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SYNTHESIS

Revealing genetic patterns across ecoregions in the northeastern Pacific of California and Baja California

Mariana Ronalda Ferrera-Rodríguez[1] | **Luis Malpica-Cruz**[2,3] | **Adrián Munguía-Vega**[4,5] | **Rodrigo Beas-Luna**[1] | **Ana Laura Flores-Morales**[1] | **Alicia Abadía-Cardoso**[1]

[1]Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico

[2]Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico

[3]ECOCIMATI, A.C., Ensenada, Baja California, Mexico

[4]Conservation Genetics Laboratory, The University of Arizona, Tucson, Arizona, USA

[5]Applied Genomics Lab, La Paz, Mexico

Correspondence
Luis Malpica-Cruz, Universidad Autónoma de Baja California, Instituto de Investigaciones Oceanológicas, Carretera Tijuana-Ensenada Km 103, Pedregal Playitas, Ensenada, BC, Mexico.
Email: lmalpica@uabc.edu.mx

Alicia Abadía-Cardoso, Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico.
Email: aabadia@uabc.edu.mx

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Abstract

Aim: We reconstructed the genetic patterns and identified the main genetic breaks of several taxa across California and Baja California coast. Additionally, we evaluated the contribution of different variables to the level of structure.

Location: California and Baja California coast.

Taxon: Fish, invertebrates, algae, seagrass and mammals.

Methods: We generated a map to reconstruct the genetic patterns using genetic information (Fst index and phylogenetic clades distribution) from a literature review of population genetics publications from 2000 to 2023. For the analysis of genetic connectivity drivers, we explored the effect of different variables representing life history traits, reproductive strategies and biogeographic variables and generated five working hypotheses which were evaluated with generalized linear models (GLMs).

Results: We identified 42 genetic breaks from 63 species across our study area. The largest number of breaks occurs from 27° N to 29° N and from 31° N to 35° N. This range includes transition zones between ecoregions such as Punta Eugenia, Baja California, Mexico and Point Conception, California, USA. We also identified Ensenada, Baja California region as a barrier to gene flow. From a transboundary perspective, we found 40 species with connectivity between California and Baja California, including 14 commercial and or recreational species. We found none of the variables explored had a clear effect on the level of genetic differentiation of the species assessed in the region.

Main Conclusion: Genetic breaks among different taxa do not distribute randomly across the latitudinal range from California and Baja California coastal area, rather they are mainly located in transition zones between marine ecoregions. The challenge to identify specific variables that explain general genetic patterns highlights the complexity that drives population connectivity processes in marine species.

KEYWORDS
biogeography, California current, genetic structure, marine ecoregions, Northeast Pacific, transboundary management

1 | INTRODUCTION

Genetic connectivity is defined as the exchange of individuals between populations, which results in gene flow and alters species' population and evolutionary dynamics (Lowe & Allendorf, 2010; Palumbi, 2003). The movement of individuals between populations favours population growth rate, gene flow and species persistence throughout adverse environmental conditions (Cowen & Sponaugle, 2009). In the marine environment, the interaction between biological, environmental factors and the oceanographic process generates different patterns of connectivity, which can range from populations with high connectivity and no genetic differentiation to isolated populations from each other, with high genetic differences (Díaz-Jaimes et al., 2010; Horne et al., 2008). The study of connectivity links ecological and evolutionary aspects, such as dispersal and migration, source and sink dynamics and population genetic structure (Selkoe et al., 2016). Thus, understanding species and population connectivity levels can contribute to the design of protected areas, invasive species control and management of transboundary species (Kool et al., 2012). Also, from a management perspective, the study of connectivity can be used to inform the identification of isolated populations of endangered species, delimitation of stocks and management units and evaluation of the impact on the exploitation of a resource (Pante et al., 2015).

Connectivity is driven by specific processes and scales. For example, in terrestrial environments, processes occur in two dimensions, whereas in marine environments, depth adds a third dimension (Waits et al., 2015). Additionally, the presence of physical barriers (e.g. mountains, rivers, seas) is frequently identified as a factor that promotes or limits connectivity in terrestrial environments. On the other hand, in marine environments, other barriers such as physical gradients (e.g. temperature, salinity), oceanographic processes (e.g. convergent currents, water masses boundaries and eddies) and habitat heterogeneity are identified as barriers (Gottscho, 2016; Pelc et al., 2009).

Particularly, connectivity in marine species is regulated by intrinsic and extrinsic factors. Intrinsic factors include species' life history aspects, such as dispersal potential, variable reproductive strategies and adult behaviour (sessile, pelagic). Extrinsic factors are related to the environment, including habitat heterogeneity, salinity, marine currents, geographic distance and biogeographic processes. The interaction between intrinsic and extrinsic factors differs among species, as well as the relevance of the variables that regulate connectivity, which leads to diversity in the patterns identified (Hernawan et al., 2021; Selkoe et al., 2010). For example, pelagic phase dynamics in some marine species, such as larval dispersal, larval transport and reproductive connectivity, promote connectivity among populations (Pineda et al., 2007). Also, juvenile, and adult movements can influence connectivity processes, particularly during reproductive migrations and when species use different habitats between developmental stages (Green et al., 2015). Therefore, it is important to consider the life history of species to understand connectivity patterns.

In recent years, the advancement in genetic tools and the incorporation of biophysical models into population studies have challenged the *open population hypothesis* that describes no genetic structure due to the lack of barriers in the marine environment and the large population sizes (Cowen et al., 2000). This new genetic+biophysical approach has revealed that processes, such as local recruitment, lead to a fine genetic structure among marine populations (Benestan et al., 2015; Mertens et al., 2018; Silva et al., 2019; Soria et al., 2012; Zhang et al., 2020).

Low connectivity between populations could result in allele fixation over time and, ultimately, in changes in allele frequencies that will create genetic breaks (Hellberg et al., 2002; Lowe et al., 2017). If these breaks occur across multiple species and regions, they may be regulated by the same barrier or process (Villamor et al., 2014). Barriers to gene flow may include strong gradients in oceanographic processes or habitat heterogeneity to different extents (Sá-Pinto et al., 2012).

On a broader time scale, several historical events have shaped connectivity patterns. For example, the final closure of the Tethys seaway (Terminal Tethyan Event) in the mid-Miocene (~16 Ma) resulted in vicariant diversification for several marine taxa (e.g. intertidal crustaceans, coral reef fishes, gastropods) (Liu et al., 2018). Likewise, the closure of the Panama Isthmus (3.1 Ma) promoted vicariance diversification as seen in several sister taxa of invertebrates and fish (Cowman & Bellwood, 2013). Besides vicariance by a physical barrier (e.g. formation of land bridges), divergence events may also occur in response to soft barriers (e.g. hydrological processes) such as those observed on reef fish families Labridae, Pomacentridae and Chaetodontidae (Cowman & Bellwood, 2013). For the Northeast Pacific region, the Baja California Peninsula rifting and formation of the Gulf of California (~5.5 Ma) promoted new habitat, disjunct distributions and divergence between north and south populations of the peninsula both for marine and terrestrial species (Bernardi, 2014; Dolby et al., 2015; Riginos, 2005). In conjunction, global climate events triggered drastic changes in marine habitats, species distribution and local adaptation. Transition to a cool and upwelling regime, during the middle Miocene, established highly productive and diverse ecosystems. A second major shift occurred during the Pleistocene with global glacial and interglacial periods where major sea level changes reduced extensive bays and estuarine habitats and enhanced rocky shore environments (Jacobs et al., 2004).

Species distribution patterns determine biogeographic regions (realms, provinces and ecoregions) at different spatial scales (Briggs & Bowen, 2012; Spalding et al., 2007). These patterns are driven by several factors, such as water temperature, historical and broad-scale isolation, geomorphology and hydrographic features (Briggs & Bowen, 2012; Spalding et al., 2007). Transition areas between biogeographic regions frequently promote reduction of gene flow resulting in genetic breaks between species populations features (Gottscho, 2016).

Genetic connectivity studies in the California and Baja California region integrate different aspects. On a geological scale, Gottscho (2016) relates tectonic processes to the location of biogeographic zones and Kelly and Palumbi (2010) highlight the effect of Cape Mendocino as a genetic barrier for intertidal invertebrates. On the other hand, Pelc et al. (2009) addressed the effect of biological traits and connectivity and reported a different response to oceanographic and coastal topography between high and restricted dispersal species. Meanwhile, Riginos et al. (2011) showed that biological traits, such as egg type and extrinsic factors as biogeographic transitions, drive the genetic structure of coastal fish. Given the high heterogeneity of the region, assessing the processes that influence the level of population connectivity is warranted, particularly to establish effective conservation and sustainable resource management strategies. In this work, we analysed genetic patterns of multiple taxonomic groups in coastal ecosystems between California and Baja California. To do this, we used phylogenetic trees and the Fst fixation index, a widely used measurement based on the variation of allele frequencies that describes populations in terms of genetic differentiation (Hedgecock et al., 2007). Although the Fst index is widely used, most analyses of genetic structure have focused on one or a few species, thus, the description and comparison between regions have been less studied. We focused our analyses on three objectives: (1) to identify barriers to gene flow and their relationship with marine ecoregions, (2) to evaluate the contribution of different variables to the level of genetic differentiation in different species and (3) to integrate genetic patterns with environmental characteristics of the region.

2 | MATERIALS AND METHODS

2.1 | Study area

The coastal region of California and the Baja California peninsula is located between 42° N and 22.7° N. It belongs to the California Current ecosystem, characterized by high productivity and species richness due to current and upwelling patterns. This system is formed by a surface current (0–200 m) of subarctic waters (10–20°C) with an equatorward direction and a countercurrent of subsurface equatorial waters (100–300 m) rich in nutrients (Durazo, 2015; Lluch-Belda et al., 2003).

The different characteristics of the water masses in the California and Baja California region and the interaction with the coastline generate transition areas and a particular biological dynamic (Durazo, 2015). According to the biogeographical classification, there are three ecoregions: Northern California, Southern California Bight and Magdalena Transition (Spalding et al., 2007) (Figure 1). The northernmost ecoregion (Northern California) spans from Cape Mendocino to north of Point Conception in California (40°–33° N), with cold waters and strong upwelling. Next, the Southern California Bight, runs from Point Conception to Punta Eugenia in Baja California (34.4°–26.3° N), with warmer waters and less intense upwelling. Finally, the Magdalena Transition extends from Punta Eugenia to the region of Los Cabos (26.7°–22.7° N), where temperate and tropical waters converge (Lluch-Belda et al., 2003; Spalding et al., 2007).

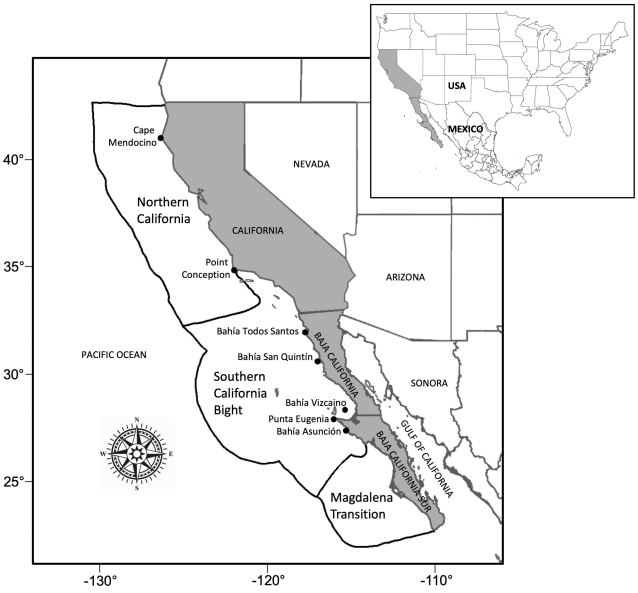

FIGURE 1 Marine ecoregions in California and Baja California: Northern California, Southern California Bight and Magdalena Transition. Points indicate the main biogeographic breaks and bays for species distribution: Cape Mendocino, Point Conception, Bahia Todos Santos, Bahía San Quintin, Bahía Vizcaino, Punta Eugenia and Bahia Asuncion.

2.2 | Literature review

We conducted an extensive literature search to evaluate the patterns of genetic structure along the coasts of California and Baja California. The review was limited to work conducted from 2000 to 2023 in different taxonomic groups (algae and seagrasses, invertebrates, fishes and marine mammals). We used three databases: Science Direct (Elsevier), SCOPUS (Elsevier) and Wiley Online Library with the following keywords: 'marine genetic connectivity', 'population structure' and 'population genetics' with the combination of words 'California', 'Northeast Pacific' and the taxonomic groups of fish, invertebrates, algae and mammals. We only considered research articles published in indexed journals and with at least one sampling site in California and one in Baja California, except modelling or in silico work in aquaculture systems. Basic information was extracted and condensed with the following data: study area (sampling sites and coordinates), species, molecular marker, genetic estimator value (Fst), location of genetic breaks and pattern of structure or connectivity described. A list of the data sources is found in the Supplementary Material S1.

2.3 | Geographic regions with genetic breaks

To identify biogeographic patterns, we constructed a map with the frequency and distribution of genetic breaks across California and Baja California. We define a genetic break as a significant discontinuity in the distribution of genetic diversity among populations in response to geological, ecological or oceanographic factors

(Narváez-Barandica et al., 2023; Rancilhac et al., 2022). Genetic breaks were identified based on three criteria. First, we used significant pairwise Fst values (a measure of genetic differentiation between populations); second, we looked for Fst values ≥0.05 (Kelly & Palumbi, 2010; Wright, 1978); and third, we used the monophyletic clades distribution from phylogenetic trees (the location gap between monophyletic clades).

Range distribution was marked by black polygons and genetic breaks by grey polygons. Spatial resolution was settled by one degree with the software QGIS (QGIS Development Team, 2022). A list of the data sources is found in the Supplementary Material S2.

We obtained a heatmap with genetic break frequency by taxonomic group to identify the latitudinal pattern of genetic breaks. We proved the hypothesis that genetic break patterns differ among taxonomic groups by applying a Fisher's test, using a frequency table with the number of species and genetic breaks (Sprent, 2011).

Also, we used chi-square tests to evaluate the frequency distributions of the breaks identified. We performed an independent test for each of the three criteria: (1) reciprocal monophyly, that aims to identify and spatially locate the genetic breaks; (2) pairwise significant Fst, that assesses how levels of genetic differentiation are distributed, including subtle differentiation; and (3) pairwise Fst >0.05 that focuses on identifying the distribution of stronger genetic structure (Dolby et al., 2015; Munguia-Vega, 2011). Analysis of each Fst category was based on the frequency distribution of Fst values. Reciprocal monophyly was based on breaks between clades on a latitudinal range from 24° N to 42° N with a resolution of 2°.

2.4 | Predictive variables of genetic divergence

We explored the effect of different variables representing life history traits, reproductive strategies and biogeographic variables on the levels of genetic structure based on the species identified in the literature review. We evaluated the influence of these biological and environmental traits across available data spanning the whole study region. We classified our variables into three major groups, the first one according to the dispersal potential during early and adult stages, including the potential dispersion based on fertilization type (i.e. pelagic larval duration, motility, internal and external fertilization). The second group was based on reproductive characteristics (i.e. reproductive aggregations and reproductive season) and the third group with broad habitat traits (i.e. temperature range and ecoregions) (Table 1). Specific information for each variable was obtained from scientific articles and publicly accessible online databases such as Fishbase (www.fishbase.se), OBIS (www.gbif.org), Sealifebase (www.sealifebase.ca) and Animal Diversity Web (animaldiversity.org). A complete list of the data is found in the Supplementary Material S3.

With this information, we formulated and tested five hypotheses on the relationship between the proposed predictive variables on the level of genetic structure among populations using the Theoretic Information Criteria (Anderson & Burnham, 2002; Burnham & Anderson, 2004). Because we wanted to identify if the genetic structure is driven by a certain type of variable, hypotheses were developed on a 'type-trait' and a mix-trait arrangement

TABLE 1 Variables predictive of genetic connectivity based on biological or ecological processes.

Biological/ecological characteristics	Variable	Hypothesis	Reference
Dispersion in the early stages of life	Pelagic larvae duration	Longer periods in the pelagic phase increase the potential for dispersal and gene flow	Treml et al. (2012); Shanks (2009); Hernawan et al. (2021)
Dispersion in the early stages of life	Reproductive strategies (gamete release and fertilization)	Pelagic fertilization offers a greater dispersal potential than fertilization on substrates, as they are immediately subject to the action of oceanographic and ecological factors	Bradbury et al. (2008); Riginos et al. (2011); Leis et al. (2013)
Dispersion in the adult phase	Mobility	In the adult phase, the ability to move can increase connectivity between populations	Bradbury et al. (2008); Pascual et al. (2017); Hernawan et al. (2021)
Reproductive characteristics	Reproductive aggregations	The formation of reproductive aggregations creates potential areas of connectivity, facilitating gene flow	Ma et al. (2018)
Reproductive characteristics	Duration of the reproductive season	Longer reproductive periods may favour gene flow between regions	Mertens et al. (2018); Treml et al. (2015)
Habitat temperature ranges	Habitat temperature	Species that are distributed over a wider temperature range may increase the level of connectivity between regions with different oceanographic characteristics	Leis et al. (2013)
Habitat heterogeneity	Ecoregions	Due to the oceanographic features among the ecoregions species with distribution across different ecoregions could show more connectivity compared to species restricted to a single ecoregion	Pascual et al. (2017); Riginos et al. (2011); Hernawan et al. (2021)

Note: Variables related to dispersal, reproduction and environmental characteristics were selected. Subsequently, their relationship with connectivity was hypothesized.

(Table 2). Based on these hypotheses, we used generalized linear models (GLMs) to evaluate the effect of our predictive variables on the level of genetic structure among fish and invertebrate populations, represented by the Fst index (Table 2). A total of 50 species (18 fish and 32 invertebrates) were included in this analysis. Data analysis and model development were done with the software R 4.03 (R Core Team, 2020).

As a first step, the assumptions of normality and homoscedasticity, as well as the degree of collinearity between the variables, were checked using visual methods (Zuur et al., 2010) (Supplementary Material A). Based on these tests, GLMs with gamma distribution were chosen. For the continuous variables, the data were scaled (Schielzeth, 2010). Finally, we used the Akaike corrected criterion (AICc) and the contribution of the predictor variables through the weight of each variable to determine the fit of the models.

3 | RESULTS

A total of 46 articles published from 2000 to 2023 met our selection criteria and were included in the analyses (Figure 2). Between 2000 and 2013, a higher number of publications met the criteria. After the peak of 2013, a decrease in the number of publications meeting the criteria was observed. We did not record any publications meeting our selection criteria in 2002, 2006, 2012, 2016 and 2019.

A total of 86 species were analysed in publications and 67 presented genetic structure data (Fst/phylogenetic data), representing seven *phyla*: Chordata, Mollusca, Arthropoda, Echinodermata, Nematoda, Heterokontophyta and Trakephyta (Figure 2). The species included 38 fish, 43 invertebrates, 2 marine mammals, 2 seagrasses and 1 algae. From these, 16 species of fish were commercially important, such as kelp bass *Paralabrax clathratus*, sand bass *P. maculofasciatus* and California sheephead *Semicossyphus pulcher*. Also, 4 species of invertebrates were commercially important, such as the red sea urchin *Mesocentrotus franciscanus*, the mussel *Mytilus californianus*, the abalone *Haliotis corrugata* and the red lobster *Panulirus interruptus*.

A total of 227 sampling sites were represented in the publications analysed across the region. We found the sampling effort was greater in California, with 145 sites compared to 82 in the Baja California peninsula. The sampling resolution per study was variable. The highest number of sampling sites per study was 58 while the lowest was 2, with an average of 13 sampling sites per publication.

The publications analysed reported the use of different molecular markers over time, which can be classified into four groups: mitochondrial DNA (mtDNA), nuclear genes, microsatellite loci and single nucleotide polymorphisms (SNPs). Mitochondrial markers were the most used (31 publications), followed by 15 with microsatellites, 10 with nuclear coding genes and 2 with SNPs. We found 19 publications that combine the use of two types of markers. The most used combination was mitochondrial and nuclear coding genes (Figure 2).

3.1 | Genetic patterns across the Californias

The levels of genetic structure that dominated the region for all taxonomic groups and all markers were low according to Fst, with values <0.02, particularly on invertebrates. However, there were also species with low connectivity and strong genetic structure (Fst between 0.25 and 0.7), such as *Girella nigricans*, *Fundulus parvipinnis*, *Leuresthes tenius*, *P. maculofasciatus*, *Stenoplax mariposa* and *Cyanoplax keepiana*. Additionally, mitochondrial markers presented higher Fst values (average Fst = 0.165) than nuclear markers (nuclear coding genes (average Fst = 0.033), microsatellites (average Fst = 0.062) and SNPs (average Fst = 0.007)).

TABLE 2 Hypotheses to explain the level of genetic structure formulated as GLM models based on the Theoretical Information Criteria approach (Anderson & Burnham, 2002; Burnham & Anderson, 2004).

Model	Hypothesis	Variable	Model
1	Genetic structure is related to the reproductive characteristics of the species	Fertility type, reproductive season, reproductive aggregation	Fst ~ fert + rep_season + rep_ag
2	Genetic structure is related to environmental characteristics	Ecoregion, temperature range	Fst ~ ecoregion + range_temp
3	Genetic structure is mediated by dispersal potential in the early stages of development, as well as environmental characteristics	Fertility type, temperature range, ecoregion	Fst ~ fert + range_temp + ecoregion
4	Genetic structure is mediated by the dispersal potential in the adult stage and its relationship with environmental characteristics	Motility, reproductive aggregation, temperature range, ecoregion	Fst ~ motility + rep_ag + range_temp + ecoregion
5	Genetic structure is mediated by the level of mobility in the adult stage and the potential for dispersal in early stages and environmental factors	Motility, fertility type, temperature range, ecoregion	Fst ~ motility + fert + range_temp + ecoregion

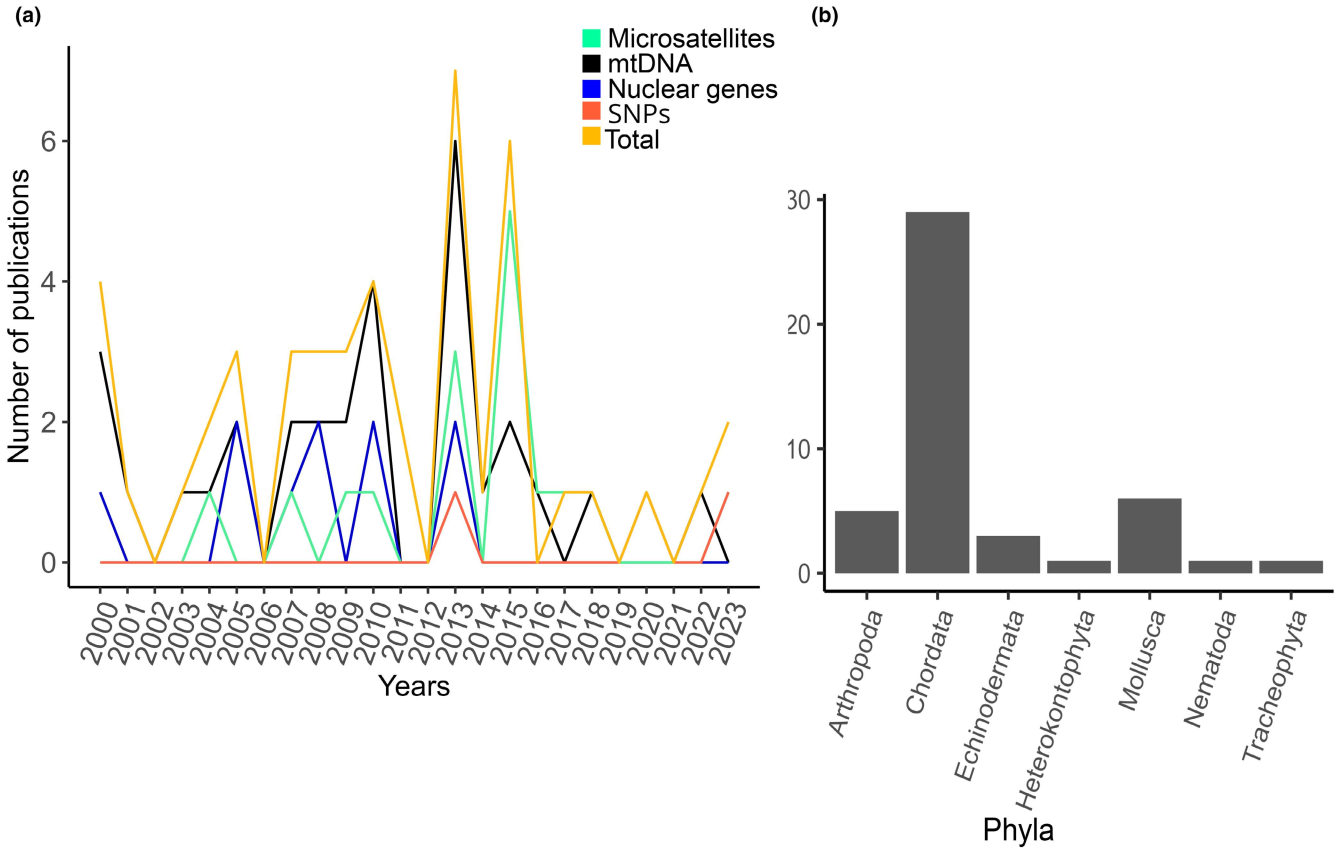

FIGURE 2 Trends on marine genetic structure publications in the northeastern Pacific region, (a) trends per year by use of genetic marker reported and (b) by phyla.

3.2 | Geographic regions and species with genetic breaks

To identify biogeographic patterns, we included the 63 species with connectivity data represented by fish, invertebrates, algae, grasses and mammals. We recorded 38 biogeographic breaks between 26° N and 39° N. For all the taxonomic groups 43% of the species present genetic breaks. For the 22 species of fish, we observed 21 breaks with 63% of species presenting genetic breaks. We also found 15 genetics breaks that represent 27% of the 33 species of invertebrates. The three species of algae and grasses presented a genetic break. Finally, only 1 of the 3 species of mammals presents a genetic break. On the other hand, 57% of all the species present homogeneous populations with no genetic breaks across the range. For recognized genetic breaks such as Punta Eugenia and Point Conception, 29% of species presented a genetic break either in one or both regions (Figure 3).

From a transboundary perspective between California (USA) and Baja California (Mexico), 35 species showed connectivity among both countries, including 13 commercial or recreational species (*G. nigricans*, *P. maculofasciatus*, *Anisotremus davidsonii*, *S. pulcher*, *Engraulis mordax*, *Sardinops sagax*, *Sebastes auriculatus*, *S. miniatus*, *M. franciscanus*, *M. californianus*, *Megastrea undosa*, *P. interruptus* and *Macrocystis pyrifera*), 9 fish, 4 invertebrates and one alga. However, some of these commercially important species presented a continuous or a break pattern throughout the larger region. For example, *P. maculofasciatus* and *A. davidsonii*, present an overall continuous population in the northern region, including the international boundary, with a single genetic break further south in Punta Eugenia. Meanwhile, *S. sagax*, *E. mordax* and *S. auriculatus* have a continuous population across the region. Among invertebrates of commercial interest, *M. californianus*, *M. undosa* and *P. interruptus* also showed continuous populations throughout California and Baja California (Figure 3).

Several genetic breaks were recorded close to the boundaries between ecoregions, highlighting the presence of biogeographic transition zones. For example, Punta Eugenia (27°–29° N), located between the SCB and Magdalena Transition ecoregions and Point Conception (35 N°) located between the Northern California and Southern California Bight ecoregions. The Ensenada area at around 32° N also stands out presenting a genetic break for several species (Figure 3).

Regarding the trends on genetic breaks presence, the distribution of breaks according to ecoregions may be biased due to the sampling effort and area of interest of the different connectivity studies analysed. For example, the Southern California Bight area was the most sampled, 58 out of 59 species had a sampling site on this ecoregion and had 23 breaks. On the other hand, distribution in the Northern California area includes 31 species and 3 breaks and in the Magdalena Transition area only 18 species were sampled, in which only one break was identified.

The distribution and number of genetic breaks between fish and invertebrates were not statistically different (Fisher's test,

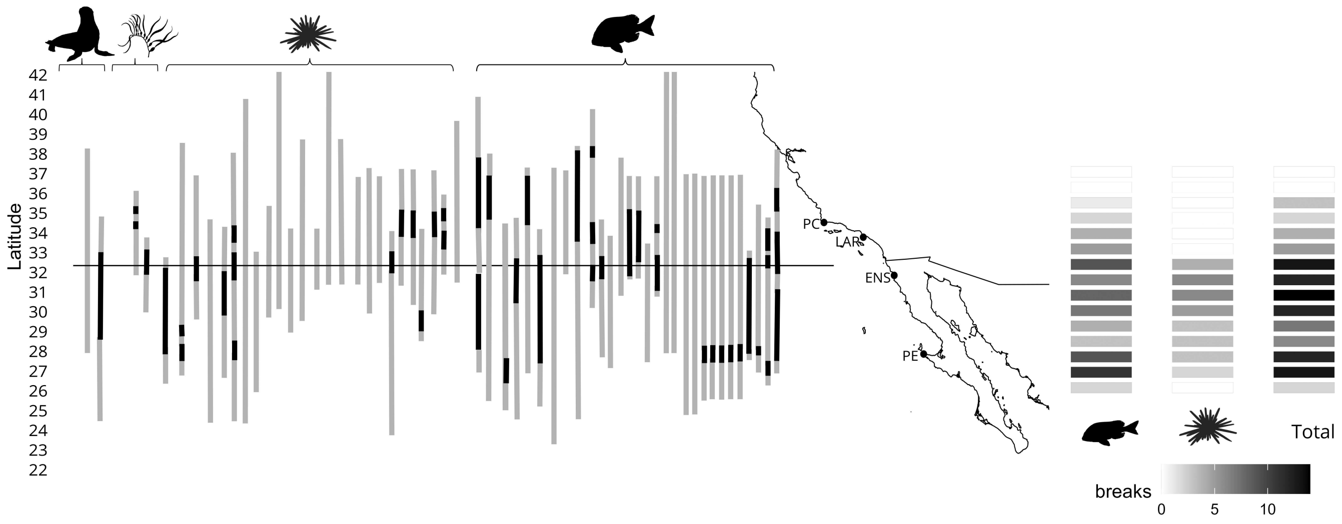

FIGURE 3 Genetic breaks across California and Baja California for different taxonomic groups. Grey bars in the centre represent the latitudinal sampling range for each species highlighting in black the genetic breaks reported in each publication along the latitudinal gradient. The heatmaps highlight the prevalence of genetic breaks by latitude. Major break zones like Point Conception (PC), Los Angeles Region (LAR), Ensenada (ENS) and Punta Eugenia (PE) are indicated. The horizontal black line represents the political border between USA and Mexico.

TABLE 3 General linear model selection table following Akaike's corrected criteria (AICc).

Model	1	3	2	5	4
(Int)	4.493	6.155	6.875	2.955	9.749
fert	+	+		+	
rag	+				
rs	2.88				
eco		+	+	+	+
temp		1.782	2.1	−0.728	−0.107
mot				+	+
Fam	G	G	G	G	G
df	6	10	8	12	10
logLik	300.45	303.1	300.31	304.73	301.47
AICc	−587.7	−582.7	−582.4	−580.3	−579.4
Delta	0	4.9	5.3	7.3	8.2
weight	0.833	0.07	0.06	0.021	0.013

Note: Contribution to variability explanation and statistic values according to each model. Variable codes are as follows: Fert (fertilization type), rag (reproductive aggregations), rs (reproductive season), eco (ecoregion), temp (temperature range) and mot (motility). Interception (int), presence of variable for each model (+).

$p = 0.95$). Algae and grasses showed genetic breaks between 34° N and 35° N (Point Conception) and between 32° N and 33° N in the SCB. Finally, out of the 3 species of mammals, only the California sea lion (*Zalophus californianus*) showed structure between a population north of Point Conception and another population south of Punta Eugenia (Figure 3).

Also, the chi-squared tests showed that the genetic breaks have a non-random distribution along the latitudinal gradient, supported by the three criteria independently: reciprocal monophyly ($p = 0.005359$), Fst significant values ($p = 0.00002$) and Fst >0.05 ($p = 0.000022$).

3.3 | Predictive variables of genetic structure

We explored each model independently and found that *ecoregion* and *motility* variables influenced the Fst values in model 5. Specifically, effects were observed for the transition zone between Northern California and Southern California ecoregion ($p = 0.0224$) with an increase in Fst values. Regarding the motility in the adult phase, sessile species had lower Fst values ($p = 0.0428$).

The models developed did not show enough evidence to explain the genetic patterns of the species included in this study (Annex 2). Following the Akaike information criterion, model 1, which includes variables linked to reproduction, had the best fit (Table 3). However, statistically, these variables were not found to influence the connectivity levels of the species.

4 | DISCUSSION

In this study, based on a literature review of 46 articles concerning the connectivity and genetic structure of marine species, we evaluated the characteristics of the most predominant genetic patterns, the molecular markers used and the study effort among multiple taxonomic groups in the coastal areas of California and Baja California. We showed that 65% of the species analysed across the USA–Mexico border are part of the same genetic group as they do not show a genetic break. These patterns suggest high levels of biological connectivity across the political boundary. From these groups, 36% of species are of commercial or recreational interest. Additionally, we found that mitochondrial DNA and microsatellite loci have been the most widely used molecular markers in population genetic studies, particularly between 2003 and 2015. The use of molecular markers developed with high-throughput sequencing methods has been incorporated gradually through time.

Employing information on Fst values and phylogenetic trees from our literature review database, we identified 42 genetic breaks between 26° and 39°N. This information is relevant for two reasons. First, it reveals the trends in population genetic studies along an ecologically and economically important transboundary region. Secondly, it shows evidence that genetic structure across different taxa is associated with specific geographic regions across the coasts of California and Baja California. In the analysis of drivers of genetic structure, the linear models showed that biological characteristics related to dispersal capacity in the early stages of development and reproductive strategies alone do not determine the levels of connectivity in marine species along the coasts of California and Baja California.

The different traits that shape connectivity patterns are also influenced by evolutionary forces. These forces may act in opposition as it happens with gene flow that homogenizes and distributes genetic variation, while natural selection enhances local adaptation. Local adaptation results in resident genotypes with a higher fitness in their native habitat than foreign genotypes (Sanford & Kelly, 2011). Generally, local adaptation tends to develop over more stable conditions that allow species to be exposed over larger periods of time to one environment type. However, in environments with changes over small scales or mosaic conditions, life history and behaviour components may also promote local adaption (Sotka, 2012). Several marine species have shown local adaptation, even among populations with high connectivity. For example, fish species have shown local adaptation related mainly to growth (*Menidia menidia*), feeding (*Gadus morhua*) and reproductive traits (*Pomacentrus coelestis*) (Conover et al., 2006). Also, intertidal invertebrates have shown local adaptation related to temperature (*Tigriopus californicus*), hypoxia (*Acatia torsia*) and predation (*Mytlius edulis*) (Sanford & Kelly, 2011).

4.1 | Genetic connectivity between California and Baja California

Our literature review showed a higher representation of fish and invertebrate species in genetic connectivity studies in the region. This result may be related to the high commercial or ecological importance of these species. For example, species of importance for fisheries generate greater interest, particularly for stock delimitation, to assess the relationship between genetics and demographic parameters, as well as for conservation and breeding studies (Smith, 1994; Thorpe et al., 2000). This pattern has been observed in regions such as the Indo-Pacific, where authors also found that more studies on genetic connectivity have focused on bony fishes, followed by molluscs and arthropods (Hernawan et al., 2021).

Overall, the connectivity patterns are diverse between species and may respond oppositely to environmental factors, like *Paralabrax clathratus*, which presents higher structure levels between the international border. This may be caused by the effect of the Ensenada Front and the result of the divergent flow, in which water moves away from each other and may reduce dispersion. Conversely, for the snail *M. undosa*, connectivity between the USA and Mexico is maintained through the Ensenada population, which presents more genetic similarity to the Californian populations than to the rest of sites studied along Baja California (Haupt et al., 2013).

Unravelling the genetic structure dynamics of populations across political boundaries is critical from an ecological and management perspective, particularly as environmental changes reshape ecosystems and species ranges (Palacios-Abrantes et al., 2020). The Southern California Bight region is shared by both countries and is considered a marine climate change hotspot with economically and ecologically important species such as sea urchin, California sheephead, abalone, sea cucumber and giant kelp (Arafeh-Dalmau et al., 2023). Estimated species distribution shifts may lead to several challenges on management, like stock delimitation, catch rate limits and fishery closures, among new regulations and conservation frameworks that may be established. Additionally, management instruments must include, regularly updated connectivity and climate adaptation criteria (Arafeh-Dalmau et al., 2023; Cisneros-Montemayor et al., 2020). The identification of genetic patterns offers a baseline for modelling different scenarios that incorporate range distribution and population dynamics. Some initial binational efforts have been made between California and Baja California to address challenges in sustainable management and mitigate climate change stressors on marine diversity (Aburto-Oropeza et al., 2018; Ramírez-Valdez et al., 2017). Therefore, when commercially or ecologically important populations occur across political boundaries their genetic structure must be considered to produce sound management strategies that ensure their sustainability.

Groups or species with less commercial value are also present in genetic structure analysis such as chitons and other rocky intertidal species, which could be used as environmental indicators (Chiarelli & Roccheri, 2014). Chitons showed a latitudinal gradient at the gene flow level, with species restricted to central California and northern regions showing panmictic populations, meanwhile, chitons in southern California and Baja California exhibit significant genetic differentiation. Data also showed that genetic structure is between species rather than a population-level pattern. Though different environmental and oceanographic variables may influence connectivity, average SST has a significant correlation with connectivity. Warmer waters may speed larval development and reduce the time and distance of larval dispersion, which results reduced connectivity levels. This temperature difference seems to drive connectivity in a stronger way than biogeographic barriers, like Point Conception, in which not all the species presented a significant structure on either side of the barrier (Kelly & Eernisse, 2007). Indeed, temperature may exert selective pressure on several marine species as is suggested on pink abalone in California and Baja California, where the two genomic groups correspond with temperate and warm waters, respectively (Mares-Mayagoitia et al., 2024).

Interestingly, the data also shows species with high Fst values (0.25–0.7), which are not commonly observed in marine species. These values may respond to several processes including incipient speciation and/or local adaptation associated to specific biological characteristics and life histories (e.g. PLD, migratory behaviour, natal homing, reproductive philopatry, environment occupied). For example, for the California killifish *Fundulus parvipinnis*, both hypotheses have been suggested, a possible process of division into subspecies enhanced by the isolation of estuarine habitats and also local adaptation due to temperature differences (Bernardi & Talley, 2000). Another example is that for *G. nigricans*, where a disjunct distribution due to habitat fragmentation has been suggested to explain such a strong differentiation, besides the effect of currents on the Punta Eugenia area (Terry et al., 2000).

4.2 | Geographic regions with genetic breaks

The genetic breaks identified in this study are distributed mainly in two ecoregions, Northern California, characterized by cooler waters and Southern California Bight, where warmer waters are present (Spalding et al., 2007). The area with the greatest number of breaks coincides with recognized biogeographic barriers, such as Point Conception and Punta Eugenia, nearly 30% of the species register breaks either in one or both regions. Some shared traits in species that present genetic breaks are reef-associated habitat, carnivore diet, PLD between 30 and 60 days, reproductive season from 3 to 8 months and presenting both demersal and pelagic gamete fertilization strategies. Species with no breaks are predominantly demersal, also have a carnivore diet and shorter PLD periods but with a wide range of reproductive seasons.

The distribution of genetic breaks along the latitudinal gradient supports the hypothesis that genetic structure in particular regions is enhanced in response to several processes, including the presence of geographic barriers, like Point Conception and Punta Eugenia. Breaks distribution suggest a northern (32°–36° N) and southern (26°–30° N) pattern. Throughout the range, other factors, such as oceanographic processes, behavioural traits like site fidelity and geographic distance may also promote the observed patterns. A latitudinal association has been reported on chitons (Kelly & Eernisse, 2007) and marine fishes (Bradbury et al., 2008). Nonetheless, some methodological issues may be considered like the difference in the number of sample sites among the several studies. The fewer the sample sites and more separate sites between geographic barriers, the more dispersed the latitudinal distribution of genetic breaks (Pelc et al., 2009; Quesada-Calderón et al., 2021).

The oceanographic characteristics and circulation in coastal California and Baja California are key factors in connectivity patterns, either facilitating the dispersal of individuals or acting as a barrier to individuals' movement. In particular, the levels of differentiation at a smaller spatial scale can be explained by these processes rather than by geographic distance (Banks et al., 2007; Xuereb et al., 2018). In addition, the organism's life histories are affected by oceanographic or geological processes and these generate genetic breaks. For example, it has been reported that the Point Conception biogeographic break has a different effect depending on the type of larva in invertebrate species (Araya-Donoso et al., 2022). Specifically, Point Conception represents a significant barrier for species with pelagic larvae, but not for benthic and low-dispersal species (Pelc et al., 2009; Wares et al., 2001).

These differences in the effects of barriers to dispersal are also observed in Punta Eugenia. Due to the convergence of different water masses, Punta Eugenia divides two oceanographic provinces (north and south) and two surface temperature regimes, one cold in spring and winter and one warm in summer and autumn (Durazo, 2015). In this area, some species like *G. nigricans*, *Gillichthys mirabilis*, *P. maculofasciatus* and *A. davidsonii* show a clear genetic differentiation between north and south (Bernardi, 2014). At the same time, *S. pulcher* and *Halichoeres semicinctus* maintain connectivity across the region (Bernardi, 2014). Moreover, species that showed genetic differentiation in the studied region also presented differentiation between the Pacific and the Gulf of California and species with a higher gene flow between the Pacific and the Gulf, maintained high connectivity around Punta Eugenia (Bernardi et al., 2003).

Eddies are another oceanographic process with an influence on the region, which may influence population dynamics. Eddies are energetic swirling, time-dependent circulations with variable extension and duration (Gulakaram et al., 2020; Rhines, 2019) and can promote or hinder connectivity processes. Bahia Vizcaino in Baja California (28.2° N) has been reported as a point of eddy formation where there is a strong anticyclonic eddy activity but can also occur to the north (Ensenada and San Quintin) and the south between 27° N and 25° N in front of Punta Eugenia, where a transition to cyclonic eddies occurs (Navarro-Olache et al., 2022; Soto-Mardones et al., 2004). Coincidently, our results show that these latitudes stand out as breaks for the dispersal of many species in Baja California (27–29° N/31° N–35° N). The role of eddies in genetic connectivity can go both ways, serving as transport of individuals from a region, which favours connectivity (Reguera-Rouzaud et al., 2020) or acting as a barrier to exchange, thus favouring genetic structure (Díaz-Viloria et al., 2009; Limer et al., 2020).

In fact, a temporal match exists between eddies formation or propagation and reproductive season for most species assessed in this study. For example, both fish and invertebrates present spawning peaks during summer when eddies are generated (e.g. *G. nigricans*, *A. davidsonii*). Additionally, for species that reproduce during fall or winter (e.g. *Pisaster ochraceus*), the effect of eddies when moving along the coast would be in larval propagation (Soto-Mardones et al., 2004). Therefore, it would be relevant to study the specific effect of eddies on the genetic connectivity of marine populations along the latitudinal gradient of the coasts of California and Baja California.

On evolutionary time scales, the formation of biogeographic breaks can be related to tectonic processes derived from the development of the Pacific fracture zones. For example, Point Conception is aligned with the Murray fracture zone and Punta Eugenia with the Shirley fracture zone. These geologic features extend to the terrestrial ecosystem, where biogeographic boundaries to species dispersal also occur (Gottscho, 2016). The range of latitude in which we report genetic breaks (27° N to 29° N and 31° N and 32° N) is also reported for terrestrial habitats on the peninsula and follows a north–south divergence pattern. Geographic events like the separation of the Baja California peninsula from the continent and the formation of the Gulf of California triggered different processes in which different habitats and ecological transition zones were formed and expanded (Dolby et al., 2015; Riginos, 2005). For example, in the Vizcaino region, there is an ecological transition zone related to increased rainfall. The divergence of cold waters off the coast at Punta Eugenia and warmer waters contribute to this change. Therefore, genetic patterns are driven by intertwined geological, ecological and climatic processes (Dolby et al., 2015).

The high levels of diversity in the Northeastern Pacific might have developed through vicariant and climatic events. Likely, a main driver of current diversity patterns observed was the shift from a warm to a cool upwelling-dominated regime in the Late Miocene. The ecological consequence was rich trophic dynamics that allowed the diversification of present coastal species like rockfish, surfperches, crabs, kelps and abalone (Jacobs et al., 2004). Conversely, during the mid-Pliocene, the upwelling regime was greatly diminished limiting diversification events. A major shift occurred during the Pleistocene with over 50 glacial cycles shaping coastal habitats. Some of the most affected habitats were estuaries, which now are highly reduced on North America's west coasts. Thus, estuarine habitats in California and Baja California were limited to a few widely separated refugia. Connectivity patterns were regulated by sea level variation and regional continental shelf topology. Isolation and recolonization dynamics were settled during glacial cycles (Dolby et al., 2018). A common genetic signature from these environmental changes is genetic bottlenecks, in which allele diversity is highly reduced, usually followed by a subsequent expansion event when adequate environmental conditions return (Marko, 2004; Neilson, 2005; Silliman, 2019).

Variations in genetic patterns among marine species due to biogeographic barriers and oceanographic processes are also present in the South Pacific. The latitudes 30° S and 42° S on the coasts of Chile are recognized as biogeographic barriers, but the species population structure response differs. For example, species like beach flee *Orchesteoidea tuberculata* and snail *Scurria scurra*, which present low dispersal potential in early stages (brooders or very short PLD period) remain isolated across these latitudes. Meanwhile species like starfish *Heliaster helianthus* and crabs *Petrolisthes violaceus* and *Metacarcinus edwardsii* present high dispersal potential given by PLD maintain gene flow between populations across these biogeographic areas (Haye et al., 2014; Veliz et al., 2022). Although both regions in either hemisphere have their own geologic, oceanographic and biogeographic, characteristics, they also share the influence of eastern boundary currents (i.e. the California current in the northern hemisphere and the Humboldt current in the southern hemisphere). Both currents generate strong upwelling systems, equatorial currents and mesoscale processes that can act as barriers to gene flow processes (Zakas et al., 2009). Transition zones on the coasts of Chile are also related to the dynamics and intensity of eddies. From 30° S to 38° S, there is an area of strong eddies and variable equatorial winds, while from 20° S to 30° S, the eddy energy decreases, but the equatorial wind stress remains constant (Hormazabal et al., 2004). Genetic breaks for multiple benthic species are reported between these two regions with the transition at 30° S.

It is interesting to note that the genetic differentiation patterns observed are present along the coasts of California and Baja California for both marine and terrestrial environments (Dolby et al., 2015; Riginos, 2005). The match of barriers producing genetic differentiation at the population level between marine and terrestrial environments is part of an intricate global ocean–atmosphere interactions (Seo et al., 2023). Atmospheric dynamics firmly guide processes such as the formation of gyres and currents, while in terrestrial environments, the movement of different air masses through convection cells and pressure changes condition the resulting climate and habitat (Farmer & Cook, 2013). Thus, the processes of genetic differentiation between ~30° in the northern and southern hemispheres for terrestrial and marine species demand much more attention and study efforts.

4.3 | Predictive variables of genetic structure

In this study, the variables evaluated in the models showed little relationship and low predictive power with the level of genetic structure (Fst). *Motility* and *ecoregion* were the only variables with significant values (Table 2); however, under the selection criteria, they did not contribute to improving the model's explanatory power.

The evidence of an effect found for the *ecoregion* variable agrees with our hypothesis and with our results on genetic breaks found for several species populations in the region. Differences between ecoregions can regulate gene flow. The transition zone between Northern California and Southern California Bight acts as a barrier that increases Fst values. This effect may be an indicator of the role of habitat heterogeneity on genetic structure (Hernawan et al., 2021). Thus, environment-related variables generate certain conditions to which the species responds with higher or lower levels of connectivity (Pelc et al., 2009).

The *motility* variable showed a negative relationship with Fst, contrary to our hypothesis. We expected that the effect of a sessile lifestyle would increase Fst levels. However, we found the opposite. One explanation may be that sessile organisms perform mass spawning and their contribution to connectivity as adults is offset by their contribution of dispersal in their early life stages (Cowen et al., 2006; Cowen & Sponaugle, 2009). Therefore, the effect of biological life history variables may differ from that expected due to their relationship with other life history factors that have a greater effect on connectivity.

The low correlation of the variables with the level of connectivity may be due to the variability in the species life histories included in the analysis and the interactions that occur with the oceanographic characteristics of the region. A similar result was reported in the Indo-Australian Archipelago where ecoregion and mobility were drivers of genetic structure but not reproductive traits, for example, fertilization strategies (Hernawan et al., 2021). Also, studies on benthic fishes have reported that transition zones contribute significantly to genetic structure (Riginos et al., 2011). Thus, environment-related variables generate certain conditions to which the species responds with higher or lower levels of connectivity.

Methodological components such as the different molecular markers used to estimate Fst values must also be considered on the interpretation of our results. The inherent characteristics of the different molecular markers are related to the level of genetic differentiation detected by Fst. For example, nuclear markers such as microsatellites and SNPs are related to lower Fst values compared to those obtained by mitochondrial markers (Gandra et al., 2021). This pattern may be related to the difference in marker mutation rate and effective size (Ne), since allele fixation tends to occur more rapidly in mtDNA than in nuclear DNA markers due to uniparental inheritance and mutation rates present variations among different markers (Ballard & Whitlock, 2004; Hernawan et al., 2021). However, it is important to consider that, in species with strong sexual selection (polygamous systems), the effective size is reduced in nuclear markers, which may increase genetic drift and allele fixation. Lower Fst values reported for nuclear markers, in particular microsatellites, may be related to their high mutation rate, which increases genetic variability among subpopulations (Hs) but reduces the Hs/Ht ratio (Balloux & Lugon-Moulin, 2002). Indeed, previous studies found significant differences between the marker and Fst values (Gandra et al., 2021; Medina et al., 2018; Riginos et al., 2011). However, other studies assessing population genetic structure across taxa have found no effect of the molecular marker used on Fst values (Hernawan et al., 2021). We consider that the bias of using different markers is compensated by the inclusion of several taxa that allow us to recognize the presence of broader genetic patterns.

Our macroecological focus across multiple taxa and life strategies suggests that the relationship between life histories and environmental characteristics act heterogeneously, making it difficult to explain connectivity patterns by a specific variable type. Additionally and relevant to consider, is that other variables not considered or readily available in our analysis could provide more information to evaluate the hypotheses used to develop our proposed models. However, the data from the present work, in conjunction with previous studies, show that connectivity is a complex process that is related to several factors and processes in which species, through their life history, may have levels of connectivity that are not coherent to what their life history traits suggest (Mertens et al., 2018).

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Luis Malpica-Cruz https://orcid.org/0000-0003-0750-1652

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BIOSKETCH

Mariana Ronalda Ferrera-Rodríguez is interested in the genetic connectivity of marine taxa in the northeast Pacific Region. This work represents a component of her Ph.D. work at Universidad Autonoma de Baja California on the connectivity patterns and genomic population of California and Baja California marine species. Mariana and the rest of the contributors collaborate on research on marine ecology, diversity, population genetics, conservation and marine resource management across the California and Baja California Peninsula region as well as in other parts of Mexico alongside fishers, NGOs and government agencies (MexCal research group, https://mex-cal.org).

Author contributions: MFR, LMC, AAC and AMV conceived the ideas; MFR, LMC and AAC analysed data and prepared the manuscript draft; AMV, RBL and ALF edited and revised the manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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