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Genetic connectivity of two marine gastropods in the Mediterranean Sea: seascape genetics reveals species-specific oceanographic drivers of gene flow

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Abstract

Oceanographic features such as currents, waves, temperature and salinity, together with life history traits, control patterns and rates of gene flow and contribute to shaping the population genetic structure of marine organisms. Seascape genetics is an emerging discipline that adopts a spatially explicit approach to examine biotic and abiotic factors that drive gene flow in marine environments. In this study, we examined factors that contribute to genetic differentiation in two coastal Mediterranean gastropods whose geographical ranges overlap but which inhabit different environments. The two species differ in several life history traits and in their dispersal capabilities. Genetic differentiation was relatively low for the trochid species *Gibbula divaricata* (F_{ST} =0.059), and high for the vermetid species *Dendropoma lebeche* (F_{ST} =0.410). Salinity emerged as the most important variable explaining the genetic structure of both species; sea surface temperature was also important for *G. divaricata*. For the more sessile *D. lebeche*, the coastline was predicted to provide important pathways for stepping-stone connectivity and gene flow. Our results provide a greater understanding of the factors influencing marine population connectivity, which may be useful to guide marine conservation and management in the Mediterranean.

KEYWORDS
Dendropoma lebeche, genetic connectivity, *Gibbula divaricata*, landscape genomics, marine conservation, multivariate optimization, population genetics, seascape genetics, UNICOR

1 | INTRODUCTION

Connectivity, defined as the interchange of individuals among populations, plays a key role in promoting population viability by favouring gene flow among demes, and allowing for demographic rescue and recolonization following local extinction, which can counteract local declines and reduce extinction vulnerability (Cowen & Sponaugle, 2009; Dulvy et al., 2003). Despite its relevance for conservation, assessing population connectivity in the marine realm is hampered by the scarce knowledge of the interplay between abiotic factors, such as oceanographic currents, fronts or environmental features, and the wide variety of life history traits typical of marine species, such as reproduction mode, offspring size, type and duration of larval development, habitat requirements and adult migratory behaviours, among others (Selkoe et al., 2015).

In recent years, marine biodiversity has faced large-scale declines worldwide (McCauley et al., 2015), with numerous species pushed to the edge of extinction and restricted to small isolated populations (Fordyce et al., 2019; Sala & Knowlton, 2006). The spawning period of many marine species is directly related to sea surface temperature (SST), and thus global warming is a critical factor impacting marine population connectivity and decline

(Przeslawski et al., 2008). While global warming is now a well-known driver of marine ecosystem collapse, less is known about the relative influence of other abiotic and biotic factors that support genetic connectivity and population resilience in oceanic systems (López-Márquez, et al., 2019a).

Among abiotic factors, sea currents are considered a predominant agent promoting connectivity for some populations, whereas for others, they act as barriers to gene flow (Treml et al., 2008). In places where sea currents interact with each other or with the coastline topography, oceanic fronts are formed, which potentially restrict connectivity, even among proximal localities. In the western and central Mediterranean Sea, six major sea fronts have been highlighted as driving factors shaping population connectivity in a wide diversity of taxa (Pascual et al., 2017). The Gibraltar Strait (GS) front, located between the Iberian Peninsula and Africa and originating from the influx of less saline Atlantic waters to the more saline Mediterranean, has been reported as a barrier to gene flow for numerous marine species (Figure 1; Galarza et al., 2009; Lowe et al., 2012; Marie et al., 2016). The Almeria-Oran Front (AOF), located between southeastern Spain and Algeria, has been proposed as an additional frontier between the Atlantic Ocean and the Mediterranean Sea (Patarnello et al., 2007; Tintoré et al., 1988). The four other oceanographic discontinuities representing potential barriers to connectivity within the Mediterranean include the Balearic Front (BF) over the Balearic Islands, the Ibiza Channel (IC) between the island of Ibiza and the Iberian Peninsula, the Sicily Channel (SC) located from southern Sicily to the Tunisian coast, and the Otranto Strait (OS) between the Adriatic and Ionian seas (Ferentinos & Kastanos, 1988; Menna et al., 2019; Ruiz et al., 2009). The OS has been recently shown to be associated with genetic structure of marine invertebrate species (López-Márquez, et al., 2019a).

Apart from oceanic currents and fronts, other abiotic factors, such as the coastline configuration and habitat distribution, may influence gene flow and genetic differentiation in coastal species. For instance, bays often act as retention zones where self-recruitment is more common compared with in open coasts (Nicastro et al., 2008). Salinity gradients have also been described as an important factor determining gene flow via their association with nearby sea currents and fronts, with variation in water physiochemistry being a strong driver of habitat suitability for many marine organisms (Millot & Taupier-Letage, 2005). For instance, the pronounced salinity gradient (2 parts per thousand) over a distance of 2 km in the Alboran Sea

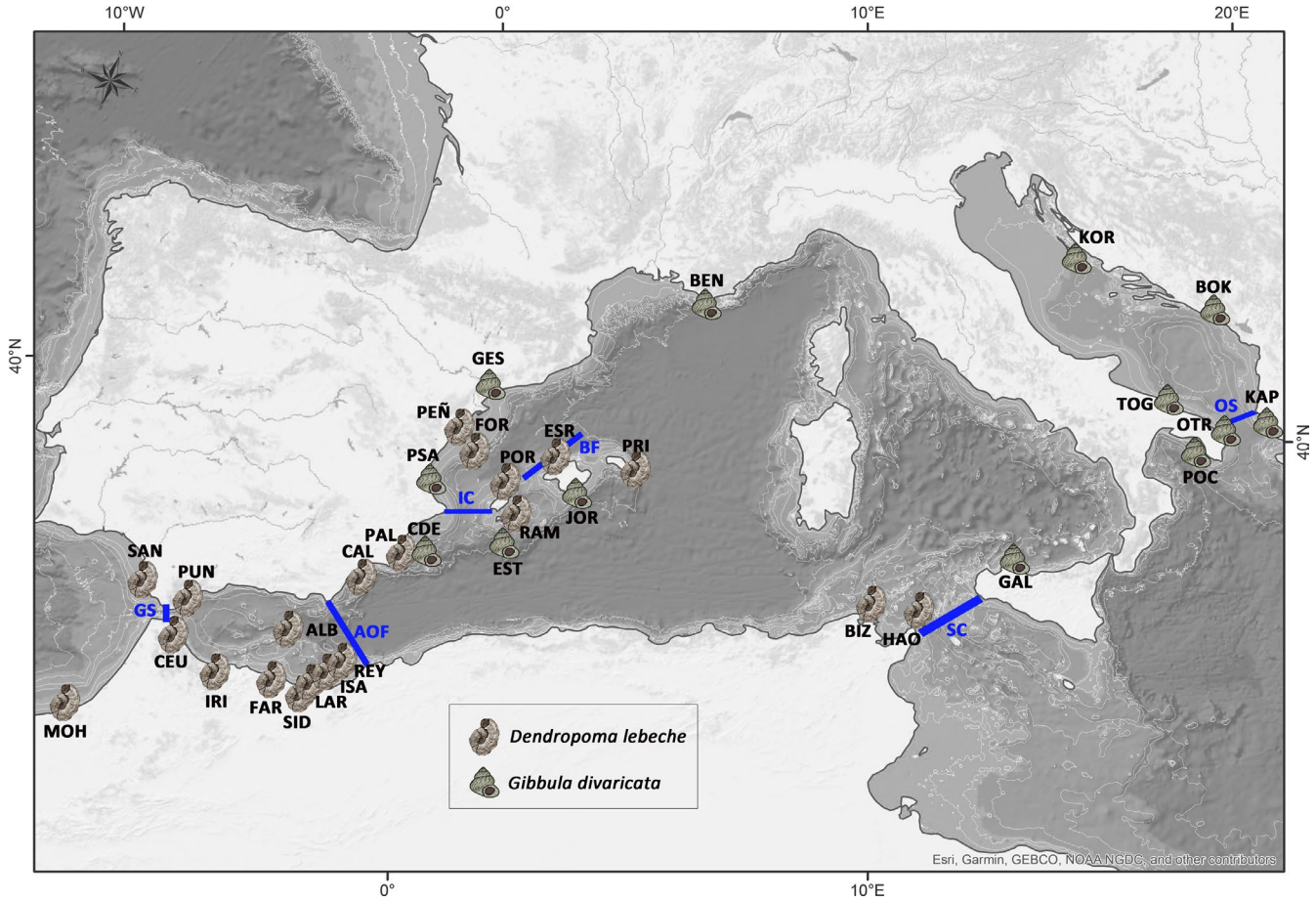


FIGURE 1 Map representing the sampling locations in the western Mediterranean Sea and proximal Atlantic Ocean and the oceanographic fronts analysed (blue lines). The acronyms of fronts (in blue): GS (Gibraltar Strait), AOF (Almeria-Oran Front), IC (Ibiza Channel), BF (Balearic Front), SC (Sicily Channel) and OS (Otranto Strait). For population codes, see Table 1

TABLE 1 Location of *Gibbula divaricata* and *Dendropoma lebeche* samples. *N* indicates the number of samples analysed from each location

Species	Location name	Label	GPS coordinates	*N*
G. divaricata	Canal del Estacio (Murcia, Spain)	CDE	37°44′49.22″N, 0°44′12.94″W	30
G. divaricata	Port Saplaya (Valencia, Spain)	PSA	39°30′38.80′′N, 0°19′5.11′′W	34
G. divaricata	Cala de Gestell (Tarragona, Spain)	GES	40°57′29.94″N, 0°52′47.78″E	23
G. divaricata	Estany des Peix (Formentera, Spain)	EST	38°43′39″N, 1°24′26″E	30
G. divaricata	Colònia Sant Jordi (Mallorca, Spain)	JOR	39°18′42.56″N, 2°59′36.28″E	21
G. divaricata	Isla de Bendor (Marseille, France)	BEN	43°7′41.80″N, 5°45′2.09″E	13
G. divaricata	Capo Gallo (Sicily, Italy)	GAL	38°12′33.21″N, 13°16′55.36″E	30
G. divaricata	Porto Cesareo (Apulia, Italy)	POC	40°11′715′′N, 17°55′ 077′′E	34
G. divaricata	San Foca, Otranto (Apulia, Italy)	OTR	40°18′12′′N, 18°24′ 17′′E	29
G. divaricata	Torre Guaceto (Apulia, Italy)	TOG	40°42′999′′N, 17°48′ 003′′E	30
G. divaricata	Kornati National Park (Croatia)	KOR	43°46′31′′N, 15°37′ 51′′E	31
G. divaricata	Boka Kotorska (Montenegro)	BOK	42°24′888′′N, 18°38′ 111′′E	35
G. divaricata	Karaburun Peninsula (Vlorë Country, Albania)	KAP	40°26′35′′N, 19° 29′ 08′′E	16
D. lebeche	Mohammedia (Morocco)	MOH	33°42′30.12″N, 7°22′44.70″W	26
D. lebeche	Sancti Petri (Cádiz, Spain)	SAN	36°23′10.64″N, 6°12′30.27″W	30
D. lebeche	Punta Carnero (Gibraltar, Spain)	PUN	36°04′21.15″N, 05°25′44.18″ W	30
D. lebeche	Ceuta (Spain)	CEU	35°53′43.76″N, 5°18′17.58″W	28
D. lebeche	Cala Iris (Morocco)	IRI	35°9′6.52″N, 4°21′58.26″W	30
D. lebeche	Faro Tres Forcas (Morocco)	FAR	35°26′8.84″N, 2°57′26.94″W	30
D. lebeche	Isla Alborán (Spain)	ALB	35°56′16.8″N, 3°2′11.4″W	30
D. lebeche	Sidi el Bachir (Morocco)	SID	35°5′20.24″N, 2°31′46.38″W	32
D. lebeche	Congreso (Islas Chafarinas, Spain)	LAR	35°10′35.3″N, 2°26′23.9″W	30
D. lebeche	Isabel II (Islas Chafarinas, Spain)	ISA	35°10′53.2″N, 2°25′53.5″W	30
D. lebeche	Rey Francisco (Islas Chafarinas, Spain)	REY	35°11′3.7″N, 2°25′22.1″W	30
D. lebeche	Calnegre (Murcia, Spain)	CAL	37°30′22.99″N, 1°25′00.92″W	31
D. lebeche	Cabo Palos (Murcia, Spain)	PAL	37°37′49.64″N, 00°42′05.19″W	30
D. lebeche	Peñíscola (Castellón, Spain)	PEÑ	40°21′40.36″N, 0°24′13.76″E	15
D. lebeche	La Foradada (Islas Columbretes, Spain)	FOR	39°52′30″N, 0°40′16.0″E	30
D. lebeche	Portinatx (Ibiza, Spain)	POR	39°6′54.86″N, 1°31′19.52″E	22
D. lebeche	Es Ram (Formentera, Spain)	RAM	38°39′13.74″N, 1°31′22.84″E	30
D. lebeche	Es Ratjoli (Mallorca, Spain)	ESR	39°38′3.60″N, 2°25′19.64″E	30
D. lebeche	Punta Prima (Menorca, Spain)	PRI	39°48′50.34″N, 4°17′6.99″E	20
D. lebeche	Bizerte (Tunisia)	BIZ	37°19′48.47″N, 9°51′53.61″E	25
D. lebeche	Cape Bon (Tunisia)	HAO	37°5′17.19″N, 11°2′5.34″E	20

drives the inflow of Atlantic water to the gyre generating the AOF (Tintoré et al., 1988).

Biotic factors driving individual mobility at the larval, juvenile and adult stages are also crucial to understand genetic structure across a seascape. Marine organisms that have life history traits associated with a long planktonic larval stage typically exhibit long-distance dispersion by sea currents, which may contribute to low genetic structure (Pascual et al., 2017). However, higher than expected genetic differentiation has been documented for numerous marine species with high dispersal capacities, contradicting the idea that the seas are open and well-connected systems (Calderón et al., 2007; Palero et al., 2008; Pérez-Ruzafa et al., 2006). As a general rule, the main dispersal stage of coastal nonsessile species is the larval phase, although juveniles and adults also disperse to some degree. For sessile species, dispersal occurs almost exclusively during the larval transport phase (Cowen & Sponaugle, 2009), although some small species can also disperse by rafting at juvenile or adult stages (Martel & Chia, 1991). Species with a long planktonic larval duration (PLD) should be more affected by abiotic factors such as oceanographic fronts. In contrast, genetic differentiation in benthic sessile species with short PLDs is thought to be determined mostly by biotic and local factors, independently of oceanographic barriers (Pascual et al., 2017).

To understand the complex interplay between abiotic and biotic factors shaping genetic structure in marine organisms requires an

integrative, spatially explicit analytical approach. Seascape genetics provides an ideal framework in which to test the role of different abiotic factors as potential drivers of genetic connectivity in marine environments (Selkoe et al., 2016). Moreover, comparative studies applying seascape genetic approaches to syntopic (co-occurring) species could provide strong inferences about the main drivers of gene flow in marine ecosystems.

In this study, we analyse such interactions among different factors that may modulate the connectivity and, therefore, the genetic structure and differentiation of two co-occurring Mediterranean species using a seascape genetic approach. Our model species include two gastropods whose ranges overlap: the top shell trochid *Gibbula divaricata* and the sessile vermetid *Dendropoma lebeche*. Both species have a coastal distribution in the Mediterranean Sea and are believed to have low dispersion capacity. Further, *D. lebeche* is a threatened reef-building species highly sensitive to direct and indirect human pressures. This species belongs to the so-called "*Dendropoma petraeum*" species complex, which according to previous molecular analysis comprises four genetically distinct clades with a west–east phylogeographical split and no geographical overlap (Calvo et al., 2009, 2015). Each of these cryptic clades roughly corresponds to a different Mediterranean sub-basin. *Dendropoma lebeche* is restricted to the southwestern Mediterranean and the nearby Atlantic coasts.

Dendropoma reefs are particularly vulnerable and, thus, greater knowledge of the processes driving their dispersal is needed. These reefs, which are threatened by human coastal development and rapid environmental changes, have been decimated or even eliminated in some areas (Galil, 2013). Therefore, given the importance of Mediterranean reef ecosystems, the cryptic species of this complex have been included in Annex II (Endangered or Threatened Species) of the Protocol for Specially Protected Areas and Biodiversity in the Mediterranean (Barcelona Convention) and Appendix II (Strictly Protected Fauna Species) of the Bern Convention (Templado et al., 2004).

Long-lived, structural invertebrates, such as *D. lebeche*, have a much lower recovery potential than small, short-lived organisms, and the limited connectivity of this gastropod decreases its recovery potential even more. Recovery often depends on intrinsic factors such as life history traits, population structure and genetic diversity, but also on extrinsic factors such as the type and magnitude of the disturbance, and the conservation and management measures applied to reduce human impacts (Lotze et al., 2011). Therefore, conserving the important intertidal reefs of *D. lebeche* requires understanding the oceanographic processes that drive their dispersal and recolonization dynamics, and conservation measures based on this knowledge must be implemented at a transnational level to protect the most important locations for local populations and network connectivity. Importantly, less than 30% of the known extent of these reefs are located within marine protected areas (MPAs) or coastal reserves (Chemello et al., 2014).

The common species *G. divaricata*, known as top shells, inhabits the Mediterranean Sea (Templado, 2011). This species shares habitat with other conspecific species as *G. rarilineata* whose morphological characteristics could overlap (López-Márquez, et al., 2019b). Although frequent, *G. divaricata* is threatened by habitat fragmentation due to human activities in the coastline.

The reproductive biology of *G. divaricata* is poorly known. It appears to reproduce continuously throughout the year (our pers. obs.), and has a planktonic larval phase that lasts only a few days (Chuckhchin, 1960). The reproductive season of *D. lebeche* begins in late April when the water temperature increases, and continues until the end of summer when the water temperature decreases (Calvo et al., 1998). This species has an entirely intracapsular development without free-swimming larvae; therefore, its dispersal seems restricted to the very sporadic rafting events of crawling juvenile snails, with self-recruitment predominately driving the maintenance of its populations (Calvo et al., 1998).

The main objective of this study was to identify and contrast the factors affecting genetic connectivity (and conversely differentiation) of two marine species with limited dispersal capacities, one common (*G. divaricata*) and the other threatened (*D. lebeche*). We assessed marine resistance to gene flow using multivariate optimization following the methodology of Shirk et al. (2010), Shirk et al. (2018) and a previously described approach for modelling wind-driven dispersal (Landguth et al., 2017) to account for the directionality of current flows in the marine environment (e.g., López-Márquez, et al., 2019a). We hypothesized that *D. lebeche* would show a stronger genetic structure given its life history traits (lack of a pelagic larval stage and a sessile adult lifestyle). In contrast, we expected *G. divaricata* to show more extensive genetic admixture among populations due to the relatively higher dispersal capability of its planktonic larvae. Given their different life history traits, we expected that connectivity among *D. lebeche* populations would be more conditioned by abiotic factors such as coastline topography and habitat features, whereas *G. divaricata* would show stronger associations with oceanographic factors such as sea currents.

2 | MATERIALS AND METHODS

2.1 | Target species

Dendropoma lebeche is a reef-building species distributed in the southwestern Mediterranean and adjacent Atlantic coasts (Templado et al., 2016). This gregarious vermetid creates symbiotic bioconstructions with crustose coralline algae (e.g., *Neogoniolithon brassica-florida*) from monolayer encrustations over rocks at low intertidal levels to large rims on the outer edge of abrasion platforms (Templado et al., 2016). Together, the gastropod and algae species give rise to irregular conglomerates on the lowest intertidal rocky coast made up of thousands of individuals, in open semi-exposed shores and the upper surface of these aggregations often coincides with the biological mean sea level. The population density in dense aggregates ranges normally between 400 and 600 individuals dm^{-2} (Templado et al., 2016). *Dendropoma lebeche* requires specific

hydrodynamic conditions that include swaying waves but not direct wave impact. It seems to withstand high temperatures and inhabits the warmest areas of the western Mediterranean where the temperature does not drop below 14°C (Chemello, 2009; Chemello & Silenzi, 2011). The coastline topography and slope of the substrate can also affect its establishment: it shows a preference for horizontal surfaces, and avoids steeply inclined slopes.

Gibbula divaricata inhabits very shallow rocky bottoms (typically, 0–1 m of depth) that are highly sheltered from wave action, including coastal lagoons, harbour areas and artificial hard structures, and tolerates some degree of pollution (López-Márquez, et al., 2019b). As such, the coastline topography and the existence of protective elements (e.g., rocky barriers or artificial coastal defence structures) is a determining factor for the occurrence of this species. Temperatures in these highly protected shallow environments are much more variable and extreme compared to SSTs in open water. Therefore, this species is probably eurythermal (i.e., it is able to tolerate wide changes in temperature). It typically has a patchy pattern of distribution, with dense populations found in more favourable habitats but not in sandy beaches and rocky coastlines exposed to waves (López-Márquez, et al., 2019b).

Between 13 and 35 specimens of *G. divaricata* or *D. lebeche* were collected from 13 and 21 sampling locations, respectively (Table 1). Trochid specimens of *G. divaricata* were collected by hand from the rocky shore, and vermetid colonies of *D. lebeche* were sampled from the rocky intertidal level by removing pieces of aggregates with a chisel and a hammer. The operculum of gastropods can prevent thorough fixation of inner tissues; therefore, individuals were first cooled to 4°C to prevent the operculum from closing, prior to the removal of the soft tissue parts. All individuals were fixed in absolute ethanol and stored at 4°C. Top-shells were deposited in the Malacological Collection at the Museo Nacional de Ciencias Naturales in Madrid (MNCN 15.05/80147. 15.05/80148. 15.05/80150. 15.05/80173).

2.2 | Study area

The study area was the Mediterranean Sea and two locations in the northeastern Atlantic Ocean (Figure 1), covering the entire known extent of the distributions of the two study species. The sampling sites included the Moroccan Atlantic coasts, the gulf of Cádiz, the Strait of Gibraltar, and the Alboran, Balearic, Tyrrhenian, Adriatic and Ionian seas.

Dendropoma lebeche, which has a discontinuous and patchy distribution, was sampled at 21 localities. Two sites were located along the Atlantic coasts close to the Mediterranean: Mohammedia (MOH) on the coast of Casablanca (Morocco) and Sancti Petri (SAN) in the Gulf of Cádiz (Spain), which are 330 km apart. One site was selected for each side of the Strait of Gibraltar, one in Algeciras (Cádiz, Iberian Peninsula; PUN), and one in Ceuta (North Africa; CEU), separated by 25 km. Seven sites were selected in the Alboran Sea along the Moroccan coast (IRI, FAR and SID), Alborán Island (ALB) and Chafarinas Islands (ISA, REY and LAR), where the greatest distance between sites is 170 km (between ALB and IRI). Two sites, ~70 km apart, were sampled in southeastern Spain (Calnegre, CAL; and Cabo de Palos, PAL). Six sites were sampled in the Balearic Sea: one off the coast of Castellón (PEÑ), another ~65 km east of Castellón near Columbretes Islands (FOR), and one off each of the four Balearic Islands, Menorca (PRI), Formentera (RAM), Mallorca (ESR) and Ibiza (POR), where the largest distance between sites is 295 km (between PRI and RAM). Finally, the most eastern sampling locations were two in the Tyrrhenian Sea along the coast of Tunisia (BIZ and HAO), separated by 120 km. More than 1,700 km separate the eastern-most (HAO) and western-most (MOH) localities (Figure 1; Table 1).

Gibbula divaricata is found on shallow, sheltered rocky bottoms or artificial hard structures throughout the western and central Mediterranean Sea and, similar to *D. lebeche*, has a patchy coastal distribution. We sampled populations of the species at 13 Mediterranean localities. We collected one in Murcia in southeastern Spain (CDE), and four in the Balearic Sea, of which two were on the Spanish coast near Valencia (PSA) and Tarragona (GES), separated by 195 km, and two were off the Balearic Islands of Formentera (EST) and Mallorca (JOR), 165 km apart. We also sampled a single locality between the Balearic and Ligurian seas in Bendor (BEN), which is a small island close to Marseille (France). Tyrrhenian sea samples were collected from Capo Gallo (GAL) (Sicily). Five localities were sampled in the Adriatic Sea: three along the eastern Adriatic coast in Albania (KAP), Montenegro (BOK) and Croatia (KOR), with a maximum distance between localities of 500 km (KAP and KOR), and two along the Apulian coast of Italy (TOG and OTR), separated by about 90 km. Porto Cesareo in the Gulf of Taranto (POC) in the northern Ionian Sea was also sampled.

The pattern of sea surface circulation in the Mediterranean Sea has been widely described by a variety of oceanic models (e.g., Fernández et al., 2005; Rio et al., 2007). We designed our sampling to ensure that most of the populations sampled were situated on different sides of the six potential dispersal barriers (SG, AOF, IC, BF, SC and OS, Pascual et al., 2017). In addition, the sampling localities represent four of the six sub-basins within the Mediterranean Sea: the western Mediterranean, Tyrrhenian, Ionian and Adriatic seas. We also included *D. lebeche* populations from two proximal Atlantic localities. In the eastern Mediterranean and the Levantine Sea, *D. lebeche* is absent (replaced by *D. anguliferum*), and *G. divaricata*, which was previously considered to be distributed throughout the entire Mediterranean Sea (Templado, 2011), has been displaced by a related species (*G. rarilineata*) from Italy to the easternmost Mediterranean (our pers. obs.).

2.3 | Genetic analysis

Genomic DNA was extracted from the foot and head tissues of the *G. divaricata* and *D. lebeche* specimens, respectively. DNA was purified using the QIAGEN BioSprint 15 DNA Blood Kit (Qiagen), according to the protocol for tissue samples, including an RNase treatment step. The DNA was quantified using a NanoDrop and the Quant-iT

dsDNA HS Assay, according to the manufacturer's instructions. Aliquots of 2 ng μl^{-1} were prepared for genotyping analyses. DNA quality was also checked on 0.8% agarose gels.

Gibbula divaricata specimens were identified to the species level by molecular determination made by DNA barcoding following Barco et al. (2013). A 658-bp fragment at the 5′ end of cytochrome *c* oxidase subunit I (COI) was amplified using the primers LCO1491 (Folmer et al.,1994) and COI-H (Machordom et al., 2003). Sequences were compared with those available in GenBank using the BLAST algorithm (Altschul et al., 1997). *Dendropoma lebeche* species identification followed a previous study (Templado et al., 2016) where the species showed a clearly delimited geographical distribution and was highly divergent at both levels of mitochondrial and nuclear genes (Calvo et al., 2009).

Twenty-three polymorphic microsatellites for *G. divaricata* (López-Márquez et al., 2016) and *D. lebeche* (López-Márquez et al., 2018), respectively, were initially tested using nested PCR (polymerase chain reaction), a method successfully applied in other species including the nemertean *Malacobdella arrokeana* (Alfaya et al., 2014) and the mollusc *Panopea abbreviata* (Ahanchédé et al., 2013). To amplify *G. divaricata* populations, a three-primer PCR (Vartia et al., 2014) was performed following the same procedure and conditions as in López-Márquez, et al. (2019b). For *D. lebeche*, the forward primer from each primer pair was fluorescently 5′ end-labelled with either 6-FAM, NED, VIC or PET, while reverse primers were pig-tailed with 5′-GTTTCTT-3′ (Brownstein, 1996). PCRs were performed as in López-Márquez et al. (2018).

Null alleles and scoring errors were examined using MICRO-CHECKER (Van Oosterhout et al., 2004), and homozygous frequencies were adjusted when the null allele frequency was estimated at >0.20. Possible loci under selection were analysed using BAYESCAN 2.1 and ARLEQUIN version 3.5 (Excoffier et al., 2005). Allelic diversity (*Na*), observed (H_O) and expected (H_E) heterozygosities and Hardy–Weinberg equilibrium (HWE) were quantified using GENEPOP version 4.0 (Raymond & Rousset, 1995) and GENALEX 6.0 (Peakal & Smouse, 2006). When required, *p*-values were corrected with the sequential Bonferroni method (Rice, 1989).

Genetic differentiation among sampling locations was measured by Wright's fixation index (F_{ST}) and standarized values (F'_{ST}, Meirmans, 2006), calculated using GENALEX. Significant values were checked with GENETIX (Belkhir et al., 2004). We used a principal coordinates analysis (PCoA) to visualize population genetic clustering based on F_{ST} values.

Estimates of the effective population size were calculated using NEESTIMATOR version 2 (Do et al., 2014) following the linkage disequilibrium method (Waples & Do, 2008).

We used STRUCTURE 2.2.3 (Pritchard et al., 2000) to infer population genetic structure using an admixture model with correlated allele frequencies and location specified as a prior. We ran 20 replicates per *K*, with *K* = 1–14 for *G. divaricata*, and *K* = 1–22 for *D. lebeche*, calculating the mean log probability of the data (lnP(*K*)), with 100,000 Markov chain Monte Carlo (MCMC) iterations following a 10,000 iteration burn-in. In order to evaluate the optimal value of *K*, we employed both ln(Pr(*X*|*K*) values (median values of Ln (Pr Data)) and Δ*K* using STRUCTURE HARVESTER (Earl & vonHoldt, 2012) and following the method proposed by Evanno et al. (2005). We also used the software STRUCTURESELECTOR (Li & Liu, 2017) to implement Puechmaille's (2016) method, which has been shown to perform better with uneven samples. CLUMPAK (Kopelman et al., 2015) was used to compare results across the 20 replicates per each *K*.

A Bayesian assignment method (Rannala & Mountain, 1997), implemented in GENECLASS (Piry et al., 2004), was used to detect putative first-generation migrants and to calculate individual probabilities of assignment to each population. For this, a MCMC resampling method with a simulation algorithm (Paetkau et al., 2004) was run using 10,000 simulated individuals and a type I error threshold of 0.05.

To test barriers to gene flow, we used BARRIER version 2.2 (Manni et al., 2004) to perform a Delaunay triangulation from the coordinates of the sampling sites using Monmonier's (1973) maximum-difference algorithm and the pairwaise F_{ST} matrix. To test barrier robustness, 100 resampled bootstrap matrices were evaluated (R function provided by Eric Petit, UMR ECOBIO CNRS, Paimpont).

2.4 | Isolation-by-distance

We analysed isolation-by-distance (IBD) using two methods. First, we performed a Mantel permutation test as implemented in GENALEX (9,999 permutations; Mantel, 1967) to analyse the correlation between linearized F_{ST} ($F_{ST}/(1 - F_{ST})$) and the log of the shortest geographical distance over water. We calculated the shortest geographical distances over water among all pairs of sampling sites by running a factorial least cost paths analysis in UNICOR (Landguth et al., 2012) on a resistance surface that had all water cells set to a value of 1 and all land cells set to a value of 1,000,000 (essentially making any land a barrier to movement). The second IBD approach used linear mixed effects modelling (LME) in the RESISTANCEGA package in R (Peterman, 2018) to calculate the Akaike information criterion (AIC; Akaike, 1973) for the F_{ST} values and the shortest geographical distance between all sampling locations.

2.5 | Seascape variables

We selected a series of environmental variables potentially related to connectivity among the mollusc populations analysed, such as those previously analysed by us in a study on the Mediterranean coral *Cladocora caespitosa* (López-Márquez, Cushman, et al., 2019) (Table 2). These included (1) ocean bathymetry, based on the global high-resolution shoreline (GSHHS) at 30 arc-second raster resolution (downloaded from EMODnet; http://www.emodnet.eu/bathymetry), (2) seawater temperature, analysed by three temporal effects: the means of monthly data (SST), and the coldest (SST_C) and warmest months (SST_W), (3) three salinity variables: the means of monthly data (SSS), and the freshest (SSS_F) and saltiest

TABLE 2 Description of the environmental variables used in the study

Acronym	Description
SSS	Salinity annual mean
SSS_F	Salinity freshest month mean
SSS_S	Salinity saltiest month mean
SST	Temperature annual mean
SST_C	Temperature coldest month mean
SST_W	Temperature warmest month mean
Shore	Resistance values for water: 50; shore: 1
Strict	Resistance values for water: 1,000; shore: 1
Water	Resistance values for water: 1
curr_01_mean	January currents mean
curr_02_mean	February currents mean
curr_03_mean	March currents mean
curr_04_mean	April currents mean
curr_05_mean	May currents mean
curr_06_mean	June currents mean
curr_07_mean	July currents mean
curr_08_mean	August currents mean
curr_09_mean	September currents mean
curr_10_mean	October currents mean
curr_11_mean	November currents mean
curr_12_mean	December currents mean
curr_win_mean	Winter currents mean
curr_spr_mean	Spring currents mean
curr_sum_mean	Summer currents mean
curr_fall_mean	Autumn currents mean

months (SSS_S) (variables 2 and 3 were obtained from the marine spatial ecology website MARSPEC; http://marspec.weebly.com/) and (4) sea surface currents collected from three depths (1, 5 and 16 m) using zonal and meridional velocities at three temporal resolutions (hourly, daily and monthly) from the Copernicus Marine environment monitoring service (CMEMS V4) at a resolution of 0.042 arc-degrees. For this final variable, we performed Mantel tests and removed highly correlated surface current variables (r >.98). After this screening, months were grouped by season and monthly means were retained. Given that depth data were highly correlated, we used a surface current depth of 1 m, as both species are generally found around this depth.

Sea surface currents were considered as directional variables (Landguth et al., 2017; López-Márquez, et al., 2019b), the bathymetric data set as cost variables (Cushman et al., 2006) and SSTs (SST, SST_C and SST_W), together with salinity (SSS, SSS_F and SSS_S), as slope variables (Cushman, et al., 2013a; Yang et al., 2013a). The functional form and magnitude of resistance relationships for slope variables were optimized by varying the shape of the response function (Bothwell et al., 2017; Shirk et al., 2010); rasters with different power functions (0.1, 0.5, 1, 1.5 and 3) were generated in ARCINFO WORKSTATION 10.2.2 (Environmental Systems Research Incorporated [ESRI], 2011). Every cell value in the raster represents the hypothesized cost to move across a specific location. To calculate cumulative cost distances among the sampling sites (Cushman et al., 2006; Dunning et al., 1992), we used UNICOR (Landguth et al., 2012) for cost and slope variables. In the case of directional variables, we used the directionality function implemented in UNICOR (Landguth et al., 2017) to calculate the asymmetric "current cost-distance" from the zonal and meridional velocities.

2.6 | Resistance hypotheses

Seascape resistance layers were developed using the same methodology as in López-Márquez, et al. (2019a). Using the bathymetric data, we classified the coastline as water pixels within 1,000 m of land, and the rest of the water pixels as open water. We designed three resistance hypotheses by assigning different resistance values to movement through the coastline versus open water: (i) *Water*, in which all water pixels were assigned a resistance value of 1, (ii) *Shore* with a resistance value of 1 for coastline and 50 for open water and (iii) *Strict* with a resistance value of 1 for coastline and 1,000 for open water (Table 3). The *Water* model represents isolation by water distance, *Shore* corresponds to high connectivity along the coastline and relatively high resistance through the open water and *Strict* limits gene flow along the coastline with very little movement allowed through open water. All rasters were resampled to 500-m resolution, and all GIS layers were processed in ARCGIS 10.3.1.

2.7 | Isolation by seascape resistance

To test how the oceanographic factors influence gene flow in both molluscs, we used a two-step procedure that uses LME coupled with AIC model selection and multivariate restricted optimization (Shirk et al., 2010) (Figure 2). This approach has been widely used and is considered one of the strongest model selection approaches currently available for comparing alternative landscape resistance models (Shirk et al., 2018).

TABLE 3 Resistance models used to test the relative resistance of movement (in terms of gene flow) along the coastline and open water for *Gibbula divaricata* and *Dendropoma lebeche*. Numbers represent hypothesized resistance values assigned to each area in the Mediterranean Sea

	Resistance values		
Model	Coastline	Open Water	Land
Water	–	1	1,000
Shore	1	50	1,000
Strict	1	1,000	1,000

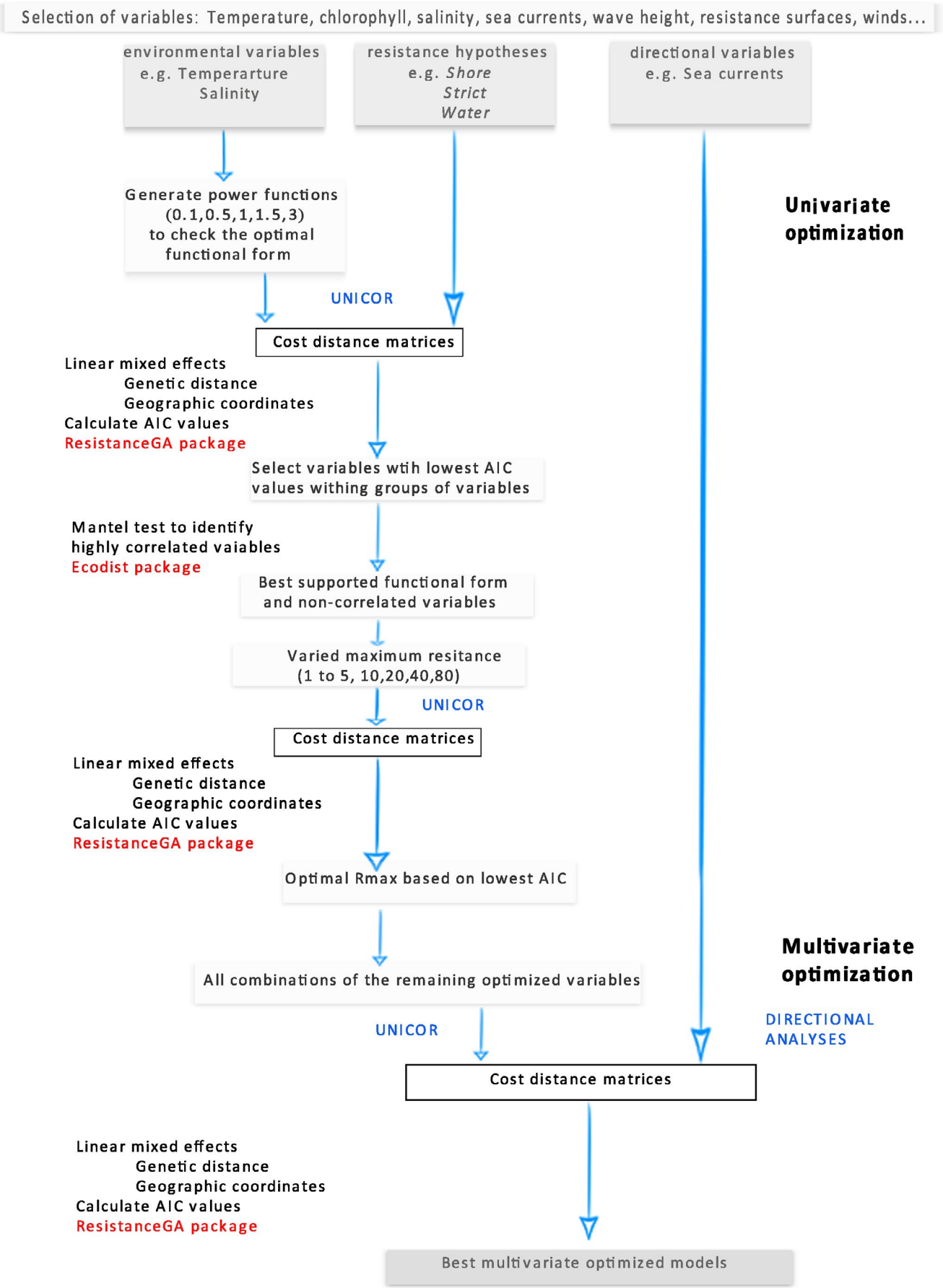


FIGURE 2 A workflow diagram of the two-step optimization procedure

The first step identified the optimal functional form and maximum resistance for each variable analysed (Shirk et al., 2010) using the ECODIST package in R (Goslee & Urban, 2007). For each set of variables, optimal functional forms and cost distance relationships were selected on the basis of the lowest within-group AIC values. In this step, we also removed variables that were highly correlated to reduce the effect of multicollinearity on model selection performance (Cushman, et al., 2013a; Shirk et al., 2018). For highly correlated variable pairs, we discarded the covariate with the higher AIC value.

Second, we used restricted optimization with initial values set at those of the best supported functional forms identified in the first step. We varied the maximum resistance (R_{max}, Shirk et al., 2010) for each variable across five levels (5, 10, 20, 40 and 80). Then, we used RESISTANCEGA to select the optimal R_{max} for each resistance hypothesis based on the lowest AIC. Next, we tested both univariate relationships between each variable and genetic differentiation, and multivariate relationships including all possible additive combinations of predictor variables (e.g., Castillo et al., 2014; Shirk et al., 2010). Sea currents were included in the final steps of the process because they could not be analysed as resistance layers due to their directional nature. Finally, the best multivariate optimized models were ranked according to AIC as in López-Márquez, et al. (2019a) (Shirk et al., 2017).

3 | RESULTS

3.1 | Genetic diversity

Mean observed and expected heterozygosities, respectively, were 0.570 and 0.743 for *Gibbula divaricata* and 0.383 and 0.399 for *Dendropoma lebeche* (Table 4). The mean number of alleles for *G. divaricata* ranged from 6.64 for EST to 8.98 for PSA. Mean allelic richness was lower in *D. lebeche*, ranging from 2.30 for SAN to 5.09 for CAL, and effective population sizes were in general higher in *G. divaricata* than in *D. lebeche* with some of their populations considered to be of infinite size (Table 4). No linkage disequilibrium (LD) between loci was observed, except for one population of *D. lebeche* (CEU) and one of *G. divaricata* (POC). Thus, the 23 polymorphic loci analysed respectively for each species were considered statistically independent. In almost all populations of both species, we detected significant deviations from HWE across different loci. Null alleles were detected in the *D. lebeche* populations of BIZ, ISA, REY, ALB, FAR, IRI, CEU, ESR and POR, and in all *G. divaricata* populations except GES. However, no significant differences were observed between pairwise F_{ST} and pairwise F_{ST} corrected for null alleles (Table S1).

3.2 | Genetic analyses and isolation by distance

Global F_{ST} revealed significant and high genetic differentiation for *D. lebeche* (F_{ST} global =0.410, p <.0001). In contrast, we found much lower, but significant, differentiation in *G. divaricata* (F_{ST} global =0.059, p <.0001). Pairwise F_{ST} values for *D. lebeche* ranged from 0.034 for ISA vs. REY to 0.416 for PRI vs. MOH. For *G. divaricata*, values ranged from 0.011 for TOG vs. OTR and also for BOK vs. KOR to 0.108 for EST vs. KAP (Table 5). These ranges increased when F'_{ST} values were calculated: 0–0.614 for *G. divaricata* and 0.068–0.863 for *D. lebeche*.

The first two axes of the PCoA explained 63.59% and 35.76% of the variation in F_{ST} for *G. divaricata* and *D. lebeche*, respectively. For *G. divaricata*, a clear separation was evident between the Adriatic (OTR, TOG, BOK, KOR and KAP) and western Mediterranean populations (EST, JOR, PSA, CDE, GES, GAL and BEN), with a single population occupying a central position (POC from the Ionian Channel location) (Figure 3). We could differentiate *D. lebeche* into five groups: (i) Atlantic plus the Gibraltar Strait (MOH, CEU and PUN), (ii) Alboran Sea (IRI, SID, LAR, ISA, REY, ALB and FAR), (iii) Spanish Levantine coast plus Mallorca (PEÑ, CAL, PAL and ESR), (iv) Tunisia (HAO and BIZ) and (v) Balearic Islands (RAM, FOR, PRI and POR) and, notably, Atlantic SAN (Figure 4).

Analysis of genetic structure based on ΔK revealed two genetically differentiated clusters for both species. Populations of *G. divaricata* were divided into an Adriatic group (OTR, TOG, KOR, BOK and KAP) and one comprising the rest of the Mediterranean populations (CDE, PSA, GES, EST, JOR, BEN and GAL), except the one from the Ionian Sea (POC), which showed signatures of admixture from Adriatic and Mediterranean populations (Figure 5). For *D. lebeche*, one cluster consisted of one of the Atlantic populations (MOH) and the Alboran (PUN, CEU, IRI, FAR, ALB, SID, LAR, ISA and REY) and Spanish Levantine coastal populations (CAL, PAL and PEÑ), while the other cluster comprised the other Atlantic population (SAN) and the Balearic (FOR, POR, RAM, PRI and ESR) and Tunisian (BIZ and HAO) populations. Some admixture was apparent between the two major groups (Figure 6).

In contrast, results based on the probability (ln (Pr($X|K$)) values and Puechmaille's (2016) estimators showed a best K value of 5 for *G. divaricata*, structured as: (i) west Mediterranean populations (CDE, PSA, GES, BEN and GAL); (ii) a cluster consisting of a few individuals from different locations (orange), mostly GES and BEN; (iii) Balearic populations (EST and JOR); (iv) western Adriatic populations (OTR and TOG) and (v) eastern Adriatic populations (KOR, BOK and KAP) with a small contribution of the western Adriatic cluster. The Ionian Sea population (POC) showed ancestors from both the western Mediterranean and the two Adriatic clusters (Figure 5).

D. lebeche showed a more structured pattern (K = 15, ln (Pr($X|K$); K = 18, Puechmaille's (2016) estimators): (i) the westernmost Atlantic population (MOH) and CEU in the Strait of Gibraltar; (ii) some individuals from CEU belong to another cluster (light blue); (iii) the Atlantic population (SAN), which also had a small contribution in two of the Balearic locations (PRI and POR); (iv) PUN in the Strait of Gibraltar; (v) a large proportion of the IRI population in the Mediterranean Moroccan coast; (vi) the rest of the mixed population of IRI together with FAR and ALB in the Alboran Sea; (vii) SID, with a small contribution from LAR, which are nearby locations on the

TABLE 4 Estimators of genetic diversity in *Gibbula divaricata* and *Dendropoma lebeche*. *Na*, number of alleles; H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient; N_e, effective population size

Population	*Na*	H_O	H_E	F_{IS}	N_e
Dendropoma lebeche					
MOH	2.56	0.299	0.306	0.044	15
SAN	2.30	0.314	0.313	0.013	53
PUN	2.35	0.257	0.261	0.034	10
CEU	2.98	0.236	0.328	0.300	0.5
IRI	3.00	0.390	0.399	0.039	74
FAR	3.13	0.327	0.336	0.043	40
ALB	2.96	0.249	0.294	0.166	18
PRI	2.62	0.363	0.356	0.001	11
SID	2.90	0.300	0.302	0.024	55
LAR	3.04	0.381	0.366	−0.023	33
ISA	3.83	0.395	0.432	0.100	75
REY	3.19	0.331	0.359	0.096	150
CAL	5.09	0.522	0.558	0.084	23
PAL	3.71	0.492	0.483	0.000	119
PEÑ	3.82	0.329	0.388	0.208	79
FOR	3.66	0.428	0.415	−0.013	73
POR	3.60	0.436	0.443	0.0328	43
RAM	4.80	0.539	0.551	0.039	32
ESR	4.03	0.450	0.481	0.085	∞
BIZ	4.22	0.554	0.537	−0.015	63
HAO	3.64	0.447	0.461	0.052	137
Mean		0.383	0.399		
Gibbula divaricata					
CDE	8.59	0.549	0.755	0.270	∞
PSA	8.98	0.598	0.777	0.233	777
GES	7.50	0.528	0.735	0.281	93
EST	6.64	0.547	0.723	0.244	382
JOR	7.61	0.552	0.722	0.231	280
BEN	8.91	0.552	0.767	0.317	246
GAL	8.18	0.533	0.766	0.301	∞
POC	8.55	0.579	0.784	0.264	97
OTR	7.15	0.578	0.731	0.219	375
TOG	7.46	0.585	0.713	0.193	∞
KOR	8.47	0.608	0.734	0.186	840
BOK	8.43	0.631	0.747	0.163	∞
KAP	7.86	0.573	0.701	0.213	31
Mean		0.570	0.743		

Mediterranean Moroccan coast; (viii) the Chafarinas Islands (LAR, ISA and REY); (ix) CAL and (x) PAL, both on the Spanish Levantine coast; (xi) the northernmost population PEÑ; (xii) Columbretes (FOR), Ibiza (POR) and almost half of the assignment in Menorca (PRI); (xiii) Formentera (RAM); (xiv) Mallorca (ESR) and (xv) the Tunisian populations (BIZ and HAO) (Figure 6). For $K = 18$, almost every population was represented by a single sampling location. The groups comprised some Alboran sea locations (IRI, FAR and ALB), the Chafarinas Islands (LAR, ISA, and REY) and the Tunisian locations (BIZ and HAO), which were assigned to one cluster each (Figure 6). The distribution and proportion of these genetic clusters were represented in pie diagrams for each population of *G. divaricata* and *D. lebeche* (Figure 7).

We detected the occurrence of strongly supported barriers (100% bootstrap support) of genetic differentiation across the studied area. These barriers corresponded to the six oceanographic

TABLE 5 F_{ST} values among *Gibbula divaricata* and *Dendropoma lebeche* populations. In bold, significant values (p <.05) following GENALEX for *G. divaricata*. For *D. lebeche*, all F_{ST} values were significant. Upper side standardized F'_{ST}

	Gibbula divaricata												
	CDE	**PSA**	**GES**	**EST**	**JOR**	**BEN**	**GAL**	**POC**	**OTR**	**TOG**	**KOR**	**BOK**	**KAP**
CDE	–	0.090	0.177	0.425	0.395	0.067	0.082	0.251	0.445	0.460	0.467	0.509	0.539
PSA	0.014	–	0.326	0.339	0.322	0.066	0.197	0.176	0.387	0.394	0.416	0.446	0.480
GES	0.040	0.036	–	0.563	0.540	0.194	0.087	0.429	0.593	0.596	0.552	0.602	0.614
EST	**0.060**	**0.050**	**0.076**	–	0.142	0.349	0.494	0.424	0.560	0.590	0.557	0.557	0.590
JOR	**0.058**	**0.050**	**0.079**	**0.034**	–	0.357	0.478	0.384	0.504	0.518	0.532	0.569	0.584
BEN	0.024	0.022	0.048	**0.059**	**0.063**	–	0.158	0.152	0.361	0.371	0.394	0.421	0.451
GAL	0.018	0.014	0.043	**0.054**	**0.055**	0.027	–	0.268	0.450	0.469	0.447	0.488	0.525
POC	**0.033**	**0.028**	**0.057**	**0.063**	**0.059**	**0.033**	**0.024**	–	0.091	0.103	0.137	0.149	0.179
OTR	**0.064**	**0.061**	**0.088**	**0.095**	**0.087**	**0.061**	**0.055**	**0.021**	–	0.000	0.102	0.109	0.174
TOG	**0.068**	**0.063**	**0.089**	**0.102**	**0.091**	**0.063**	**0.059**	**0.022**	0.011	–	0.104	0.120	0.167
KOR	**0.075**	**0.067**	**0.087**	**0.094**	**0.091**	**0.068**	**0.063**	**0.028**	**0.024**	**0.023**	–	0.023	0.002
BOK	**0.074**	**0.068**	**0.088**	**0.091**	**0.094**	**0.066**	**0.062**	**0.028**	**0.024**	**0.025**	**0.011**	–	0.016
KAP	**0.089**	**0.083**	**0.103**	**0.108**	**0.107**	**0.082**	**0.079**	**0.039**	**0.039**	**0.036**	0.014	0.015	–

	Dendropoma lebeche																				
	MOH	**SAN**	**PUN**	**CEU**	**IRI**	**FAR**	**ALB**	**SID**	**LAR**	**ISA**	**REY**	**CAL**	**PAL**	**PEÑ**	**FOR**	**POR**	**RAM**	**ESR**	**PRI**	**BIZ**	**HAO**
MOH	–	0.849	0.747	0.598	0.753	0.803	0.776	0.751	0.729	0.743	0.781	0.626	0.736	0.758	0.832	0.829	0.774	0.720	0.858	0.761	0.761
SAN	0.397	–	0.828	0.863	0.751	0.744	0.785	0.783	0.798	0.739	0.748	0.685	0.750	0.765	0.518	0.418	0.485	0.748	0.426	0.692	0.743
PUN	0.354	0.383	–	0.655	0.659	0.775	0.797	0.786	0.705	0.635	0.647	0.600	0.694	0.730	0.814	0.850	0.767	0.756	0.806	0.786	0.773
CEU	0.239	0.402	0.281	–	0.565	0.729	0.702	0.628	0.650	0.716	0.728	0.459	0.621	0.554	0.781	0.853	0.742	0.619	0.789	0.713	0.725
IRI	0.323	0.315	0.266	0.196	–	0.301	0.430	0.574	0.506	0.538	0.515	0.401	0.596	0.589	0.697	0.764	0.710	0.635	0.744	0.657	0.220
FAR	0.364	0.308	0.343	0.298	0.105	–	0.085	0.159	0.128	0.135	0.130	0.154	0.236	0.244	0.248	0.288	0.232	0.247	0.277	0.221	0.226
ALB	0.348	0.331	0.372	0.283	0.150	0.085	–	0.188	0.134	0.164	0.163	0.141	0.242	0.241	0.260	0.316	0.260	0.232	0.294	0.221	0.264
SID	0.329	0.356	0.377	0.241	0.224	0.159	0.188	–	0.137	0.191	0.214	0.151	0.244	0.220	0.264	0.300	0.237	0.235	0.259	0.222	0.232
LAR	0.292	0.340	0.288	0.235	0.173	0.128	0.134	0.137	–	0.072	0.092	0.133	0.232	0.221	0.269	0.303	0.227	0.211	0.263	0.217	0.255
ISA	0.261	0.303	0.232	0.281	0.186	0.135	0.164	0.191	0.072	–	0.034	0.146	0.236	0.253	0.246	0.279	0.212	0.228	0.271	0.206	0.261
REY	0.353	0.328	0.244	0.294	0.191	0.130	0.163	0.214	0.092	0.034	–	0.166	0.252	0.254	0.269	0.319	0.235	0.245	0.307	0.249	0.279
CAL	0.221	0.248	0.201	0.140	0.102	0.154	0.141	0.151	0.133	0.146	0.166	–	0.103	0.118	0.153	0.202	0.149	0.107	0.178	0.143	0.160
PAL	0.298	0.295	0.280	0.227	0.203	0.236	0.242	0.244	0.232	0.236	0.252	0.103	–	0.215	0.216	0.254	0.188	0.164	0.217	0.209	0.210
PEÑ	0.309	0.318	0.297	0.176	0.190	0.244	0.241	0.220	0.221	0.253	0.254	0.118	0.215	–	0.265	0.278	0.193	0.209	0.242	0.231	0.206

(Continues)

TABLE 5 (Continued)

	Dendropoma lebeche																				
	MOH	SAN	PUN	CEU	IRI	FAR	ALB	SID	LAR	ISA	REY	CAL	PAL	PEÑ	FOR	POR	RAM	ESR	PRI	BIZ	HAO
FOR	0.374	0.189	0.358	0.312	0.248	0.248	0.260	0.264	0.269	0.246	0.269	0.153	0.216	0.265	—	0.122	0.153	0.156	0.147	0.179	0.185
POR	0.350	0.145	0.365	0.342	0.283	0.288	0.316	0.300	0.303	0.279	0.319	0.202	0.254	0.278	0.122	—	0.096	0.188	0.130	0.187	0.185
RAM	0.279	0.150	0.283	0.264	0.236	0.232	0.260	0.237	0.227	0.212	0.235	0.149	0.188	0.193	0.153	0.096	—	0.175	0.131	0.154	0.156
ESR	0.282	0.294	0.302	0.210	0.200	0.247	0.232	0.235	0.211	0.228	0.245	0.107	0.164	0.209	0.156	0.188	0.175	—	0.199	0.208	0.216
PRI	0.416	0.171	0.367	0.340	0.290	0.277	0.294	0.259	0.263	0.271	0.307	0.178	0.217	0.242	0.147	0.130	0.131	0.199	—	0.206	0.216
BIZ	0.295	0.245	0.317	0.256	0.210	0.221	0.221	0.222	0.217	0.206	0.249	0.143	0.209	0.231	0.179	0.187	0.154	0.208	0.206	—	0.148
HAO	0.304	0.276	0.314	0.257	0.220	0.226	0.264	0.232	0.255	0.261	0.279	0.160	0.210	0.206	0.185	0.185	0.156	0.216	0.216	0.148	—

fronts previously described (GS, AOF, IC, BF, SC and OS, Figure 1). For *D. lebeche*, GS, AOF, IC and BF were identified as supported barriers. For *G. divaricata*, IC, BF, SC and OS were well-supported barriers. Other barriers, although less well-supported, also appeared to be important for *G. divaricata*, such as the one between OTR and KOR on opposite coasts of the Adriatic Sea.

We identified 30 individuals as potential first-generation migrants for *G. divaricata*, and six for *D. lebeche*, representing 8.43% and 1.04% of the 356 and 579 individuals analysed, respectively (Table 6). Highly significant associations were found between linear F_{ST} and shortest ocean path distances for both species (for *G. divaricata*, Mantel R =.389, p =.001, and for *D. lebeche*, R =.137, p =.0002). Model selection revealed *Water* as the best-supported resistance model for both species (i.e., IBD over water) compared with the others (i.e., *Shore* and *Strict*, Table S2).

3.3 | Isolation by seascape resistance

3.3.1 | Univariate optimization

For *G. divaricata*, genetic differentiation was best described by strongly convex slope functions for salinity and SST (0.1 for SSS, SSS_F, SSS_S, SST and SST_C), with SST_W described by a moderate slope function (0.5). *D. lebeche* also exhibited strongly convex slope functions (0.1) for SSS, SSS_F, SSS_S, SST and SST_W, whereas SST_C was described by a slightly concave slope function (Tables S3 and S4).

Mantel correlations showed that, for *G. divaricata* and *D. lebeche*, respectively, 11 and four variables were correlated with an r >.98 (Table S5). For highly correlated variable pairs, we retained the variable with the lowest AIC, resulting in five retained for *G. divaricata* and six for *D. lebeche* (Table S6).

Next, we identified the maximum resistance (R_{max}) for each of the retained variables. For *G. divaricata*, the optimal R_{max} was 20 for *Strict* (i.e., 20 times the minimum resistance value), 40 for salinity, and 80 for *Shore* and for salinity in the saltiest month. In *D. lebeche*, the optimal R_{max} was 20 for SST and 80 for salinity and for SST in the warmest months (Tables S7 and S8).

3.3.2 | Multivariate optimization

All combinations of the five and six variables identified for *G. divaricata* and *D. lebeche*, respectively, using univariate optimization were then assessed via multivariate optimization. Currents, as directional variables, were included in the final step (e.g., López-Márquez, Cushman, et al., 2019a). AIC values calculated for the monthly mean of currents and currents grouped by season were identical, and thus we only retained the mean of September for further analyses. Two sets of variable combinations were generated, one including the slope variables and the other including the slope variables plus current velocities (Table S9).

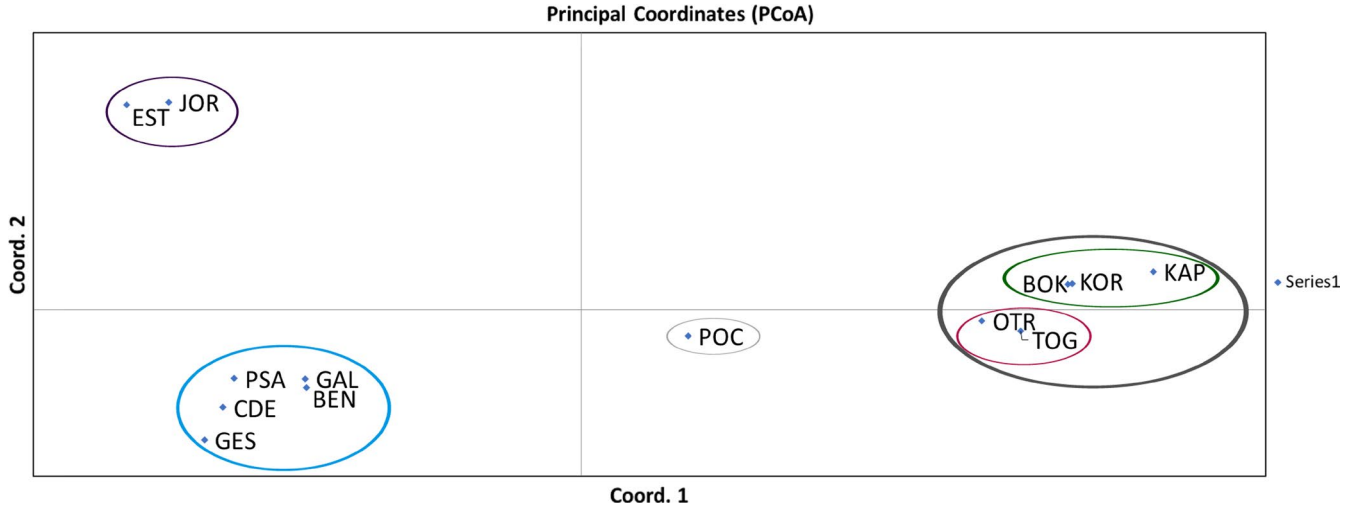
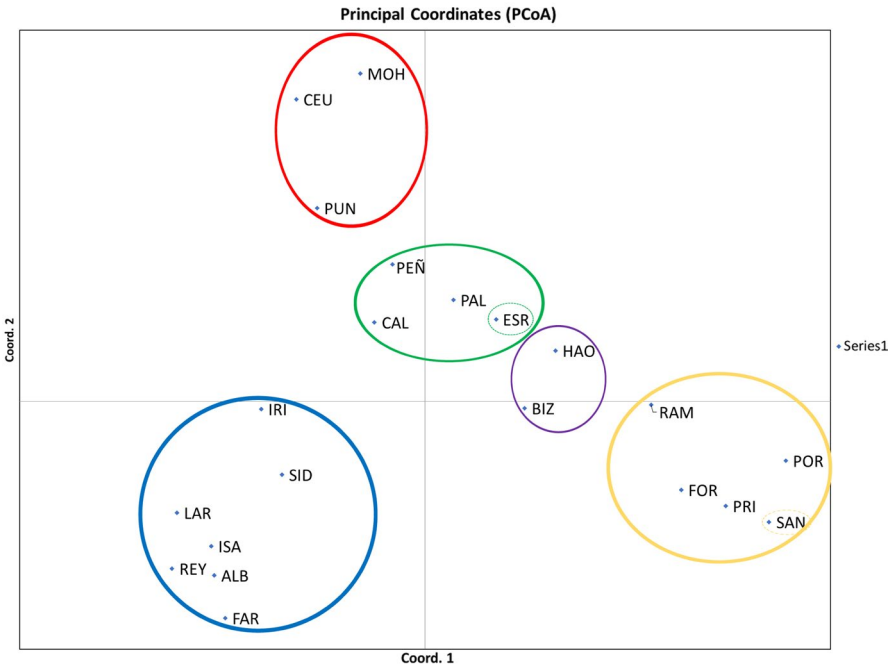


FIGURE 3 Results of a principal coordinates analysis (PCoA) detecting population genetic clustering for *Gibbula divaricata*. F_{ST} values among populations showed a variation of 63.59% explained by the two first axes

FIGURE 4 Results of a principal coordinates analysis (PCoA) detecting population genetic clustering for *Dendropoma lebeche*. F_{ST} values among populations showed a variation of 35.76% explained by the two first axes



Salinity gradients emerged as the most well-supported hypothesis driving genetic differentiation for both species. For *G. divaricata*, the next best supported hypothesis was sea temperature combined with sea surface currents (m3c) (ΔAIC of 5.31); however, for *D. lebeche*, it was *Shore* (ΔAIC of 0.13). Also, there was support for 18 top models for *D. lebeche* (i.e., ΔAIC <4). Additionally, salinity (i.e., SSS, SSS_S, or SSS_F) was included in eight of 10 top models and accounted for 11 of the 20 total number of variables (55%) in those models for *G. divaricata*. Likewise, it appeared in nine of 10 top models and accounted for 17 of the 23 total number of variables (74%) in those models for *D. lebeche*. In summary, our results suggested that multiple factors including salinity, SST, sea currents and movement by rafting of crawling juveniles along the coastline were driving gene flow for both species, with salinity appearing to be the most important driver for both species (Table 7).

4 | DISCUSSION

We utilized a multivariate optimization seascape genetic methodology to identify underlying processes driving spatial genetic patterns in two Mediterranean gastropods, *Gibbula divaricata* and *Dendropoma lebeche*. This relatively new approach, first applied in the Mediterranean coral *Cladocora caespitosa* (López-Márquez, et al., 2019a), uses multivariate restricted optimization (Shirk et al., 2010) with linear mixed effects modelling (Shirk et al., 2018). Using this

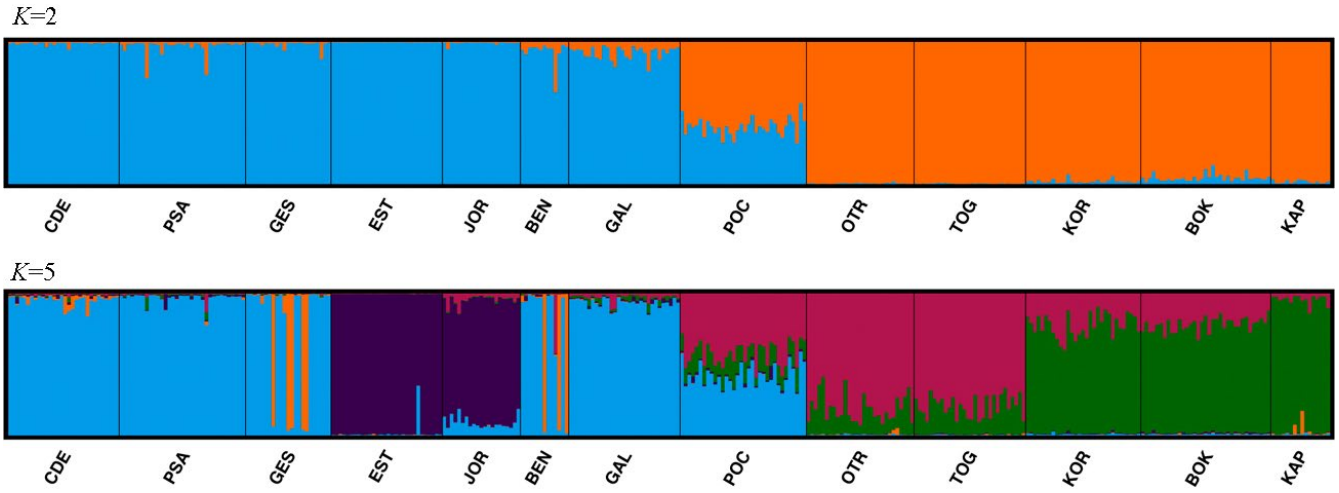


FIGURE 5 STRUCTURE result selected by CLUMPAK for the 13 locations of *Gibbula divaricata* for $K = 2$ and $K = 5$

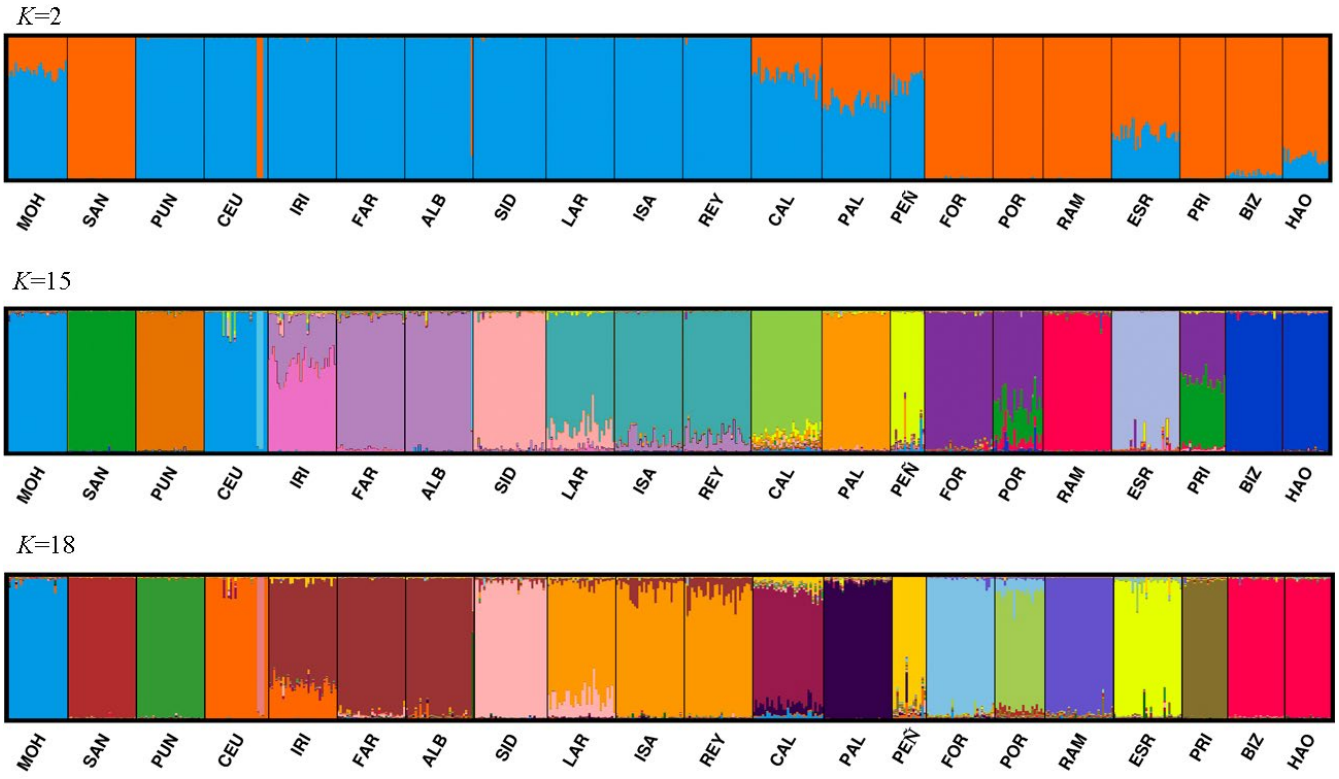


FIGURE 6 STRUCTURE result selected by CLUMPAK for the 21 locations of *Dendropoma lebeche* for $K = 2$, $K = 15$ and $K = 18$

approach, we evaluated the relative effect and functional response of a range of seascape variables (e.g., salinity, temperature, shoreline topography and sea currents) on the genetic connectivity of the two gastropods.

Salinity gradients emerged as an important driver of gene flow for both gastropods, although in *D. lebeche* there is highly limited gene flow, and all locations have a large degree of genetic isolation.

In marine systems, the seawater is well mixed except at thermohaline density fronts and contact zones between eddies, gyres and other physical oceanographic features that separate water masses. These transition areas can act as semipermeable barriers or retention zones for planktonic larvae (Galarza et al., 2009). Therefore, it is likely that a salinity gradient acts primarily as a proxy for water mixing. Indeed, we found that explicit modelling of water mixing through a directional analysis of resistance due to currents predicted the level of genetic differentiation observed for both species. The proximity of locations along coastlines also influenced gene flow for *D. lebeche*, and SST in combination with sea currents

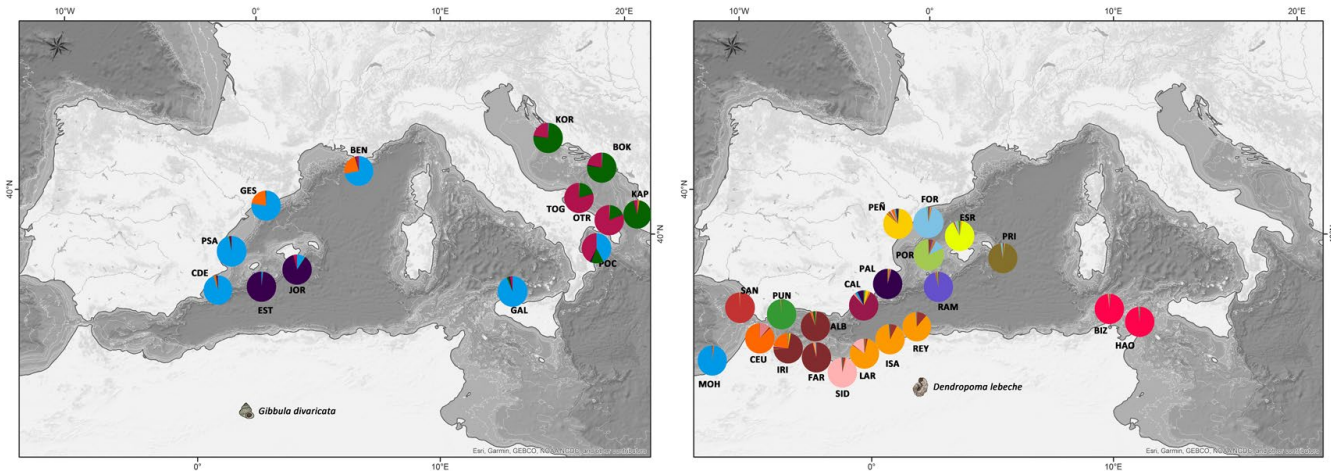


FIGURE 7 Maps with pie diagrams representing the distribution and proportion of the genetic clusters detected by STRUCTURE in each population for *Gibbula divaricata* and *Dendropoma lebeche*

was influential for *G. divaricata*. These results are consistent with the theoretical hypotheses that predict species with a lower dispersal capacity are more affected by distance and coastline topography compared with species with a higher dispersal potential, which are more strongly impacted by oceanographic fronts defined by currents. The Mediterranean is a concentration basin: lower water levels and higher water evaporation in the east has led to a salinity gradient that increases from west to east, excluding the area comprising the Spanish Levantine coast and the Balearic Islands, which is characterized by its own salinity gradient (Coll et al., 2010). Annual mean SST gradually increases from north to south and west to east (Figure 8).

We focused on the two gastropod species studied because they have largely overlapping geographical ranges but inhabit different microenvironments. They also differ in their life history traits (e.g., sessile and gregarious vs. free-living snails; filter feeder vs. grazer; reproductive period from late spring to late summer vs. long reproductive periods throughout the year; intracapsular vs. planktonic larvae). Genetic structure patterns in the two species revealed noteworthy differences in population connectivity: *G. divaricata* showed evidence of long-distance gene flow, whereas *D. lebeche* presented a marked structure consistent with more limited and local gene flow. Strikingly, a seascape genetic analysis revealed that similar drivers of gene flow operate in both species, with many of the same factors, in particular salinity gradients, determining population differentiation in the two taxa. Therefore, differences in larval development (planktonic vs. entirely encapsulated) or other life history traits can lead to substantially different patterns of genetic structure, even when the same abiotic factors modulate that structure.

The genetic structure of the trochid species *G. divaricata* revealed a clear division between western Mediterranean and Adriatic Sea populations. The genetic clusters mainly correspond to four groups: one distributed along the coastline from the Spanish Levantine coast to Sicily, one comprising the Balearic populations and two along the western and eastern coasts of the Adriatic Sea, plus some differentiated individuals. The population structure of *G. divaricata* is largely consistent with those of other marine species in this region (e.g., Bahri-Sfar et al., 2000; Carreras et al., 2019; Riesgo et al., 2019), although we generally observed higher F_{ST} values in our study. Currents moving from north to south parallel to the Spanish Levantine coast form eddies that result in fronts that isolate the Balearic Islands (Millot, 1999). A complex regimen of currents also creates barriers within the Adriatic Sea (Barale et al., 2005). These barriers, together with changes in environmental parameters (salinity), appear to drive population differentiation in several marine species (Borsa et al., 1997; Luttikhuizen et al., 2008; Rindi et al., 2020).

For the vermetid species, *D. lebeche*, we detected much stronger genetic structure: almost every location formed a different genetic cluster except for the three clusters that grouped, respectively, two sites in the Alboran Sea, the three in the Chafarinas Islands and the two in Tunisia. This pattern coincides with the oceanographic discontinuities previously described by Pascual et al., (2017) and Bellisario et al., (2019). Moreover, genetic differentiation is up to five times higher in *D. lebeche* than in *G. divaricata* when comparing the same locations (e.g., between Formentera and Mallorca within the Balearic Islands). One migrant was found between very distant locations (PAL–ALB) for *D. lebeche* separated by the AOF. This scenario could be explained by occasional rafting events (achieved through mucous drogue secreted by crawling juveniles) seeming to allow stepwise dispersal, sometimes over relatively long distances (Calvo et al., 2009). Given the co-occurrence pattern of the two species, and their nearly identical exposure to abiotic factors, the strong difference in genetic structure appears to be largely driven by differences in their life history strategies.

Our results clearly show that the primary genetic structure in both studied species coincides with the main biogeographical regions delimited by thermohaline density fronts in the western and central Mediterranean. This structure is mainly driven by salinity gradients and SST (notedly in the warmest months, when reproduction peaks), with the distance separating locations along the coastline also being important for the sessile *D. lebeche*.

TABLE 6 Migrant test for *Gibbula divaricata* and *Dendropoma lebeche*. For each site (for acronyms, see Table 1), individuals are presented according to their sampling site in columns, and in rows, to their assignment to the destination population. The last column lists the total number of individuals that were not assigned to the population from which they were sampled. *N* indicates the number of samples analysed from each location

Gibbula divaricata

	ORIGIN													
POP	**PSA**	**KAP**	**BOK**	**KOR**	**TOG**	**OTR**	**POC**	**BEN**	**EST**	**JOR**	**CDE**	**GAL**	**GES**	**Total**
PSA							1	1			5	3	1	11
KAP				1										1
BOK		2		1										3
KOR		1									1			2
TOG						3								3
OTR			1		1									2
POC						2							1	3
BEN		1					1							2
EST														-
JOR									2					2
CDE	1													1
GAL														–
GES														–
Total	1	4	1	2	1	5	2	1	1	–	6	3	2	30
N	34	16	35	31	30	29	34	13	30	21	30	30	23	

Dendropoma lebeche

	ORIGIN					
POP	**PEÑ**	**PAL**	**ISA**	**REY**	**ALB**	**Total**
PEÑ						–
PAL	1				1	2
ISA				2		2
REY			2			2
ALB						–
Total	1	–	2	2	1	6
N	15	30	30	30	30	

4.1 | Management implications

Results from this study will facilitate a greater understanding of the factors influencing population connectivity of target coastal marine invertebrates in complex oceanic environments. For example, seeing the dominant effects of salinity gradients and of shoreline dispersal (for sedentary species) can help researchers to predict areas of importance for dispersal linkages within and among populations and to identify areas for conservation prioritization (e.g., López-Márquez, et al., 2019a).

In recent decades, marine fauna has been increasingly threatened by human activities such as overfishing and pollution accelerated by climate change (McCauley et al., 2015). The Mediterranean Sea is especially sensitive to these impacts and to global warming (Lejeusne et al., 2010). Along with pollution, over-exploitation and invasive species, habitat modification, fragmentation, degradation and loss are widely considered some of the most serious threats to Mediterranean biodiversity (Templado, 2014). Due to habitat fragmentation or loss, connectivity between populations of many species has been interrupted or reduced. A decrease in available habitats for a species leads to a reduction in the number of both donor and potential recipient populations, which consequently become more isolated and decrease in size and abundance (Airoldi et al., 2008). Moreover, when the population density of a species decreases, reproductive success also often decreases, especially in broadcasting invertebrates ("Allee effect") (Courchamp et al., 2008). This has important impacts on population stability and community dynamics. Furthermore, local extinction of nondispersing species or those with

low dispersal capacity (such as the studied gastropods) prevents their recovery. Seascape genetic analyses that can predict the rate and pattern of population connectivity, prioritize areas for connectivity conservation, and guide management and development planning will be essential to proactively and effectively conserve marine biodiversity in the Mediterranean Sea and elsewhere. Coastal development decreases the available habitat for *Dendropoma* reefs and hinders connectivity among remaining populations. By contrast, coastal development can favour connectivity between populations of *G. divaricata*, since this top shell adapts well to artificial structures and harbour areas.

Despite the ecological relevance of the biogenic *Dendropoma* reefs, rarely are they subjected to accurate management (Chemello et al., 2014). Action plans for *Dendropoma* reef protection must be extended, and its management improved, at the scale of the entire Mediterranean Sea. Therefore, implementation of a basin-wide conservation strategy that includes the monitoring of both protected and unprotected reefs is essential to effectively protect this neglected but important coastal habitat. Having accurate information on population connectivity is fundamental to optimize their protection (Milazzo et al., 2016). The resistance model produced in this study could be used to build empirically based corridor priority maps, as has been done for a number of mammalian species (e.g., Cushman, Landguth, et al., 2013b, 2018; Kaszta et al., 2020). Such connectivity mapping and prioritization can then be used as the basis of proactive spatial planning to guide establishment of new coastal and marine protected areas and to regulate coastline development in the most vulnerable and important locations.

Most conservation measures for marine biodiversity focus on the establishment of MPAs and much has been written about their role as exporters of fish biomass and larvae to surrounding areas (e.g., Sale et al., 2005). The effectiveness of MPAs for biodiversity conservation will be limited if exported larvae do not find appropriate places to settle outside of these areas. Furthermore, if larvae are not imported from outside MPAs, then there will be a genetic impoverishment of their resident populations and limited means of demographic rescue or recolonization (Templado, 2014). There are a number of benefits of protecting representative habitats using well-enforced MPAs (McCook et al., 2010), but nevertheless protected

TABLE 7 Best models ranked according to AIC values (for acronyms, see Table 2)

Models	Variables	AIC
Gibbula divaricata		
m1	SSS_S	−454.70
m3c	SST +Current	−449.39
m14	SSS_S +Shore	−448.07
m14c	SSS_S +Shore + Current	−443.85
m12	SSS_S +SSS	−440.28
m13	SSS_S +SST	−438.43
m12c	SSS_S +SSS + Current	−437.83
m124	SSS_S +SSS + *Shore*	−437.08
m2	SSS	−437.04
m3	SST	−436.89
Dendropoma lebeche		
m1	SSS	−634.23
m6	*Shore*	−634.10
m12	SSS +SSS_F	−633.89
m1c	SSS +Current	−633.82
m12c	SSS +SSS_F + Current	−633.29
m123	SSS +SSS_F + SSS_S	−632.80
m13	SSS +SSS_S	−632.73
m14	SSS +SST	−632.43
m124	SSS +SSS_F + SST	−632.16
m123c	SSS +SSS_F + SSS_S +Current	−632.16

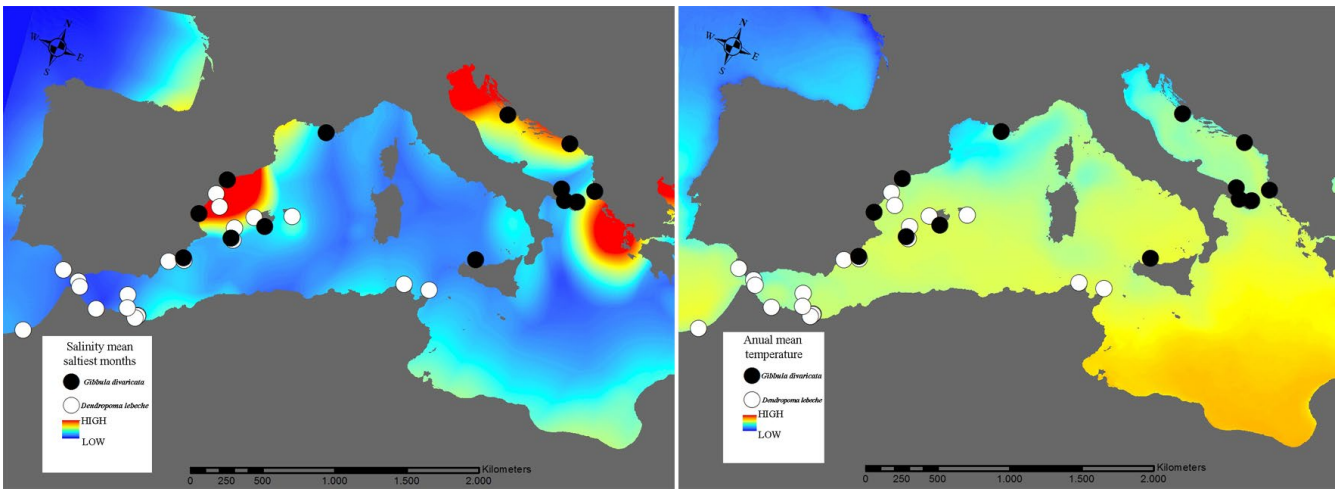


FIGURE 8 Spatial variation of salinity mean values in the saltiest months, and annual mean temperatures in the study area. Black and white dots represent the sampling locations of *Gibbula divaricata* and *Dendropoma lebeche*, respectively

area coverage within MPAs alone is not a sufficient indicator for meeting global biodiversity targets.

Effective protection of *Dendropoma* reefs may be enhanced through a network of small no-take reserves rather than few, widely spaced large MPAs. As suggested by Harrison et al., (2020), small networks of marine reserves yield stabilizing benefits that ensure a consistent larval supply to replenish decimated populations. Further, for an integrated conservation of the entire *Dendropoma* reef system, it would be appropriate to develop a marine spatial planing (*sensu* Gissi et al., 2019) or zoning management (McCook et al., 2010), taking into account a set of biological and ecological features (i.e., life history traits, population connectivity, spatial distribution, structural complexity and the potential for regime shifts) along with human impacts. Besides, to designate an effective spatial zoning or a network of small MPAs, the distance and direction in which marine larvae disperse is a primary ecological issue (Sale et al., 2005). Effective MPAs, or networks of these, must be both net exporters to sustain surrounding population, and largely self-sustaining populations (Catalano et al., 2020). Therefore, design of a network of MPAs should entail a balance involving correct choice of size, number and placement and must be established as a network of optimally located sites that support local populations and connectivity among them (Halpern, 2003).

The Mediterranean Sea is an ideal laboratory in which to investigate changes derived from global warming, and the differential responses of species to it, while also obtaining data on the population structure and genetic diversity of selected species (the "gene-climate approach" of Lo Brutto et al., 2011). Inferences on past and contemporary temporal variations in effective population size and genetic variability can be drawn from such genetic studies. These parameters are of primary importance as they provide evidence of the presence of endangered populations and predict the influence of environmental changes on individual species (Templado, 2014). Moreover, long-lived engineer invertebrates, such as *D. lebeche*, can be useful indicators of both short- and long-term changes in Mediterranean ecosystems, thus providing insight into ecosystem responses to changes (Duarte et al., 1999). Likewise, *Dendropoma* reefs have been used as natural archives of past sea-level and surface temperature variations (Chemello & Silenzi, 2011).

By understanding the relationship between oceanographic parameters, genetic differentiation and genetic diversity, we can test predictions about the potential impacts of global climate change in the studied species, particularly given the strong influences of temperature and salinity, which are both likely to be sensitive to climatic warming. In short, seascape genetics can help characterize the responses of marine organisms to those threats and infer their resiliency, thus helping in the important task of marine biodiversity conservation.

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AUTHOR CONTRIBUTIONS

Designed research: V.L.M., J.T. and A.M. Performed research: V.L.M., J.T., A.M., S.C., H.Y.W. and H.B. Contributed new reagents or analytical tools: A.M., S.C., H.Y.W. and H.B. Analysed data: V.L.M., S.C., H.Y.W. and H.B. Wrote the paper: V.L.M., J.T., A.M., S.C., H.Y.W. and H.B.

DATA AVAILABILITY STATEMENT

Microsatellite genotypes are available at https://datadryad.org/stash/share/cTQBLTYtn9fo8GO-A5yoptR06iU_I4qI-1MG4WJj2P8

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SUPPORTING INFORMATION

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

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