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RESEARCH ARTICLE

# Global-scale genetic structure of a cosmopolitan cold-water coral species

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## Abstract

1. When considering widely distributed marine organisms with low dispersal capabilities, there is often an implication that the distribution of cosmopolitan species is an artefact of taxonomy, constrained by the absence of characters for delimiting either sibling or cryptic species. Few studies have assessed the relationship among populations across the global range of the species' distribution, and the presence of oceanographic barriers that might influence gene flow among populations are underestimated.
2. In this study, evolutionary and ecological drivers of connectivity patterns have been inferred among populations of the cold-water coral *Desmophyllum dianthus*, a common and widespread solitary scleractinian species, whose reproduction strategy and larval dispersal are still poorly unknown.
3. The genetic structure of *D. dianthus* was explored using 30 microsatellites in 347 specimens from 13 localities distributed in the Mediterranean Sea and Atlantic and Pacific Oceans.
4. Results clearly reveal genetically differentiated populations in the Northern and Southern Hemispheres ($F_{ST}$ = 0.16, $F_{SC}$ = 0.01, $F_{CT}$ = 0.15, *P*-values highly significant), and Chilean and New Zealand populations with independent genetic profiles.
5. Marine connectivity patterns at different spatial scales are discussed to characterize larval dispersal and gene flow through the Northern and Southern Hemispheres.

**KEYWORDS**

cold-water corals, cosmopolitan species, gene flow, larval dispersal, microsatellite, molecular ecology, population structure

## 1 | INTRODUCTION

The paradox of marine species with limited larval dispersal capability and global distribution and its resolution has been discussed by several authors (Bleidorn, Kruse, Albrecht, & Bartolomaeus, 2006; Hauquier, Leliaert, Rigaux, Derycke, & Vanreusel, 2017; Hutchings & Kupriyanova, 2018; Katz et al., 2005; Kawauchi & Giribet, 2014; Klautau et al., 1999; Logares, 2006; Pérez-Portela, Arranz, Rius, & Turon, 2013; Salgado-Salazar, Rossman, & Chaverri, 2013; Weiner, Aurahs, Kurasawa, Kitazato, & Kucera, 2012; Zeppilli, Vanreusel, & Danovaro, 2011). The studies of various marine organisms with putative cosmopolitan distributions (e.g. polychaetes, ciliates, sipunculids, sponges, ciliates, ascidians, nematodes) have always demonstrated the existence of a complex of species, or an artefact distribution. Exceptions seem to appear in the deep sea: Hutchings and Kupriyanova (2018) suggest that conditions at greater depths may be more conducive to dispersal and/or more homogeneous than in shallow coastal ecosystems, thus facilitating the persistence of widespread species, such as polychaetes, through evolutionary time.

Cold-water corals play a major ecological role as ecosystem engineers (habitat-forming species) in the deep sea, locally enhancing biodiversity on the continental shelf and slope (Roberts, Wheeler, Freiwald, & Cairns, 2009; Rogers, 1999). Many cold-water coral species display an apparently wide distribution (Cairns, 1994, 1995), reinforcing the notion that cosmopolitanism is a common occurrence in the deep sea, although only a few rigorous tests of connectivity and genetic diversity have been presented to date. Typically, cold-water corals are extremely slow-growing organisms; some species can live several centuries, providing an important habitat and a valuable archive of past environmental conditions in their skeletal chemistry (Montagna, McCulloch, Taviani, Remia, & Rouse, 2005; Montagna & Taviani, 2019; Robinson et al., 2014). Nevertheless, as occurs in many other marine ecosystems, deep-sea coral reefs are imperilled by direct and indirect human activities, particularly fishing and hydrocarbon industries, which are progressively exploiting deeper waters (Risk, Heikoop, Snow, & Beukens, 2002; Roberts et al., 2009). Conservation strategies and efforts are closely related to the biological and ecological knowledge of the target organisms. Unfortunately, the biological understanding of corals inhabiting the deep sea is limited by logistical difficulties of studies at extreme depths; indirect methods have to be used to infer the demography, biology, and ecology of these organisms. Although several genetically based studies target cold-water and temperate corals (Boavida et al., 2019; Costantini et al., 2011; Costantini, Fauvelot, & Abbiati, 2007; Dahl, Pereyra, Lundälv, & André, 2012; Herrera, Shank, & Sánchez, 2012; Le Goff-Vitry, Pybus, & Rogers, 2004; Miller, Rowden, Williams, & Häussermann, 2011; Morrison et al., 2011), a large number of coral species and geographic areas are still understudied. Unlike pelagic organisms, which are able to disperse as adults, marine benthic organisms show a great variety and capability of larval dispersive modes. Especially when direct observations are not possible, as is the case with deep-sea species, molecular genetics plays a key role in investigating and understanding the larval dispersal and demographic connectivity.

The cold-water coral *Desmophyllum dianthutheres* is a globally important cold-water coral, being common in all ocean basins (Cairns, 1994, 1995). The species displays a remarkable longevity, with morphologically indistinguishable ancestors dating back to the early Pleistocene, but possibly as early as the Miocene (Vertino et al., 2019). Mitochondrial and nuclear DNA sequence data have revealed the existence of common haplotypes throughout its range (Addamo, Reimer, Taviani, Freiwald, & Machordom, 2012; Miller et al., 2011), suggesting it is truly a cosmopolitan species, although some biogeographical barriers to contemporary gene flow do exist (e.g. across ocean basins of the Southern Hemisphere; Miller et al., 2011). Furthermore, molecular studies within the Mediterranean (Addamo et al., 2012; Boavida, Becheler, Addamo, Sylvestre, & Arnaud-Haond,- 2019; Costantini, Addamo, Machordom, & Abbiati, 2017) and among southern Australian seamounts (Miller & Gunasekera, 2017) indicate widespread dispersal, at least at the scale of hundreds of kilometres. Nevertheless, to date, no study has assessed the relationship between populations across the global range of the species. Hence, the relative importance of historical and contemporary gene flow in structuring and maintaining global populations remains unknown.

Studying the dynamics of populations is fundamental for understanding the ecology and evolutionary processes in marine environments, and for developing an effective plan to protect marine biodiversity (Cowen & Sponaugle, 2009). In this context, this study aims to estimate the genetic diversity in the cosmopolitan coral *D. dianthus* across its range and explore the role of contemporary connectivity in maintaining its global distribution and local populations. Thirty polymorphic microsatellite loci were used to determine the population structure of *D. dianthus* from 13 localities across the Northern and Southern Hemispheres. Potential larval connectivity dispersal with patterns of isolation by distance and oceanographic and genetic barriers with their significance for ongoing management and conservation in the deep sea are also discussed.

## 2 | METHODS

### 2.1 | Species studied

*Desmophyllum dianthus* occurs in the upper bathyal zone (200–2,500 m); it is generally associated with the reef-building species *Desmophyllum pertusum* (syn. *Lophelia pertusa*; Addamo et al., 2016), *Madrepora oculata*, and *Solenosmilia variabilis* (Roberts et al., 2009; Trotter et al., 2019; Zibrowius, 1980). However, records at shallower depths exist from 45 m depth in New Zealand fjords (Grange, Singleton, Richardson, Hill, & deL Main, 1981), and from 8 m depth in Chilean fjords (Försterra & Häussermann, 2003). *Desmophyllum dianthus* is a slow-growing coral (0.5–2 mm year$^{-1}$, exceptionally up to 3.6 mm year$^{-1}$ in shallow water) with a long lifespan (up to 200 years old) (Adkins, Henderson, Wang, O'Shea, & Mokadem, 2004; Jantzen et al., 2013; Roberts et al., 2009), and hypothetical lecithotrophic larvae capable of long-distance dispersal (Miller et al., 2011; Thresher, Adkins, & Thiagarajan, 2011). Notwithstanding, populations do not

appear to be panmictic either across depths or ocean basins, at least in the Southern Hemisphere (Miller et al., 2011). No studies on larval behaviour of *D. dianthus* have been published so far; thus, predictions of larval dispersal potential are impossible. However, applying a modal analysis to the size frequency distribution of live-caught and sub-fossil specimens, Thresher et al. (2011) made inferences on recruitment periodicity, growth, and mortality rates: regular episodic recruitment events occur approximately every 25 years, with a range of 9.2–15.1% constant adult (>30 mm corallum width) mortality rate. Recently, Feehan, Waller, and Häussermann (2019) published the first study on reproduction strategy of *D. dianthus* from the Patagonian fjords. The study confirmed the coral as a dioecious broadcast spawning species with a highly seasonal mode of reproduction, spawning at the end of austral winter (August) and beginning gamete production in early spring (September).

## 2.2 | Samples and study area

Coral tissue was sampled and preserved in absolute ethanol from specimens of *D. dianthus* collected during 18 voyages occurring between 2002 and 2012. Sampling took place in 13 localities and at different depth ranges: six in the Mediterranean Sea (315–1,350 m), three in the North Atlantic Ocean (500–1,069 m), one in the South Atlantic Ocean (757–1,629 m), and three in the South Pacific Ocean (20–1,200 m) (Figure 1). The sampling techniques, including the distance between locations, vary between year and sites. Further information and details are provided in Supporting Information Data S1.

The spatial scale across which the samples were collected is from tens to ten thousands of kilometres (up to maximum of 25,000 km). To achieve greater statistical power, and after testing the absence of genetic differentiation among samples of very close localities, those sampling sites that were represented by only two to five specimens were pooled into one locality. This was the case of the samples for localities finally named as ADR, ION, BAL, and SIC. The lack of small-scale structure within these areas has already been demonstrated in previous studies (Boavida, Becheler, Addamo, et al., 2019; Costantini et al., 2017).

## 2.3 | Microsatellite genotyping and characterization

Total genomic DNA was extracted from the mesenteric tissue of 347 *D. dianthus* specimens using the Qiagen BioSprint 15 DNA Blood Kit (Qiagen Iberia S.L., Madrid, Spain), with slight modifications, including the optional RNase treatment and an extended period of proteinase K lysis (overnight incubation at 55°C). DNA concentration was quantified using a Qubit 2.0 fluorometer (Thermo Fisher Scientific, Madrid), and diluted to a final concentration of 2 ng $\mu l^{-1}$. Thirty-one microsatellite loci developed for *D. dianthus* (25 markers from Addamo et al., 2015; six markers from Miller &

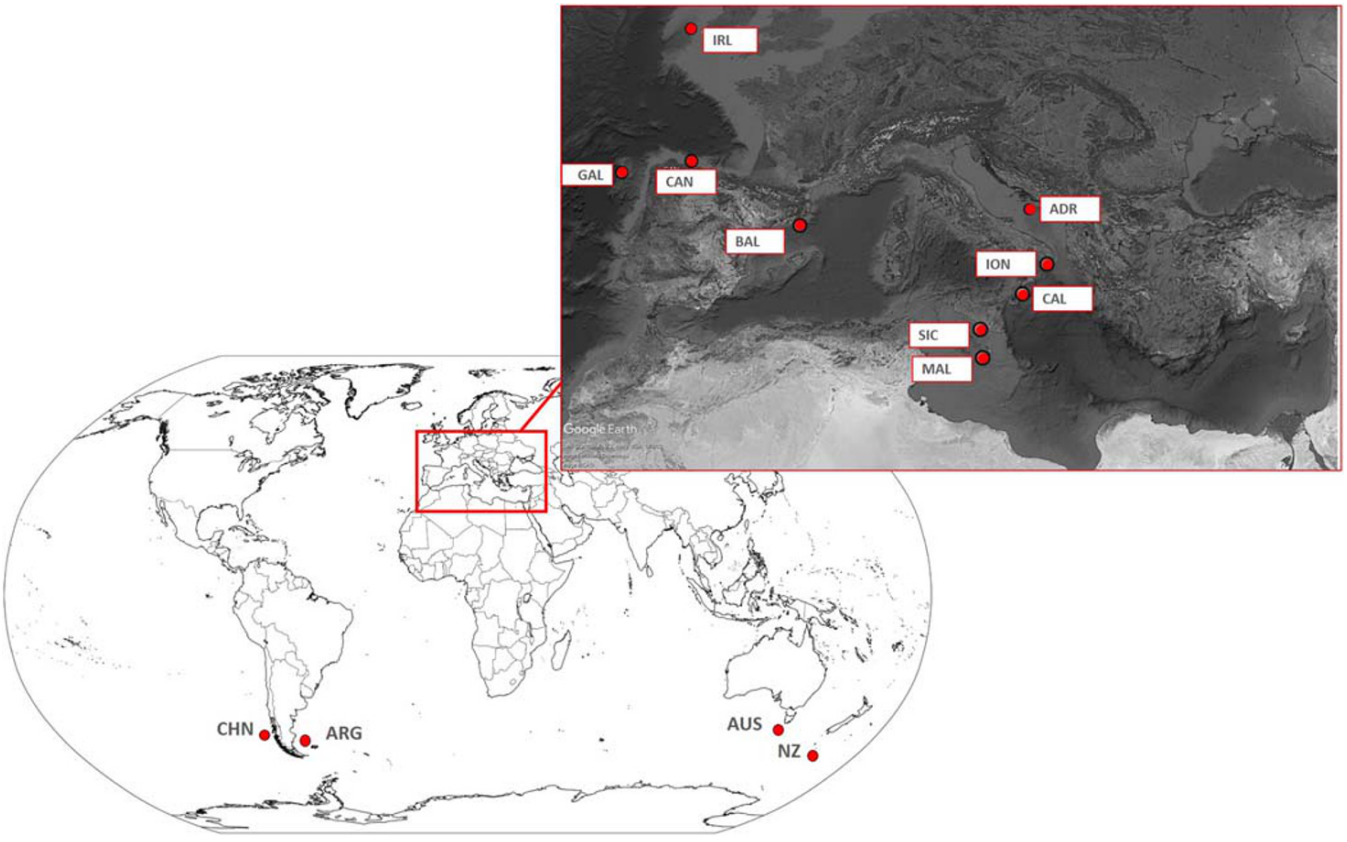


**FIGURE 1** Map of *Desmophyllum dianthus* collection localities

Gunasekera, 2017) were organized in one tetraplex, seven triplexes, and three duplexes by Multiplex Manager 1.0 (Holloley & Geerts, 2009) and analysed in each sample. Multiplex polymerase chain reactions (PCRs) were performed using 1X Qiagen Multiplex PCR Master Mix (Qiagen, Hilden, Germany), and following the PCR conditions described in Addamo et al. (2015). Fluorescently labelled PCR products were run on an ABI PRISM 3730 DNA Sequencer (Applied Biosystems), scored using the GeneScan-500 (LIZ) size standard (Thermo Fisher Scientific, Madrid), and analysed with the GeneMapper software (Applied Biosystems). Estimates of null allele frequency, error scoring, and large allele dropout were calculated with the Brookfield-1 method (Brookfield, 1996) using Micro-Checker (Van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Owing to possible asexual reproduction of corals (e.g. via budding), individuals with identical multilocus genotype were identified using the index of probability of identity (the probability of two individuals sharing the same genotype) calculated using GenAlEx 6.5 (Peakall & Smouse, 2012). Genotypic linkage disequilibrium was computed by exact test using Genepop 4.1 (Raymond & Rousset, 1995; Rousset, 2008) and GenAlEx 6.5 (Peakall & Smouse, 2012) to test the gene association for each pair of loci at each sampled locality, and analysis of significance was tested with Markov chain Monte Carlo. Sequential Holm–Bonferroni correction (Holm, 1979) was applied to the multiple tests. The detection of genetic markers exhibiting locus-specific effects associated with non-neutral selection (outliers) was made with different methods: the coalescent simulator built in LOSITAN (Antao, Lopes, Lopes, Beja-Pereira, & Luikart, 2008), the Bayesian calculation performed in BayeScan v2.01 (Fischer, Foll, Excoffier, & Heckel, 2011), and the hierarchical method implemented in Arlequin v.3.5 (Excoffier & Lischer, 2010).

## 2.4 | Genetic diversity and structure

Genetic variability within localities was estimated as observed heterozygosity $H_o$, expected heterozygosity $H_e$, and unbiased expected

**TABLE 1** Summary statistics for each locality of *Desmophyllum dianthus*

| Sampling location | Code | Statistic | *N* | $N_a$ | $N_e$ | *I* | $H_o$ | $H_e$ | $uH_e$ | $F_{st}$ | Pa (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Adriatic Sea | ADR | Mean | 23.900 | 9.433 | 5.230 | 1.762 | 0.631 | 0.749 | 0.765 | 0.146 | 54 |
| | | SE | 0.427 | 0.745 | 0.523 | 0.096 | 0.036 | 0.025 | 0.026 | 0.045 | – |
| Ionian Sea | ION | Mean | 39.267 | 11.333 | 5.321 | 1.809 | 0.607 | 0.749 | 0.759 | 0.177 | 17 |
| | | SE | 0.593 | 1.003 | 0.549 | 0.102 | 0.035 | 0.027 | 0.027 | 0.044 | – |
| Calabria | CAL | Mean | 30.133 | 10.367 | 5.090 | 1.776 | 0.621 | 0.747 | 0.759 | 0.157 | 49 |
| | | SE | 0.348 | 0.914 | 0.476 | 0.097 | 0.034 | 0.026 | 0.027 | 0.039 | – |
| Malta | MAL | Mean | 30.733 | 10.433 | 4.962 | 1.753 | 0.615 | 0.741 | 0.753 | 0.157 | 25 |
| | | SE | 0.335 | 0.951 | 0.510 | 0.095 | 0.036 | 0.025 | 0.025 | 0.046 | – |
| Strait of Sicily | SIC | Mean | 42.067 | 11.733 | 5.553 | 1.862 | 0.587 | 0.765 | 0.774 | 0.239 | 12 |
| | | SE | 0.489 | 0.995 | 0.603 | 0.097 | 0.039 | 0.023 | 0.023 | 0.044 | – |
| Balearic Sea | BAL | Mean | 12.667 | 7.500 | 4.776 | 1.624 | 0.621 | 0.720 | 0.751 | 0.130 | 23 |
| | | SE | 0.241 | 0.575 | 0.479 | 0.096 | 0.042 | 0.032 | 0.033 | 0.046 | – |
| Galicia | GAL | Mean | 20.300 | 9.267 | 5.038 | 1.764 | 0.582 | 0.761 | 0.780 | 0.234 | 26 |
| | | SE | 0.296 | 0.761 | 0.452 | 0.083 | 0.033 | 0.019 | 0.020 | 0.040 | – |
| Cantabria | CAN | Mean | 14.367 | 9.800 | 5.934 | 1.894 | 0.604 | 0.792 | 0.821 | 0.246 | 57 |
| | | SE | 0.182 | 0.731 | 0.554 | 0.085 | 0.034 | 0.016 | 0.017 | 0.038 | – |
| Ireland | IRL | Mean | 6.933 | 5.867 | 4.344 | 1.509 | 0.599 | 0.717 | 0.773 | 0.153 | 44 |
| | | SE | 0.046 | 0.395 | 0.413 | 0.076 | 0.041 | 0.021 | 0.023 | 0.057 | – |
| Argentina | ARG | Mean | 12.533 | 7.567 | 4.471 | 1.530 | 0.566 | 0.672 | 0.700 | 0.157 | 73 |
| | | SE | 0.171 | 0.667 | 0.478 | 0.117 | 0.053 | 0.040 | 0.042 | 0.055 | – |
| Chile | CHN | Mean | 34.000 | 9.967 | 4.800 | 1.491 | 0.514 | 0.621 | 0.630 | 0.146 | 70 |
| | | SE | 0.557 | 1.340 | 0.890 | 0.150 | 0.051 | 0.051 | 0.052 | 0.044 | – |
| Australia | AUS | Mean | 30.933 | 10.533 | 4.975 | 1.609 | 0.571 | 0.666 | 0.677 | 0.128 | 57 |
| | | SE | 0.346 | 1.087 | 0.661 | 0.136 | 0.043 | 0.041 | 0.042 | 0.038 | – |
| New Zealand | NZ | Mean | 31.200 | 11.533 | 6.002 | 1.818 | 0.584 | 0.728 | 0.740 | 0.190 | 99 |
| | | SE | 0.435 | 1.173 | 0.788 | 0.130 | 0.046 | 0.039 | 0.040 | 0.048 | – |
| Total | | Mean | 25.310 | 9.641 | 5.115 | 1.708 | 0.592 | 0.725 | 0.745 | 0.174 | |
| | | SE | 0.550 | 0.262 | 0.161 | 0.030 | 0.011 | 0.009 | 0.009 | 0.013 | |

Abbreviations: $H_e$, expected heterozygosity; $H_o$, observed heterozygosity; *F*, fixation index; *I*, Shannon's information index; *N*, sample size; $N_a$, number of alleles; $N_e$, number of effective alleles; Pa, percentage of private alleles; $uH_e$, unbiased expected heterozygosity.

heterozygosity $uH_e$ (Table 1). Tests for departures from Hardy–Weinberg equilibrium (HWE; locality by each locus) were also calculated. The inbreeding coefficients of individuals relative to each subpopulation $F_{IS}$ and to the total population $F_{IT}$ and the effect of subpopulation compared with the total population $F_{ST}$ were estimated for each locus separately and for all loci. Moreover, allelic richness $N_A$ and private allelic richness $P_A$ were calculated for each locality. Computations were made using GenAlEx 6.5.

To investigate population structure, the number of genetic clusters $K$ from multilocus genotype data was inferred with a Bayesian model-based approach implemented in STRUCTURE v2.3.4 (Falush, Stephens, & Pritchard, 2003). Bayesian analyses of genetic admixture model, including the information of sampling localities (LOCPRIOR), were run with settings including 100,000 Markov chain Monte Carlo interactions after a burn-in of 10,000 iterations. Ten independent chains were run to test each value of $K$ from 1 to 20. The results from STRUCTURE were then processed in STRUCTURE HARVESTER (Earl, 2012), STRUCTURE SELECTOR (Li & Liu, 2018), and CLUMPAK (Kopelman, Mayzel, Jakobsson, Rosenberg, & Mayrose, 2015) to detect the best-fit number of genetic clusters representing the genetic discontinuity of the data. The highest mean $\ln Pr(X|K)$ (Pritchard, Stephens, & Donnelly, 2000), the $\Delta K$ (Evanno et al., 2005), and MedMeaK, MaxMeaK, MedMedK, and MaxMedK (Puechmaille, 2016) were all considered to identify and evaluate the optimum value of $K$. Each cluster identified in the initial STRUCTURE run was analysed separately using the same settings to identify potential within-cluster structure (Evanno et al., 2005). Pairwise genetic distances $F_{ST}$ between clusters suggested by STRUCTURE and population assignment were calculated using GenAlEx 6.5. Microsatellite data were also subjected to analysis of molecular variance (AMOVA), implemented in Arlequin 3.5, to evaluate genetic differentiation among populations. To define a phylogeographic structure, spatial AMOVA among localities was tested for several clusters of populations (from 1 to 7) using SAMOVA 1.0. This method maximizes the proportion of genetic variance due to differences between a user-defined number of groups $K$, and assigns localities to groups, considering that they must be geographically adjacent and genetically homogeneous. $F$-statistics estimated the proportion of genetic variability found among populations $F_{ST}$, among populations within groups $F_{SC}$, and among groups $F_{CT}$. In particular, $F_{CT}$ is the index associated with simulated genetic barriers (Dupanloup, Schneider, & Excoffier, 2002).

## 2.5 | Genetic–spatial correlation and demographic parameters

Samples were analysed for isolation-by-distance using Mantel test implemented in GenAlEx 6.5. The regression of linearized $F_{ST}$ (i.e. $F_{ST}/(1 - F_{ST})$) versus marine geographic distance (kilometres), and depth distance (metres) was performed to assess the correlation between depth, genetic, and geographic distances. Marine geographic distances between localities were calculated using Google Earth (Google Inc., 2009) and considering the most direct marine route.

Detection of first-generation migrants was determined with GeneClass2 (Piry et al., 2004), setting the frequency-based method with Monte Carlo resampling, minimum number of 10,000 simulated individuals, and 0.01 for type I error (alpha) value.

Mutation-scaled effective populations size (Theta), and past (im) migration rates between populations were estimated using the coalescence-based program Migrate-n v3.6.4 (Beerli, 2009).

# 3 | RESULTS

Tests for linkage disequilibrium yielded approximately 1% significant tests of linked loci (after sequential Holm–Bonferroni correction) among a total of 5,655 pairwise comparisons. However, lack of homogeneity of significant physical linkage detected in GenPop 4.1 and GenAlex 6.5 led to the rejection of the hypothesis of linkage disequilibrium and all loci were considered as independent. In total, 347 specimens were initially analysed using 31 microsatellite loci. All loci were successfully genotyped in all populations, but one locus (DdL97) was excluded from the final data set due to PCR failure in more than 30% of all individuals (randomly across the complete sample). The mean probability of two corals having identical genotypes (probability of identity) was estimated at $3.0 \times {}^{-11}$ based on the extreme situation that all individuals were in full-sibling relationships (considering the combination of all 30 loci). Only two individuals (both from the same sampling locality in the Strait of Sicily) had identical multilocus genotypes and were considered as belonging to the same individual or clone. Thus, one of them was removed from the data set for subsequent analyses. Hence, the final analyses were performed with 346 different multilocus genotypes.

Null allele frequencies, calculated by locus per sampling locality, revealed a homozygosity excess across 10 loci (DdB118, DdC102, DdL7, DdL22, DdL41, DdL51, DdL58, DdL84, DdL90, and DdL109; Supporting Information Data S2) following Brookfield-1 adjustments. Outlier tests computed under different criteria determined inconsistent results: none of the analyses were simultaneously significant for a certain locus, hence the hypothesis that loci could be under selection has been rejected.

## 3.1 | Genetic diversity and structure

All loci were polymorphic, with a total number of alleles per locus ranging from three (DdL86) to 21 (C6), with a mean value of nine alleles per locus. The ratio of allelic richness to private allelic richness for each locality showed that localities from the Southern Hemisphere had the highest frequency of private alleles (Table 1). By locality, the observed heterozygosity $H_o$ was lowest in the Chilean population (CHN, 0.52 ± 0.05) and greatest in the Mediterranean population (ADR, 0.63 ± 0.04), whereas the unbiased expected heterozygosity $uH_e$ varied between 0.63 ± 0.05 (CHN) and 0.82 ± 0.02 (CAN) (Table 1).

The optimal values of genetic clusters *K* representing the genetic discontinuity among *D. dianthus* individuals were identified by the three approaches: highest mean lnPr(*X*| *K*) (Pritchard et al., 2000), Δ*K* (Evanno et al., 2005), and MedMeaK, MaxMeaK, MedMedK, and MaxMedK (Puechmaille, 2016; Supporting Information Data S3). Analyses of populations structure indicated two main genetic clusters of *D. dianthus* (*K* = 2), based on optimal *K* designed by Evanno (Δ*K*), corresponding to localities in the Northern Hemisphere (Mediterranean Sea–North Atlantic Ocean), on one side, and the Southern Hemisphere (South Atlantic Ocean–Pacific Ocean), on the

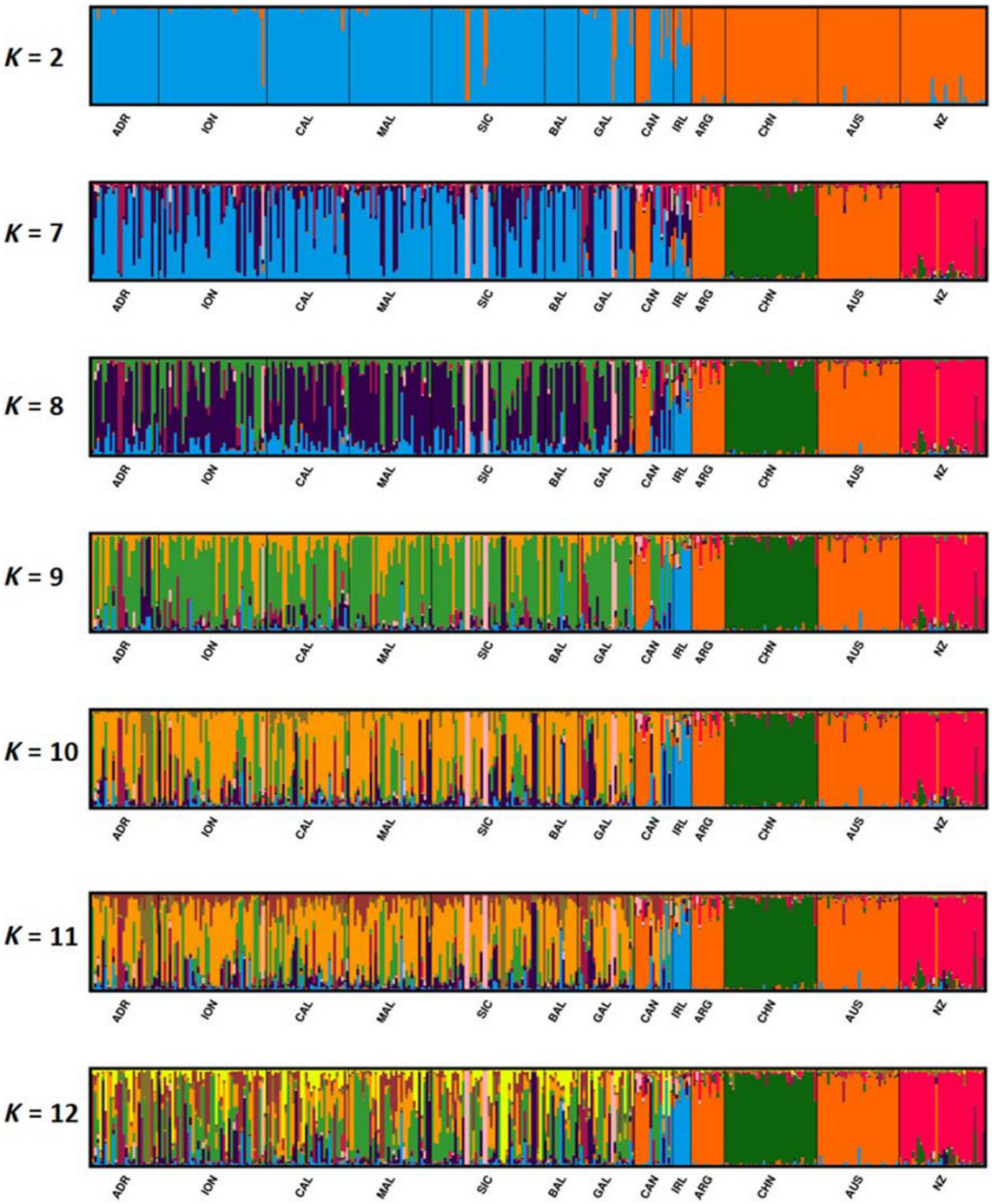


**FIGURE 2** Proportional membership of *Desmophyllum dianthus* individuals from sequential cluster analyses using STRUCTURE SELECTOR and CLUMPAK. The clusters are shown with the vertical bars representing each individual broken into coloured segments based on the proportion of the genome estimated to have originated from each cluster. Localities were structured in two main clusters (*K* = 2), based on optimal *K* designed by Evanno (Δ*K*), and in a range of clusters *K* = 7–12, based on optimal *K* designed by Puechmaille (MaxMeanK). Localities in Northern Hemisphere: ADR, ION, CAL, MAL, SIC, BAL, GAL, CAN, and IRL. Localities in Southern Hemisphere: ARG, CHN, AUS, NZ. For complete locality names, see Table 1

other. Localities were also structured in a range of higher values of genetic clusters ($K$ = 7–12), based on optimal $K$ designed by Puechmaille (MaxMeanK; Figure 2). Indeed, further structuring was detected within each main cluster, whereby the *D. dianthus* specimens of the Southern Hemisphere were subdivided clearly into three different genetic clusters (ARG + AUS, NZ, and CHN) and the specimens of the Northern Hemisphere were further subdivided into two genetic clusters: localities in (a) the Mediterranean Sea + GAL and GAL, and (b) CAN + IRL (Figure 2). Nevertheless, the CAN population apparently shares a genotype descendant with another group (AUS + ARG) from the Southern Hemisphere. In concordance with these results, the GenAlEx population assignment test estimated full self-population attribution (100%) for individuals from CHN and NZ, partially for individuals from AUS and ARG (93% and 84% respectively), whereas most of the individuals from the Mediterranean Sea and North Atlantic Ocean sites were assigned to other localities from the same marine area (82.4%). These results define the five population groups as the most probable structure of populations. In addition, the genetic distance among individuals (Figure 3) and the population differentiation estimated through AMOVA indicated appreciable differences among all five population group pairs (total $F_{ST}$ = 0.146, $P$ = 0.000) and an observed variation of 14.59%. The highest $F_{ST}$ values were observed between CHN and Mediterranean Sea + GAL (0.216) and between AUS + ARG and Mediterranean Sea + GAL (0.167) (Supporting Information Data S4).

## 3.2 | Genetic–spatial correlation and demographic parameters

Similarly, population differentiation with genetic barriers among five population groups were also indicated with SAMOVA (Figure 4). The phylogeographic structure identified AUS + ARG, CHN, NZ, CAN + IRL, and Mediterranean Sea + GAL as geographically homogeneous and maximally differentiated from each other ($F_{ST}$ = 0.16, $F_{SC}$ = 0.01, $P$-values highly significant), with clear genetic barriers ($F_{CT}$ = 0.15, $P$-values highly significant). A significant semipermeable natural barrier ($F_{CT}$ = 0.05, $P$ = 0.03) between the Mediterranean Sea and North Atlantic Ocean was detected: IRL, CAN, and Mediterranean Sea + GAL ($F_{ST}$ = 0.05, $F_{SC}$ = 0.002, $P$-values highly significant).

Furthermore, positive and highly significant genetic–spatial correlation was also detected from the Mantel test ($P$ = 0.1). Pairwise genetic distances between original localities increased significantly with geographic distances, showing an evident pattern of isolation by distance on the large spatial scale (Figure 5a). Localities appeared clustered in two major genetic divergence groups. The first cluster, including specimens from the Mediterranean Sea and the North Atlantic Ocean (marine distance range 0–5,000 km), showed a genetic differentiation ($F_{ST}$ range 0.008–0.1) smaller than the second cluster ($F_{ST}$ range 0.05–0.18), which is represented by two subgroups: (a) ARG–CHN and Mediterranean Sea–North Atlantic Ocean (marine distance range 8,000–17,000 km) and (b) AUS–NZ and Mediterranean Sea–North Atlantic Ocean (marine distance range >20,000 km). In contrast, significant low genetic–depth correlation was detected from the Mantel test ($P$ = 0.06) (Figure 5b, Supporting Information Data S5).

The estimated effective population size varied among different groups, with the lowest being 0.002 (NZ) and the highest 0.019 (IRL + CAN); NZ is about 10% of IRL + CAN. The credibility interval for the size of NZ is 0.00053 to 0.0090, and for IRL + CAN it is 0.01780 to 0.02113. Considering these intervals, the most extreme values for the size ratio NZ/IRL + CAN were a minimum of 0.25% and a maximum of 33.3% (Supporting Information Data S6). Asymmetric migration patterns characterized the gene flow direction across the five population groups, of which CHN, AUS + ARG, and NZ had the lowest number of migrants of first generation. The highest past (im) migration rate was detected from Mediterannean Sea + GAL to IRL + CAN (Supporting Information Data S6). Further studies should be performed in order to investigate in-depth and at regional scale the events responsible of the estimated migration.

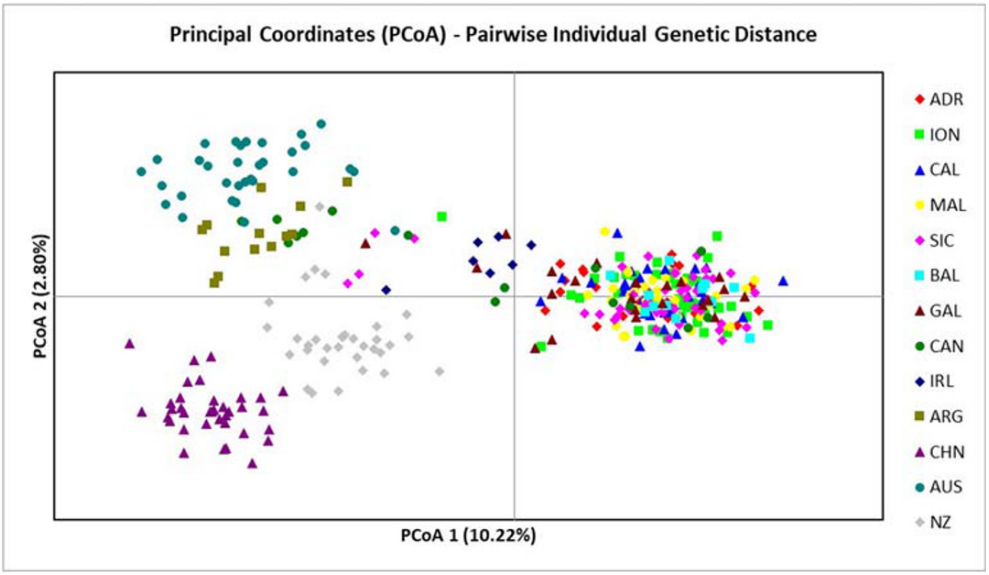


**FIGURE 3** Plot of principal coordinates analyses of pairwise individual genetic distance, classified by localities. For the complete locality names, see Table 1

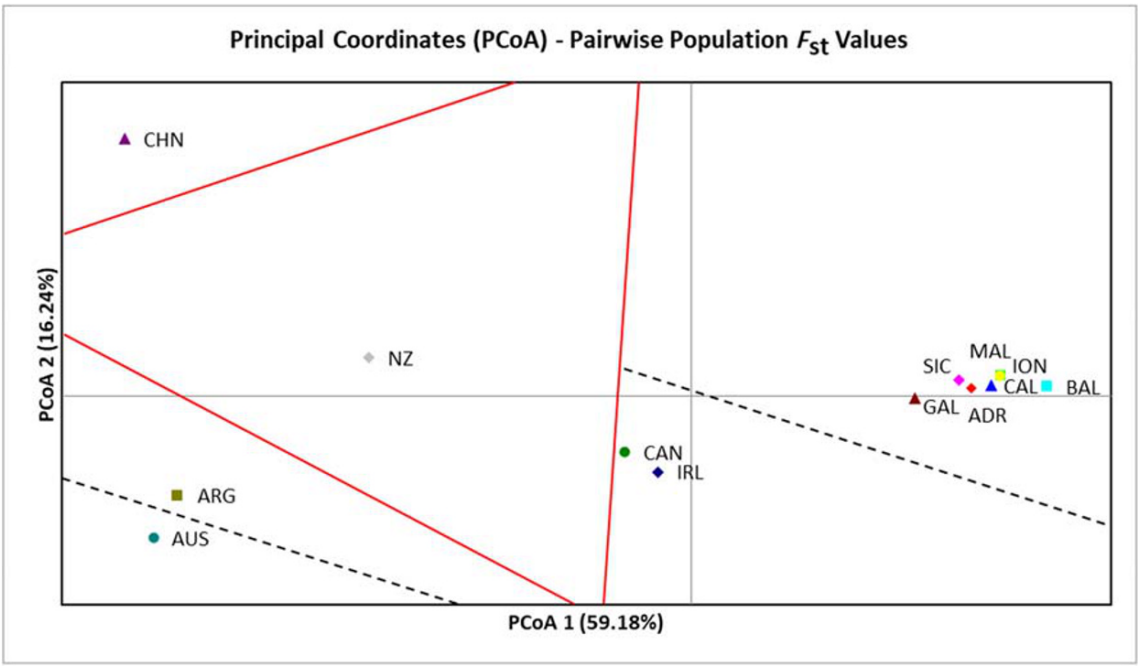


**FIGURE 4** Plot of principal coordinates analyses of all microsatellite data, classified by localities, with corresponding impermeable (red continuous line) and semipermeable (black dotted line) genetic barriers estimated using SAMOVA 1.0

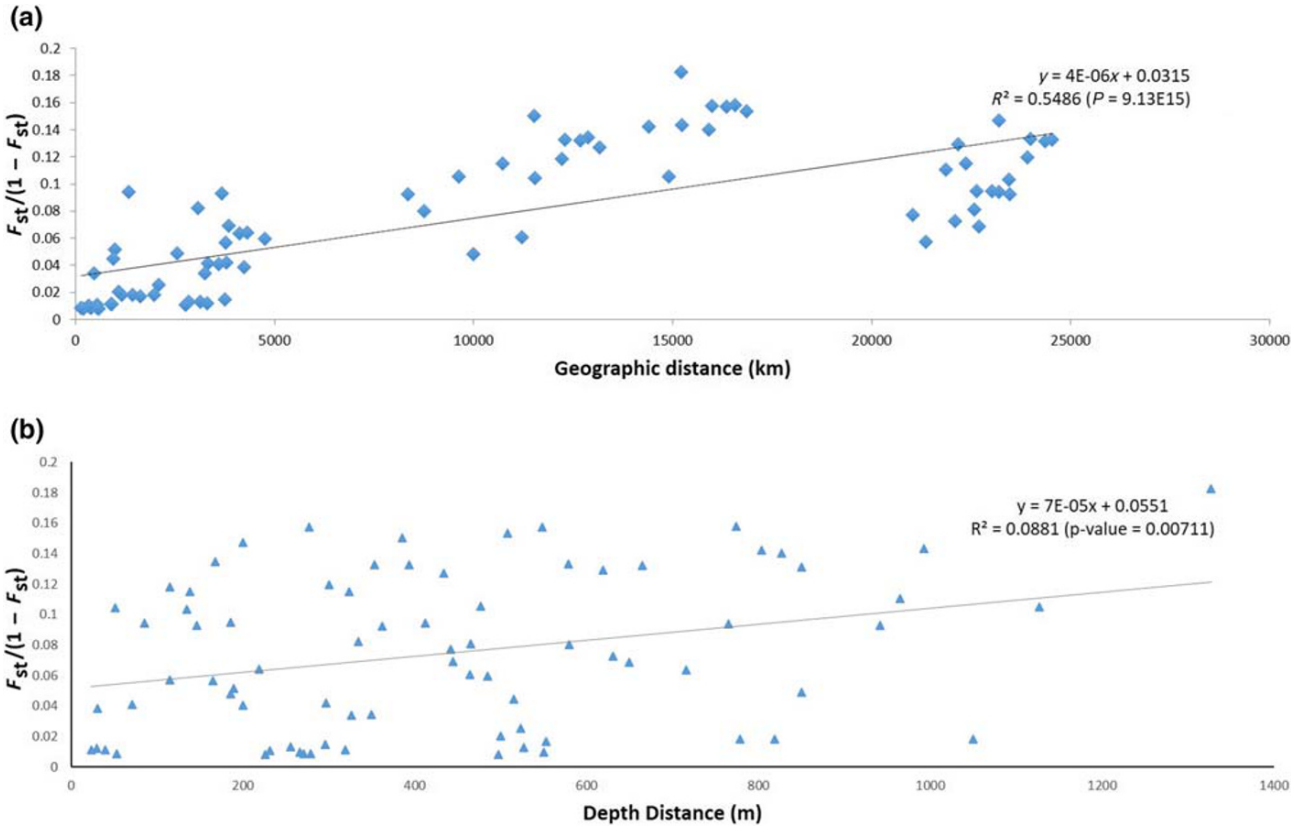


**FIGURE 5** Mantel test for correlation between (a) geographic or (b) depth distances and genetic distances among *Desmophyllum dianthus* localities

## 4 | DISCUSSION

Despite several studies (Bleidorn et al., 2006; Hauquier et al., 2017; Hutchings & Kupriyanova, 2018; Katz et al., 2005; Kawauchi & Giribet, 2014; Klautau et al., 1999; Logares, 2006; Pérez-Portela et al., 2013; Salgado-Salazar et al., 2013; Weiner et al., 2012; Zeppilli et al., 2011) demonstrating that globally distributed species with low dispersal capabilities generally are species complexes with a hidden diversity of cryptic species, morphomolecular taxonomy did not uncover these in *D. dianthus* (Addamo et al., 2015). This deep-sea species seems to be a monospecies with a cosmopolitan distribution (Addamo et al., 2012). The results, combined with the low larval dispersal capability that characterizes its sibling species *D. pertusum* (syn. *L. pertusa*) and oceanographic features, lead to the hypothesis of genetic breaks and biogeographic boundaries in marine regions at different spatial scales.

In this study, the genetic diversity of cosmopolitan cold-water coral *D. dianthus* populations has been compared both in the Northern and Southern Hemispheres. Diversity estimates of *D. dianthus* populations and potential physical dispersal barriers might also be affected by the different ecosystem habitats and oceanographic features that characterize each study area. Whereas in the South-west Atlantic Ocean and South-east Pacific Ocean the sampling sites are mostly represented by fjord and seamount environments, in the Mediterranean Sea and North Atlantic Ocean they mainly relate to canyons and outer shelf situations. Porlier, Garant, Perret, and Charmantier (2012) and Hauquier et al. (2017), for example, demonstrated that the genetic structure can be also linked to habitat types, suggesting that although individuals have high dispersal ability, local adaptation might reduce gene flow among populations located in different habitats. In this study the results revealed a clear difference in demographic history of five population groups, and the presence of semipermeable biogeographical barriers in the Mediterranean Sea and North Atlantic Ocean could contribute to the differentiation observed using microsatellites. Nevertheless, further studies with seascape genetics approaches need to be undertaken at a regional scale, investigating the effects of habitat composition between populations on genetic differentiations.

### 4.1 | Spatial–genetic structuring and oceanographic connectivity

A clear genetic structure exists in *D. dianthus* across its distribution range, indicating that different eco-evolutionary processes (e.g. larval dispersal capacity, community dynamics) and oceanographic factors might drive the strong genetic differentiation between the hemispheres and among locations within each hemisphere.

At a global scale, strong genetic discontinuities were detected between the Northern and Southern Hemispheres. Even though, the sample size of the boreal population is twice that of the austral one, the $N_A$ observed is similar in both hemispheres, whereas the $H_o$ in the Southern Hemisphere is lower (heterozygosity deficit) than the one detected in the northern counterpart. In addition, $P_A$ is much higher in the southern localities (>70%), suggesting that distinct ecological (biotic and abiotic factors) and demographic events (e.g. bottleneck or vicariance processes) have affected the Southern Hemisphere more deeply. Although a clear isolation-by-distance pattern indicates a restricted gene flow among geographically distant populations, evidence of a potential corridor between both hemispheres arises from North Atlantic Ocean populations (e.g. Cantabria and Ireland), where some individuals shared their genetic profile with the Southern Hemisphere clusters (Argentina). Connections between Northern and Southern Hemispheres could be facilitated by intermediate populations (stepping stones), although samples of potential intermediate populations were not available at the time of the study (e.g. *D. dianthus* samples from Brazil and/or Azores) to test this hypothesis. Equally, differentiation between populations might be underestimated because of homoplasy, due to the relative rapid evolution rate of microsatellites.

Within each hemisphere, multiple processes (e.g. larval behaviour, dispersal potential, selection, and oceanographic features) that influence gene flow and connectivity could contribute to patterns of differentiation in *D. dianthus*. In the Southern Hemisphere, strong genetic discontinuities between Australia, New Zealand, and Chile were detected, indicating potential vicariance or adaptation to environmental changes at regional scale, as shown for *D. pertusum* in the North Atlantic Ocean (Morrison et al., 2011). The southern hemispheric populations encompass three distinct marine habitats (seamounts: Australia and New Zealand; shelf: Argentina; and fjord: Chile), and the genetic variation could reflect the different oceanographic features. Significant genetic differentiation with depth strata was documented in previous studies (Miller et al., 2011), indicating limited vertical larval dispersal, and explaining the differences observed between Australian (∼1,000 m) and New Zealand (∼400 m) seamount populations despite their relative proximity. The samples from Chile are of a shallow-water population (up to 23 m), so isolation and divergence from deep populations is unsurprising. Similar results were also obtained from *D. pertusum* populations in Norwegian fjords and offshore waters: Le Goff-Vitry et al. (2004) revealed that fjord subpopulations were highly genetically differentiated from the continental margin subpopulations, suggesting a very low gene flow between these groups. On the contrary, the similarity between Australia and Argentina is unexpected. Both samples were collected at comparable depths (∼1,000 m), from a seamount and continental shelf respectively. This similarity suggests that deep currents might play a key role in connectivity and supports the notion that connections in the deep sea are greater than in shallow waters, facilitating cosmopolitanism (Hutchings & Kupriyanova, 2018). In this case, ocean currents, such as the Subantarctic Front, Antarctic Intermediate Water,the Antarctic Circumpolar Current, and Circumpolar Deep Water (Hartin et al., 2011; Peterson & Witworth, 1989; Sloyan, Talley, Chereskin, Fine, & Holte, 2010), might drive the gene flow between populations of the South Atlantic and Pacific Oceans.

Within the Northern Hemisphere, similar findings were observed for the North Atlantic Ocean and the Mediterranean Sea. The genetic differentiation by geographic pattern is broken by unexpected low gene flow between Cantabria and Galicia and high genetic similarity between Galicia and the localities from the Mediterranean Sea. In the first case, the restricted gene flow between both marine areas might be explained by the hydrographical and dynamic features of the sampling areas in Cantabria and Galicia. Le Goff-Vitry et al. (2004) and Morrison et al. (2011) demonstrated that a highly heterogeneous submarine orography (e.g. narrow canyons) and hydrology (e.g. seasonal upwelling system or eastward shelf–slope current, a prolongation of the Iberian Poleward Current in the Gulf of Biscay) can contribute to the genetic differentiation between populations by limiting larval distribution of *D. pertusum* in the North Atlantic Ocean, and likewise other species (Koutsikopoulos & Le Cann, 1996; Quinteiro, Rodríguez-Castro, & Rey-Méndez, 2007; Rivera et al., 2013; Sánchez & Gil, 2000). In the second case, the unexpected connectivity between Galicia and Mediterranean Sea populations could be explained by the Mediterranean Water Vein (MW). This is a poleward current that tends to contour the south-western slope of the Iberian Peninsula, transporting salty and warm MW over a great distance (Cherubin et al., 1997; Iorga & Lozier, 1999). The MW effect decreases from the western Spanish coast up to the northern coast of Galicia (Fraga, Mouriño, & Manríquez, 1982). All these considerations and the current results have led to the rejection of the hypothesis of Galicia as a potential corridor between the North Atlantic and the Mediterranean Sea.

Although recent studies demonstrated that genetic diversity and connectivity of shallow-water benthic invertebrate populations within the Mediterranean Sea—for example, *Dendropoma petraeum* (Calvo, Templado, Oliverio, & Machordom, 2009) and *Astroides calycularis* (Casado-Amezúa, Goffredo, Templado, & Machordom, 2012)—are usually associated with the marine biogeographic regions identified for the Mediterranean Sea (Bianchi & Morri, 2000), no substantial genetic differentiation with such geographical boundary patterns was detected among *D. dianthus* individuals analysed from different Mediterranean localities. Nevertheless, it is also important to note that all individuals analysed in this study were sampled in the Western Mediterranean Sea. Since the Mediterranean Sea displays oceanographic differences among sub-basins, and the merging of the whole basin in a single bio-province has been questioned based on different approaches (Malanotte-Rizzoli & Pan-Med Group, 2012), further analyses should be performed, including on samples of *D. dianthus* from the Eastern Mediterranean Sea.

Low connectivity and declining genetic variability along a depth gradient was reported in previous studies for *D. dianthus* populations in the South Pacific Ocean (Miller et al., 2011), as well as in the Mediterranean Sea for the octocoral *Corallium rubrum* (Costantini et al., 2010, 2011). Findings from this study indicate submarine orography and hydrology as major key players in the genetic differentiation. Further tests at different scales and with a larger sample sizes are needed to substantiate these conclusions.

## 4.2 | Conservation and management implications

Inferring genetic variation and making genetic data available at different spatial scales play a key role in conservation management. When the reproductive and developmental biology of a species is unknown, data on genetic variation and gene flow are relevant for understanding the biological or ecological events that could affect the species over time. If a coral population, for example, is negatively impacted by human pressures and it is known that gene exchange exists between populations, then the overall genetic diversity of the species would not be so damaging at certain sites, since these may be recolonized over time by sexually produced larvae (Le Goff-Vitry et al., 2004). If, on the other hand, there is no gene exchange, it could be fatal for the affected population. The exercise of studying *D. dianthus* populations at a large geographic scale might be used as a starting point for further analyses at a smaller scale and focused on conservation measures of specific areas. In the case of a catastrophic event affecting a population in the Northern Hemisphere, our results suggest, for example, that the gene flow between Mediterranean Sea and Atlantic Ocean might play a role allowing the recolonization (source–sink model) of the damaged area. On the contrary, in the Southern Hemisphere, where Chilean samples represent a differentiated population, any negative event could dramatically damage it. Taking into consideration that in one of three fjords where dense coral banks are described (Häussermann & Försterra, 2007) there was a mass mortality killing of *D. dianthus* specimens along approximately half the fjord (Försterra et al., 2014), and in a second fjord that was subject to intense fish farming (Clement, Grünewald, Aquilera, & Rojas, 2002), which can also negatively affect coral populations (Häussermann, Försterra, Melzer, & Meyer, 2013), there is almost no potential source for population recovery. The corresponding Chilean gene pool would be lost, thus affecting the genetic diversity of the entire species in the area. Therefore, special attention should be paid to the Chilean fjord populations and their conservation, by controlling, for instance, the contamination due to intensive aquaculture in the surrounding areas. Finally, although New Zealand individuals appear to be genetically distinct, in the case of dramatic events the population could, in principle, be replenished from adjacent populations (e.g. Macquarie Ridge Seamount 5, Chatham Rise; Miller & Gunasekera, 2017).

Population genetic studies at a global scale can help to prioritize some areas as 'hot spots', but further studies exhaustively sampling understudied areas can help to give a better picture of genetic connectivity at the local scale and be fundamental for effective local conservation management plans.

Although the overall relationship between genetic structure and marine life histories seems to match generally, there is a growing number of exceptions that provide powerful insights into the relationships between physical and biological oceanography (Palumbi, 2004). Genetic population studies on a global scale provide an overview of population structure and connectivity, which in turn can identify potential genetic breaks and biogeographic boundaries in marine regions, which is important for effective marine conservation. The scientific results of molecular studies need to be used more frequently

by policymakers as support to their work in achieving the international goal of sustainable management of marine resources.

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## AUTHOR CONTRIBUTIONS

AMA and AM contributed to the design of the study. Sample collection was performed by AMA, MJK, HV, and MT. DNA extraction, sequencing, and data analysis was performed by AMA. The manuscript was written by AMA with contributions from all authors.

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## SUPPORTING INFORMATION

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

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