Landscape Ecol (2019) 34:2649–2668
https://doi.org/10.1007/s10980-019-00911-x

RESEARCH ARTICLE

Seascape genetics and connectivity modelling for an endangered Mediterranean coral in the northern Ionian and Adriatic seas

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Received: 22 April 2019 / Accepted: 23 September 2019 / Published online: 10 October 2019

Abstract

Context Spatially heterogeneous oceanographic properties such as currents, waves, and biogeochemical gradients control the movement of gametes and larvae of marine species. However, it is poorly understood how such spatial dynamics may shape the genetic connectivity, diversity, and structure of marine populations.

Objectives We applied a seascape genetics framework to evaluate the relationships between marine environmental factors and gene flow among populations of the endangered Mediterranean pillow coral (*Cladocora caespitosa*).

Methods We modelled gene flow among locations in the Adriatic and northern Ionian Seas as a function of sea surface temperature, salinity, currents and geographic distance. Isolation by distance and isolation by resistance hypotheses were then compared using model optimization in a generalized linear mixed effects modelling framework.

Results Overall genetic differentiation among locations was relatively low (F_{ST} = 0.028). We identified two genetic groups, with the northernmost location segregating from the rest of the locations, although some admixture was evident. Almost 25% of the individuals analysed were identified as putative migrants and a potential barrier to gene flow was identified between the northern and central-southern basins. The best gene flow models predicted that genetic connectivity in this species is primarily driven by the movement along the coastlines and sea surface currents.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10980-019-00911-x) contains supplementary material, which is available to authorized users.

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Conclusions A high percentage of self-recruitment and relatively low migration rates has been detected in the studied populations of *C. caespitosa*. Its fragmented distribution along the coast can be predicted by stepping-stone oceanographic transport by coastal currents among suitable habitat patches.

Keywords *Cladocora caespitosa* · Marine connectivity · Linear mixed effects models · Model optimization · Seascape ecology · Landscape genetics

Introduction

The field of landscape genetics has seen rapid development over the last two decades (e.g. Manel et al. 2003; Balkenhol et al. 2015; Cushman et al. 2018), yet seascape genetic studies are still scarce (Selkoe et al. 2015; Ahrens et al. 2018). Storfer et al. (2010) pointed out that only about 15% of landscape genetic studies were conducted in fresh water systems and only 6% in marine environments. Seascape genetics, has been used to investigate dispersal patterns as a function of observed pairwise genetic differentiation, detection of dispersal barriers to gene flow, and for testing alternative ecological hypotheses regarding factors affecting the genetic structure of marine populations (Galindo et al. 2006; Coscia et al. 2012).

Undertaking spatial genetic studies in the marine environments has been particularly difficult because of the dual challenges of collecting data related to seascape features and marine species population genetics (e.g. Balkenhol et al. 2009; Storfer et al. 2010; Selkoe et al. 2016). Early work in seascape genetics highlighted the limitations of applying simple population genetic models to the highly complex, multi-dimensional and scale-dependent context of marine ecosystems (Selkoe et al. 2016). In particular, anisotropic patterns of transport in eddies and gyres that differ seasonally, interannually and at different depths of the water column lead to complex patterns of episodic gene flow. Large population sizes and long dispersal distances often limit genetic differentiation in marine species and it has long been assumed that their local populations were demographically open (e.g. Waples 1990; Hedgecock et al. 1992; Whitlock and McCauley 1999). Nevertheless, there is growing evidence that larvae of some species do remain near their source population thus increasing self-recruitment and limiting population connectivity (e.g. Sponaugle et al. 2002; Strathmann et al. 2002). Most marine species have a two-phase life cycle (pelagic larvae and benthic adults). The free larvae can disperse tens to hundreds of kilometres during their larval period, while the benthic or sedentary adults are often aggregated in spatially restricted habitats (Cowen and Sponaugle 2009). Currents often cause diffusion and dilution of clouds of dispersing larvae, but varied spatial and temporal heterogeneity of physical and biological factors (such as temperature, salinity, pH, nutrients or predators) play important roles in their transport, arrival to suitable places and subsequent settlement and survival. In certain situations, these contact zones along the fronts between opposing currents, can become potential barriers and increase the concentration and aggregation of dispersing larvae (Siegel et al. 2003; Mann and Lazier 2006; Woodson and McManus 2007). Furthermore, local-scale oceanographic retention dynamics, such as offshore eddies or counter currents, can limit the dispersal of larvae and may significantly increase local retention and self-recruitment (Pineda et al. 2007).

Among studies that looked at spatial population structure and connectivity in marine systems (e.g. Selkoe et al. 2008; Selkoe and Toonen 2011; Liggins et al. 2013; Riginos and Liggins 2013; Pinsky and Palumbi 2014; Dalongeville et al. 2018), few have investigated the scales, effect sizes, and functional forms of relationship between spatial marine processes and population structure and gene flow. Additionally, the highly connected, multi-scale, spatially and temporally complex nature of marine ecosystem dynamics leads to genetic pattern-process relationships that require a scale-dependent, spatially-explicit and individual-based framework to properly discern. The relative influence of seascape variables on genetic structure of marine populations can be identified by testing alternative ecological hypotheses in a seascape genetic framework (e.g. Storfer et al. 2007). Such a framework should address both spatial and temporal scale, particularly with respect to differences in environmental conditions, current direction and speed at different depths in the water column and changes in these vectors over time. Research in terrestrial environments has shown that optimizing scale, effect size and functional form are all effective and essential to

obtain a clear and accurate understanding of the processes affecting gene flow (Shirk et al. 2010; Castillo et al. 2014; Shirk et al. 2018).

The main goal of this study was to adapt the optimization approaches described above to identify the factors that drive gene flow of a temperate scleractinian coral species in the northern Ionian and Adriatic seas (Mediterranean Sea). We analysed the genetic structure of the reef-forming Mediterranean coral *Cladocora caespitosa* (Linnaeus 1767) and estimated the connectivity of its populations using microsatellite markers along a complex coastlines and current patterns. This Mediterranean endemic coral is found in a wide variety of habitats, from shallow waters to $\sim$ 35 m deep (Bellan-Santini et al. 2002). It typically forms isolated colonies or beds, or occasionally large dense banks (Kersting and Linares 2012) or true reefs (Kružić and Benković 2008). They are sensitive to high hydrodynamism (e.g. strong waves), but can tolerate intense sustained currents, and a complex and irregular coastline favours the settlement of this coral and development of coral banks (Chefaoui et al. 2017). The spawning period of this species is short, synchronous and seasonal: in the western Mediterranean it occurs at the end of the summer when sea surface temperature (SST) begins to fall (Kersting et al. 2013b), while in the Adriatic Sea it takes place at the beginning of the summer when SST begins to rise coinciding with a full moon (Kružić et al. 2008). Eggs are released by the polyps in a mucous coating, while sperm is freely released in sperm bundles. Fertilization may be enhanced by synchronous spawning and egg retention on the colony surface (Kružić et al. 2008). This mechanism may force the planulae to remain near the parental colonies, likely contributing to the patchy and contagious distribution of the coral (Kersting and Linares 2012), as does potential asexual reproduction by fragmentation or polyp removal (Kružić et al. 2008). Therefore, the reproductive biology of this coral results in limited dispersal capability, with self-recruitment predominating over less frequent longer-distance dispersal events (Casado-Amezúa et al. 2014; Kersting et al. 2014). The biological traits and the patchy and discontinuous distribution of *C. caespitosa*, along with the distinctive physical features of the Adriatic Sea, provide a complex scenario in which both patchy and continuous factors influence its population connectivity.

The relatively low dispersal capability of the species, its slow life history strategy and low recovery potential (Kersting et al. 2014) combined with long-term impacts of climate-change (Kersting et al. 2013a) has led to its decline in distribution and overall abundance, with increasingly isolated populations. Thus, it was listed as an endangered species on the IUCN Red List (Casado-Amezúa et al. 2015). Therefore, it is urgent to identify those factors involved in its dispersal and genetic connectivity. To this aim, we: (1) conducted the first analysis of gene flow in a marine system using multi-variate restricted optimization to identify effects sizes and interactions of environmental factors and (2) applied previously described approaches developed in modelling wind-driven seed dispersal to account for directionality of current flows. To date, no seascape genetics study has optimized relationships with directional resistance due to currents and cumulative resistance due to the spatial rate of change of marine environmental variables. Thus, to accomplish the first goal, the methodology followed was the same as Shirk et al. (2010, 2018) using the best current method of model selection (linear mixed effects modelling), and for the second, the effects of directionality of sea surface currents on genetic differentiation was analysed using the methods developed by Landguth et al. (2017) in terrestrial systems. The cumulative differences in environmental resistance have been successfully applied to model continuous genetic differentiation across in tree (Cushman et al. 2016; Bothwell et al. 2017) and shrub species (Yang et al. 2015) in terrestrial environments. Here we show that these landscape genomic methods can also be successfully applied to solve the challenge of understanding gene flow in complex marine environments.

Materials and methods

Study area

Our study area extends across the Adriatic and the northern Ionian seas (central Mediterranean; Fig. 1). The sampling sites correspond to a pilot study area of the European project COCONET (EU Seventh Framework Programme), where genetic studies for different marine species such as the sea urchin *Paracentrotus lividus* (Paterno et al. 2017), the seagrass *Posidonia*

oceanica (Jahnke et al. 2017) and the top shell *Gibbula divaricata* (López-Márquez et al. 2019), were performed in order to produce guidelines for the networks of Marine Protected Areas institution (Boero et al. 2016). The Adriatic Sea is divided into three well differentiated sub-basins: the northern basin (average depth = 35 m; maximum depth ∼ 170 m), the middle basin (average depth = 140 m; maximum depth ∼ 270 m), and the southern basin which presents a wide depression (depth range = 200 m–1270 m) (Russo and Artegiani 1996). The hydrological connection between the Adriatic and Ionian seas occurs through the Otranto Channel, which is ∼ 70 km in width and ∼ 800 m in depth (Ferentinos and Kastanos 1988).

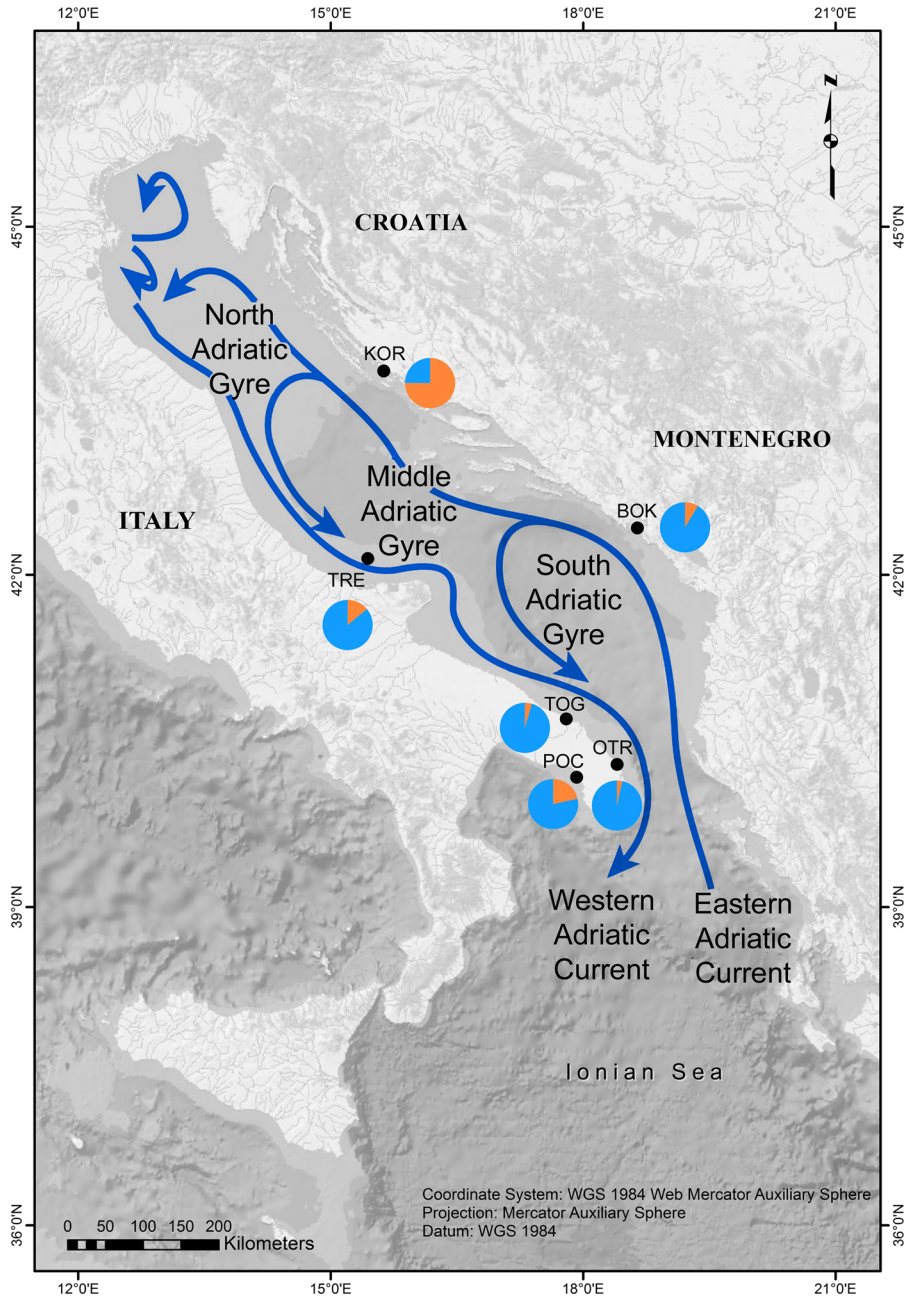

Fig. 1 Map representing the sampling locations in the Adriatic Sea and the global surface circulation (Adapted from Melià et al. 2016). Blue and orange in pie diagrams indicate distribution and proportion of the two genetic clusters detected by STRUCTURE in each population

Hydrological circulation in the Adriatic Sea is cyclonic and is dominated by two main currents (Fig. 1). The Eastern Adriatic Current (EAC) flows to the north, along the eastern side of the Adriatic Sea, while the Western Adriatic Current (WAC) flows back to the south along the western coasts (Russo and Artegiani 1996). Additionally, each of the three sub-basins (northern, middle and southern) is dominated by their own cyclonic gyres (Fig. 1), which vary seasonally in their intensity of water circulation. However, the southern sub-gyre tends to persist year-round (Russo and Artegiani 1996). Between the Ionian and Adriatic Seas, the Otranto Channel allows Ionian waters to enter and mix with the EAC (Poulain and Hariri 2013). The general pattern of the currents favours connectivity along coastlines; nevertheless, long-distance dispersal between eastern and western coasts is achievable via Adriatic sub-gyres (Carlson et al. 2016). Thus, seascape connectivity through this basin is primarily influenced by circulation of the EAC and WAC across the three sub-regions, but connectivity is also driven by temporal connections within sub-gyres (Melià et al. 2016).

In the study area, *C. caespitosa* has a discontinuous and patchy distribution, often as aggregated colonies. We collected samples of *C. caespitosa* from six localities. Five were located in the central and southern sectors of the Adriatic Sea (Table 1; Fig. 1). Among these, two were located along the eastern coast of the Adriatic Sea, including the Telašćica Nature Park (Kornati; KOR) in Croatia and Boka Kotorska (BOK) in Montenegro. Three others were set along the western coast, including the Tremiti island (TRE), Torre Guaceto (TOG) and Otranto (OTR). The sixth population was located in Porto Cesareo (POC) in the Gulf of Taranto (Italy) in the northern part of the Ionian Sea. Distances between sampling locations ranged from 160 km (BOK and KOR) to 600 km (KOR and POC). Distances between western locations ranged from 240 km (TRE and TOG) to 450 km (TRE and POC). Our sampling localities represent two of the three sub-basin areas within the Adriatic Sea and a population from the Ionian Sea, situated at different sides of potential dispersal barriers (e.g. deep water areas) (Fig. 1).

Genetic analysis

Individual polyps from 28 to 35 colonies were collected by SCUBA diving at each of the six sampling locations. Sampled colonies were separated by at least 1 m to avoid collection of clones. Four to six polyps (from each colony) were carefully excised and placed into labelled bags. Samples were stored in vials of absolute ethanol and preserved at 4–10 °C until molecular procedures were performed. All necessary permits were obtained for the described field studies. DNA from the sample soft tissue was extracted for 190 absolute ethanol-fixed polyps using the manufacturer's protocol of the QIAGEN BioSprint 15 DNA Blood Kit (Qiagen Iberia S.L., Madrid, Spain). Using the Quant-iT dsDNA HS Assay, DNA was measured and diluted to a final concentration of 0.3 ng/µl. All samples were genotyped for nine polymorphic microsatellite loci previously isolated for this species by Casado-Amezúa et al. (2011). PCR amplifications were performed as described in Casado-Amezúa et al. (2011). To facilitate genotyping, 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). All fluorescently labelled PCR products were run on an ABI PRISM 3730 DNA Sequencer (Applied Biosystems) and scored using the GeneScan-500 (LIZ size standard). Electropherograms were analysed with GENEMAPPER software 3.0 (Applied Biosystems).

Table 1 Location of *Cladocora caespitosa* samples

Location Name	Code	GPS coordinates	N
Boka Kotorska (Montenegro)	BOK	42°25.147′N; 18°40.608′E	28
Kornati (Croatia)	KOR	43°51.384′N; 15°16.086′E	33
Tremiti Island (Italy)	TRE	42°8.233′N; 15°31.196′E	34
Torre Guaceto (Italy)	TOG	40°42.868′N; 17°48.096′E	35
San Foca, Otranto (Italy)	OTR	40°6.543′N; 18°31.169′E	32
Porto Cesareo (Italy)	POC	40°13.176′N; 17°55.402′E	28

MICRO-CHECKER v2.2.3 (Van Oosterhout et al. 2004) was used to test for null alleles.

We quantified allelic diversity (Na), observed (Ho) and expected (He) heterozygosities and Hardy–Weinberg equilibrium (HWE) for each locus within sampling locations using GENEPOP v4.0 (Raymond and Rousset 1995) and GENALEX 6.0 software (Peakal and Smouse 2006). *P*-values were corrected with the sequential Bonferroni method (Rice 1989). We checked for the existence of clones using GENALEX, and estimated genetic differentiation among sampling locations with Wright's fixation index (F_{ST}) using Weir and Cockerham's estimators in GENETIX v.4.03 (Belkhir et al. 2004). We visualized population genetic clustering with principal coordinates analysis (PCoA) on F_{ST} values in GENALEX, and further used STRUCTURE 2.2.3 software (Pritchard et al. 2000) to infer population genetic structure. We used an admixture model with correlated allele frequencies and location specified as a prior. We ran 20 replicates per K, for K = 1–10 (surpassing the number of localities to count on possible unsampled differentiated populations) to calculate the mean log probability of the data (lnP(K)), based on 100,000 Markov chain Monte Carlo (MCMC) iterations following a 10,000 iteration burn-in. We evaluate the optimal value of K by considering both the highest mean likelihood value (L(K)), and ΔK as calculated using STRUCTURE Harvester (Earl and vonHoldt 2012) and the method proposed by Evanno et al. (2005). We used Clumpak (Kopelman et al. 2015) to compare results across the 20 replicates per each K, and identify the most likely number of populations. Using the optimal K, we performed a hierarchical analysis of molecular variance (AMOVA) in ARLEQUIN v3.5 (Excoffier et al. 2005) using 1000 permutations. Next, we tested each locus for deviation from neutrality. We conducted an F_{ST} outlier analysis with LOSITAN (Antao et al. 2008), testing each locus for deviations from neutral expectations of the relationship between heterozygosity and F_{ST}. We also used BAYESCAN 2.01 (Foll 2012) to test for evidences of selection versus a neutral model, using a Bayes factor, and following Jeffreys's (1961) scale of evidence. The parameters used were: burn-in = 50,000, thinning interval = 30, number of outputted iterations = 5000, number of pilot runs = 50, and length of pilot runs = 5000.

To identify putative first-generation migrants among populations, we used a Bayesian assignment method (Rannala and Mountain 1997) as implemented in GENECLASS (Piry et al. 2004). In order to calculate individual probabilities of assignment to each population, a MCMC resampling method with simulation algorithm (Paetkau et al. 2004) was performed using 10,000 simulated individuals and a type I error threshold of 0.05.

We tested for barriers to gene flow by computing Delaunay triangulation from the GPS coordinates using Monmonier's (1973) maximum-difference algorithm with the pairwaise F_{ST} matrix (BARRIER v.2.2 software, Manni et al. 2004). Barrier robustness was assessed with 100 resampled bootstrap matrices (R function courtesy of Eric Petit, UMR ECOBIO CNRS, Paimpont).

Isolation by distance

We quantified isolation by distance (IBD) among all locations as the correlation between linearized F_{ST} ($F_{ST}/(1 - F_{ST})$) and the log of geographic distance using the Mantel permutation test implemented in GENALEX (10,000 permutations; Mantel 1967). Geographic distance was computed as the shortest ocean path between sampling locations. IBD was also analysed by linear mixed effects modelling (LME) using resistanceGA package in R and calculating Akaike information criterion (AIC; Akaike 1973) for the F_{ST} values and the shortest geographic distance between all locations. For all model selection we used AIC from LME with resistanceGA, as it has been recently demonstrated to be the best model selection approach for landscape genetic studies under a wide range of conditions (Shirk et al. 2017).

Selection of environmental variables

We selected a set of variables that previous studies have shown can affect the biology, and potentially the connectivity, of our study species (e.g. Peirano et al. 2005; Kersting et al. 2013b; Chefaoui et al. 2017). These variables included sea surface temperature, salinity, bathymetry and sea surface currents. We further investigated temporal effects of sea water temperature, including means of monthly data (sst), coldest months (sst_c) and warmest months (sst_w). Data represent the time period from September 2002 to August 2010. Sea surface water temperature has been reported as a key factor controlling

gametogenetic cycles or larvae release periods in this Mediterranean coral (Kersting et al. 2013b). Salinity data was obtained from 1955 to 2006; we assessed the influences of means of monthly data (sss), freshest (sss_f) and saltiest months means (sss_s). Salinity has been previously shown to influence both coral skeleton growth and polyp behaviour (Peirano et al. 2005). All six variables (sst, sst_c, sst_w, sss, sss_f and sss_s) were obtained from the ocean climate layers for marine spatial ecology website MARSPEC (http://marspec.weebly.com/). Bathymetry data was downloaded from EMODnet (http://www.emodnet.eu/bathymetry). All data were constrained to a common land mask based on the global self-consistent, hierarchical and high-resolution shoreline (GSHHS), at 30 arc-second raster resolution. Land was classified as NoData in all raster grids.

Sea currents were obtained from a coupled hydrodynamic-wave model implemented over the whole Mediterranean basin by Copernicus Marine environment monitoring service (CMEMS V4) and extended into the Atlantic Sea for a better understanding of the water exchange through the Strait of Gibraltar (downscaled from 0.042 arc degree resolution). Zonal and meridional sea current velocities from 2016 to 2018 were obtained for three different depths (1, 5 and 16 m) and three temporal resolutions (hourly, daily and monthly). Because we expected some correlation among the current datasets, we computed mantel tests between all pairs. Following assessment of multicollinearity, we retained monthly and seasonal (winter, spring, summer and fall) means for all years. Furthermore, as all depths were highly correlated, we chose to use current at 1-m depth in the analysis.

Sea surface temperatures (sst, sst_c and sst_w) and salinity (sss, sss_f and sss_s) were evaluated as slope variables (Cushman et al. 2013; Yang et al. 2013), sea surface currents (means by months and by seasons) were assessed as directional variables (Landguth et al. 2017), and the three bathymetry resistance layers were evaluated as cost variables (Cushman et al. 2006) (Table 2). Following the approach originally developed by Shirk et al. (2010) to optimize the functional form and magnitude of resistance relationships, we varied the shape of the response function for the slope variables, generating rasters with a range of power functions (0.1, 0.5, 1, 1.5 and 3) using ARCINFO WORKSTATION 10.2.2 (Environmental Systems Research Incorporated (ESRI), Redlands, CA, USA, 2011). Each raster cell value represents the hypothesized cost to move across a given location. We then used UNICOR (Landguth et al. 2011) to calculate cumulative cost distances among all sampled populations pairs (Dunning et al. 1992; Cushman et al. 2006). For the directional sea surface currents, we used the directional functionality in UNICOR (e.g. Landguth et al. 2017) to calculate asymmetric "current cost-distance" from the zonal and meridional velocities.

Data related to human pressures on the environment (human footprint) was included not for LME analysis, but to make inferences or evaluations of potential threats and conservation status of the populations analysed. Information related to navigable waterways, population density or roads (among others) in 2009, integrated in the human footprint map, was

Table 2 Description of the environmental variables used

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:1000; 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	Fall currents mean

downloaded from the Wildlife conservation society (http://wcshumanfootprint.org) (Venter et al. 2016).

Development of resistance surfaces

Based on bathymetry, we delimited two different areas in the Adriatic Sea: open water and coastline. We classified all water pixels within 1000 m of land as coastline. We then tested three resistance hypotheses (*Water, Shore, Strict*, see below) by assigning different values to land, open sea and coastline raster cells. The land surface, where dispersal is not possible for this species, was assigned a maximum value of 1000. We assigned a uniform resistance of 1 for movement through all water pixels (*Water*). This resistance model reflects isolation by waterbody distance or the shortest ocean path through the marine system. For the *Shore* hypothesis, we assigned a resistance of 1 for coastline and a resistance of 50 for open water. This resistance model suggests high gene flow along the shallow coastlines and moderately high resistance through open water. For the *Strict* hypothesis, we assigned a resistance of 1 to coastline and a resistance of 1000 to open water (Table 3). This resistance model represents a situation where gene flow is restricted to stepping stone dispersal along the coastline and where open water is effectively as resistant to gene flow as land. Rasters were resampled to 500 m resolution; all GIS layers were processed in ArcGIS 10.3.1.

Modelling isolation by seascape resistance

We first identified the optimal functional form and maximum resistance for each variable using linear mixed effects modelling coupled with multivariate restricted optimization (Shirk et al. 2010, 2018). To understand how the ocean environment influences gene flow for this Mediterranean coral, we used the same modelling method (i.e., LME coupled with model selection using AIC) to rank support among alternative seascape resistance hypotheses. This has recently been shown to be the most robust model selection method for comparing alternative landscape genetic models (Shirk et al. 2018). We identified optimal functional forms and cost distance relationships for each set of variables based on lowest within-group AIC values (for small sample sizes; Burnham and Anderson 2002) using the Ecodist package in R (Goslee and Urban 2007). Mantel tests identified highly correlated variables, which have been shown to affect model selection performance (Cushman et al. 2013; Shirk et al. 2018), and those with higher AIC values were dropped.

In the second phase of the restricted optimization, we varied maximum resistance (R_{max}, Shirk et al. 2010) of the best supported functional form for each variable across five levels (5, 10, 20, 40 and 80, respectively). As before, for each of these forms of the variables we calculated cost-distance matrices with UNICOR and then computed AIC from LME in resistanceGA. We again selected the optimal R_{max} for each resistance hypothesis based on lowest AIC.

In the final step of the restricted optimization, we performed an iterative loop wherein the relationship of each variable with genetic distance was tested singly and in all possible additive combinations (e.g. Shirk et al. 2010; Castillo et al. 2014.). Currents as directional variables were added at the end of the process given they are non-transitive and cannot be added as resistance layers due to their directionality. We then produced a final ranking of AIC for the best multivariate optimized models using LME.

Table 3 Resistance models to test the relative resistance of movement along the coastline and open water on gene flow in *C. caespitosa*

Model	Resistance values		
	Coastline	Open Water	Land
Water	–	1	1000
Shore	1	50	1000
Strict	1	1000	1000

Numbers represent hypothesized resistance values assigned to each area in the Adriatic Sea

Results

Genetic variability

Prior to running population genetic analyses, we removed 13 individuals that were identified as clones. Overall, we detected relatively high heterozygosity (observed and expected heterozygosity mean values 0.472 and 0.498 respectively, Table 4) with a mean number of alleles ranging between 5.33 for KOR to

Table 4 Estimators of genetic diversity in 190 samples of *Cladocora caespitosa*

	N_a	H_o	H_e	F_{IS}
BOK	5.556	0.474	0.499	0.066
KOR	5.333	0.476	0.527	0.111
TRE	5.778	0.458	0.486	0.073
TOG	5.444	0.481	0.490	0.036
OTR	5.556	0.426	0.462	0.096
POC	5.667	0.518	0.522	0.028
Mean	5.556	0.472	0.498	0.068

N_a number of alleles, H_o observed heterozygosity, H_e expected heterozygosity, F_{IS} inbreeding coefficient

5.77 for TRE. No linkage disequilibrium between loci was observed in any of the populations, and thus the nine polymorphic loci were considered statistically independent.

After sequential Bonferroni correction, all localities demonstrated significant deviations from HWE for different loci. Null alleles frequencies were checked with MICRO-CHECKER at each locus in each sample, and for TRE and POC populations null alleles were detected. This could result from problems associated with amplification, scoring or mutations in the sequences where the primers were designed. For the rest of the populations the disequilibrium could be explained by having a high number of different alleles (from 10 to 17) related to the number of samples (28–35). However, no significant differences were observed between pairwise F_{ST} and pairwise F_{ST} corrected for null alleles. AMOVA analyses showed that the 97.16% of genetic variation was observed within populations (Table 5).

Assessing marker neutrality, LOSITAN found that none of the nine microsatellites showed significantly higher or lower F_{ST} values than neutral expectations. However, BAYESCAN showed two loci (Cc-L4 and Cc-L21) as potential outliers under positive selection. Considering the lack of agreement between both methodologies, all loci were considered for further analyses.

Population differentiation and isolation by distance

Global F_{ST} revealed significant but low genetic differentiation (F_{ST} global = 0.028, $p < 0.0001$). Pairwise F_{ST} values ranged between 0.0001 for TOG vs. POC to 0.0432 for KOR vs. OTR (Table 6). Croatian population (KOR), was significantly differentiated from the other localities, presenting the lower value respect to POC (F_{ST} = 0.019). The F_{ST} values among populations represented in the PCoA analysis showed that 92.78% of the variation was explained by the first two axes. The first axis of the PCoA separated OTR, TRE and TOG from the rest of the locations in the Adriatic Sea (Fig. 2). Within those groups, a separation of TOG from OTR and TRE, and KOR from BOK and POC is evidenced.

Analysis of population genetic structure identified $K = 2$ as the best-supported number of clusters. One is comprised only by the northern Adriatic population (KOR), while all other sites in the central and southern Adriatic and the Ionian (TRE, BOK, TOG, OTR, POC) comprise the other cluster. Although two different groups were detected, we also found substantial evidence of admixture between them (Fig. 3).

We observed the occurrence of moderate but strongly supported barriers in genetic differentiation across the studied area (100% bootstrap support). The strongest barrier was located between the northern and central-southern basins, dividing KOR from the rest of populations. We also identified a secondary barrier

Table 5 AMOVA analyses for six populations of *C. caespitosa* divided into the two groups detected by Structure

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among groups	1	8.254	0.050	2.35
Among populations within groups	4	10.932	0.010	0.49
Within populations	374	777.206	2.078	97.16
Total	379	796.392	2.138	

P values for all results were significant ($P < 0.0001$)

Table 6 F_{ST} values among *C. caespitosa* populations

	BOK	KOR	TRE	TOG	OTR	POC
BOK	0	**0.04705**	**0.04143**	**0.02360**	**0.04602**	**0.01122**
KOR	**0.02241**	0	**0.08613**	**0.06155**	**0.08743**	**0.04041**
TRE	**0.02072**	**0.04181**	0	**0.01523**	**0.00729**	**0.02675**
TOG	**0.01173**	**0.02972**	**0.00768**	0	**0.00371**	**0.00035**
OTR	**0.02343**	**0.04322**	0.00377	0.00191	**0**	**0.02665**
POC	0.00538	**0.01883**	**0.01307**	0.00017	**0.013329**	**0**

Upper side standardized F_{ST}. In bold significant values ($P < 0.05$)

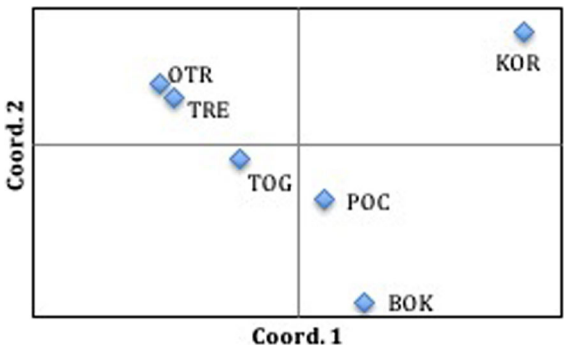

Fig. 2 Results for principal coordinates analysis (PcoA). F_{ST} values among populations showed a variation of 92.78% explained by the two first axes

dividing the East and West coasts of the Adriatic Sea. We further identified 46 individuals as potential first generation migrants, representing almost 25% of the 190 individuals analysed; most of them were considered coming from unknown populations (Table 7). No significant association was found between linear F_{ST} and shortest ocean path distances (Mantel $R = 0.063$, $p = 0.144$). In addition, LME analyses showed that the *Water* resistance model (i.e., isolation by waterbody distance) ranked worst in AIC compared to the other resistance models (i.e., *Shore* and *Strict*), indicating existence of significant heterogeneity of gene flow as functions of seascape variables (Table 8).

Isolation by seascape resistance

Univariate optimization

Testing the best shape for the slope variables, varying the response function with different power functions, showed that the best shape ($\Delta AIC = 0$) was 0.1 for sss_s and sst_c, 0.5 for sss_f and 3 for sss, sst and sst_w (Table 9 and AIC ranking in Table 10). Results for Mantel test correlations showed high values between all 72 combinations of variables (see Supplementary Table 1). This identified 11 variables that were correlated with Mantel $r > 0.98$ (see Table 11). Among this pool of 11 highly correlated variables we removed those that had higher AIC values than the variables they were correlated with. This resulted in five variables that were retained for the second step of the univariate optimization: *Shore* and *Strict*, salinity in the saltiest month (sss_s), salinity monthly mean with a power function of 3 (sss_3) and sea surface temperature in the coldest month with the power function 0.1 (sst_c_0.1) (Table 12).

The second step of the univariate optimization varied the maximum resistance (R_{max}) of these five retained variables and identified the R_{max} with the lowest AIC. The result was a R_{max} of 5 for the salinity, 10 for *Strict* and R_{max} of 80 for salinity in the saltiest month and temperature in the coldest month (Table 13).

Fig. 3 STRUCTURE result selected by Clumpak for the six locations of *C. caespitosa* in the Adriatic (BOK, KOR, TRE, TOG and OTR) and Ionian Seas (POC) $K = 2$

Table 7 Assignment test for *Cladocora caespitosa* at the six Adriatic and Ionian populations

Population	Self	Origin						Unknown	Total
		BOK	KOR	TRE	TOG	OTR	POC		
BOK	20	–	–	–	–	–	–	8	8
KOR	24	–	–	–	–	–	1	8	9
TRE	23	–	1	–	–	1	3	6	11
TOG	29	1	–	–	–	2	1	2	6
OTR	26	1	–	1	–	–	1	3	6
POC	22	–	–	–	–	–	–	6	6
Total	144 (75.78%)	2	1	1	0	3	6	33	46(24.21%)

For each site (acronyms as in Table 2), individuals are presented in rows according to their sampling site and classified as individuals assigned to their own population (Self) and those assigned to other sites or to an unknown population. The last column lists the total number and percentage of individuals that were not assigned to the population from which they were sampled

Table 8 Ranking of AIC values for the cost variables analysed

Variables	AIC
Shore	− 86.290938
Strict	− 83.690859
Water	− 82.707071

The final form of the five retained variables was: (1) *Strict,* R_{max} of 10, (2) *Shore* (3) salinity in the saltiest month, 0.1 power function and R_{max} of 80, (4) sea temperature in the coldest month, 0.1 power function and R_{max} of 80 and (5) salinity, 3 power function and R_{max} of 5 (Table 14).

Multivariate optimization

We then computed all combinations of the five retained optimized variables. Currents as directional variables were included a posteriori to the models created. Previously, we detected that AIC values calculated for the monthly mean of currents and grouped by seasons resulted identical (see Supplementary Table 2); therefore, we chose to include just one directional variable for further analyses. Then, we created two sets of variable combinations: one set including current effects and the other set without current effects (Table 15). Hypothesis ranking according to AIC values for all possible combinations of variables showed that *Strict* was the most supported hypothesis of the genetic differentiation, with a ΔAIC of 1.973 from the next most supported hypothesis (*model12*). This *Strict* model hypothesized that larvae movement along coastline would best explain gene flow. The surface of paths for this model, showing the cumulative density of optimal routes between populations, is represented in Fig. 4 (where data of human footprint were overlapped). The next best model, *model12*, was a hybrid of *Strict* and *Shore*, which also supported the hypothesis that gene flow was due to larvae movement along the coastline. The next hypothesis best supported is the combination of *Strict* and *Shore* with the sea surface currents (*model12c*) (Table 16).

Discussion

The temperate coral *Cladocora caespitosa* is physiologically and morphologically similar to typical tropical reef-building corals in being zooxanthellate, colonial, and able to form extensive bioherms that may fuse in reef-like structures (Kružić et al. 2008). However, it can be considered that it inhabits in a ‘‘thermally marginal sea” regarding what has generally been considered as ‘‘optimal’’ in terms of coral growth and survival. In fact, the distribution and abundance of *C. caespitosa* is currently reduced overall in the Mediterranean with respect to its recent fossil remnants, so it is considered a relict species from the subtropical late Pliocene and Quaternary periods

Table 9 Different shape for the slope variables, varying the response function with different power functions (0.1, 0.5, 1, 1.5 and 3)

Variable	Power	AIC	AICmin	ΔAIC
sss	0.1	− 82.705		0.003
sss	0.5	− 82.672		0.036
sss	1	− 82.701		0.007
sss	1.5	− 82.708		0.001
sss	**3**	**− 82.709**	− 82.709	0
sss_f	0.1	− 82.691		0.037
sss_f	**0.5**	**− 82.728**	− 82.728	0
sss_f	1	− 82.713		0.014
sss_f	1.5	− 82.708		0.020
sss_f	3	− 82.709		0.019
sss_s	**0.1**	**− 82.903**	− 82.903	0
sss_s	0.5	− 82.866		0.036
sss_s	1	− 82.812		0.090
sss_s	1.5	− 82.771		0.131
sss_s	3	− 82.712		0.190
sst	0.1	− 82.675		0.033
sst	0.5	− 82.670		0.038
sst	1	− 82.696		0.012
sst	1.5	− 82.706		0.002
sst	**3**	**− 82.709**	− 82.709	0
sst_c	**0.1**	**− 82.735**	− 82.735	0
sst_c	0.5	− 82.680		0.054
sst_c	1	− 82.687		0.047
sst_c	1.5	− 82.705		0.029
sst_c	3	− 82.709		0.026
sst_w	0.1	− 82.668		0.040
sst_w	0.5	− 82.678		0.030
sst_w	1	− 82.694		0.014
sst_w	1.5	− 82.704		0.004
sst_w	**3**	**− 82.708**	− 82.708	0

Zero values of ΔAIC indicate the best shape (in bold). For acronyms see Table 2

and the remaining populations are patchily distributed across the entire Basin (Peirano et al. 2009).

In light of global, and especially marine, biodiversity decline, seascape genetics offers a valuable tool for understanding the major factors influencing connectivity and genetic diversity in marine ecosystems. Connectivity among populations, and patterns of dispersal and gene flow, are primarily determined by the physical characteristics of the landscape occupied

Table 10 Ranking of AIC values for cost (*Shore*, *Strict* and *Water*) and slope variables (sss_s, sst_c, sss_f, sss, sst and sst_w) with the best power function selected (For acronyms see Table 2)

Variables	Power	AIC
Shore	–	− 86.2909
Strict	–	− 83.6909
sss_s	0.1	− 82.903
sst_c	0.1	− 82.7351
sss_f	0.5	− 82.7288
sss	3	− 82.709
sst	3	− 82.709
sst_w	3	− 82.7089
Water	–	− 82.7070

Table 11 Variables correlated with a R coefficient $r > 0.98$ from Mantel test analyses (For acronyms see Table 2)

Variables	R coefficient
sss_f–sss_s	0.9881447
sst–sss_f	0.9962337
sst_w–sss_f	0.9962317
Water–sss_f	0.9962799
sss_f–sss	0.996234
sst–sss	1
sst_w–sss	1
Water–sss	0.9999964
sst_w–sst	1
Water–sst	0.9999964
Water–sst_w	0.9999965

Table 12 AIC ranking for the five selected variables and their power function selected for the second step of the univariate optimization (For acronyms see Table 2)

Variables	Power	AIC
Shore	–	− 86.2909
Strict	–	− 83.6909
sss_s	0.1	− 82.903
sst_c	0.1	− 82.7351
sss	3	− 82.709

Table 13 Values for Akaike information criterion (AIC) for the variables selected for the second step of the univariate optimization

Variables	Power	R_{max}	AIC
Shore	**–**	**–**	**– 86.2909**
Shore	–	5	– 83.9345
Shore	–	10	– 83.8872
Shore	–	20	– 83.8808
Shore	–	40	– 83.8743
Shore	–	80	– 86.2559
Strict	–	–	– 83.6909
Strict	–	5	– 86.7353
Strict	**–**	**10**	**– 88.3134**
Strict	–	20	– 86.5953
Strict	–	40	– 86.3742
Strict	–	80	– 86.0781
sst_c	0.1	5	– 82.6939
sst_c	0.1	10	– 82.7351
sst_c	0.1	20	– 82.7671
sst_c	0.1	40	– 82.7901
sst_c	**0.1**	**80**	**– 82.8026**
sss_s	0.1	5	– 82.8628
sss_s	0.1	10	– 82.903
sss_s	0.1	20	– 82.9353
sss_s	0.1	40	– 82.9552
sss_s	**0.1**	**80**	**– 82.9717**
sss	**3**	**5**	**– 82.7091**
sss	3	10	– 82.7090
sss	3	20	– 82.7090
sss	3	40	– 82.7089
sss	3	80	– 82.7089

Variables are rescaled to different R_{max} (5, 10, 20, 40). In bold, best R_{max} for the variable (lowest AIC) (For acronyms see Table 2)

Table 14 Summary of final variables selected with the best power function and R_{max} (For acronyms see Table 2)

Variables	Power	R_{max}	AIC
Strict	–	10	– 88.3134
Shore	–	–	– 86.2909
sss_s	0.1	80	– 82.9717
sst_c	0.1	80	– 82.8026
sss	3	5	– 82.7091

by a species and the biological life-history traits of that species. Connectivity and gene flow, in turn, shape the patterns of genetic structuring of a species (López-Márquez et al. 2019).

In this study, two genetic clusters were detected in the northern and central-southern part of the Adriatic Sea, respectively, among the analysed populations of the coral *C. caespitosa.* Low differentiation and some admixture between the two groups suggest moderate levels of connectivity among populations, except for the northern Adriatic and Ionian populations, where higher levels of differentiation were found. Nevertheless, the genetic indices are similar in the different populations (e.g. H_e ranged from 0.462 to 0.527). Curiously, the two highest H_e values are presented by the most differentiated populations, Kornati and Porto Cesareo. In any case, this H_e range is comparable to the one found for this species in the western Mediterranean (H_e ranged from 0.444 to 0.543), using the same set of markers (Casado-Amezúa et al. 2014). The difference between our study and that of Casado-Amezúa et al. (2014) is that here the heterozygote deficit was a general trend. This result is not unusual in corals (e.g. Ayre and Hughes 2000; Severance and Karl 2006; Goffredo et al. 2009; Polato et al. 2010; Casado-Amezúa et al. 2012; Zayasu et al. 2018; Evans et al. 2019), and can be an indication of biological and demographical features of the analysed populations (e.g. population effective size, inbreeding, population mixing, non-random mating or asexual reproduction). Our results suggest that some genetic exchange still exists between the Adriatic populations and thus, the weight of asexual reproduction (about the 7% of the studied colonies were clones) could be the clue to, at least partially, explain the higher heterozygosity deficit in the Adriatic populations in respect to the western Mediterranean ones.

Another shared characteristic of the studied populations is self-recruitment, estimated to ~ 75%, among Adriatic populations, and 69–90% among the western Mediterranean populations (Casado-Amezúa et al. 2014). This agree with the assumed limited capacity of coral larvae to disperse, compared with the planktotrophic larvae of other marine invertebrates since coral planulae are primitive larvae with poor swimming abilities (Harrison and Wallace 1990). Because there are migrant *C. caespitosa* specimens of unknown origins, further studies with expanded study area is needed to investigate the global distribution of

Table 15 Left column: models (m) tested with the respective slope variables

Models	Variables	Models	Variables
m1	*Strict*	m1c	*Strict* + current
m2	*Shore*	m2c	*Shore* + current
m3	sss_s	m3c	sss_s + current
m4	sst_c	m4c	sst_c + current
m5	sss	m5c	sss + current
m12	*Strict* + *Shore*	m12c	*Strict* + *Shore* + current
m13	*Strict* + sss_s	m13c	*Strict* + sss_s + current
m14	*Strict* + sst_c	m14c	*Strict* + sst_c + current
m15	*Strict* + sss	m15c	*Strict* + sss + current
m23	*Shore* + sss_s	m23c	*Shore* + sss_s + current
m24	*Shore* + sst_c	m24c	*Shore* + sst_c + current
m25	*Shore* + sss	m25c	*Shore* + sss + current
m34	sss_s + sst_c	m34c	sss_s + sst_c + current
m35	sss_s + sss	m35c	sss_s + sss + current
m45	sst_c + sss	m45c	sst_c + sss + current
m123	*Strict* + *Shore* + sss_s	m123c	*Strict* + *Shore* + sss_s + current
m124	*Strict* + *Shore* + sst_c	m124c	*Strict* + *Shore* + sst_c + current
m125	*Strict* + *Shore* + sss	m125c	*Strict* + *Shore* + sss + current
m134	*Strict* + sss_s + sst_c	m134c	*Strict* + sss_s + sst_c + current
m135	*Strict* + sss_s + sss	m135c	*Strict* + sss_s + sss + current
m145	*Strict* + sst_c + sss	m145c	*Strict* + sst_c + sss + current
m234	*Shore* + sss_s + sst_c	m234c	*Shore* + sss_s + sst_c + current
m235	*Shore* + sss_s + sss	m235c	*Shore* + sss_s + sss + current
m245	*Shore* + sst_c + sss	m245c	*Shore* + sst_c + sss + current
m345	sss_s + sst_c + sss	m345c	sss_s + sst_c + sss + current
m1234	*Strict* + *Shore* + sss_s + sst_c	m1234c	*Strict* + *Shore* + sss_s + sst_c + current
m1235	*Strict* + *Shore* + sss_s + sss	m1235c	*Strict* + *Shore* + sss_s + sss + current
m1245	*Strict* + *Shore* + sst_c + sss	m1245c	*Strict* + *Shore* + sst_c + sss + current
m1345	*Strict* + sss_s + sst_c + sss	m1345c	*Strict* + sss_s + sst_c + sss + current
m2345	*Shore* + sss_s + sst_c + sss	m2345c	*Shore* + sss_s + sst_c + sss + current
m12345	*Strict* + *Shore* + sss_s + sst_c + sss	m12345c	*Strict* + *Shore* + sss_s + sst_c + sss + current

Right column: models tested with the respective slope variables including the velocity of the currents (c) (For acronyms see Table 2)

C. caespitosa and to evaluate the effects of distant dispersal on the species genetic structure, even if such distant dispersal occurs only sporadically.

Our results showed that populations of *C. caespitosa* were slightly differentiated and connected by a relatively low migration rates, leading to low genetic distance even at a relatively large spatial scale. It should be borne in mind that rare successful migration events might be sufficient to preserve the natural levels of connectivity. Population genetic structure results from past historical events and present reproductive and dispersal patterns. Our results suggest that at the spatial and temporal (due to the markers) scales analysed in this study, the present population pattern is determined and maintained by present low larval dispersal rather than colonization history.

In addition to quantifying genetic connectivity and the population structure of the coral *C. caespitosa* in the studied area, our analysis is the first seascape genetics study that has combined multivariate

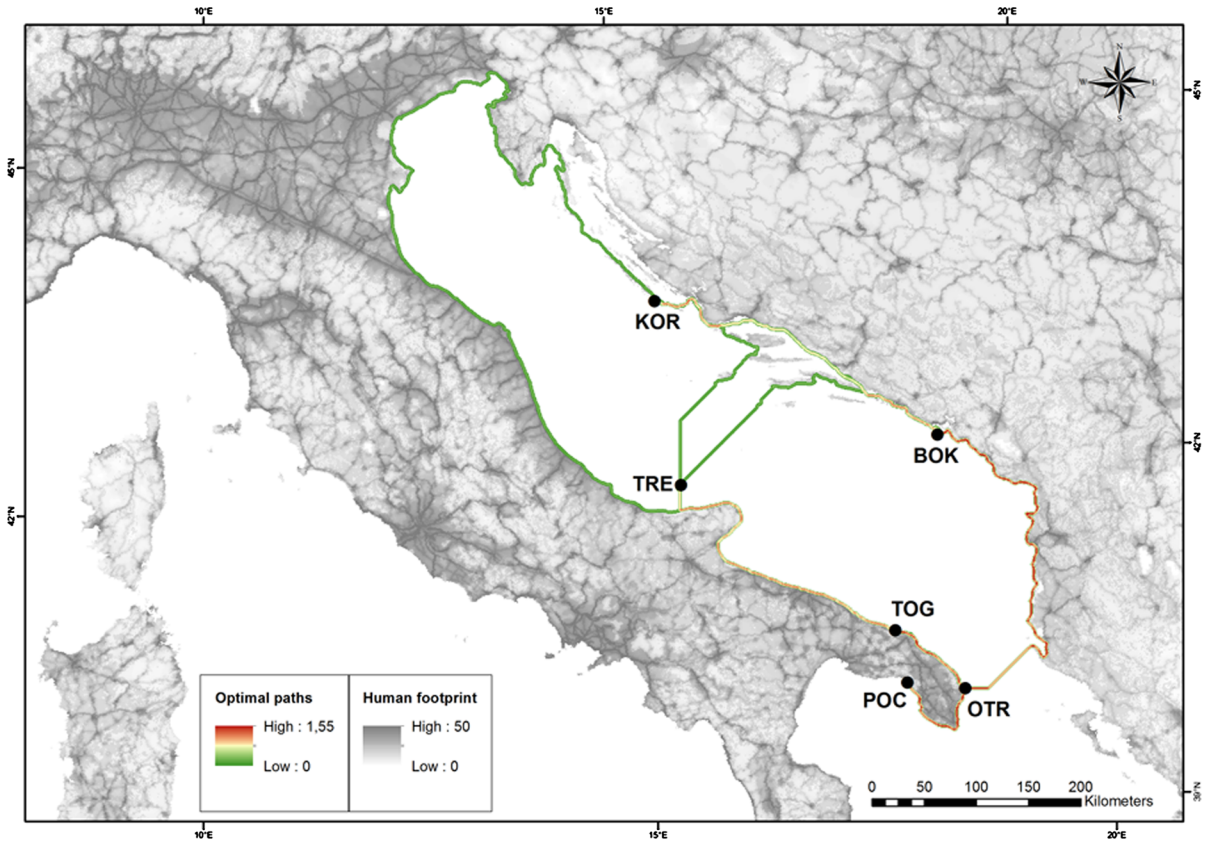

Fig. 4 Map representing the most supported hypothesis of the genetic differentiation (*Strict*) showing the cumulative density of optimal paths resulted from the unicorn analysis between all populations. This information was overlapped with the human footprint (Venter et al. 2016)

Table 16 Best models ranking according to AIC values (For acronyms see Table 2)

Models	Variables	AIC
m1	*Strict*	− 88.3134
m12	*Strict* + *Shore*	− 86.3396
m2	*Shore*	− 86.2909
m12c	*Strict* + *Shore* + current	− 85.1553
m2c	*Shore* + current	− 84.4309
m1c	*Strict* + current	− 84.2947
m125	*Strict* + *Shore* + sss	− 83.4709
m25	*Shore* + sss	− 83.4631
m15	*Strict* + sss	− 83.4232
m123	*Strict* + *Shore* + sss_s	− 83.4077

restricted optimization (Shirk et al. 2010) that has been shown to effectively identify drivers and optimize relative resistance values (e.g. Castillo et al. 2014) with a linear mixed effects objective function for ranking models, which has recently been shown to outperform other model selection approaches in a wide range of contexts (Shirk et al. 2018). In addition, this is one of the first seascape genetics studies to quantitatively evaluate and combine the relative effects and functional response form of a range of seascape variables, such as salinity, temperature, current flow, and shoreline topography. Importantly, given the dominant effect of ocean currents in larval transport it is an important advance to be able to use directional resistance modelling to predict connectivity in the non-isotropic context of sea currents, as has been recently done for pollen dispersal with wind (e.g. Landguth et al. 2017). In combination, the multivariate restricted optimization with linear mixed effects modelling, optimizing the relative effects and functional response form for a range of important seascape

variables, allowed this study to comprehensively evaluate a very large hypothesis space and gives us high confidence in our conclusions.

Gene flow of the studied scleractinian coral is affected primarily by proximity along coastline stepping stones, which has been previously noted in a top-shell species, *Gibbula divaricata* (López-Márquez et al. 2019). Secondarily to connectivity of sea surface currents, which likely determine the directions and velocities of larvae movement. Thus, it is important to assess the movement along the coastlines and how it is influenced by the currents. Fragmented distributions of the species along the coast can be predicted by stepping-stone oceanographic transport and habitat availability.

Factors that drive the distribution and reef development of this Mediterranean coral have been previously addressed by Chefaoui et al. (2017), pointing to phosphate concentration, low wave height and complex shorelines as the main determinants of the distribution of the species. However, that kind of approach could have limitations due to the fact that different biotic factors (as interactions with other species, mainly competition with photophilic algae) and dispersal abilities may also influence the distribution of *C. caespitosa*, the growth of its colonies, and therefore, connectivity among its populations (Chefaoui et al. 2017). The fact that the species prefers particular habitats must be coupled with the availability and distribution of such habitat and the capacity of the larvae to reach locations with suitable conditions, and this is determined not only by these limiting conditions but also by other factors that impede/favour larvae transport. We have demonstrated that in this species larvae transport in the Adriatic Sea is concentrated along the coastline and is driven to a lesser degree by sea surface currents. Nevertheless, other variables here analysed as the salinity or the sea surface temperature, and previously noted as variables that could affect potentially the connectivity, resulted to have lesser weight than expected.

We conclude that a combination of suitable habitat, oceanographic transport and hydrological factors provides strong prediction of genetic structure. These relationships provide insight into the mechanisms of dispersal and the role of life-history traits. Our results highlight the importance of spatially-explicit modelling of stepping stone dynamics and oceanographic directional transport, coupled with habitat suitability, to better describe and predict marine population structure and differentiation in species with limited dispersal capacity, as has been pointed out by Buonomo et al. (2016). As Perry and Larcombe (2003) suggested, may be more appropriate that these kinds of temperate coral settings be considered not as restricted or disturbed reef systems, but as alternative states of coral assemblages. Much more research is needed to understand the dynamics of these so called marginal reefs.

Understanding the processes that influence genetic connectivity and those which identify the environmental factors likely to affect population connectivity are necessary to address effective long-term conservation and management strategies. The fact that the larvae seem to follow the coastline to disperse suggests high risk of impedance of gene flow by coastal development, along with pollution plumes from rivers or submarine outfall pipes close to the shore. Pollution, has exponentially increased in the last decades and mostly affects developing countries, which is the case around the study area (Fig. 4). Construction of infrastructures and industrial installations, as well as the development of facilities for the growing human settlements, are factors responsible of the loss of marine habitats (Schubel 1994; Heerhartz et al. 2014). Obviously, this is part of a complex problem, since these factors act together with natural ones (erosion, climate variability, storms, etc.) and their synergy gives rise to the current population dynamics (Harley et al. 2006; Clynick et al. 2008; Nicholls et al. 2016). Elahi et al. (2015) consider that it is not possible to understand local biodiversity trends without information about local human activities besides the ecological context. Even if not numerous, different examples were given, as that of *Posidonia oceanica* (Montefalcone et al. 2010) where fragmented habitats due to both human and natural causes explain population structure observed. Thus, perturbation of the connectivity along the coastline can be due to natural processes, but it is dramatically increased in this Anthropocene era, and could be especially important in species such as *C. caespitosa* that is suffering regression in different areas, but also could be a general problem for coastal species.

Given widespread and ongoing declines of coral populations around the world, this study provides a timely evaluation of the major factors influencing genetic diversity, connectivity, and resilience of a

temperate coral species threatened by a climate change.

Acknowledgements This research was funded by the European project CoCoNET "Towards COast to COast NETworks of marine protected areas (from the shore to the high and deep sea), coupled with sea-based wind energy potential" from the VII FP of the European Commission (Grant Agreement No. 287844) and the Spanish Ministry of Economy and Competitiveness (Grant reference: CTM2014-57949-R). We want to thank Antheus s.r.l and many people who helped collecting samples. Thanks to Computational Biogeography and photography laboratories of the MNCN and to Melinda Modrell for the revision of the language.

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