many places. For example, the San Clemente-San Isidro transform fault (Dickinson & Butler, 1998) limits the continental

shelf along northwestern Baja California, and the San Bruno, San Andreas and Hosgri-San Gregorio faults delimit the shelf in the San Francisco Bay area (Figure 1; Clifton, Hunter, & Gardner, 1988). In contrast, the Tosco-Abrejos transform fault delimiting the edge of the shelf south of Pt. Eugenia is farther offshore (Spencer & Normack, 1979) than those north (Dickinson & Butler, 1998; Michaud

et al., 2007; Plattner, Malservisi, & Govers, 2009). Consequently, the continental shelf is broad from Bahía Vizcaíno region southward and narrow in northwestern Baja California and southern/central California.

#### 4.1.2 | Gulf of California coast

The Gulf has steep nearshore bathymetry in the west (the peninsula) and broader, lower-gradient bathymetry in the east (mainland Mexico). Several factors account for this gradient asymmetry. The steepness of the Gulf's peninsular coast is largely associated with active tectonics. The axis of rifting shifted from the eastern to western Gulf (Aragón-Arreola & Martín-Barajas, 2007; Bennett, Oskin, & Iriondo, 2017) about 3 Mya (Stock, 2000), making rift-related vertical tectonic movement more recent in the western Gulf and steepening the eastern escarpment of the Baja California peninsula (Mark, Gupta, Carter, Mark, & Gautheron, 2014). The eastern Gulf became an incipient passive margin when the rifting axis moved west. Peninsula-sourced sediment supply and fluvial erosion are also more limited in the western Gulf due to aridity and smaller catchments on the peninsula that drain mostly to the Pacific from the narrow, west-tilted peninsula. The mainland (eastern) coast receives a greater sediment supply from rivers draining the Sierra Madre Occidental mountains aided by summer monsoon-associated precipitation (Nava-Sánchez, Gorsline, & Molina-Cruz, 2001). In the northern Gulf, ancient Colorado River sediment discharge contributed to deltaic formation and low-gradient nearshore topography (Brusca, Álvarez-Borrego, Hastings, & Findley, 2017; Carriquiry & Sanchez, 1999). In summary, active tectonics and limited sediment supply in the western Gulf maintain a steeper nearshore topography than in the eastern Gulf.

#### 4.2 | Shelf geomorphology and habitat patterns

According to our habitat models, steeper coasts host fewer, smaller estuarine refugia than broad coasts. Many of these narrow coastlines remain too steep to form estuaries today; they instead host rocky-shore intertidal and reef habitats (Bernardi, 2000; Dawson, 2001; Dawson et al., 2002; Hendrickx, Brusca, & Reséndiz, 2014). STRUCTURE results (Figure 4) show that refugia along steep coastlines generate distinct groups more often than refugia along broad coasts (Figure 4, Tables S8, S9). Populations along broad coasts have higher allelic richness and broad-coast refugia probably had greater genetic connectivity during lowstand due to larger size, greater proximity and/or greater openness to the ocean (Spies & Steele, 2016), which can facilitate connectivity.

#### 4.3 | Pacific coast refugia and genetics

Our habitat models predicted three estuarine refugia during lowstand along ~2,100 km of northeastern Pacific coastline, which correspond in number and geographic location to the three genetic groups for each species (Figure 4). All present-day estuaries south of

Punta Eugenia fall within the predicted Bahía Magdalena refugium, which show significantly higher mean allelic richness than populations northward. Populations south of Punta Eugenia also lack differentiation (Figure S6, Tables S5, S6), supporting the notion of Bahía Magdalena as a large, stable refugium.

Our habitat models suggest that aside from the Vizcaíno and N. Concepcion refugia, all populations north of Punta Eugenia were extirpated at lowstand and recolonized as habitat re-formed during postglacial sea level rise. Results from ABC tests confirm that this scenario is favoured in the genetic data over alternate refuge scenarios and isolation by distance (Figure 5). There are some interspecific differences in the level of genetic mixing between genetic groups (Figure 4A), which can be attributed to differences in freshwater tolerance (Griffith, 1974; Rao, 1974), dissolved oxygen tolerance (Courtois, 1976b) or life history characteristics; for example, *F. parvipinnis* adheres its eggs to substrates, which may reduce larval migration (Fritz, 1975; Williams & Brown, 2008).

#### 4.3.1 | San Francisco Bay

*Gillichthys mirabilis* is our only study species that occurs in SFB. The northern range limit for *F. parvipinnis* and *Q. y-cauda* is in Morro Bay, north of Point Conception. Our habitat models suggest that SFB was not a refugium, consistent with previous work (Atwater, 1979; Malamud-Roam et al., 2006, 2007), which indicates that SFB estuary only reached its modern extent ~6 kya. STRUCTURE results (Figure 4) and tree reconstructions (Figures S4, S5) support lowstand extirpation of SFB because those individuals are not genetically differentiated as expected if they persisted in isolation during the LGM. Moreover, ABC analyses unequivocally support extirpation and recolonization scenarios from the other three Pacific refugia for SFB. Surprisingly, recolonizations of SFB appear to have come from up to 1,800 km to the south, a region downstream of the south-flowing California Current. The strength of this current may have changed since the LGM (Kennett & Kennett, 2000). A weakened California Current or strengthened north-flowing Davidson counter-current could have facilitated northward colonization, as can occur during modern El Niño (ENSO) events (Byrne, Bernardi, & Avise, 2013; Goddard, Gosliner, & Pearse, 2011; Johnson et al., 2009; Lea & Rosenblatt, 2000; Zacherl, Gaines, & Lonhart, 2003). The waters of SFB are warmer than nearshore waters at the same latitude (Conomos, 1979) and could probably sustain warmer-adapted species after colonization.

Colonization of SFB via anthropogenic transfers of *G. mirabilis* used as live bait is unlikely because bait use postdates (Turner & Sexsmith, 1967) the documentation of *G. mirabilis* as human food in the 19th century (Lockington, 1877; Love, 2012), and because *G. mirabilis* was generally only used as bait for recreational fishing in southern California and inland freshwater fishing (Miller, 1952; Turner & Sexsmith, 1967).

Extralimital populations, such as *G. mirabilis* in SFB, are often sinks in which genetic diversity is "imported" from the rest of a species' range through metapopulation dynamics. If our inferences are

correct, then during consecutive glacial cycles SFB populations may have been extirpated repeatedly and act as genetic sinks over evolutionary time despite repeated recolonizations. However, if coastal sea-surface temperatures increase under anthropogenic climate change and species accommodate this increase by shifting ranges northward (e.g., Ficke, Myrick, & Hansen, 2007; McFarlane, King, & Beamish, 2000; Roessig, Woodley, Cech, & Hansen, 2004), then in the next few centuries, the SFB population may become part of the contiguous range and no longer be a genetic sink.

#### 4.4 | Gulf coast refugia and genetics

*Quietula y-cauda* and *Gillichthys mirabilis* inhabit steeper estuaries in the Gulf than the Pacific (Table S2), and within the Gulf, the habitats are significantly steeper on the western side than eastern side. Our paleohabitat models suggest that Gulf habitat area was reduced by 85% at the LGM lowstand relative to today (Figure 3B). Increasing habitat area between ~15 and 5 kya appears to be nearly exponential and driven primarily by the large northern and eastern habitats. This habitat increase occurred later in the Gulf than the Pacific (~12 kya vs. ~8 kya), probably the result of different shelf geomorphologies (Figure 2).

A combination of paleohabitat models and ABC analyses favour a model with two western refugia (Francisquito and Zacatecas), a northern Gulf refugium and three eastern refugia (Figure 5). The two western refugia were small and produced genetically distinct populations (Figure 4B); the northern and eastern refugia appear to have maintained genetic connectivity, perhaps because they were larger, more numerous and more geographically proximate, which would be facilitated by the broader, tectonically passive shelf in this region (Figure 2).

The physical footprint of the Gulf decreased at lowstand, bringing eastern and western coastal populations closer (Deng & Hazel, 2010). At the latitude of Isla Tiburón, trans-Gulf populations are separated by only ~70 km at lowstand relative to 100 km at present. Proximity, potentially also aided by seasonal gyre circulation in this region (Marinone, 2003; Soria et al., 2014), may have facilitated trans-Gulf migration.

#### 4.5 | Theoretical framework for sea level refugia

We propose the following framework to explain how physical processes control coastal habitat distribution and genetic connectivity through time. Tectonic processes such as rifting, uplift and faulting, in combination with wave erosion and sediment supply, shape the regional geomorphology and coastlines of tectonically active margins. These processes largely determine grade (steepness) and width of the continental shelf, which dictate where estuaries (and likely other coastal habitats) can form (Jacobs et al., 2011). Sea level oscillations over this heterogeneous shelf topography during glacial cycles alternatively eliminate and re-form estuarine habitat. Consequently, biological populations exhibit genetically distinct clades resulting from isolation in lowstand refugia, as well as genetically admixed,

intervening populations recolonized from adjacent refugia. Less tectonically active or broader coasts tend to have larger and/or more genetically interconnected refugia, whereas refugia on steeper coasts are fewer in number, smaller and more genetically isolated. Glacially mediated isolation–admixture patterns are commonly observed in phylogeography (Hewitt, 2000, 2004). This scenario differs in that sea level change is a global phenomenon of relatively equal magnitude and may therefore contribute to extirpation–isolation–recolonization processes in coastal species globally. Furthermore, sea level change operates over longer timescales by other processes, such as large-scale tectonics and changes in global, not just Northern Hemisphere, ice volume (Miller, 2005). Therefore, a sea level mechanism could also diversify coastal taxa over deeper geologic timescales.

#### 4.6 | Application to other habitats

Many phylogeographic studies within the Gulf have focused on rocky intertidal (Deng & Hazel, 2010; Hurtado, Frey, Gaube, Pfeiler, & Markow, 2007; Hurtado et al., 2010), rocky shore (Riginos, 2005; Riginos & Nachman, 2001), sandy substrate (Byrne et al., 2013; Hurtado et al., 2013; de Jesús Suárez-Moo et al., 2013), reef (Lin, Sánchez-Ortiz, & Hastings, 2009) and offshore pelagic (Segura, Rocha-Olivares, Flores-Ramírez, & Rojas-Bracho, 2006) species. As with estuaries, these other habitats are discontinuously distributed along coastlines (Riginos & Nachman, 2001). While the location of lowstand refugia would differ by habitat type, patterns of extirpation–recolonization, as revealed here with estuaries, should be applicable to these other habitat types as well. For example, rocky intertidal/reef habitat is common on the western side of the Gulf and less abundant on the eastern side—the opposite pattern observed for estuarine habitat (Hendrickx, Brusca, Cordero, & Ramírez, 2007). Lowstand refugia for rocky-shore associated species may therefore have been commonplace in the western Gulf and less so in the eastern Gulf—again, opposite to our results for estuaries. By influencing population connectivity, over repeated glaciations sea level refugia may have substantially contributed to the phylogeographic patterns observed in the studies referenced above.

#### 4.7 | Incipient speciation

We find differentiation between Pacific and Gulf populations of *Quietula y-cauda* and *Gillichthys mirabilis* (Figure S7), inferred from reduced  $F_{ST}$  values (Table S5) and reciprocal monophyly in microsatellite tree topologies (Figure S4). Bernardi et al. (2003) previously documented incipient speciation in eight rocky-shore fish species with similar distributions (but see Simison, 2005; Bernardi, 2014). They hypothesized that the warm waters of interglacial periods limited migration around the tip of the peninsula. Our results reveal similar levels of differentiation between Pacific and Gulf populations as previously observed (Bernardi, 2014; Bernardi et al., 2003; Maldonado, Davila, Stewart, Geffen, & Wayne, 1995; Terry et al., 2000), but we suggest that isolation in sea level refugia also

contributed to this differentiation. Lowstand isolation may be particularly important in species absent from the southwestern Gulf, such as *G. mirabilis*. Differences in tidal regimes and temperature variability (Álvarez-Borrego, 2011; Argote, Amador, Lavín, & Hunter, 1995; Bustos-Serrano & Castro-Valdez, 2006; Bustos-Serrano, Millan-Núñez, & Cajal-Medrano, 1996; Ellingson, 2012), mangrove distributions (Aburto-Oropeza et al., 2008; Whitmore et al., 2005), seasonal upwelling (Juillet-Leclerc & Schrader, 1987; Lluch-Cota, 2000; Zeitzschel, 1969) and faunal distributions (Briggs & Bowen, 2012; Hastings, 2000) between the Pacific and the Gulf also probably subject populations to different selection pressures (Littler & Littler, 1981). Consequently, differential ecological adaptation may have occurred during lowstand isolation if population connectivity was low as our results suggest.

## 5 | CONCLUSION

We performed range-wide paleohabitat modelling of tidal estuaries and comparative population genetic assessments of three codistributed estuarine fishes over ~4,600 km of coastline to assess population connectivity over the past ~20 kyrs. We suggest the proximate mechanism controlling estuarine habitat connectivity over time is the interaction of changing sea level with regionally variable continental shelf topography. The ultimate mechanism underlying estuarine habitat distribution through time, and thus genetic population structure in part, is the combination of tectonic and sediment processes that shape the shelf topography itself. This framework may be operating along other coastal habitats globally and be a significant driver of genetic diversification and population structure during Pleistocene (and earlier) sea level changes. Our sea level habitat models explained modern-day genetic patterns better than alternative scenarios that included isolation by distance and seaways, and our results have potentially broad explanatory power for phylogeographic patterns of species from other habitat types across this region and elsewhere.

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## DATA ACCESSIBILITY

Mitochondrial DNA sequences are available at NCBI GenBank (KY484184–KY464476, *cytB*; KY464477–KY464835, *mtCR*; Table S10). All data are available via Dryad (<https://doi.org/10.5061/dryad.gm1td>). Sampling information is in the Supporting Information.

Genbank accession numbers used for *Fundulus sciadicus* are EU182727.1, EU182728.1, EU182729.1.

## AUTHOR CONTRIBUTIONS

G.A.D. and D.K.J. conceived of this study with input from LTF. G.A.D. collected data and R.A.E. contributed data. G.A.D. and D.K.J. analysed and interpreted results. G.A.D. drafted the manuscript; all authors critically revised the manuscript and gave approval for publication.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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