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ORIGINAL PAPER

Genetic insights into recolonization processes of Mediterranean octocorals

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Abstract

Marine ecosystems are strongly impacted by the consequences of human activities, such as habitat destruction or artificialization and climate change. In the Mediterranean Sea, sessile benthic species, and particularly octocorals, have been affected by mass mortality events linked with positive thermal anomalies. The future survival of octocoral populations impacted by global change will depend on their recolonization abilities facing local extirpation or important modification of their habitat. We studied these processes in Mediterranean octocorals in two situations: the colonization of artificial substrates (wrecks) by the red gorgonian *Paramuricea clavata*, and the recolonization following mortality events in the yellow gorgonian *Eunicella cavolini*. With microsatellite markers (seven for *P. clavata*, five for *E. cavolini*), we analyzed the genetic diversity of populations on artificial substrates and their differentiation from other neighboring populations. For *P. clavata* the populations on artificial substrates were not or lowly differentiated from the closest populations (1.3–1.6 km) on natural substrates, and showed similar levels of genetic diversity. Artificial substrates can then be considered as an interesting substitute for natural substrates for this species. For *E. cavolini* we did not detect any variation in diversity or relatedness following recuperation after mortality events. In both cases, our results suggest the input from different populations in the recolonization process, which helps in maintaining the genetic diversity. These results are useful for the management of these species and of associated ecosystems.

Introduction

Marine biodiversity is increasingly impacted by global and local pressures such as climate change, overfishing, introduction of invasive species, habitat destruction and pollution (Boudouresque et al. 2017; Gattuso et al. 2018). The

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combination of these pressures questions the possibility of evolution and persistence of numerous marine species. Whereas the global impact of human activities on biodiversity is still increasing, different solutions (from reduction of greenhouse gas concentrations to manipulation of ecological adaptation and habitat restoration) are explored to mitigate this impact in the marine realm, but with uncertainties regarding their efficiency and trade-offs (Gattuso et al. 2018).

Additionally, coastal areas face an expansion of artificial structures such as dikes, offshores structures or even wrecks (Dafforn et al. 2015). The development of artificial structures can have contrasting consequences on marine biodiversity such as habitat loss or indirect modifications of the environment (Dafforn et al. 2015). Conversely, artificial structures can provide new habitats, and act as artificial reefs and connectivity nodes. Artificial structures can increase habitat complexity in seabed, complexity which has been impacted by activities such as trawling. Therefore, despite their negative effects, artificial structures can be considered as potential management tools in a context of global change. The future of marine biodiversity will then depend on the evolutionary trajectories of populations in this changing and anthropized environment. These evolutionary trajectories include the possibility of genetic adaptation, acclimatization, gene flow, recolonization and range shift (Bell and Collins 2008). Global change can then be considered as a wide scale adaptive challenge for many species, submitting biodiversity to important and new selective pressures (Otto 2018).

In this context, population genetics can be used to study genetic connectivity, the possibility of sustaining gene flow among habitats, including artificial ones, and the recolonization processes following disturbances. For example, a study of two scleractinian species, *Pocillopora damicornis* and *Seriatopora hystrix*, has shown a recolonization pattern mainly from neighbouring populations, but with occasional more distant sources (Starger et al. 2010). It is also important to consider the consequences of recolonization on genetic diversity, for example through founder effects. A founder effect will lead to changes in allele frequencies between source and sink populations, and to a reduction in genetic diversity (Allendorf et al. 2017). Nevertheless, this is not always the case. For instance, in the gastropod *Nucella lapillus*, no significant genetic effect of local extinction and recolonization was detected, despite a priori low dispersal abilities (Colson and Hughes 2004). Depending on the ecology of the species (e.g. age at sexual maturity), the strength of founder effects during recolonization will vary ranging from drastic reduction of intra-population genetic diversity and an increase in genetic differentiation between populations, to a lack of effect (Austerlitz et al. 2000). The type of habitat (natural/artificial) can also impact the level of genetic diversity, as observed in the gastropod *Patella caerulea* where populations on urban structures showed less genetic diversity than populations on natural rocky habitats (Fauvelot et al. 2009).

The Mediterranean Sea, with a combination of an important species diversity and strong human pressures including climate change, is a hotspot of biodiversity (Coll et al. 2010, 2012; Cramer et al. 2018). Mass mortality events induced by thermal anomalies have been observed in the last decades in the northern Mediterranean (Garrabou et al. 2009; Verdura et al. 2019). These mortality events have impacted several sessile groups of species such as sponges and octocorals. For a given species, the impact was different among regions and depths (Garrabou et al. 2009). Global (e.g. warming) or local (e.g. habitat destruction) pressures can lead to population decline or extinction (extirpation). This combination of human pressures raises the question of the survival of octocoral populations facing global change, which is linked to their adaptive potential. For example, octocoral populations from different depths show in some cases different thermotolerance levels, and this diversity could be important for adaptive evolution (Haguenauer et al. 2013; Ledoux et al. 2015; Pivotto et al. 2015). At a metapopulation level, population decline or extirpation can be compensated by migration from other populations, which can have positive demographic and genetic effects (Ronce 2007). In this context, the aforementioned increasing availability of artificial substrates should be considered, as artificial structures can allow the development of new local populations and modify the connectivity network. Studying the recolonization abilities of octocorals at a genetic level, on natural and artificial substrates, is therefore of paramount importance to better understand their future evolution and conservation.

Population genetic studies of Mediterranean octocorals have regularly evidenced a significant genetic differentiation at short distance, from a few tens to hundred meters. This was the case, at different levels, for the red coral *Corallium rubrum* (e.g. Costantini et al. 2007; Ledoux et al. 2010a, b; Pratlong et al. 2018), the red gorgonian *Paramuricea clavata* (Mokhtar-Jamai et al. 2011; Arizmendi-Mejía et al. 2015), and the yellow gorgonian *Eunicella cavolini* (Masmoudi et al. 2016; Cánovas-Molina et al. 2018). This marked genetic structure could be the result of a combination of reduced mean dispersal distance (Ledoux et al. 2010a), an important genetic drift, and of priority effect (Orsini et al. 2013). Studying the genetic diversity of recently colonized or recolonized sites would then be interesting to better understand the processes shaping the genetic structure of these species. For example, a founder effect along with a priority effect could lead to a persistent genetic differentiation at unexpected short distance. Genetic data on recolonization are scarce in Mediterranean octocorals. Arizmendi-Mejía et al. (2015) observed that a recently established population of *P. clavata* in Ibiza island (Balearic Islands, East Spain),

probably originated from several source populations, which can explain its relatively high levels of genetic diversity compared to the other investigated populations. In the same species, a lack of marked founder effect was also suggested during recolonization process following last glacial maximum (Ledoux et al. 2018). Focusing on *Eunicella cavolini*, Cánovas-Molina et al. (2018) suggested that colonies established on artificial reefs in the area of Marseille (South-East France) could come from different populations.

In the present study, we propose to extend our knowledge regarding colonization processes in these species with two case studies: the colonization of two artificial substrates (wrecks) by *P. clavata*, and the recolonization of a natural substrate after a strong mortality event in *E. cavolini*. In both cases, we aim to estimate the contribution of neighboring populations to the newly (re)colonized population. We also test if the dynamics of these colonizations are associated with founder events (i.e. a reduction in genetic diversity, or a differentiation of the new populations from neighbouring ones). This study sheds new light on the origin of short distance genetic differentiation in Mediterranean octocorals and should improve our understanding regarding the evolution of marine biodiversity in changing and artificializing seascapes.

Materials and methods

Sampling and population history

All colonies were sampled by scuba diving. Regarding *P. clavata*, we sampled two populations established on the ships «Donator» (DON) and «Le Grec» (GRE), both ships wrecked in 1945 in the same area in southeastern France. Eight additional populations on natural substrates were sampled, with increasing distance from the wrecks, up to the Marseilles area for the most distant sites (up to 75 km by sea; Table 1; Fig. 1). The distance with the closest population on natural substrate (SAR) is around 1.3 km for GRE and 1.6 km for DON. The sample size for *P. clavata* varied between 29 and 39 colonies. For *E. cavolini*, we focused on the sampling of four populations around the island of Ischia (Tyrrhenian Sea, West Italia; Table 1; Fig. 1) which experienced strong mortality events: Sant'Angelo (SAN), Secca delle Formiche (SFV), and La Nave (LAN) where mortality was documented in 2002, 2003, 2005 (except in LAN) and 2009 (Gambi et al. 2006, 2010; Garrabou et al. 2009; Cigliano and Gambi 2007; Gambi 2014), and La Grotta Azzurra at Palinuro (GAZ, Salerno; 15–25 m depth), a semi-submerged cave where a strong mortality event was registered in October 2008, with 77% of dead colonies at 15 m depth (Gambi et al. 2010), and a slight recovery of the population already observed in July 2011 (Gambi and Barbieri 2012). We also sampled two populations that, to our knowledge, did not experience any recent mortality event: the Nisida island (NISB, Gulf of Naples), and the Secchitello bank (UST, Ustica island, North Sicily) where *E. cavolini* is distributed relatively deep (below 30 m depth). In the sites affected by mortality events we likely sampled both young *E. cavolini* individuals and residual individuals which recruited before the mortality events. These *E. cavolini* populations were sampled in June and July 2013. Therefore we sampled from 4 to 11 years after mortality events for impacted populations. Regarding the evolution of density and the size structure of *E. cavolini* at the site GAZ after the 2008 mortality event (Gambi and Barbieri 2012), samples mainly come from colonies recruited after this event. The sample size for *E. cavolini* varied between 14 and 38 colonies. For both species, 3–4 cm fragments from an apical branch were sampled from each colony, and stored in ethanol 95% at – 20 °C before DNA extraction.

Microsatellite markers

DNA extraction was performed according to Mokhtar-Jamai et al. (2011), Ribout and Carpentieri (2013), and Masmoudi et al. (2016) depending on the samples. The *P. clavata* colonies have been genotyped with , Para10, Para12, Para14, Para17, Pard and Para2-37 as in Molecular Ecology Resources Primer Development Consortium et al. (2010) and Mokhtar-Jamai et al. (2011). Data from GAB, PTV, MTM, RIO, RIS and IMP were available from Mokhtar-Jamai et al. (2011). The *E. cavolini* colonies have been genotyped with the loci S14, C21, C30, C40 and Mic56 following Masmoudi et al. (2016).

Genetic diversity

We identified repeated multilocus genotypes (MLGs) and we computed the probability of occurrence of multiple MLGs under sexual reproduction with the poppr 2.8.3 R package (Kamvar et al. 2014, 2015). For all following analyses, we kept one representative of each MLG. Observed and expected heterozygosities were computed with the Genetix 4.05 software (Belkhir et al. 1996–2004). Allelic richness was estimated with a rarefaction procedure with the ADZE software (Szpiech et al. 2008), and by excluding for each species the sample with the lowest number of colonies.

Genetic structure within and among populations

Departures from panmixia were tested with the Genepop 4.5.1 software with an exact test and with heterozygote deficiency as an alternative hypothesis (Rousset 2008). The level of relatedness within populations was computed with the estimator of Wang (2002) implemented in

Table 1 Samples description: codes of sampling sites, GPS coordinates, depth, sample size without repeated MLGs (*N*), mean number of alleles per locus rarefied for *g* individuals (Ar (*g*); $g=29$ for *Paramuricea clavata*, except for PQL with $g=12$; and 14 for *Eunicella cavolini*, except UST with $g=10$)

Site	Code	GPS	Depth (m)	Year	*N*	Ar (*g*)	H_O	H_E	F_{IS}
Paramuricea clavata									
Pointe du Vaisseau	PTV	42°59′42.9″ N 6°24′24.2″ E	20–25	2008	29	7.2	0.59	0.63	**0.06**
Donator wreck	DON	42°59′35.9″ N 6°16′26.1″ E	34	2011	33	7.6	0.58	0.62	**0.08**
Le Grec wreck	GRE	42°59′37.0″ N 6°16′42.0″ E	34	2011	33	7.7	0.61	0.65	**0.06**
Sec de Sarraniers	SAR	42°59′16.3″ N 6°17′30.2″ E	40	2011	35	7.5	0.57	0.61	**0.08**
Gabinière	GAB	42°59′21.5″ N 6°23′49.2″ E	22–25	2008	32	7.8	0.63	0.69	**0.09**
Les Mèdes	PQL	43°01′43.0″ N 6°14′28.0″ E	31	2009	29	4.6	0.61	0.73	**0.16**
Montrémian	MTM	43°01′07.2″ N 6°21′46.0″ E	20–25	2008	29	6.1	0.57	0.64	**0.12**
Riou Marseille	RIO	43°10′21.66″ N 5°23′25.16″ E	20–25	2008	35	8.5	0.60	0.71	**0.15**
Riou Marseille	RIS	43°10′21.66″ N 5°23′25.16″ E	40	2008	30	8.0	0.66	0.73	**0.10**
Impériales Marseille	IMP	43°10′22.79″ N 5°23′35.39″ E	41	2007	39	8.3	0.63	0.72	**0.12**
Eunicella cavolini									
Nisida Island (Napoli)	NISB	40°47′22.8″ N 14°09′42.0″ E	20	2013	16	3.8	0.54	0.58	0.08
Secca Formiche di Vivara (Ischia)	SFV	40°44′20.45″ N 13°58′45.08″ E	15	2013	38	4.5	0.64	0.65	0.01
Sant'Angelo (Ischia)	SAN	40°41′30.58″ N 13°53′37.76″ E	18–20	2013	31	4.6	0.53	0.65	**0.20**
La Nave (Ischia)	LAN	40°42′25.35″ N 13°51′12.73″ E	20–25	2013	25	5.4	0.59	0.71	**0.17**
Grotta Azzura (Palinuro, Salerno)	GAZ	40°1′53.01″ N 15°16′9.01″ E	15	2013	32	4.9	0.66	0.70	**0.06**
Ustica Island Secchitello (Palermo)	UST	38°41′25.54″ N 13°10′25.35″ E	35–38	2013	14	4.0	0.61	0.63	0.04

Values in bold correspond to significant test of panmixia after FDR correction at a 0.05 level

H_O observed heterozygosity, H_E expected heterozygosity, F_{IS} multilocus

the COANCESTRY software (Wang 2011). To compare the levels of relatedness between populations we used the bootstrap approach of COANCESTRY with 1000 resamplings. The level of genetic differentiation was estimated with the F_{ST} estimate of Weir and Cockerham (1984). Previous studies did not detect a strong impact of null alleles for the loci analysed here in each species (Mokhtar-Jamaï et al. 2011; Masmoudi et al. 2016). Nevertheless, regarding the F_{IS} values observed here and in previous studies, and the missing data observed in some populations (see results), we also estimated F_{ST} with a correction for null allele from the FreeNA software (Chapuis and Estoup 2007). Genic differentiation between populations was tested with the exact test procedure implemented in Genepop. To estimate the relative differentiation of each population, we computed the population-specific F_{ST} in GESTE (Foll and Gaggiotti 2006; Gaggiotti and Foll 2010).

The genetic differences among individuals were visualized thanks to a Principal Component Analysis (PCA; function dudi.pca) with the Adegenet R package (Jombart 2008). We made an individual clustering analysis with the STRUCTURE software (Pritchard et al. 2000) with 10^6 iterations for the burn-in and 10^6 iterations for the main analysis, 10 replicates for each *K*, and by testing $K=1$ to $K=6$ in the two species. We used an admixture model with correlated allele frequencies. The results were visualized with the POPHELPER website (Francis 2017; https://www.pophelper.com/).

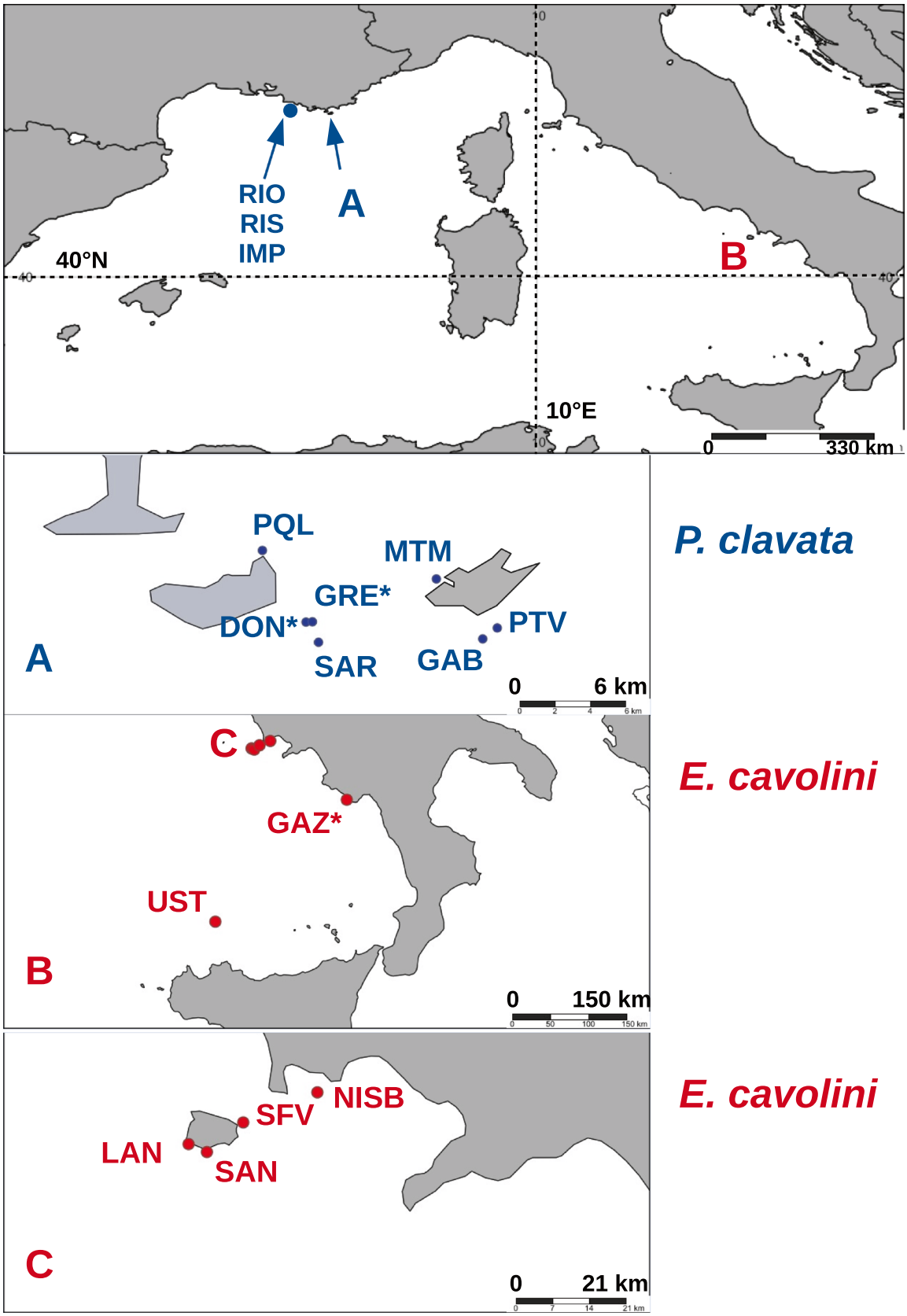

Fig. 1 Sampling locations for *Paramuricea clavata* and *Eunicella cavolini*. Asterisks indicate populations issued from colonization (wrecks for *P. clavata*) or recolonization after mortality event (*E. cavolini*). Maps were produced with SimpleMappr (Shorthouse 2010)

To infer the genetic origin of populations installed on artificial substrates (DON and GRE for *P. clavata*), and of new recruits after a complete recolonization (GAZ for *E. cavolini*), we used the GENECLASS2 software (Piry et al. 2004) with the option to infer individual assignment, using all other populations as references. We used the Rannala and Mountain (1997) criterion, and the membership probability was computed according to Paetkau et al. (2004), with 1000 simulated individuals, and a type I error of 0.01.

Results

Occurrences of repeated MLGs

For *P. clavata*, five pairs of repeated MLGs were observed: two in the GRE population, one in MTM, one in DON, one in RIS. The corresponding probability of occurrence of repeated genotypes under sexual reproduction (psex) ranged from 7×10^{-9} to 2×10^{-5}. For *E. cavolini*, three MLGs were detected more than once, all in the NISB population: one was repeated nine times (psex = 0.010), another one five times (psex = 0.014) and another one two times (psex = 0.014). The overall frequency of missing genotypes was around 17% for *E. cavolini* (mainly concentrated in the SFV and LAN populations), and 10% for *P. clavata* (mainly in PQL).

Genetic diversity and structure within populations

When considering rarefied allelic richness for *P. clavata*, the DON and GRE wreck populations had an Ar(29) of 7.6 and 7.7, respectively, similar to the value observed for the neighbouring population SAR (7.5; Table 1). The expected heterozygosity for DON and GRE was 0.62 and 0.65 respectively, whereas it was 0.61 for SAR, the lowest value found here. Regarding *E. cavolini*, the rarefied allelic richness for GAZ (recolonized population; sample size $N = 32$) was the second highest value after the LAN population ($N = 25$), with Ar(14) = 4.9 and 5.4, respectively. The same trend was observed when considering expected heterozygosity, with values of 0.70 and 0.71 for GAZ and LAN, respectively. NISB and UST, for which we have no indication of mortality events, showed the lowest allelic richness and expected heterozygosity values, but with small sample sizes in both cases (Table 1).

For *P. clavata*, all samples showed a significant deviation from panmixia, with heterozygote deficiencies varying from 0.06 (PTV and GRE) to 0.16 (PQL). For *E. cavolini*, three samples over six showed a significant deviation from panmixia, and heterozygote deficiencies varied from 0.01 (SFV) to 0.20 (SAN).

Regarding relatedness levels for *P. clavata*, the PTV and MTM populations showed higher mean relatedness than most other populations, whereas GAB, PQL and RIO tended to have lower mean relatedness than other populations (Table 2). There was no clear tendency for the wreck populations DON and GRE. For *E. cavolini*, NISB and SFV showed higher mean relatedness than other populations.

Genetic differentiation and origin of new recruits

Regarding population differentiation, the global F_{ST} estimate was 0.04 for *P. clavata*, and 0.08 for *E. cavolini*. For both species, all pairwise differentiation tests were significant, apart from the comparison between GRE and SAR for *P. clavata*, two sites separated by 1.3 km (Table 3). For *P. clavata,* the differentiation between DON and SAR was low (uncorrected pairwise $F_{ST} = 0.02$; corrected pairwise $F_{ST} = 0.03$; spatial distance: 1.6 km), but significant. For *E. cavolini* and focusing on the recolonized GAZ population, the lowest differentiation was observed with the LAN population ($F_{ST} = 0.08$, for corrected and uncorrected estimates; distance 140 km). The mean pairwise F_{ST} for the comparison involving GAZ was 0.1 and 0.07 for the uncorrected and corrected estimates, respectively. Accordingly, GAZ was then slightly more differentiated or at the same level of differentiation than the other populations, except UST (range 0.04–0.11 and 0.02–0.12 for the uncorrected and corrected estimates, respectively).

Local F_{ST} are presented in Table 4. For *P. clavata*, the PQL population displayed a higher local F_{ST} than other populations, and the corresponding 95% confidence interval did not overlap with those of other populations. For *E. cavolini*, the highest local F_{ST} was observed for NISB, but with a 95% confidence interval overlapping with those of other populations. None of the (re)colonized populations showed significantly different values.

The PCA analysis of *P. clavata* did not show any clear structure pattern, with only a few individuals from IMP and RIS separated from the other ones on axes 1 and 2 (Fig. 2). For *E. cavolini*, the main pattern was a distinction of GAZ and UST samples on axes 1 and 2, respectively. The individuals of these two populations were genetically diverse as shown by their quite wide distribution on the PCA axes.

The results of the individual clustering are presented in Fig. 3. For *P. clavata*, we present the results for $K = 2$ to $K = 5$ since there was no informative distinction above this value. At $K = 2$, one can observe a gradient between two clusters, a major one around Marseille (RIO, RIS, IMP), and a minor one increasing in frequency in other populations. At $K = 3$, GAB, MTM and PTV are separated from the rest. At $K = 5$, we also observe a slight distinction of two populations: MTM and RIS. The wreck populations DON and GRE appear related to the SAR population. In all cases, the separation among clusters was not complete. For *E. cavolini*, we present the results for $K = 2$ to $K = 4$, there was no

Table 2 Comparisons of relatedness levels

(A) *P. clavata*

	PTV	DON	GRE	SAR	GAB	PQL	MTM	RIO	RIS
PTV									
DON	**0.083*** **								
GRE	**0.074*** **	-0.0092							
SAR	**0.065*** **	-0.018	-0.0094						
GAB	**0.11*** **	**0.031*** **	**0.032*** **	**0.041*** **					
PQL	**0.12*** **	**0.036*** **	**0.045*** **	**0.054*** **	0.013				
MTM	-0.019	**-0.1*** **	**-0.093*** **	**-0.084*** **	**-0.13*** **	**-0.14*** **			
RIO	**0.14*** **	**0.053*** **	**0.062*** **	**0.071*** **	**0.03*** **	0.017	**0.16*** **		
RIS	**0.076*** **	-0.0073	0.0019	0.011	**-0.03*** **	**-0.043*** **	**0.095*** **	**-0.06*** **	
IMP	**0.11*** **	**0.029*** **	**0.038*** **	**0.047*** **	0.0056	-0.0073	**0.13*** **	**-0.024*** **	**0.036*** **

(B) *E. cavolini*

	NISB	SFV	SAN	LAN	GAZ	UST
NISB						
SFV	**0.14*** **					
SAN	**0.21*** **	**0.071*** **				
LAN	**0.3*** **	**0.15*** **	**0.081*** **			
GAZ	**0.21*** **	**0.073*** **	0.0026	**-0.079*** **		
UST	**0.2*** **	**0.2*** **	-0.0061	-0.087**	-0.0086	

Comparison of within-population relatedness levels based on the estimator of Wang (2002), (A) for *Paramuricea clavata*, and (B) for *Eunicella cavolini*. Each comparison corresponds to the observed difference in mean relatedness between population in column and population in row. Blue and red values indicate significantly positive and negative differences respectively

*Extreme values based on 1000 bootstraps, with the corresponding percentiles: 5%

**Extreme values based on 1000 bootstraps, with the corresponding percentiles: 2.5%

***Extreme values based on 1000 bootstraps, with the corresponding percentiles: 1%

informative distinction above this value. GAZ and UST are separated from other populations at $K=2$ while GAZ and UST are separated at $K=3$. At $K=4$ there is a distinction of GAZ from other populations which are almost equally admixed among the three other clusters. Nevertheless, some individuals in GAZ seem more related to other populations than to the blue cluster dominant in this population.

The results of assignment analyses are presented in supplementary Table 1. For *P. clavata*, if we arbitrarily consider a threshold of 0.95 for membership probabilities, three over 33 individuals of DON could be related to SAR, six to PQL, three to RIO and one to IMP (this individual also showed high probability for RIO). For GRE, three over 33 individuals could be related to SAR, and seven over 33 to PQL. For *E. cavolini*, eight individuals over 32 displayed high membership probability for the LAN population. In both cases several individuals displayed very low membership probabilities for all the tested populations suggesting that they come from non-sampled sites.

Discussion

Spatial patterns of recolonization

Our data allow discussing and comparing the dispersal and recolonization abilities of two Mediterranean octocoral species. For *P. clavata*, we observed a genetic proximity between the samples on the two wrecks DON and GRE, and the nearest population of natural substrate SAR. The differentiation was very low (and even non-significant for GRE) between these two populations and SAR, 1.2 km apart. The longevity of *P. clavata* may reach 50–100 years, but their age is difficult to estimate, for example due to variation in

Table 3 Pairwise F_{ST} values for (A) *Paramuricea clavata*, and (B) *Eunicella cavolini*

(A)	DON	GRE	SAR	GAB	MTM	PTV	PQL	RIO	RIS	IMP
DON	–	**0.02**	**0.03**	**0.05**	**0.05**	**0.05**	**0.08**	**0.01**	**0.04**	**0.03**
GRE	**0.01**	–	**0.01**	**0.03**	**0.05**	**0.06**	**0.06**	**0.02**	**0.05**	**0.03**
SAR	**0.02**	**0.00**	–	**0.03**	**0.05**	**0.05**	**0.10**	**0.03**	**0.06**	**0.04**
GAB	**0.04**	**0.04**	**0.04**	–	**0.04**	**0.05**	**0.10**	**0.03**	**0.07**	**0.04**
MTM	**0.05**	**0.06**	**0.07**	**0.04**	–	**0.04**	**0.13**	**0.04**	**0.08**	**0.06**
PTV	**0.03**	**0.05**	**0.05**	**0.04**	**0.05**	–	**0.13**	**0.04**	**0.07**	**0.06**
PQL	**0.04**	**0.04**	**0.06**	**0.05**	**0.10**	**0.06**	–	**0.08**	**0.06**	**0.06**
RIO	**0.01**	**0.02**	**0.04**	**0.03**	**0.04**	**0.03**	**0.04**	–	**0.03**	**0.01**
RIS	**0.05**	**0.06**	**0.07**	**0.07**	**0.08**	**0.06**	**0.06**	**0.02**	–	**0.03**
IMP	**0.03**	**0.04**	**0.04**	**0.03**	**0.06**	**0.05**	**0.05**	**0.01**	**0.03**	–

(B)	GAZ	LAN	NISB	SAN	SFV	UST
GAZ	–	**0.08**	**0.08**	**0.07**	**0.06**	**0.05**
LAN	**0.08**	–	**0.12**	**0.07**	**0.07**	**0.11**
NISB	**0.11**	**0.05**	–	**0.03**	**0.05**	**0.07**
SAN	**0.10**	**0.04**	**0.04**	–	**0.02**	0.07
SFV	**0.09**	**0.04**	**0.06**	**0.04**	**–**	0.07
UST	**0.10**	**0.13**	**0.12**	**0.11**	**0.12**	–

Below diagonal: standard F_{ST} estimates (Weir and Cockerham 1984); above diagonal: F_{ST} estimates from FreeNA. Values in bold correspond to significant genic differentiation after FDR correction at a 0.05 level

Table 4 Estimates of local F_{ST} with 95% highest probability density interval (HPDI)

Population	Mean	95% HPDI
P. clavata		
DON	0.08	0.0556; 0.109
GRE	0.08	0.0545; 0.107
SAR	0.07	0.0471; 0.0950
GAB	0.05	0.0327; 0.0768
MTM	0.12	0.0779; 0.162
PTV	0.08	0.0514; 0.109
PQL	0.23	0.165; 0.295
RIO	0.03	0.0205; 0.0498
RIS	0.07	0.0489; 0.0960
IMP	0.05	0.0327; 0.0671
E. cavolini		
GAZ	0.15	0.0940; 0.208
LAN	0.18	0.117; 0.238
NISB	0.30	0.188; 0.427
SAN	0.17	0.107; 0.235
SFV	0.22	0.142; 0.302
UST	0.24	0.144; 0.332

growth rate or breakage of some branches (Linares et al. 2007). The age of the wrecks is known (more than 70 years), which sets an upper limit to population age, but not the age of the sampled colonies. Some colonies sampled here could then not only correspond to the first generation of founders, but also be descendants from these founders, or descendants from more recent migrants. We can consider two non-mutually exclusive explanations to the observed low differentiation among wrecks and surrounding populations. First, the initial recruits came from the SAR population, with no or low enough founder effect that would have induced initial differentiation. Second, gene flow from SAR after colonization could have contributed to the genetic homogeneity of *P. clavata* at that scale. The lack of founder effect in *P. clavata* was related to the late sexual maturity observed in this species (Coma et al. 1995; Ledoux et al. 2018). Indeed, during the years following the foundation of a new population, the expansion of the population is mainly due to new migrants and not to local reproduction. This increases the effective population size until the first reproductive event buffering the founder effect (Austerlitz et al. 2000). Even if significant, the low differentiation observed with other populations than SAR points to the possible participation of these populations to the newly founded ones as well. This is supported by assignment analysis indicating a contribution of PQL. In their study of a recently founded population of *P. clavata*, Arizmendi-Mejía et al. (2015) identified multiple source populations at distances ranging from 300 m to around 1 km, which is similar to our results. The larval duration of *P. clavata* has been estimated between 8 and 25 days in laboratory, which could allow long distance dispersal (Linares et al. 2008). The assignment of three individuals to a population from Marseille can correspond to such long distance dispersal. Similarly, Padrón et al. (2018) suggested

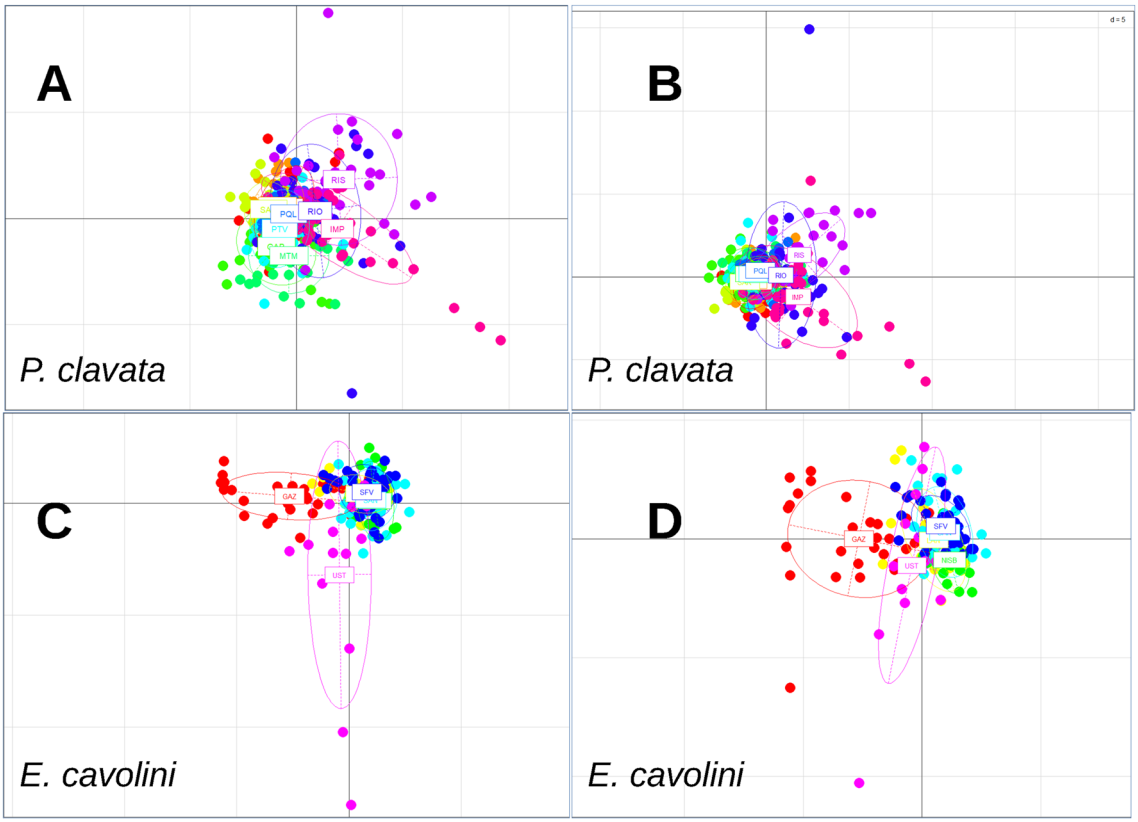

Fig. 2 Plots of PCA results. **a** *Paramuricea clavata* with axis 1 (2.7% of variance) horizontal and axis 2 (2.4% of variance) vertical; **b** *P. clavata* with axis 1 horizontal and axis 3 (2.2% of variance) vertical. **c** *Eunicella cavolini* with axis 1 (4.7% of variance) horizontal and axis 2 (4.4% of variance) vertical; **d** *E. cavolini* with axis 1 horizontal and axis 3 (3.9% of variance) vertical

that connectivity among coastal populations of *P. clavata*, possibly at tens of kilometres, had contributed to their recovery after mortality events. Nevertheless, surface brooding and larval behavior (negative phototaxis), and a short swimming phase may reduce the realized dispersal in this species (Linares et al. 2008). In that case, we should consider that non-sampled and closer population(s) could have contributed to the mixed diversity of the wreck populations.

For *E. cavolini*, the colonies sampled in GAZ should be mainly new recruits following the 2008 mortality event. These recruits could correspond to local recruitment from the few remaining colonies (Gambi and Barbieri 2012). There was no significant reduction in genetic diversity at that site compared to other populations. This could mean that there was enough surrounding colonies to sustain population recovery; for example one can note that the mortality event was less strong at 25 m, and this would constitute a possible refugia. Additionally, recruits could have come from different populations, as suggested by the genetic differences among individuals shown by clustering and multivariate analyses. The origin of these foreign recruits in the GAZ population is not clear based on our sampling. The assignment analysis suggested the possibility of LAN as origin of the recruits in GAZ. LAN and GAZ are distant from around 140 km apart. This is at odd with the local differentiation usually observed for this species (Cánovas-Molina et al. 2018). It seems more probable that non-sampled populations, either genetically akin to LAN, or corresponding to another genetic group, contributed to this signal of distant recolonization of GAZ. In a preliminary study of the colonization of artificial reefs by *E. cavolini*, it was difficult to precisely identify the population(s) of origin, but potential source populations could be distant by two to three kilometres from these artificial structures (Cánovas-Molina et al. 2018). There is no information on the larval biology of *E. cavolini* to further interpret these results. In the congeneric species *E. singularis*, the settlement could be possible within 30 h (Weinberg 1979), but it would be interesting to formally characterize the larval phase duration in *E. cavolini*.

In any case, the analysis of the colonized or recolonized populations in the two species studied here clearly indicates a mixed origin of the recruits. Recolonization from mixed origins, with sporadic distant input, has also been observed in hexacorals (Underwood et al. 2007; Starger et al. 2010). In the case of *E. cavolini* (GAZ), this was done in a relatively short time after mortality event (mortality in 2008, sampling

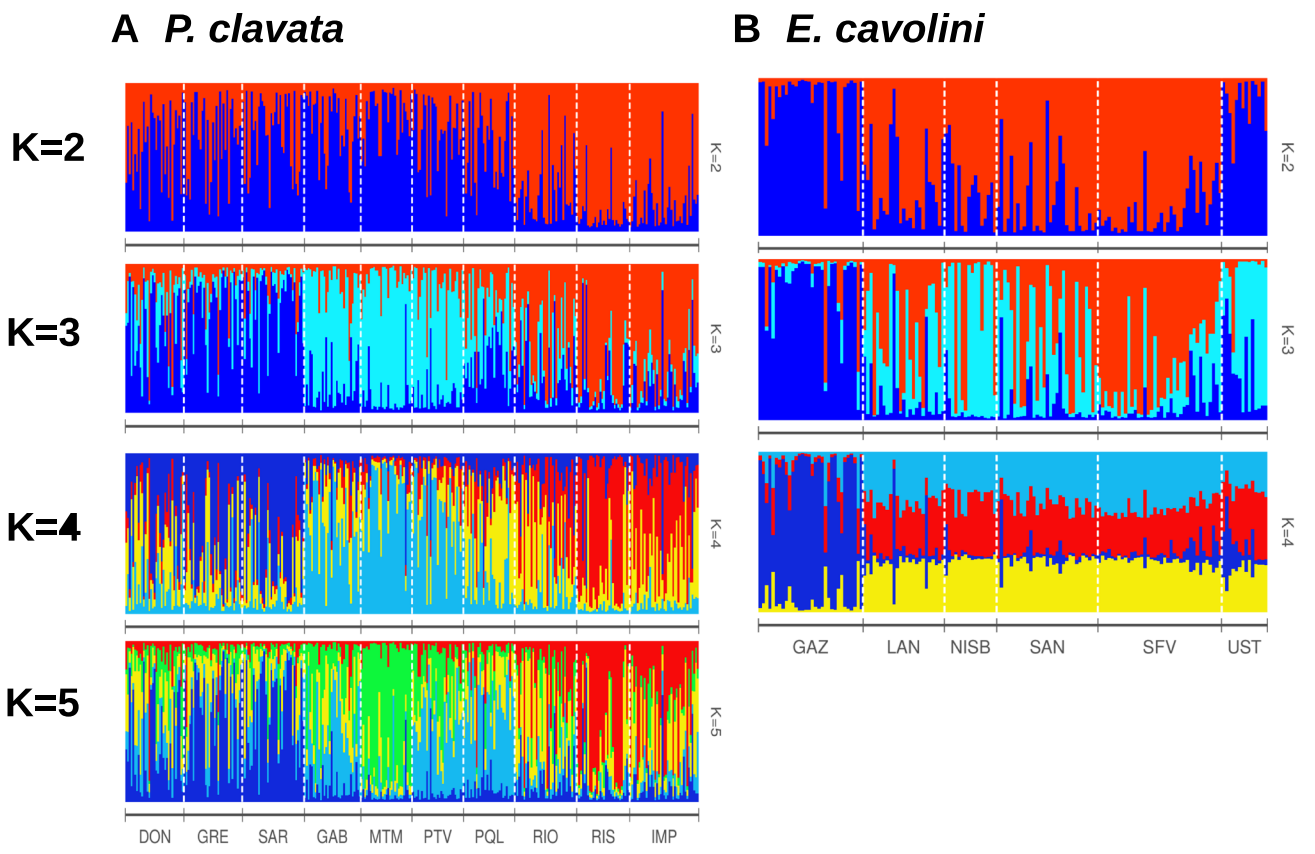

Fig. 3 Results for the individual clustering analysis with STRUCTURE for **a** *Paramuricea clavata* and **b** *Eunicella cavolini*

in 2013). Interestingly, Cupido et al. (2012) have observed an increase in recruitment for *P. clavata* following mortality events, possibly because a greater space availability. This could both limit the erosion of genetic diversity (see below), and allow gene flow from other populations. From a methodological point of view, our results underline that studying recolonization in Mediterranean octocorals should not only consider neighbouring populations, but increase the sampling effort to distant populations.

Consequences on the genetic diversity of the populations

We did not observe any impact of colonization or recolonization in the population diversity of both species, or with local F_{ST} reflecting local drift. One can note that the expected heterozygosities observed here for *E. cavolini* are higher than those previously reported by Cánovas-Molina et al. (2018), and in the range of values obtained for populations from western Mediterranean by Masmoudi et al. (2016), but in both cases with a microsatellite panel partly different from the one used here.

As already mentioned, in the case of *E. cavolini* most other populations analysed here suffered from mortality events which may have reduced their genetic diversity as well. Regarding *P. clavata*, the levels of diversity observed here are in the lower range of those observed by Mokhtar-Jamai et al. (2011) or Pérez-Portela et al. (2016), again with a partially different panel of microsatellite markers. In the case of this species, depth has been shown to be positively correlated with genetic diversity (Pilczynska et al. 2019). Even if the sampling scheme does not allow a precise study of this question, a similar tendency was observed here with a mean expected heterozygosity of 0.67 for the depth range 20–34 m, and 0.69 for 40–41 m. In both species we observed significant heterozygote deficits in most populations. This is in line with previous observations of departures from panmixia in Mediterranean gorgonians (e.g. Ledoux et al. 2010b; Mokhtar-Jamaï et al. 2011). These departures have been explained by a combination of inbreeding and null alleles, and this does not seem linked with patterns of recolonization here.

The retention of genetic diversity and the lack of change in relatedness following recolonization can be the consequence of the mixed origin of the recruits. In *E. cavolini*,

we did not observe any genetic effect of mortality events either. Nevertheless detecting such effects of mortality might require the comparison of more populations, and cohorts within populations, with more information on the date and impact of mortalities. In *P. clavata*, Pilczynska et al. (2016) did not detect any reduction in genetic diversity following mortality event as well. One can note that to have a genetic impact, any demographic shrinkage should be sustained over several generations (Allendorf 1986), whereas we consider here only a very low generation number. Additionally, partial mortality of colonies, long generation time (Lippé et al. 2006), late sexual maturity (Ledoux et al. 2018), and an increase in recruitment (Cupido et al. 2012) can buffer the genetic impact of bottlenecks or demographic accidents on populations. As shown here, in a metapopulation context, exchanges from more or less distant populations will also limit the genetic consequences of mortality events. These conclusions might be different on a longer term. The low survivorship success of the early stages, despite the high investment in the production of gametes in *P. clavata* (Coma et al. 1995), suggests that the species may have a low capacity to recover during large or frequent disturbances (Linares et al. 2008). More generally, if climate change induces strong and recurrent scale mortality events, this might lead to a reduction of larval recruitment of different species. This has been observed in scleractinians of the Great Barrier Reef after mass bleaching event (Hughes et al. 2019).

In a context of population fragmentation, and anthropization of coastal areas, it is important to consider the role of artificial structures as potential substrates for settlement and to enhance biodiversity. In the Bay of Marseille, after 11 years of immersion, artificial reefs are already colonized by several octocoral species, such as *E. cavolini*, *E. singularis* and *E. verrucosa* (Guillemain et al., unpublished data). Our results show that the colonization of wrecks did not lead to a reduction of genetic diversity at a given range depth for *P. clavata*. Similarly, Ordóñez et al. (2013) did not observe any significant difference in genetic diversity between populations of the ascidian *Microcosmus squamiger* on artificial and natural substrates. Conversely a lower genetic diversity was observed for the limpet *Patella caerulea* on artificial structures compared to natural rocky substrates (Fauvelot et al. 2009). Such different results are probably linked to different population dynamics, and to different interaction with the substrates according to the species. It will then have different consequences on the role of these new substrates and associated populations in the connectivity and genetic diversity of populations. In the case of octocorals, our results indicate that artificial substrates provide good opportunities for the development of new populations, or the extension of existing ones. Artificial substrates situated at a few kilometres from natural populations can possibly be colonized and allow the development of new populations. It will be interesting to extend connectivity studies in this context to test if these populations could have other impacts, such as for example act as stepping stone to allow gene flow between previously isolated areas.

Factors driving short distance differentiation in Mediterranean octocorals

Genetic differentiation at short distance has been repeatedly observed in Mediterranean octocorals (e.g. Costantini et al. 2007; Ledoux et al. 2010a; Mokhtar-Jamai et al. 2011; Cánovas-Molina et al. 2018). Several factors could contribute to such patterns. First a short mean dispersal distance has been inferred from the analysis of local genetic structure, and from the observation of related individuals at a very short distance in the red coral *C. rubrum* (Ledoux et al. 2010a). This may seem at odd with the long larval survival (up to 42 days) estimated for this species in aquarium (Martínez-Quintana et al. 2015). Also, the observation of a short-distance differentiation does not preclude for the presence of sporadic more distant exchanges allowing gene flow at a larger metapopulation scale. Such discrepancy between the spatial scale of genetic structure and the duration of larval phase has been observed for example in the fish *Elacatinus lori* (D'Aloia et al. 2015), calling to more detailed study of factors driving connectivity. Second, genetic drift is the other important driver of genetic structure, and analyses of local genetic structure pointed to a relatively low effective size in the red coral *C. rubrum* (Ledoux et al. 2010a). Finally, priority effect at the genetic level can increase genetic differentiation, when the arrival of new recruits is limited by the presence of already installed individuals (isolation by colonization; Orsini et al. 2013). Our results, and previous ones (Arizmendi-Mejía et al. 2015), suggest that in a metapopulation context, colonization or recolonization may not be limited by dispersal. Available habitat, either artificial or natural, following mortality, seem to be easily recolonized, at least in a metapopulation context. A temporal survey over several generations, or indirectly the comparison of different cohorts, would allow estimating the strength of isolation following the founding of new populations.

Perspectives

Our results show the possibility of successful (in terms of genetic diversity) colonization or recolonization in Mediterranean gorgonians, including on artificial substrates. These data will be useful for the spatial design of similar studies in these species. The use of a higher number of markers such as SNPs could increase the power of assignment analyses as well (e.g. Glover et al. 2010; Benestan et al. 2015). Finally, it would be interesting to study the adaptation of

these species to new substrates with population genomics approaches (Manel et al. 2016). As this may be difficult in a context of strong genetic structure (Pratlong et al. 2018), such results based on microsatellite loci in different species will be useful to choose the best sampling scheme.

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Data availability All genotypes have been deposited in the Zenodo database under reference: https://doi.org/10.5281/zenodo.3724056

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Sampling authorizations All sampling have been performed with authorizations from the corresponding local authorities.

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