# **RESEARCH PAPER**



#### Journal of Biogeography

WILEY

# Oceanographic heterogeneity influences an ecological radiation in elasmobranchs

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#### **Funding information**

Australian Research Council, Grant/Award Number: DP110101275 and FT130101068; Macquarie University

Handling Editor: Michael Dawson

# Abstract

**Aim:** During ecological speciation, reproductive isolation is predicted to evolve between populations adapted to different biotic or abiotic environments despite the absence of geographical isolation. Regions of oceanographic heterogeneity (e.g. current interfaces, habitat transition zones, ecological gradients) are strong candidates for the presence of ecologically divergent natural selection, but their role in the radiation of elasmobranch species is yet to be tested. We used an integrative framework to assess the relative influence of oceanographic heterogeneity and geological history on the diversification of an elasmobranch genus.

Location: Gulf of California (GC) and Baja California Peninsula (BCP), Mexico.

Taxon: Shovelnose guitarfish (genus Pseudobatos).

**Methods:** We sampled 210 *Pseudobatos* specimens from four distinct but physically connected oceanographic regions within the GC and in the BCP. We used genetic (mtDNA sequences and AFLP genotypes) and environmental (six oceanographic variables) datasets to clarify phylogenetic relationships, demographic history and evolutionary divergence among populations, and to test for associations between ecologically driven selection and reproductive isolation.

**Results:** Phylogenetic and population genetic evidence exposed five distinct lineages of *Pseudobatos* in the region, including four cryptic lineages in the GC. Phylogeographic analyses indicate a recent history of ecologically driven diversification associated with the Gulf's young oceanographic environment and its four ecologically discrete regions. This hypothesis was supported by seascape genetics, ecological niche modelling and by tests of selection.

**Main conclusions:** We propose an adaptive radiation for the genus *Pseudobatos* linked with habitat heterogeneity of the GC. Our study likely represents the first assessment of an ecological radiation in the highly diverse elasmobranch group. It capitalizes on the environmental and biogeographic settings of the GC to offer a new perspective about the application of integrative approaches to study divergent natural selection and diversification in the sea.

#### KEYWORDS

ecological speciation, evolutionary radiation, isolation by environment, marine biodiversity, phylogeography, seascape genomics

### 2 | Journal of Biogeography 1 | INTRODUCTION

Many species appear to evolve by the process of 'ecological diversification' in which reproductive isolation evolves between populations adapted to different environments or ecological niches (Nosil, 2012; Schluter, 2009; Via, 2009). Theoretical and empirical evidence for ecological speciation has recently accumulated, challenging the dominant paradigm of physical mechanisms of diversification that underpin allopatric speciation (Beheregaray, Cooke, Chao, & Landguth, 2015; Teske et al., 2019). Nevertheless, links between diversification and natural selection are not always evident, and the role of ecological adaptation and divergence in the speciation process remains controversial (Nosil, 2012; Seehausen et al., 2014).

In marine ecosystems, spatial population disjunctions that resulted in speciation are often associated with vicariant events or with oceanographic discontinuities (Bowen, Rocha, Toonen, & Karl, 2013; Gaither, Toonen, Robertson, Planes, & Bowen, 2010). Regions of oceanographic heterogeneity (e.g. current interfaces, habitat transition zones, ecological gradients) are potentially strong candidates for the presence of ecologically based divergent selection between environments. Yet, the role of oceanographic heterogeneity as a driver of ecological diversification has not been satisfactorily addressed (Grummer et al., 2019; Riginos, Crandall, Liggins, Bongaerts, & Treml, 2016). Assessing geographical isolation and divergent natural selection in the ocean should benefit from studies of regional biotas exposed to active geological history and complex oceanography. In this context, the Gulf of California (GC) and the adjacent Baja California Peninsula (BCP) provide an ideal study region. The geomorphological history of the Gulf has been particularly dynamic (Dolby, Bennett, Lira-Noriega, Wilder, & Munguía-Vega, 2015; Murphy & Aguirre-Leon, 2002; Umhoefer et al., 2018), and its current oceanographic conditions show high temporal and spatial variability (Ortega, Álavarez-Borrego, Arriaga, Renner, & Bridge, 2010). The processes underpinning the formation of the GC and the BCP are thought to have started ~12 million years ago (Mya), with the detachment of a proto-peninsula from the mainland and the formation of the southernmost GC (Dolby et al., 2015; Umhoefer et al., 2018). Tectonic activity transported the proto-peninsula and a volcanic archipelago 300 km north-west, allowing the flood of the northern GC ~6 Mya. At that time, the southernmost part of the GC was connected to the Pacific Ocean by seaways between islands. By ~3 Mya emerging land attached these islands and the proto-peninsula, closing the seaways and forming the BCP (Dolby et al., 2015; Murphy & Aguirre-Leon, 2002). In spite of these key events between ~6 and 3 Mya, the Colorado river delta established 4.5 Mya but continued to experience smaller fluctuation after that time (Dorsey, O'Connell, McDougall, & Homan, 2018); the Ballenas Channel formation was completed only ~2 Mya (Nagy & Stock, 2000); and recent volcanic activity and overriding plate uplifts changed dramatically the south-west coast of BCP ~2-1 Mya (García Sánchez et al., 2019; Mark, Chew, & Gupta, 2017; Sutherland et al., 2012). This combination of older and younger events was integral to the recent (i.e. Pleistocene) establishment of four oceanographic regions inside the GC, which are physically connected

but have ecologically distinctive features (Figures 1 and 2d; Lluch-Cota et al., 2007; Ortega et al., 2010). Briefly, the open gulf (OG) is largely influenced by oceanic waters with relatively low productivity (< 0.6 mg Cla/m<sup>3</sup>) and small annual variation in temperature (22–30°C). The lower gulf (LG) has intermediate productivity (< 1.5 mg Cla/m<sup>3</sup>) and more variable thermodynamics (18-32°C). The islands region (IG) has channels that are over 500 m deep and is characterized by strong tidal-mix upwelling that maintain high productivity (> 3 mg  $Cla/m^3$ ) and low annual temperatures (11-22°C). The upper gulf (UG) has shallow waters (average < 100 m), high salinity (up to 40‰), large temperature variation (9–38°C), high productivity (> 2.5 mg  $Cla/m^3$ ) and large tidal ranges (> 6 m; Lluch-Cota et al., 2007; Ortega et al., 2010). Previous genetic studies of marine organisms from the GC-BCP have mainly focused on vicariant biogeography (Bernardi, 2014; Castillo-Páez et al., 2014; Riginos, 2005; Sandoval-Castillo & Rocha-Olivares, 2011: Sandoval-Castillo, Rocha-Olivares, Villavicencio-Garavzar, & Balart, 2004), with few exceptions (e.g. García-De-León et al., 2018; Sandoval-Castillo & Beheregaray, 2015).

Allopatric speciation does not fully account for the diversity of sharks and rays because elasmobranchs show relatively moderate to high potential for dispersal (Compagno, 1990; Speed, Field, Meekan, & Bradshaw, 2010), which often translates to high gene flow among localities. Few studies have suggested ecological diversification between pairs of elasmobranch species (Griffiths et al., 2010; Walter et al., 2017). However, to the best of our knowledge, an ecological radiation has so far not been described for any elasmobranch. Elasmobranchs are an evolutionary success story, having shown long-term diversity, adaptive radiations and sophisticated morphological, ecological and behavioural specializations (Compagno, 1990; Dean, Wilga, & Summers, 2005; Musick, Harbin, & Compagno, 2004; Sorenson, Santini, & Alfaro, 2014). With around 1,000 species, elasmobranchs are the second most diverse group of vertebrates in the oceans (Compagno, 2005; Last et al., 2016). This high species diversity is most likely underestimated because of their highly conserved morphology and lack of extensive taxonomic studies (Ebert & Compagno, 2007; Last, 2007). One such example is the guitarfish family Rhinobatidae; one of the oldest families of modern elasmobranchs with around 31 species (Last et al., 2016). Guitarfishes generally show high levels of morphological stasis, few diagnostic characters and limited interspecific morphological differentiation (Cappetta, Ginter, & Hampe, 1987; Last et al., 2016; Randall & Compagno, 1995), making it particularly difficult to delineate divergent lineages. The taxonomy of Rhinobatidae in the GC-BCP region is confusing, but three species of the genus Pseudobatos are currently accepted: P. glaucostigmus (speckled guitarfish), P. leucorhynchus (whitenose guitarfish) and P. productus (shovelnose guitarfish) (Last et al., 2016). However, Sandoval-Castillo et al. (2004) reported two cryptic allopatric mitochondrial DNA (mtDNA) lineages of P. productus, one distributed along the GC, and one along the Pacific Coast (PC) of the BCP. Both the recognized and cryptic species of Pseudobatos span a vast area in the GC and in the BCP with complex oceanography. As such, they offer an ideal opportunity to assess stages of speciation and the relative roles of vicariant biogeography and natural selection in the formation of elasmobranch species.

**FIGURE 1** The Gulf of California (GC) and the Baja California Peninsula (BCP) in Mexico, showing the 16 sampling sites for *Pseudobatos*. Study regions (colour coded) are the Pacific Coast (PC) and the four bioregions inside the Gulf: the upper gulf (UG), the islands region (IG), the lower gulf (LG) and the open gulf (OG). Table indicate the number of samples collected per site



Here, we used an analytical framework that integrates phylogenetics, phylogeography, genome scans and environmental modelling to assess the influence of geomorphological history and oceanographic heterogeneity on the diversification of Pseudobatos from the GC-BCP region. First, genetic divergence, migration rates, reproductive isolation and the delineation of cryptic lineages were assessed with phylogenetic and population genetic methods. Coalescent-based phylogeographic simulations were then conducted to test the fit of the genetic data to population histories predicted by competing evolutionary hypotheses. The latter is needed because ecological speciation usually requires a study system in which the existence of a dominant allopatric phase is unlikely in the context of evolutionary history (Endler, 1982). Finally, analyses based on seascape genetics, ecological niche modelling and tests for selection were used to assess oceanographic, ecological and geographical factors underpinning divergence. We predict that our integrative framework will detect associations between genetic and environmental divergence while accounting for the effects of geographical distance and historical biogeography (sensu, Beheregaray et al., 2015). We hypothesize that the Pseudobatos lineages from the GC-BCP have a recent history of ecologically driven diversification linked to oceanographically defined regions. This study capitalizes on the environmental and biogeographic settings of the GC-BCP to apply integrative genetic-based methods to study divergent natural selection and diversification in elasmobranchs.

# 2 | MATERIALS AND METHODS

#### 2.1 | Sampling

Muscle tissue of 210 *Pseudobatos* were collected from 16 legal artisanal fisheries landing sites, covering the oceanographic bioregions of the GC and the PC of the peninsula (Figure 1). These were identified in the field as shovelnose (*P. productus*; n = 189) and as speckled guitarfish (*P. glaucostigmus* [Pg]; n = 21). Whitenose guitarfish (*P. leucorhynchus*) from the Gulf of Tehuantepec (~1,400 km south of the GC) and Brazilian guitarfish (*P. horkelii*) from Brazil were included as outgroups. Our sample includes all recognized taxa of *Pseudobatos* in the GC.

#### 2.2 | DNA analysis

We used a salting out protocol (Sunnucks & Hale, 1996) to extract genomic DNA. From 199 samples (178 shovelnose and 21 speckled guitarfish, Table S2), approximately 800 bp of the mtDNA control region (mtCR) was sequenced following Sandoval-Castillo and Beheregaray (2015). Nuclear data were generated for 183 samples (169 shovelnose and 14 speckled guitarfish, Table S2) using a modified protocol of amplified fragment length polymorphism (AFLPs; Zenger, Stow, Peddemors, Briscoe, & Harcourt, 2006) and loci determined using AFLPscore 1.4 (Whitlock, Hipperson, Mannarelli, Butlin, & Burke, 2008; locus threshold = 25%, phenotype-calling relative threshold = 10%). Error rate was assessed by running 24 samples twice from the DNA extraction step and using a mismatch error rate analysis in AFLPscore. Monomorphic loci (< 5% or > 95% all individuals) were excluded.

### 2.3 | Oceanographic dataset

Average annual oceanographic data of six key variables (temperature, salinity, oxygen saturation, nutrients concentration, total chlorophyll and bathymetry) for the last 100 years were obtained from the NOAA World Ocean Data Base (Boyer et al., 2018). Gridded maps at ~10 km<sup>2</sup> resolution of each oceanographic variable were generated using the DIVA algorithm in



**FIGURE 2** Maps of the Gulf of California and Baja California Peninsula showing the putative vicariant events (a–c), the current bioregions (d), and the geographical distribution of inferred *Pseudobatos* lineages (e). Baja California Peninsula (BCP), Southern Peninsula Seaway (SPS), Middle Peninsula Seaway (MPS), upper gulf (UG), islands region (IG), lower gulf (LG), open gulf (OG), Pacific Coast (PC), *P. glaucostigmus* (*Pg*), million years ago (Mya). The bottom diagram shows eleven phylogeographic hypotheses for diversification of *Pseudobatos* from the GC-BCP tested using approximate Bayesian computation (ABC) in DIYABC 2.1. Hypotheses include vicariance and ecological radiation events (H1a; H1b; H1c), vicariant events only (H2a; H2b; H2c; H2d; H4a; H4b), and ecological radiation only (H3a; H3b)

ODV.5.2 (Schlitzer, 2015). These cover a quadrant from 103° to 117°W and 19° to 33°N that includes all sampling localities (Figure 1).

#### 2.4 | Statistical analyses

## 2.4.1 | Phylogenetic and genealogical analyses

jModelTest 2 (Darriba, Taboada, Doallo, & Posada, 2012) was used to select the most appropriate substitution model for the mtCR dataset based on Bayesian information criterion. Phylogenetic analysis was performed using Bayesian inference in MrBayes 3.2 (Ronquist et al., 2012; replicates = 3, chains = 8, generations = 10,000,000, sampling every 100 generations, burnin = 1,000,000). Genealogical relationships among mtCR haplotypes were inferred in TCS 1.2 (Clement, Posada, & Crandall, 2000; confidence connection=>95%).

# 2.4.2 | Genetic structure and demographic history

Genetic differentiation among localities was assessed by pairwise  $\Phi_{ST}$  (mtCR) in Arlequin 3.5 (Excoffier & Lischer, 2010) and  $F_{ST}$  (AFLP) in AFLP-SURV 1.0 (Vekemans, 2002). Hierarchical population structure was tested for both the mtDNA and AFLP

datasets (see Supporting Information) using an AMOVA in Arlequin. Here genetic variation was partitioned within sampled localities, among localities, and among mtCR lineages (PC, UG, IG, LG and Pg). Genetic structure and the most likely number of populations was assessed for the AFLP data with an approach for dominant markers in Structure 2.3.4 (Hubisz, Falush, Stephens, & Pritchard, 2009; admixture model with correlated alleles, burnin = 100,000 iterations = 1,000,000). Historical demographic parameters ( $\theta$  as population sizes, and M as gene flow between populations) were estimated for the mtDNA data based on a full migration model using Migrate-N 3.6 (Beerli, 2006; slice proposal distribution, exponential with windows prior distribution, long chain = 1, burn-in = 10,000, run = 1,00,000, replicates = 7, static heating with five chains = 1, 1.5, 3, 6 and 100). Parameters were scaled by a mutation rate  $\mu$  = 1.3 × 10<sup>-07</sup> based on an average substitution of 8  $\times$  10<sup>-3</sup> substitutions per site per million years (Duncan, Martin, Bowen, & De Couet, 2006) and generation time of 16 years (Villavicencio-Garayzar, 1993). Finally, the time to the most recent common ancestor was inferred for all phylogroups (i.e. major mtDNA lineages) using BEAST 1.7 (Drummond, Suchard, Xie, & Rambaut, 2012; standard priors, burn-in = 1,000, generations = 10,000,000, replicates = 5). Since a calibrated molecular clock is not available for Pseudobatos, we applied a widely used clock for sharks of 0.8% per million years (Corrigan, Huveneers, Schwartz, Harcourt, & Beheregaray, 2008; Dudgeon et al., 2012).

#### 2.4.3 | Detection of natural selection

Outlier AFLP loci under divergent selection were identified using two Bayesian  $F_{ST}$ -outlier approaches. First, we used Mcheza (Antao & Beaumont, 2011) to run pairwise comparisons between phylogroups. For each analysis null distributions of  $F_{ST}$  were generated using 50,000 simulations, a  $\theta$  of 0.01, and a confidence interval of 99%. Loci identified in more than two comparisons were considered outliers (Campbell & Bernatchez, 2004). BayeScan 2.1 (Foll & Gaggiotti, 2008) was also used to calculate  $F_{ST}$  coefficients and decompose them into a locus-specific component ( $\alpha$ ) and a populationspecific component ( $\beta$ ). Only those loci with very strong evidence for selection (log10BF > 1.5) were considered (Jeffreys, 1961). To further reduce false positives, only loci classified as outliers by both methods were considered as candidate loci for selection.

#### 2.4.4 | Ecological isolation

Environmental distances were estimated as the difference of each oceanographic variable between sampling sites. Geographical distances between sites were measured along the coastline using GoogleEarth (2017). We then used SAM (Joost, Kalbermatten, & Bonin, 2008) to calculate multiple univariate logistic regressions to test for association between allele frequency of each of the 541 AFLPs and the five environmental variables. Associations were considered significant only if both G and Wald tests rejected the noassociation model at a 2.3E-9 threshold. In addition, the contribution of geographical and environmental factors to inferred genetic patterns, and the correlations between genetic structure (i.e. measured by mtDNA  $\Phi_{\rm ST}$  and AFLP  $F_{\rm ST}$ ) and geographical and environmental distances were assessed using partial Mantel tests in IBSWS 3.23 (Jensen, Bohonak, & Kelley, 2005; permutation = 10,000). We also used a partial redundancy analysis (RDA) to assess genotype-environmental associations between the five oceanographic variables and the allele frequencies of the candidate loci. The best model was selected using a backwards-stepwise selection procedure. Then the significance of the final model and each environmental variable was assessed by 1,000 ANOVA permutations. To determine the extent of ecological overlapping between taxa (i.e. phylogroups), predictive distribution models were generated using maximum entropy in MaxEnt 3.4.1 (Phillips, Anderson, Dudík, Schapire, & Blair, 2017). This predicts taxa environmental suitability of each cell in a gridded map. Two or three commercial fisheries sites per locality (9-15 per taxon) were used as the taxa presence dataset, and gridded maps of six oceanographic variables were used as environmental layers. A receiver operating characteristic (ROC) analysis was performed and the area under the ROC curve (AUC) was used to evaluate the discrimination power of the predicted distribution (Phillips & Dudík, 2008). In addition, symmetric extremal dependence indices (SEDIs) were calculated using the R package MAXENTOOLS 1.1.0 (Scavetta, 2019). Niche overlap among phylogroups was quantified using niche similarity indices (I) and tested using identity tests in 'ENMTools'

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0.2 (Warren, Glor, & Turelli, 2010). For the identity test, a null distribution of overlapping score between taxa was generated based on 1,000 occurrence point pseudoreplicates per taxon. Niche identity was rejected when the actual observed *I* index was significantly lower than that expected for the pseudo-replicated dataset.

# 2.4.5 | Assessing alternative scenarios of evolutionary divergence

DIYABC 2.1.4 (Cornuet et al., 2014) was used to test competing phylogeographic hypotheses (Figure 2). Results from Migrate-N were used to set each extant population size. Major historical geological events were used to set putative splitting times: (a) the end of the formation of the gulf 6 Mya (Oskin & Stock, 2003), (b) the opening of a seaway crossing Baja California in the southern part of the gulf 3 Mya (Helenes & Carreño, 1999), and (c) the opening of a putative seaway at mid-peninsula 3 Mya (Ochoa-Landin, Ruíz, Calmus, Pérez-Segura, & Escandon, 2000) or 1 Mya (Murphy & Aguirre-Leon, 2002). We tested 11 hypotheses (Figure 2c): three that include vicariance and ecological radiation events (H1a; H1b; H1c), six that consider only the vicariant events (H2a; H2b; H2c;H2d; H4a; H4b) and two considering ecological radiation only (H3a; H3b) (details in Supporting Information). For each evolutionary model, 1,000,000 datasets were simulated using the priors in Table S1. Subsequently, 60 summary statistics were calculated for each scenario and the empirical dataset. The probability of each scenario was calculated using logistic regression of simulated datasets against the linear discrimination components of the empirical data. We then calculate both type I and II error rates per scenario (see Supporting Information).

#### 3 | RESULTS

#### 3.1 | Genetic diversity and loci classification

Fifty-two mtCR haplotypes and 541 nuclear loci were resolved for all samples. Haplotype diversity was moderate to high (0.551 to 0.952). All nuclear loci were polymorphic with expected heterozygosity ranging from 0.313 to 0.407 (Table S2). Of the 541 nuclear loci, 39 candidates for selection (7.2%) were detected by both outlier methods (Mcheza detected 68 loci and BayeScan 44; Table S3).

# 3.2 | Cryptic genetic diversification of *Pseudobatos* lineages

Nuclear and mitochondrial data provided strong evidence for five lineages of *Pseudobatos* in the GC-BCP region. One lineage (Pg) corresponds to all organisms identified in the field as *P. glaucostigmus*. Samples originally identified as *P. productus* comprised four discrete lineages that show strong ecological differentiation. Each lineage was found in a different oceanographically delimited ecological Journal of Biogeography

region, namely the UG, Islands (IG), PC and LG (Figure 2d,e). In contrast, the P. glaucostigmus lineage occurs in both the OG and in the LG, in sympatry with the LG cryptic lineage of P. productus. The inferred lineages comprise five moderately supported clades (> 0.78 Bayesian support), with four (LG, Pg, UG and PC-IG) being reciprocally monophyletic (Figure 3a). Phylogenetic subdivision is reflected in strong genetic structure across the 16 sites (mtDNA  $\Phi_{sT}$  = 0.876, p < .01; AFLP  $\rm F_{ST}$  = 0.139, p < .01;  $\Phi_{\rm PT}$  = 0.282, p < .01). AMOVA shows that molecular variation is best explained by differences between bioregions (mtDNA  $\Phi_{\rm CT}$  = 0.869, p < .01; AFLP  $\Phi_{\rm RT}$  = 0.244, p < .01; Table S4). Bayesian clustering analyses suggest heterogeneous genomic divergence: Neutral loci showed moderate differentiation and substantial admixture between lineages: on the other hand, the 39 AFLP candidate loci showed complete differentiation and nil or very low admixture (Figure 3b; K = 5). Here, all individuals were allocated accurately to each mtCR lineage with very little to no nuclear gene flow or introgression between them (Figure 3b). This agrees with estimates of historical migration in which all pairwise migration parameters (m) from Migrate-N point to a higher probability distribution near zero (Table S5). Overall, the inferred levels of genetic and genealogical differentiation suggest that the five *Pseudobatos* lineages are mostly reproductively isolated.

#### 3.3 | Hypothesis testing of an ecological radiation

Out of the 11 hypotheses assessed, DIYABC results supported with high confidence the hypothesis of a single and recent ecological radiation (H3a, p > .86; Figure 4; Table S7).

### 3.4 | Ecological isolation and niche modelling

There was statistical support for correlations between genetic distance and nutrient concentration, oxygen saturation, and bathymetry, even after controlling for the effect of geographical distance (Table 1). Allele distributions of 57 (10.5%) of 541 AFLP loci were significantly associated with at least one oceanographic variable



**FIGURE 3** (a) Phylogenetic relationships between *Pseudobatos* complex from the Gulf of California–Baja California Peninsula (GC-BCP) region (coloured squares) based on a Bayesian analysis. Shown in the tree are posterior probabilities for each lineage in brackets and the estimated time to the most recent common ancestor in millions of years. The *P. leucorhynchus* from Mexico and *P. horkelii* from Brazil were used as outgroups. (b) Genetic groups of the *Pseudobatos* species complex from the GC-BCP identified with a Bayesian clustering method. Analyses were conducted with 502 neutral AFLP loci (top) and with 39 candidate AFLP loci (bottom). (c) Ecological niche models for lineages of *Pseudobatos* from the GC-BCP using six oceanographic data layers. MaxEnt suitability probability values are listed in a graded series. Pacific Coast (PC), islands region (IG), upper gulf (UG), *P. glaucostigmus* (Pg), lower gulf (LG), area under the ROC curve (AUC) and symmetric extremal dependence indices (SEDI)

**FIGURE 4** (a) Logistic regression posterior probability of the different evolutionary models described Figure 2 and ran in DIYABC. With model H3a (ecological radiation ~1 Mya.) being the best supported. (b) PCA of summary statistics of priors, posterior and observed dataset from model H3a showing that the selected model posterior explains correctly the observed dataset



**TABLE 1** Correlations between<br/>genetic differentiation and geographical<br/>and ecological distances for lineages of<br/>*Pseudobatos* from the Gulf of California<br/>and Baja California Peninsula. Q values<br/>(false discovery rate) are based on partial<br/>Mantel tests of mitochondrial control<br/>region (mtDNA), neutral AFLP loci<br/>(AFLP) and AFLP loci including outliers<br/>(AFLP Sel). Values highlighted in bold are<br/>statistically significant at a false discovery<br/>rate of 5%

				Controlling by geographical distance		
	mtDNA	AFLP	AFLPSel	mtDNA	AFLP	AFLPSel
Geographical distance	0.008	0.008	0.016			
Temperature	0.004	0.004	0.048	0.253	0.438	0.927
Salinity	0.004	0.010	0.016	0.934	0.216	0.344
Oxygen saturation	0.11	0.262	0.030	0.107	0.236	0.028
Nutrients	0.003	0.004	0.008	0.043	0.06	0.021
Chlorophyll-a	0.662	0.258	0.163	0.401	0.367	0.420
∆Temperature	0.016	0.003	0.021	0.692	0.239	0.517
Bathymetry	0.102	0.209	0.001	0.116	0.315	0.012

Bold indicates statistical significant value.

(Table S3; Figure S4). Furthermore, 26 of these loci were also candidate loci detected by both outlier analyses (Table S3), and environmental variation explained 68.2% of the genetic variation present in the candidate loci (p < .001; Figure S4).

Environmental niche modelling showed high entropy with nil to moderate geographical overlap (Figure 3c). Niche identity was rejected for all pairs of lineages, with moderate *I* index values, except for LG versus Pg (Table S6). The latter lineages are sympatric and show high niche overlap.

## 4 | DISCUSSION

Diversification in elasmobranchs has been traditionally associated with vicariant biogeographic history and dispersal limitations (Dudgeon et al., 2012; Musick et al., 2004; Sandoval-Castillo, 2019). Our work showcases the role of isolation by environment in generating and maintaining diversity in this group and suggests that mobility might not hinder speciation in sharks and rays. This adds to cumulative evidence of the importance of heterogeneous marine -WILEY- Journal of Biogeography

# 4.1 | Multiple cryptic species of *Pseudobatos* in the Gulf of California and adjacent coast

A range of analytical methods based on mtDNA and nuclear data provided strong evidence for five lineages of Pseudobatos in the GC-BCP region, including four cryptic lineages within P. productus. These show strong concordance with oceanographically delimited ecological regions (Figure 2d,e). The UG lineage of P. productus appears more closely related to the morphologically distinct P. glaucostigmus (Figure 3b). The other P. productus lineages (LG, PC and IG) are also highly divergent and show nil historical gene flow with other Pseudobatos lineages from the region. It is conceivable that the LG lineage might represent the spiny guitarfish P. spinosus, a taxon described based on a single museum specimen (Günther, 1870). Although morphological data from three specimens suggest that P. spinosus occurs in one locality from the LG (Castro-Aguirre & Pérez, 1996), this taxon has since been synonymized with P. productus (Compagno, 2005). There are no described taxa or synonyms that could be associated with the other cryptic lineages, but reproductive data suggest the existence of distinctive groups in the GC and the PC (Romo-Curiel, Sosa-Nishizaki, Pérez-Jiménez, & Rodríguez-Medrano, 2017; Villavicencio-Garayzar, 1993). Delimiting species on the basis of genetic data can be controversial, but the phylogenetic distinction and levels of genetic differentiation depicted here, in conjunction with results about niche partition and ecological divergence, satisfy a number of different properties used to delineate species. These include operational criteria used in species concepts such as the biological (Dobzhansky, 1950; Mayr, 1942) and some versions of the phylogenetic (Nelson & Platnick, 1981) concept. Thus, a total of four cryptic lineages with likely different stages of evolutionary separation are reported here for P. productus in the GC-BCP region.

# 4.2 | Population history and hypothesis testing of an ecological radiation

Our results suggest a combined impact of the BCP on initial isolation of *Pseudobatos* lineages (PC vs. GC), followed by an ecological radiation at around 1 Mya within the GC. Adaptive radiations are prompted by ecological opportunities in scenarios where incipient lineages are exposed to a wealth of evolutionarily accessible habitats and resources (Kennedy et al., 2017; Losos, 2010; Pontarp & Wiens, 2017). Historical environmental changes and associated range expansions (e.g. Hewitt, 2000) have resulted in opportunities for adaptive divergence and niche specialization (Rodrigues &

Diniz-Filho, 2016). The establishment of the present-day heterogeneous environmental setting of the GC took place between ~2 and 1 Mya, after the final formation of the BCP and the main bathymetric features of the GC (García Sánchez et al., 2019; Mark et al., 2017; Sutherland et al., 2012). We hypothesize that these events, in combination with the mid-Pleistocene transition (1.2-0.8 Mya; Chalk et al., 2017), created ecological opportunities that likely promoted adaptive phenotypic differences between the lineages of Pseudobatos. Despite the inferred strong genetic and ecological divergence (see below), there are no known conspicuous adaptive traits in morphology between Pseudobatos lineages from the GC (Márguez-Farías, 2007; Romo-Curiel et al., 2017). Morphological stasis through different stages of cladogenesis has been reported for several groups (Barley, White, Diesmos, & Brown, 2013; Beheregaray & Caccone, 2007; Bickford et al., 2007; Van Bocxlaer & Hunt, 2013), including elasmobranchs (Ebert & Compagno, 2007; Jones et al., 2017; Last, 2007). One possibility is that rates of morphological diversification in elasmobranchs are limited by the interaction of genetic and developmental constraints, as in some invertebrates (Appeltans et al., 2012; Beldade, Koops, & Brakefield, 2002; Eldredge et al., 2005). Alternatively, the apparent morphological stasis could be due to relatively low niche differentiation within the Gulf (Cothran, Henderson, Schmidenberg, & Relyea, 2013; Scriven, Whitehorn, Goulson, & Tinsley, 2016). The adaptive traits involved in this radiation could also have a physiological basis. In fact, a transcriptomic study of a teleost group has shown that physiological traits linked to environmental tolerances can be under strong selection and delimit sister species ranges across climatic gradients (Sandoval-Castillo et al., 2019). Understanding whether elasmobranch radiations respond by becoming less morphologically diverse in scenarios of relatively limited ecological opportunity (e.g. Corrigan & Beheregaray, 2009), either because of limited developmental paths or due to physiological adaptations, requires currently unavailable phenotypic data. These data, in conjunction with refined statistical approaches that directly link the tempo of lineage diversification to the tempo of phenotypic evolution (Moen & Morlon, 2014) are needed to assess the adaptive nature of the radiation and to conduct a taxonomic revision of Pseudobatos.

### 4.3 | Ecological adaptation and speciation

The first requirement for ecological speciation is a source of divergent selection, and some of the main triggers of divergent selection are habitat structure or contrasting niches (Schluter, 2001). The predicted niche models provide support for ecological partition among *Pseudobatos* lineages and are congruent with habitat heterogeneity and structure proposed for the GC with respect to productivity, oxygen, salinity, temperature, nutrients and bathymetry (Ortega et al., 2010). We also detected contrasting patterns of differentiation between the neutral and candidate loci datasets. Analyses with neutral data showed relatively moderate admixture between *Pseudobatos* lineages and suggests some level of gene flow. During early stages of speciation (as expected for Pseudobatos in the GC), gene flow can prevent the evolution of adaptive divergence (Via, 2012). However, substantial population divergence and rapid speciation between ecologically dissimilar populations in the face of ongoing gene flow has been reported for several organisms (e.g. Beheregaray & Sunnucks, 2001; Bernatchez et al., 2010; Cooke, Chao, & Beheregaray, 2012; Cooke, Landguth, & Beheregaray, 2014; Sandoval-Castillo et al., 2018). On the other hand, Pseudobatos lineages are completely differentiated based on candidate loci (Figure 3b). Long-term reproductive isolation facilitates the accumulation of neutral divergence that could be confused with genetic differentiation associated with traits under selection (Rundle & Nosil. 2005; Via, 2009). However, the Bayesian analyses suggest a relatively short time to the most recent common ancestor of Pseudobatos lineages (< 1.5 Mya; Figure 3a), a scenario consistent with the young age of the heterogeneous environment of the GC. In addition, heterogeneous genomic divergence has been associated with variation in recombination rates during the process of adaptive diversification with gene flow (Roesti, Hendry, Salzburger, & Berner, 2012; Tine et al., 2014). Thus, we consider that Pseudobatos in the GC-BCP exemplifies a radiation involving divergent natural selection with gene flow.

Genetic-environmental associations provide additional evidence for divergent selection that might eventuate in ecological speciation (Bierne, Welch, Loire, Bonhomme, & David, 2011; Stucki et al., 2017). Here, positive trends between genetic distance and three oceanographic variables remained significant after controlling for geographical distance (Table 1). Allele distributions of 26 of 39 outlier loci were significantly associated with at least one oceanographic variable (Table S3; Figure S4). Moreover, the inferred ecological isolation among Pseudobatos lineages (Figure 3c; Table S6) suggests an important role of natural selection in their diversification. The different oceanographic dynamics create sharp dissolved oxygen and nutrients concentration gradients between bioregions in the GC, with some hypoxic and nearly anoxic areas in the LG and OG and highly productive areas in the UG, IG and LG (Lluch-Cota et al., 2007). We propose that the development of metabolic specializations associated with differences in oxygen concentration and diet along ecologically distinct bioregions influenced the radiation of Pseudobatos in the GC. Oxygen consumption requirements differ between species of elasmobranchs (Speers-Roesch et al., 2012), and low oxygen saturation creates selective pressure for physiological adaptations (Renshaw, Wise, & Dodd, 2010; Routley, Nilsson, & Renshaw, 2002). Although nutrient concentration may not directly affect predators such as elasmobranchs, this factor is strongly correlated with primary productivity, which in turn affects abundance and diversity of prey (Korpinen, Jormalainen, & Pettay, 2010). In fact, a key feature of the evolutionary success of elasmobranchs relates to their ecological and anatomical feeding specializations that allowed them to radiate into numerous niches (Ferguson, Higdon, Tallman, Fisk, & Hussey, 2014; Walter et al., 2017; Wilga, Motta, & Sanford, 2007).

The lack of conspicuous morphological differences among lineages suggests that sexual selection might be unlikely. However, divergent habitat preferences are known to generate reproductive isolation if mating occurs in the preferred habitat (Rundle & Nosil, Journal of Biogeography

2005), which can be considered as a type of sexual selection (Oring & Lank, 1982). Species of Pseudobatos, including P. productus, show strong habitat preferences for reproduction (Márquez-Farías, 2007; Villavicencio-Garavzar, 1993). These can be manifested as fidelity of some individuals to mating locations (reproductive philopatry), a driver of genetic structure in several elasmobranchs (Corrigan, Huveneers, Stow, & Beheregaray, 2015; Portnoy & Heist, 2012; Sandoval-Castillo & Beheregaray, 2015). For instance, for bonnethead sharks (Sphyrna tiburo), philopatry was suggested to facilitate sorting of locally adaptive genetic variation among locations and environments (Portnoy et al., 2015). Philopatric behaviour can be a form of prezygotic sexual selection and that might contribute to the patterns observed here (Nosil, Funk, & Ortiz-Barrientos, 2009). We hypothesize that divergent habitat preferences for reproduction, potentially linked to gradients in oxygen, nutrients and bathymetry, have influenced the evolution of reproductive isolation among Pseudobatos lineages in the GC.

A limitation of our study is that genome scans were based on anonymous AFLP dominant markers. Genome-wide marker panels, whole genomes and transcriptomes can now be used to better delineate barriers to gene flow, selection gradients and isolation by environment, and to identify gene regions and phenotypic traits involved in adaptation (Grummer et al., 2019; Rellstab, Gugerli, Eckert, Hancock, & Holderegger, 2015; Riginos et al., 2016; Sandoval-Castillo, 2019). Regional-scale studies in sharks and rays should test for population diversification across heterogeneous environments while controlling for spatial genetic autocorrelation and vicariant biogeographic history (Beheregaray et al., 2015). These surveys would also benefit from a priori spatial delineation of adaptive phenotypes. Such studies are expected to contribute substantially to integrative taxonomic efforts (Dayrat, 2005) and to the conservation and management of elasmobranchs worldwide (Sandoval-Castillo, 2019).

#### ACKNOWLEDGEMENTS

We thank O. Sosa-Nishizaki, A. Rocha-Olivares, J. Ramirez-Gonzales, K. de-la-Rosa, C. Perez-Jimenez, F. Galvan-Magaña and the fisheries communities from the Gulf of California and the Baja California Peninsula for assistance with fieldwork. We also thank S. Corrigan, G. Cooke, C. Attard and K. Gates for comments on an earlier manuscript. Tissue samples were obtained from artisanal fisheries landings and following Mexican legislation (NOM-029 and NOM-059). This work was funded in part by the Australian Research Council (DP110101275 and FT130101068 to LBB) and by Macquarie University (travel grant and PhD scholarship to JSC). This is publication #59 of the Molecular Ecology Group for Marine Research (MEGMAR). We thank Prof Michael Dawson and two anonymous reviewers whose comments have greatly improved this manuscript.

#### DATA AVAILABILITY STATEMENT

AFLP genotypes, mtDNA sequences, sample coordinates and environmental data used in analyses are available on Figshare Digital Repository (DOI: 0.6084/m9.figshare.10317203) and on GenBank (accession numbers: MT134048-MT134099).

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#### BIOSKETCH

Jonathan Sandoval-Castillo is broadly interested in elasmobranch biogeography. This work represents a component of his PhD work at Macquarie University. Luciano Beheregaray supervised Sandoval-Castillo during his PhD and heads the Molecular Ecology Lab at Flinders University (http://www.molecularecology.flinders.edu.au/).s

Author contributions: JSC and LB conceived the study and wrote the manuscript; JSC did the fieldwork, and generated and analysed the data.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Sandoval-Castillo J, Beheregaray LB. Oceanographic heterogeneity influences an ecological radiation in elasmobranchs. *J Biogeogr.* 2020;00:1–13. <u>https://</u> doi.org/10.1111/jbi.13865