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Mariana Padrón, Federica Costantini, Lorenzo Bramanti, Katell Guizien, Marco Abbiati. Genetic connectivity supports recovery of gorgonian populations affected by climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, Wiley, 2018, 28 (4), pp.776-787. 10.1002/aqc.2912 . hal-02354737

HAL Id: hal-02354737

<https://hal.archives-ouvertes.fr/hal-02354737>

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This is the peer reviewed version of the following article:

Padrón M, Costantini F, Bramanti L, Guizien K, Abbiati M. Genetic connectivity supports recovery of gorgonian populations affected by climate change. *Aquatic Conserv: Mar Freshw Ecosyst*. 2018;28:776–787

which has been published in final form at:

<https://doi.org/10.1002/aqc.2912>

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Genetic connectivity supports recovery of gorgonian populations affected by climate change

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Funding information

MARES Doctoral Programme, Grant/Award Number: FPA 2011-0016; PRIN 2011 project 'Coastal bioconstructions: structure, function and management'; PRIN 2011 project, Grant/Award Number: 2015J922E4; MARES is a joint doctorate programme, Grant/Award Number: FPA 2011-0016

Abstract

1. Climate-induced threats are increasingly affecting marine populations worldwide. In the last few decades, several gorgonian species have been affected by mass mortality events in the north-west Mediterranean, putatively linked to local sea temperature increases during heatwaves. For many benthic sessile species, recovery after disturbances depends upon larval supply shaping the connection among populations.
2. In the Ligurian Sea, genetic analyses showed that some *Paramuricea clavata* populations recovered after mass mortality events; however, the patterns of connectivity, and the potential role of migration in supporting the recovery of the populations of *P. clavata*, across its distribution range within the Ligurian Sea are still unknown.
3. In this study, the population genetic structure and migration patterns of *P. clavata* populations have been analysed across seven sites in the Ligurian Sea, some of which have been affected by mass mortality events.
4. Evidence of a population bottleneck was found in most of the populations studied. Significant genetic differentiation was found among *P. clavata* populations, reflecting habitat fragmentation at a regional scale, except for two populations found 20 km apart. Continuing gene flow between distant populations was also revealed. Empirical data suggest that gene flow among populations may have contributed to support their recovery from mass mortality events.
5. The study identified populations in the central part of the Ligurian Sea that can be strategic for the regional persistence of the species. These findings highlight that the preservation of key populations could maintain connectivity and gene flow in the metapopulation, and increase the resilience of the species.

KEYWORDS

benthos, climate change, coastal, coral, dispersal, disturbance, genetics, invertebrates

1 | INTRODUCTION

Marine biodiversity on a global scale is under growing pressure from environmental alteration caused by human activities, including climate change (Hoegh-Guldberg & Bruno, 2010). Trends of increasing seawater temperature, decreasing ocean pH, and sea-level rise, along with the higher frequency and magnitude of extreme climatic events (e.g. storms and heatwaves), are threatening marine species and habitats (Doney et al., 2012). The threshold of populations and habitat resilience to climatic disturbance is still an open question in contemporary ecology and conservation biology, however (Wernberg, Russell, Thomsen, & Connell, 2014).

Severe and sudden reductions in population size (i.e. demographic bottleneck) caused by mass mortality events are expected to lead to a loss of genetic diversity, primarily allelic diversity, and eventually cause a genetic bottleneck (Lacy, 1987). Furthermore, within this context, genetic drift may amplify the loss of genetic variation in isolated populations, and potentially lead to inbreeding (Nei, Maruyama, & Chakraborty, 1975). Nonetheless, the loss of genetic diversity caused by a population collapse can be offset or reversed by migration processes (Crow & Kimura, 1970; Keller et al., 2001). Therefore, connectivity among populations is an asset for the recovery of the pre-disturbance demographic structure and genetic diversity of the population.

In marine sessile benthic species, migration between distant populations ensured by larval dispersal is expected to be a key aspect of resilience (Almany et al., 2009). The role of migration patterns in the recovery after disturbance is controversial, however: although it is possible to forecast wide larval dispersal ranges with biophysical modelling (Lipcius et al., 2008; Shanks, Grantham, & Carr, 2003), gene flow, as assessed with molecular tools, appears to be more restricted, as a result of filtering by settlement and recruitment processes (Pineda, Hare, & Sponaugle, 2007). Despite several works assuming the importance of connectivity to the persistence of sessile benthic species populations, empirical evidence on how patterns of larval dispersal confer resilience to populations remains rare (Bramanti, Iannelli, Fan, & Edmunds, 2015; Caplins et al., 2014; Gilmour, Smith, Heyward, Baird, & Pratchett, 2013; Magris, Pressey, Weeks, & Ban, 2014; Underwood, Smith, van Oppen, & Gilmour, 2007; Vollmer & Palumbi, 2007). Investigating the genetic diversity and the structure of marine populations can provide estimations of their ability to withstand perturbations, and of their rate of recovery (Hughes, Inouye, Johnson, Underwood, & Vellend, 2008; Kovach et al., 2015; Van Oppen & Gates, 2006). In particular, the assignment of individuals to the population of origin can provide more detailed inference on larval migration patterns among populations (Waser & Strobeck, 1998).

During the last two decades, several mass mortality events coinciding with anomalous temperature increases (heatwaves) have affected benthic sessile species along the rocky shores of the north-western Mediterranean Sea (Cupido, Cocito, Sgorbini, Bordone, & Santangelo, 2008; but see Rivetti, Frascchetti, Lionello, Zambianchi, & Boero, 2014). Among the species affected, gorgonians (Cnidaria, Octocorallia) were the most damaged, with a local loss of more than 50% in density and biomass (Bramanti, Magagnini, De Maio, & Santangelo, 2005; Cerrano et al., 2000; Coma et al., 2009; Cupido

et al., 2008; Garrabou et al., 2009; Santangelo et al., 2015). Gorgonians are characterized by long life span and slow growth, which along with the low fecundity of small colonies delays their recovery after disturbance (Linares, Coma, Garrabou, Díaz, & Zabala, 2008), even when negative density-dependent control of recruitment is removed (Santangelo et al., 2015). Similarly to other habitat-forming species, gorgonians have an important role in promoting and stabilizing associated assemblages, such as biogenic reefs. Therefore, the conservation of these assemblages also depends on the capability of gorgonian species to respond to climate change and increasing human disturbance (Ponti et al., 2014).

Among the gorgonian species affected by mass mortalities, the red gorgonian *Paramuricea clavata* (Risso, 1826) suffered the most drastic reductions in density and biomass over a broad spatial scale, reaching up to 80% of colonies affected in the Gulf of Genoa in 1993 (Rivetti et al., 2014). The impact of reported mass mortality events on the demographic structure and dynamics of several populations has been assessed (Cupido et al., 2009; Santangelo et al., 2015; Santangelo, Bramanti, & Iannelli, 2007). The recovery of these populations has been attributed to local replenishment (Santangelo et al., 2015), overlooking the role of larval immigration from other source populations, based on the assumption of low larval dispersal in *P. clavata* (Mokhtar-Jamaï et al., 2011). Nevertheless, in the last couple of years genetic studies have revealed a mixed pattern of isolation by distance and clustering on a regional scale, with connectivity occurring among neighbouring, fragmented populations (Arizmendi-Mejía et al., 2015; Pérez-Portela et al., 2016; Pilczynska, Cocito, Boavida, Serrão, & Queiroga, 2016). In the Ligurian Sea, genetic analyses conducted on a local scale have suggested that, after mass mortality events, the recovery of *P. clavata* populations dwelling below 20 m in depth was the result of larval supply from deeper populations (>60 m in depth), presumably not affected by mass mortality (Pilczynska et al., 2016). Nonetheless, although decreases in mortality rates with depth have been observed for this species (Linares et al., 2005), it has been shown that below 20 m of depth *P. clavata* populations can be affected by mass mortalities (Huete-Stauffner et al., 2011). In the present work we extended the geographical scale (from local to regional) and the bathymetrical range (down to 40 m) of sampling in order to test: (i) whether *P. clavata* populations dwelling between 25 and 40 m of depth in the Ligurian Sea show signatures of a genetic bottleneck as a consequence of mass mortality events; and (ii) the occurrence of gene flow among those populations.

To answer these questions, the genetic diversity, genetic structure, and regional migration patterns of the coastal *P. clavata* populations in the Ligurian Sea were analysed.

2 | MATERIAL AND METHODS

2.1 | Sampling

Colonies of the red gorgonian *P. clavata* were sampled by scuba diving at seven locations (from 25 to 40 m in depth) in the Ligurian Sea in May 2014 (Figure 1). All the samples were considered as coastal populations, regardless of depth. Small (<3 cm) branch fragments from 26

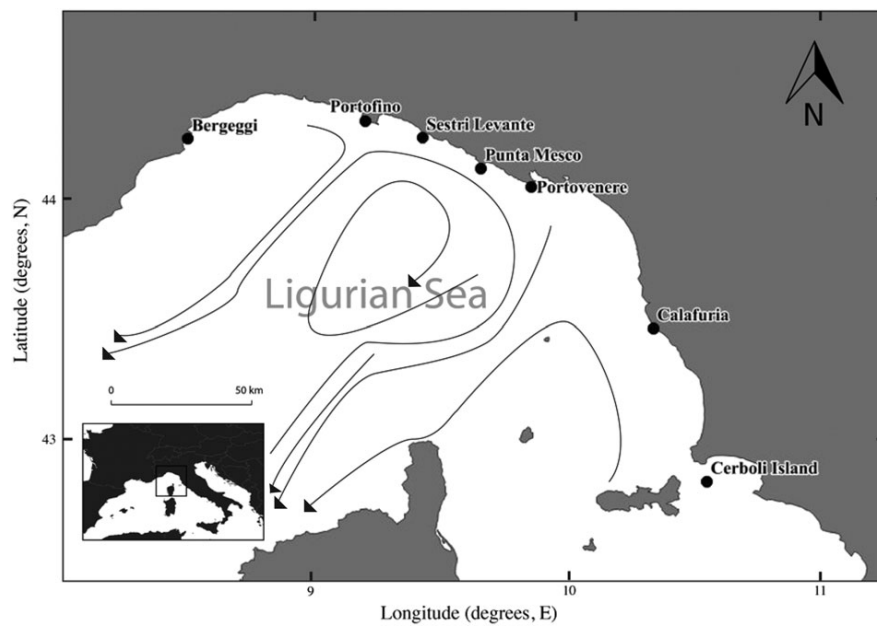


FIGURE 1 Map of the seven sampling locations of *Paramuricea clavata* in the Ligurian Sea. Black lines represent the simulated surface currents averaged during summer (the spawning season for *P. clavata* in the Mediterranean Sea; Linares et al., 2008), according to Pinardi and Masetti (2000) and Rossi et al. (2014)

to 37 colonies were collected at two different sites per location (separated by distances of between 30 m and 1 km), except in Punta Mesco and Cerboli Island. At those two locations, colonies were sampled only at one site because of restricted sampling permission by the Marine Protected Area authorities (Table 1). All samples were preserved in 95% ethanol and stored at 4°C.

The sampling design of *P. clavata* populations includes sites in which populations of the species were affected by mass mortality events: Portofino, Punta Mesco, and Portovenere. In the Ligurian Sea, mass mortality events as a result of heatwaves were reported in 1999 and 2003. In Portovenere, the pre-disturbance density of 35 individuals/m² was reduced by approximately 70% (Cupido et al., 2008; Santangelo et al., 2015). A reduction of two-thirds of the population density was reported in Portofino (Cerrano et al., 2005), whereas in Punta Mesco, *P. clavata* was also heavily affected by mortality down to depths of 25 m (Peirano, Sgorbini, Cupido, Lombardi, & Cocito, 2009). Although to our knowledge no literature has been published on mass mortality events of *P. clavata* in other locations within

the Ligurian Sea, recreational divers reported observing dead gorgonian colonies in Calafuria in 1999 (L. De Nigris, pers. comm.). Moreover, other sessile invertebrates were affected by the increases in water temperature in the area of Bergeggi (Parravicini et al., 2010).

2.2 | Microsatellite genotyping

Total genomic DNA was extracted from 372 colonies using the DNA extraction kit NucleoSpin Tissue by Macherey-Nagel. All individuals were genotyped at six polymorphic microsatellite loci developed for *P. clavata*, as used in Mokhtar-Jamaï et al. (2011): Parcla09, Parcla10, Parcla12, Parcla14, Parcla17 (Molecular Ecology Resources Primer Development Consortium et al., 2010), and Par_d (Agell, Rius, & Pascual, 2009). Genotyping was carried out on an ABI 3130 Genetic Analyser using an internal size standard (GeneScan 600 LIZ; Applied Biosystems, Foster City CA, USA), and allele scoring was performed using PEAK SCANNER SOFTWARE 1.0 (Applied Biosystems).

TABLE 1 Sampling locations of *Paramuricea clavata* in the Ligurian Sea

Location	Marine Protected Area	Site	Site ID	Latitude	Longitude	Depth (m)	Samples
Bergeggi	Area Marina Protetta Isola di Bergeggi	Bergeggi 1	BER1	44.2416	8.4461	37	32
		Bergeggi 2	BER2	44.2416	8.4461	38	30
Portofino	Area Marina Protetta di Portofino	Punta del Faro	POF1	44.1753	9.1308	36	31
		Isuela	POF2	44.1903	9.1851	40	31
Sestri Levante	No	Punta Baffe 1	SES1	44.2482	9.3963	30	32
		Punta Baffe 2	SES2	44.2482	9.3963	30	32
Punta Mesco	Area Marina Protetta delle Cinque Terre	Punta Mesco	PME	44.1247	9.6322	29	26
Portovenere	Parco Naturale Regionale di Porto Venere - Area di Tutela Marina	Secca Tinetto	POV1	44.0122	9.5104	25	30
		Parete Grotta	POV2	44.0126	9.5102	25	32
Calafuria	No	Gorgonie Rose 1	CAL1	43.2812	10.2002	35	32
		Gorgonie Rose 2	CAL2	43.2812	10.2002	25	29
Cerboli Island	No	Cerboli Island	CER	42.8555	10.5469	30	37

2.3 | Genetic diversity

Repeated multilocus genotypes were searched using GENODIVE 2.0b23 (Meirmans & van Tienderen, 2004). Observed and Nei's (1987) unbiased expected heterozygosity (H_O and H_E , respectively) were estimated using GENETIX 4.05 (Belkhir, Borsa, Chikhi, Raufaste, & Bonhomme, 2004). Allelic richness (A_r) was estimated using FSTAT 2.9.3.2 (Goudet, 2001), whereas private allelic richness (A_p) was calculated with a rarefaction procedure using HP-RARE software (Kalinowski, 2005). Linkage disequilibrium was tested for all loci using GENEPOP 4.2 (Rousset, 2008), as implemented for online use (<http://genepop.curtin.edu.au>). The test for Hardy–Weinberg equilibrium was computed for each locus using the null hypothesis of no heterozygote deficiency, and the level of significance was calculated with a Markov chain algorithm with default parameters (100 batches and 1000 iterations per batch). Single and multilocus F_{IS} values were estimated using Weir and Cockerham's (1984) fixation index in GENEPOP. The presence of null alleles was estimated using the expectation maximization (EM) algorithm (Dempster, Laird, & Rubin, 1977) in FREENA (Chapuis & Estoup, 2007).

Evidence of recent changes in effective population size as a result of the mass mortality events that affected *P. clavata* populations in the region during the past decade (Cupido et al., 2012) were tested using BOTTLENECK 1.2.02, following the two-phase model (TPM; Piry, Luikart, & Cornuet, 1999), with 95% single step mutation and a variance among multiple steps of approximately 12. A Wilcoxon's test was used, as suggested by Piry et al. (1999), for a data set of less than 20 loci. *P* values were corrected for multiple comparisons using false discovery rate (FDR) corrections (Benjamini & Hochberg, 1995).

2.4 | Population genetic structure

Population genetic structure was estimated using both the global and the pairwise F_{ST} estimates of Weir and Cockerham (1984) with GENEPOP, and following the excluding null allele (ENA) method in FREENA. The significance of pairwise genetic differentiation among sites was computed with an exact test using the default parameters in GENEPOP (100 batches and 1000 iterations per batch).

For linkage disequilibrium and F_{ST} estimates, FDR corrections (Benjamini & Hochberg, 1995) were applied in order to adjust significance levels for multiple comparisons.

Isolation by distance (IBD) was tested at a regional scale through correlation between pairwise $F_{ST}/(1 - F_{ST})$ values and the logarithm of the geographical distance between sites, with a Mantel test (Mantel, 1967), using the ISOLDE program implemented in GENEPOP. Geographical distances were measured in GOOGLE EARTH by using set points (determined as the centre of the area of distribution where the samples were collected), and measuring both Euclidean and along-the-coast distances. All of the individuals sampled from a given site shared the same geographical coordinates. The significance level of correlation between genetic differentiation and geographical distance among samples was computed using 10 000 permutations.

To estimate the extent of gene diffusion, multilocus genotypes were autocorrelated within spatial distance classes using the kinship

coefficient of Loiselle, as implemented in SPAGED1 1.4. This revealed the distance at which the random effects of genetic drift, not gene flow, are the primary determinants of genetic composition (Hardy & Vekemans, 2002). Significant positive coefficients suggest that colonies within a specific distance class are more genetically related than colonies randomly taken from any distance class. The first x-intercept of the autocorrelogram, which corresponds to the average distance at which the genetic similarity between any two quadrats drops below 0.0, is termed the 'genetic patch size' (Sokal & Wartenberg, 1983). Spatial distance intervals for kinship comparisons were constructed in such a way that the number of pairwise comparisons within each distance interval was approximately constant (between 3000 and 8000 pairs among distance classes). A total of 14 distance classes were considered: class 1, 0–14 km; class 2, 14–26 km; class 3, 26–31 km; class 4, 31–37 km; class 5, 37–56 km; class 6, 56–80 km; class 7, 80–94 km; class 8, 94–102 km; class 9, 102–117 km; class 10, 117–131 km; class 11, 131–156 km; class 12, 156–178 km; class 13, 178–214 km; and class 14, 214–250 km. The significance of the observed versus expected coefficients was tested for each class using 10 000 random permutations of locations.

To evaluate the number of clusters (*K*) in the data set without prior information regarding the geographic location of the colonies, a Bayesian method implemented in STRUCTURE 2.3.4 was used (Falush, Stephens, & Pritchard, 2003, 2007; Pritchard, Stephens, & Donnelly, 2000). STRUCTURE was run under the admixture model, choosing the assumption of correlated allele frequencies and the option of recessive alleles to cope with null alleles, as suggested by Falush et al. (2007). The mean and variance values of log likelihoods were estimated for the number of clusters, from *K* = 1 to *K* = 12. Ten runs were performed for each *K* with 500 000 iterations and a burn-in period of 50 000. In order to identify the number of clusters that best fit the data, the resulting output files were then analysed based on the rate of change in the log probability of data between successive *K* values, using the Evanno method in STRUCTURE HARVESTER 0.6.94, as implemented online (<http://taylor0.biology.ucla.edu/structureHarvester/>) (Earl & von Holdt, 2011). For the chosen *K*, the results were averaged using CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007), and the graphical representation was performed in DISTRUCT 1.1 (Rosenberg, 2004). A hierarchical analysis of molecular variance (AMOVA; 1000 permutations) was performed in ARLEQUIN 3.5 (Excoffier, 2005) using the clusters (*K* = 6) defined by STRUCTURE.

2.5 | Migration patterns

First-generation migrants and long-term migration rates were estimated as proxies of genetic connectivity among the clusters identified by STRUCTURE. First-generation migrants were detected using the Bayesian computation of Rannala and Mountain (1997) (*n* = 10000; α = 0.05) in GENECLASS 2.0 (Piry et al., 2004). Considering the possibility of long dispersal via stepping stones, the level and direction of gene flow over the last several generations among clusters was estimated by performing a maximum-likelihood based analysis. MIGRATE-N 3.6 was used to estimate theta (Θ) and the mutation-scaled migration rate *M* based on microsatellite data (Beerli & Felsenstein, 2001). Theta is

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defined as $4N_e\mu$ for a diploid system with nuclear microsatellite loci, where N_e is the effective population size and μ is the mutation rate per generation and site. M is defined as m/μ , representing the relative contribution of immigration and mutation to the variability brought into the population, whereas m is the fraction of new immigrants found in the population per generation. This calculation was run five times following the recommendations of Beerli (2009), and the results were averaged.

3 | RESULTS

3.1 | Genetic diversity

All the microsatellite loci were polymorphic. No repeated multilocus genotypes were found. Allelic richness (A_r) and private allelic richness (A_p) among sites were 5.96 ± 0.52 and 0.40 ± 0.15 , respectively. Allelic richness ranged from 4.96 for BER1 to 6.55 for POV2. The private allelic richness varied from 0.08 for SES2 to 0.58 for POV1. Observed (H_o) and unbiased expected heterozygosity (H_E) ranged from 0.49 for CER to 0.71 for SES2, with a mean value of 0.59 ± 0.06 , and from 0.67 for BER1 to 0.76 for POF1, with a mean value of 0.70 ± 0.03 (Table 2). No significant linkage disequilibrium was found among loci ($P > 0.05$ after FDR correction). Estimates of null allele frequencies varied between 0 for Parcla09, Parcla10, Parcla12, Parcla14, and Par_d, to 0.26 for Parcla12.

Multilocus estimates of F_{IS} ranged between 0.04 (BER1) and 0.33 (CAL1 and CER). All values were significantly different from zero ($P < 0.001$, mean = 0.20 ± 0.08), with the exception of BER1 (Table 2). All populations showed significant levels of heterozygosity deficiency; however, significant deviations from Hardy-Weinberg were not found for all loci in all populations. The high frequency of null alleles found for locus Parcla12 in some populations did not explain the levels of heterozygote deficiency, given that heterozygote deficiency was still significant when Parcla12 was excluded from the analysis.

Despite these populations being considered as unaffected by recent mass mortality events, recent changes in effective population

size resulting from an excess of the expected heterozygosity (a signal of a population bottleneck) were revealed at almost all locations (BER2, POF2, SES1, POV1, and CER; $P < 0.05$), with the exception of Punta Mesco and Calafuria (Table S2).

3.2 | Population genetic structure

The global multilocus F_{ST} indicated strong genetic differentiation of *P. clavata* populations between sites ($F_{ST} = 0.154$; $P = 0.0001$). Pairwise F_{ST} values ranged from 0 to 0.181, and almost all were significantly different after FDR correction (Table 3). Pairwise F_{ST} values for sites located less than 50 m apart (BER1 versus BER2, SES1 versus SES2, POV1 versus POV2, and CAL1 versus CAL2), and two sites separated by approximately 20 km (PME versus POV2), but all within a 10-m depth range, did not significantly differ. No significant differences were found between pairwise F_{ST} values and pairwise F_{ST} values corrected for null alleles (Student's *t*-test, $P = 0.163$), which suggests that the effect of null alleles was negligible.

A significant but weak pattern of isolation by distance (IBD) was detected for both measures of geographic distance: straight line ($R^2 = 0.23$; $P < 0.01$) and along the coast ($R^2 = 0.21$; $P < 0.01$) (Figure S1).

Six genetic clusters with different levels of admixture were identified by the Bayesian clustering analysis ($K = 6$, $\Delta K = 12.26$; Figure 2; for $K = 2$ to $K = 5$, see Figure S2): (i) BER1 and BER2 comprised the Bergeggi cluster (BER), with a coefficient of population membership of 90%; (ii) POF1 and POF2 formed the Portofino cluster (POF), with a coefficient of population membership of 66%; (iii) SES1 and SES2 comprised the Sestri Levante cluster, with a coefficient of population membership of 77% (SES); (iv) PME, POV1, and POV2 were grouped in the Portovenere and Punta Mesco cluster (PMP), with a coefficient of population membership of 60%; (v) CAL1 and CAL2 formed the Calafuria cluster (CAL), with a coefficient of population membership of 70%; and (vi) CER made up the Cerboli cluster (CER), with a coefficient of population membership of 80%. The results of the AMOVA confirmed the clustering structure ($P < 0.001$; Table S1).

TABLE 2 Parameters of genetic diversity for 12 sites of *Paramuricea clavata* at six microsatellite loci

Location	Site	H_o	H_E	A_r	A_p	F_{IS}
Bergeggi	BER1	0.65	0.67	4.96	0.13	0.04
	BER2	0.63	0.73	5.42	0.2	0.17
Portofino	POF1	0.61	0.66	5.24	0.55	0.22
	POF2	0.64	0.76	6.29	0.5	0.21
Sestri Levante	SES1	0.59	0.68	6.01	0.34	0.14
	SES2	0.71	0.70	6.34	0.3	0.14
Punta Mesco	PME	0.56	0.70	6.41	0.51	0.20
Portovenere	POV1	0.55	0.69	6.32	0.42	0.21
	POV2	0.58	0.69	6.55	0.28	0.10
Calafuria	CAL1	0.52	0.74	6.25	0.55	0.33
	CAL2	0.54	0.68	5.54	0.42	0.27
Cerboli	CER	0.49	0.71	6.19	0.62	0.33
	Mean value	0.59 ± 0.06	0.70 ± 0.03	5.96 ± 0.52	0.40 ± 0.15	0.20 ± 0.08

Abbreviations: H_o , observed heterozygosity; H_E , unbiased expected heterozygosity; A_r , allelic richness; A_p , private allelic richness; F_{IS} , Weir and Cockerham's (1984) estimate of Wright's (1951) fixation index, with significant values in bold (0.05 threshold after Bonferroni correction).

TABLE 3 Pairwise F_{ST} values among *Paramuricea clavata* sites in the Ligurian Sea

	BER1	BER2	POF1	POF2	SES1	SES2	PME	POV1	POV2	CAL1	CAL2	CER
BER1	0											
BER2	0.004	0										
POF1	0.116	0.116	0									
POF2	0.132	0.144	0.066	0								
SES1	0.127	0.131	0.089	0.125	0							
SES2	0.099	0.096	0.069	0.108	0.011	0						
PME	0.158	0.149	0.097	0.143	0.083	0.066	0					
POV1	0.141	0.139	0.095	0.136	0.088	0.092	0.061	0				
POV2	0.125	0.116	0.094	0.122	0.086	0.074	0.037	0.029	0			
CAL1	0.189	0.181	0.139	0.177	0.111	0.081	0.143	0.177	0.164	0		
CAL2	0.112	0.117	0.089	0.139	0.075	0.052	0.103	0.121	0.112	0.032	0	
CER	0.143	0.145	0.074	0.138	0.091	0.079	0.071	0.062	0.094	0.154	0.102	0

Significant values, after false discovery rate (FDR) correction, are highlighted in bold ($P < 0.05$).

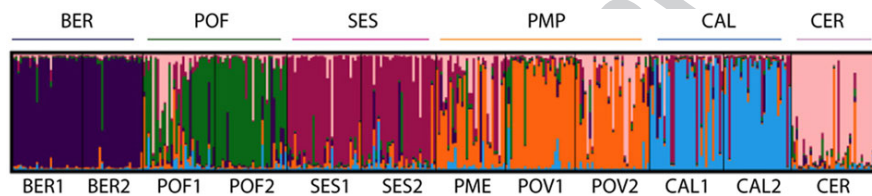


FIGURE 2 Population genetic structure of *Paramuricea clavata* in the Ligurian Sea, as revealed by STRUCTURE. Each individual is represented by a vertical line, where different colours indicate the individual proportion of membership to each cluster ($K = 6$). Key: Bergeggi (BER), purple; Portofino (POF), green; Sestri Levante (SES), fuchsia; Punta Mesco and Portovenere (PMP), orange; Calafuria (CAL), blue; and Cerboli (CER), pink

The kinship coefficient of Loiselle was positive and significant for the 0–14 km ($P < 0.01$, 95% CI = -0.0002 to 0.0002) and 14–26 km ($P < 0.01$, 95% CI = -0.002 to 0.008) distance classes

(Figure 3). The genetic patch size was estimated to be 26 km.

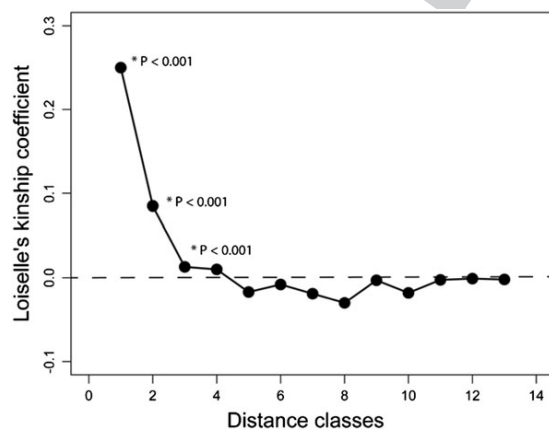


FIGURE 3 Autocorrelogram of *Paramuricea clavata* populations based on the kinship coefficient of Loiselle, estimated for multilocus genotypes within 13 spatial distance classes. The spatial distance classes were designated in such a way that the number of pairwise comparisons within each distance interval is approximately constant: class 1, 0–1 km; class 2, 2–23 km; class 3, 23–28 km; class 4, 28–40 km; class 5, 40–75 km; class 6, 75–89 km; class 7, 89–104 km; class 8, 104–125 km; class 9, 125–153 km; class 10, 153–177 km; class 11, 177–229 km; class 12, 229–251 km; and class 13, 251–283 km

3.3 | Patterns of recent and long-term migration

Overall, migration was bidirectional among all locations. Recent migration revealed by the analysis of first-generation migrants showed that the clusters of PMP and POF were the major sources of emigrants (40.62 and 28.12%, respectively). On the other hand, the clusters of BER and CAL were identified as the smallest source of emigrants, with 3.12% in both cases (Figure 4). In terms of immigrants, the clusters CAL and PMP received the highest proportion (15.9 and 14.81%, respectively), with the latter receiving immigrants for almost all other clusters (except BER). On the contrary, the cluster BER received the lowest number of immigrants (3.33%), all of them coming from the neighbouring cluster POF.

Patterns of long-term migration resulting from the maximum likelihood-based analysis using MIGRATE-N revealed that values of M ($M = m/\mu$; migration/mutation) were > 1 for all locations, meaning that the effect of migration (m) is larger than the effect of mutation (μ) (Table S3). Migration rates among clusters identified by STRUCTURE decreased with increasing distance between locations. Nonetheless, evidence of migration among the most distant locations (>250 km) was found (Table 4). The cluster that received most immigrants over multiple generations was PMP (mean $M = 18.02 \pm 8.17$), whereas the CAL cluster was identified as the one receiving the fewest immigrants (mean $M = 7.78 \pm 4.76$). In terms of source of emigrants to all other populations, the SES cluster had the highest value (mean $M = 18.68 \pm 9.21$), and the CER cluster had the lowest (mean

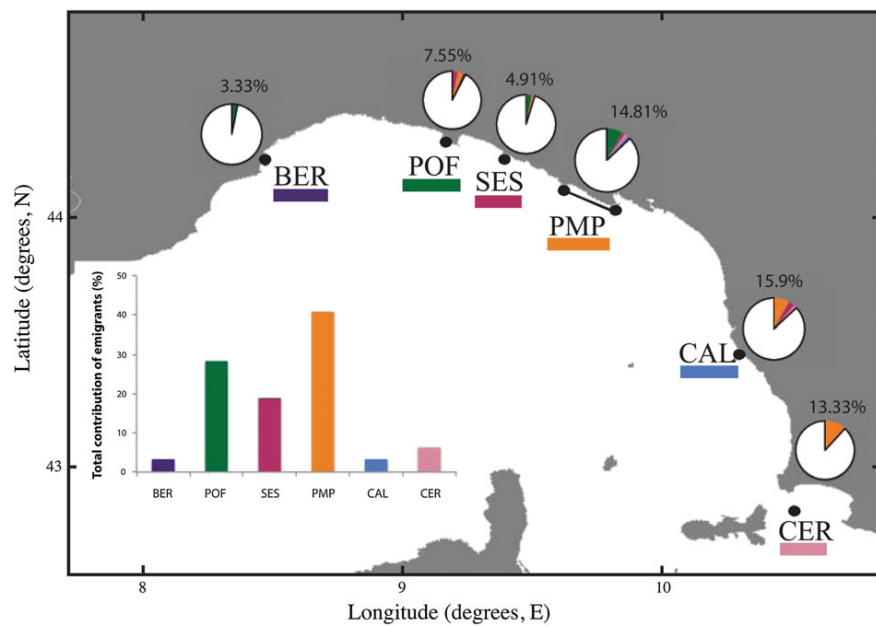


FIGURE 4 Pattern of first-generation migration among *Paramuricea clavata* populations in the Ligurian Sea. The pie charts represent recruitment in each cluster. The white portion indicates the proportion of self-recruits, whereas the colours represent immigrants from other locations. The bar plot indicates the contribution of emigrants (%) of each cluster: Bergeggi (BER), purple; Portofino (POF), green; Sestri Levante (SES), fuchsia; Punta Mesco and Portovenere (PMP), orange; Calafuria (CAL), blue; and Cerboli (CER), pink

TABLE 4 Long-term migration rates M ($= m/\mu$; migration/mutation) among genetic clusters of *Paramuricea clavata* in the Ligurian Sea, as revealed by the maximum likelihood-based analysis using MIGRATE-N (M)

		Destination						Mean
		BER	POF	SES	PMP	CAL	CER	
Source	BER	0	1.60	16.00	13.18	6.81	7.56	9.03 ± 5.65
	POF	1.81	0	14.15	21.48	4.04	10.99	10.49 ± 7.92
	SES	20.40	26.69	0	26.57	4.63	15.13	18.68 ± 9.21
	PMP	16.62	13.30	17.50	0	15.89	27.70	18.20 ± 5.53
	CAL	5.17	5.47	13.79	22.59	0	3.14	10.03 ± 8.12
	CER	5.49	1.62	9.84	6.29	7.50	0	6.15 ± 3.02
	Mean	9.89 ± 8.10	9.73 ± 10.61	14.25 ± 2.88	18.02 ± 8.17	7.78 ± 4.76	12.90 ± 9.37	

$M = 6.15 \pm 3.02$). The effective number of migrants per generation N_{em} ($= 4M$) was >0.22 at all sites.

Even though migration over such a large distance (>250 km) may be a rare occurrence, the level of migration ($>10\%$) between clusters more than 60 km apart (PMP towards CAL and CER clusters), compared with the relative exchange of migrants among neighbouring clusters ($<8\%$; e.g. POF and SES, 20 km apart), suggests that dispersal over 60 km may be more common than previously thought; however, the lowest level of migration (3.33%) was also found in one cluster (BER) located less than 60 km away from its closest neighbour (POF).

4 | DISCUSSION

Genetic evidence of population bottlenecks was found in most of the populations of *P. clavata* studied in the Ligurian Sea. Contemporary and long-term patterns of migration showed that all of the studied *P. clavata* populations are connected by larval dispersal.

4.1 | Genetic diversity and structure

The levels of genetic diversity among different *P. clavata* populations dwelling between 25 and 40 m of depth in the Ligurian Sea were similar to those found among shallow and deep populations in the same region, and in the north-west Mediterranean (Arizmendi-Mejía et al., 2015; Mokhtar-Jamaï et al., 2011; Pilczynska et al., 2016). Departures from Hardy-Weinberg equilibrium, as well as high F_{IS} values and evidence of heterozygote deficit have been previously reported in *P. clavata* populations (Mokhtar-Jamaï et al., 2011; Pérez-Portela et al., 2016; Pilczynska et al., 2016). This is a common occurrence in gorgonian species, mainly attributed to the low dispersal capabilities of the larvae (Gutiérrez-Rodríguez & Lasker, 2004; Ledoux et al., 2010).

The global F_{ST} value ($F_{ST} = 0.154$) was similar to what was previously reported for the species in the Ligurian Sea (Pilczynska et al., 2016), also indicating a high level of genetic differentiation among populations between 25 and 40 m of depth. In contrast, reported levels of genetic differentiation (F_{ST}) among *P. clavata* populations ranging from 30 to 55 m of depth in the Balearic Islands (global

F_{ST} = 0.035; Arizmendi-Mejía et al., 2015) were much lower than those found in this study. Nonetheless, non-significant F_{ST} values were found among most pairs of sites separated by 50–100 m, and generally at similar depths.

4.2 | Evidence of population bottleneck

In contrast with with Pilczynska et al. (2016), who found no evidence of a genetic bottleneck in two populations at 20–31 m of depth, a signal of a recent and drastic reduction of *P. clavata* effective population size was found in most of the populations studied (at depths of 25–40 m), with the exception of Punta Mesco and Calafuria. The findings corroborate previous studies reporting mass mortality events in populations dwelling at depths deeper than 20 m (in Sardinia, at depths of 20–40 m, Huete-Stauffer et al., 2011; in the north-western Mediterranean, at depths of 50–70 m, Pérez-Portela et al., 2016). Hence, the absence of a genetic bottleneck in Calafuria and Punta Mesco is striking.

Although very unlikely, it is possible that those populations were indeed not affected by mass mortality events: in Punta Mesco, the affected colonies were only reported down to 25 m of depth (Peirano et al., 2009), whereas mass mortalities have not been reported in Calafuria. Nonetheless, it is worth considering that high recruitment, either from reproduction of local survivors or through migration, could have cancelled the signature of a genetic bottleneck. Indeed, immigration rates in Calafuria and Punta Mesco were the highest in the region. Nonetheless, it is also worth mentioning the potential bias resulting from the methodological limitations of reconstructing the demographic history of populations from genetic data, which could have led to underestimating the number of populations that underwent a drastic decline in population size (Girod, Vitalis, Leblois, & Fréville, 2011; Peery et al., 2012).

A closer look at the Punta Mesco and Portovenere cluster (PMP) showed that mass mortality events of similar intensity were recorded in the two sites of Portovenere over 10 years ago. Also, both populations had started recovering a few years after that, but at different rates (Cupido et al., 2012). Results of the present study showed higher immigration in one of the two sites within Portovenere, with the site with lower immigration showing a signature of genetic bottleneck. Although demographic bottlenecks may be recurrent in Portovenere, migration among coastal populations may help maintain local genetic diversity and offset population collapse, making the signature of a bottleneck undetectable (Aguilar, Jessup, Estes, & Garza, 2008; Spong & Hellborg, 2002). Similarly, in Portofino, a mass mortality event was documented in 1999, and even though the mass mortality event dramatically reduced the reproductive potential of the native population, after 3 years gorgonian colony densities were greater than before the mortality event (Cerrano et al., 2005). The estimated age of first reproduction of *P. clavata* is 3 years. Therefore, enhanced recruitment following mortality should be attributed to immigration. The large number of immigrants in Portofino supports this hypothesis.

Despite no reports of *P. clavata* mass mortality events in Bergeggi, Parravicini et al. (2010) reported heatwaves affecting other sessile invertebrates. The genetic bottleneck signature observed in one of the Bergeggi sites suggests that mass mortality events could have

affected *P. clavata* populations in this area before 1999, and its permanence highlights the vulnerability of populations with low immigration rates.

Another potential explanation for the observed deficiency of heterozygotes among the studied populations could be the mixing of different gene pools, which would cause a Wahlund effect. This hypothesis has been proposed already for *P. clavata* populations in the Mediterranean Sea (Mokhtar-Jamaï et al., 2013), and for the Mediterranean red coral, *Corallium rubrum* (Costantini, Fauvelot, & Abbiati, 2007).

4.3 | Patterns of migration

The analyses of first-generation migrants and long-term migration revealed a pattern of bidirectional connectivity among all *P. clavata* populations examined. The percentage of individuals identified as first-generation migrants in a population (up to 15.9%), as well as the maximum dispersal distance of *P. clavata* found in this study (which ranged from 140 km to over 200 km, based on short-term and long-term migration, respectively), were larger than previously reported for shallower populations in the Ligurian Sea (20 km; Pilczynska et al., 2016), but were similar to values reported by Mokhtar-Jamaï et al. (2011), who found that despite strong genetic structure, some gene flow could still occur over short and longer distances (up to 160 km) across the Mediterranean Sea. Unlike the study of Arizmendi-Mejía et al. (2015), connectivity among populations of *P. clavata* in the Ligurian Sea was found between non-neighbouring clusters, but was not homogeneous throughout the region.

These findings, combined with the weak correlation found between genetic and geographic distance, demonstrate, as previously proposed by Pérez-Portela et al. (2016), that other factors rather than geographical distance alone may influence the pattern of genetic structure among *P. clavata* populations. Effective migration, in fact, is the result of the filtering of dispersal potential related to larval traits (e.g. pelagic larval duration, larval buoyancy, and behaviour) by environmental pre- and post-settlement drivers, such as hydrodynamics, predation pressure, and local geomorphological features (Lortie et al., 2004).

According to these results, the most important sources of migrants were the sites located in the central part of the Ligurian Sea, which is consistent with the large-scale separation of currents that occurs in front of Portovenere (Pinardi & Masetti, 2000). This flow separation results in two hydrodynamic provinces (Rossi, Ser-Giacomi, López, & Hernandez-García, 2014). Although the Ligurian current bordering the narrow continental shelf induces a rapid directional drift along the coast north-west of Portovenere, the detachment of meso-scale gyres south-east of Portovenere promotes higher regional retention with diffuse dispersal in the Gulf of La Spezia and north Tyrrhenian Sea. The hydrodynamic province identified north-west of Portovenere extends along the French coast to Marseille, suggesting that migrants proceeding from the north-western Ligurian Sea (e.g. Bergeggi) should be found in that location. This hydrodynamic pattern also supports the observation that the population of Bergeggi receives five times less immigrants than the population of Calafuria, and that a higher level of gene flow occurred towards the eastern part of the Ligurian Sea.

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It is also worth noting that although connectivity among coastal *P. clavata* populations provided an important contribution to the recovery of populations affected by mass mortality events, it may not be the only explanation for their upturn, and migration from deeper populations should not be excluded (Pilczynska et al., 2016). In any case, the present study shows that an effective number of migrants per generation of less than 5% was not sufficient for some populations (Bergeggi and Sestri Levante) to compensate their genetic divergence resulting from the combined effects of mutation and genetic drift.

4.4 | Implications for conservation in the context of global change

According to climate change projections, the rising of ocean temperatures and increasing frequency of extreme heatwave events (de Madron et al., 2011; Meehl et al., 2000), could lead to more frequent and more severe demographic breakdowns, especially in small and isolated populations. *Paramuricea clavata* is an extremely vulnerable species to extreme climatic conditions, which may cause severe depletions. It is generally assumed that heatwaves affect mainly shallow populations; however, during the heatwave of September 1999, unusual temperatures were recorded down to at least 32 m in depth (Bramanti et al., 2005), and genetic data demonstrate that populations of *P. clavata* between 25 and 40 m in depth have also been affected by drastic reductions in population size, highlighting that extreme climatic events impact coastal populations down to at least 40 m in depth. Nonetheless, this study provides evidence that *P. clavata* larvae are able to move among populations up to a distance of tens of kilometres, promoting population resilience and recovery from disturbance through the arrival of propagules from other locations.

Connectivity has become an increasingly important element in spatial conservation planning (Olds et al., 2016); however, only few studies have actually provided empirical data on the role of connectivity in population recovery following disturbance. Larval connectivity is remarkably relevant in sessile marine invertebrates, which rely on pre-settlement processes for dispersal. The protection of populations identified as sources of migrants would help the regional persistence of the species. The identification of key source populations may be of great value for the implementation of conservation measures and regional spatial planning in the context of increasing global climate-related disturbance. Nonetheless, seascape genetic inference can be strongly influenced by the recent demographic history of populations. Demographic stability can regulate gene flow, when recruitment in benthic populations is limited by a lack of space (Padrón & Guizien, 2016). Therefore, this study highlights the importance of integrating demographic and genetic data (see Arizmendi-Mejía et al., 2015).

In the Ligurian Sea, several Marine Protected Areas have been established based on the natural value of the habitats and/or administrative requirements. This study suggests that the spatial arrangement of the Ligurian Sea network of MPAs is effective in maintaining connectivity among *P. clavata* populations in the study area. Moreover, the distance between MPAs is in the range of the dispersal distance of the species. Therefore, in case of future disturbances, the network of MPAs in the Ligurian Sea would support the recovery of the populations. Nonetheless, it remains necessary to test the deep refugia

hypothesis, given that in the event of a disturbance affecting all shallow populations, deep populations would become of utmost importance. Taking this into consideration, it would be thus fundamental to promote the creation of offshore MPAs that could be incorporated into the existing MPA network, and ensure connectivity among shallow and deep populations. Furthermore, the eastward direction of gene flow in the study area suggests that connectivity should be further investigated in populations located west of Bergeggi, to provide a pattern of the connectivity across national borders and foster the creation of transnational MPA networks.

ACKNOWLEDGMENTS

This work was (co-)funded through a MARES grant. MARES is a joint doctorate programme selected under Erasmus Mundus coordinated by Ghent University (FPA 2011-0016) (for extra information, see <http://www.mares-eu.org>), and by the PRIN 2011 project 'Coastal bioconstructions: structure, function and management' and the PRIN 2015 (MIUR) project 'Resistance and resilience of Adriatic mesophotic biogenic habitats to human and climate change threats' (2015J922E4). The authors are grateful to the administration of the Portofino and Arcipelago Toscano Marine Protected Areas for the authorization to collect valuable samples of *Paramuricea clavata*. We are grateful to Silvia Cocito et al. for providing the samples from Punta Mesco. We also thank D. Aurelle for constructive comments. We give particular thanks to L. De Nigris, T. Garcia, L. Castellano, and Gruppo Archeosub Labronico for invaluable help in underwater sampling and logistics.

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SUPPORTING INFORMATION

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

How to cite this article: Padrón M, Costantini F, Bramanti L, Guizien K, Abbiati M. Genetic connectivity supports recovery of gorgonian populations affected by climate change. *Aquatic Conserv: Mar Freshw Ecosyst.* 2018;1-12. <https://doi.org/10.1002/aqc.2912>

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