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Out of the Mediterranean? Post-glacial colonisation pathways varied among cold-water coral species

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3 **1 i. Out of the Mediterranean? Post-glacial colonisation pathways varied among cold-water coral**
4 **2 species**

5
6 **3 ii. Running title: Contrasting deep corals recolonisation paths**

7
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49 vi. Abstract and keywords:

50 **Aim.** To infer cold-water corals post-glacial phylogeography and assess the role of Mediterranean Sea
51 glacial refugia as the origin for the recolonisation of the North-eastern Atlantic Ocean.

52 **Location.** North-eastern Atlantic Ocean and Mediterranean Sea.

53 **Taxon.** *Lophelia pertusa*, *Madrepora oculata*.

54 **Methods.** We sampled cold-water corals using remotely operated vehicles and performed one
55 geological corer for coral and sediment dating. We characterized spatial genetic patterns
56 (microsatellites and a nuclear gene fragment) using networks, clustering and measures of genetic
57 differentiation.

58 **Results.** Microsatellite and sequence data were congruent, and showed a contrast between the two
59 cold-water coral species. Populations of *L. pertusa* are not genetically structured across the North-
60 eastern Atlantic, present a dominant pioneer haplotype, local haplotype radiations and a majority of
61 endemic variation in lower latitudes. *M. oculata* populations are differentiated across the North-eastern
62 Atlantic, and genetic lineages are poorly admixed even along neighbouring sites.

63 **Conclusions.** Our study shows contrasting post-glacial colonisation pathways for two key habitat-
64 forming species in the deep-sea. The cold-water coral *L. pertusa* has likely undertaken a long-range
65 (post-glacial) recolonisation of the North-eastern Atlantic directly from refugia located along southern
66 Europe (Mediterranean Sea or Gulf of Cadiz). Contrastingly, the stronger genetic differentiation of
67 *M. oculata* populations mirrors the effects of long-term isolation in multiple refugia. We suggest that
68 the distinct and genetically diverged, refugial populations initiated the post-glacial recolonisation of
69 North-eastern Atlantic margins, leading to a secondary contact in the northern range and reaching
70 higher latitudes much later, in the late Holocene. This study highlights the need to disentangle the
71 influence of present day dispersal and evolutionary processes on the distribution of genetic
72 polymorphism, to unravel the influence of past and future environmental changes on connectivity in
73 the cosmopolitan deep-sea ecosystems associated to cold-water corals. Marine phylogeography, Deep-
74 sea, Cold-water corals, Last Glacial Maximum, *Lophelia pertusa*, *Madrepora oculata*, Glacial marine
75 refugia

76 vii. Main text

77 Introduction

1
2
3 78 Cold-water corals (CWC) are amongst the most charismatic marine ecosystems in the deep ocean
4 79 (>200 m), supporting abundant and diverse biomass (Milligan *et al.*, 2016). Deep-reef habitats rely
5 80 upon the frame-building capability of several coral species, notably *Lophelia pertusa* and
6 81 *Madrepora oculata* (Linnaeus, 1758). The two species intermingle and anastomose in reefs in the
7 82 North-eastern Atlantic Ocean (NE Atlantic; Arnaud-Haond *et al.*, 2017). Yet, ever rising
8 83 anthropogenic pressures in the deep-sea, like fisheries (Pusceddu *et al.*, 2014), oil and gas exploitation
9 84 (Cordes *et al.*, 2016) and deep-sea mining (Wedding *et al.*, 2015), threaten vulnerable CWC.
10 85 Protection of key deep-sea ecosystems is, therefore, an urgent priority, particularly in the face of
11 86 global change, and strategic Marine Protected Areas, thoroughly assessed for their genetic
12 87 connectivity, need to be established. Nonetheless, obtaining sufficient specimens and applying
13 88 statistically robust sampling designs for genetic studies in the deep-sea remain challenging (Becheler
14 89 *et al.*, 2017). While CWC connectivity has been assessed along the North Atlantic Ocean at the local
15 90 and regional scale (LeGoff-Vitry *et al.*, 2004; Morrison *et al.*, 2011; Dahl *et al.*, 2012; Becheler *et al.*,
16 91 2017), effective conservation warrants information at the NE Atlantic basin scale (Fenberg *et al.*,
17 92 2012). Spatial distribution analyses of genetic diversity can be used to detect connectivity pathways
18 93 across reefs, and to define key areas for the conservation of biodiversity.

23
24 94 Similarly, the present-day geographic distribution of many terrestrial and marine species and their
25 95 genetic diversity is influenced by environmental gradients, contemporary dispersal and recent climatic
26 96 events, notably the Last Glacial Maximum, LGM, (26 - 19 ka; Hewitt, 1996, 1999, 2004; Petit *et al.*,
27 97 2003; Maggs *et al.*, 2008; Clark, 2009). Repeated Pleistocene glaciations are known to impact deep-
28 98 sea ecosystems (Bouchet & Taviani, 1992; Sabelli & Taviani, 2014; Vertino *et al.*, 2014). However,
29 99 their impact on CWC in particular remains understudied. Deep-sea species may not respond similarly
30 100 to coastal species, because biological assemblages, environmental gradients and dispersal patterns are
31 101 fundamentally different among ecosystems and geographical areas (Kousteni *et al.*, 2015; Shum *et al.*,
32 102 2015).

35 103 The biogeographic connectivity between Mediterranean and NE Atlantic CWC during and after the
36 104 Pleistocene (ca. 2.7 Ma to 12 ka) glacial events can partially be inferred from paleo-records
37 105 (Supplementary Paleo-history). While CWC have maintained a continuous presence in the
38 106 Mediterranean Sea at least since the early Pleistocene (Vertino *et al.*, 2014), CWC in the NE Atlantic
39 107 may have been more affected, with consequent local demise during the LGM (Frank *et al.*, 2011).
40 108 Notably, the last cold oscillation, during the Younger Dryas (12.9-11.7 ka), represented a favourable
41 109 period for CWC reef growth in the western Mediterranean Sea as well as in adjacent Atlantic regions
42 110 at the Gulf of Cadiz and African margins (Schröder-Ritzrau *et al.*, 2005; McCulloch *et al.*, 2010;
43 111 Taviani *et al.*, 2011b). In contrast, growth episodes of CWC in the NE Atlantic have been restricted to
44 112 warm climate stages and coral fossils are absent from strata corresponding to glacial episodes (Frank
45 113 *et al.*, 2009). Radiometric dating shows that NE Atlantic CWC are younger than the ones from the
46 114 Mediterranean Sea, with ages estimated to be post-LGM (under 12,000 years; Freiwald & Roberts,
47 115 2005; Schröder-Ritzrau *et al.*, 2005), producing a NE Atlantic CWC age-gradient from south to north
48 116 (summarized in Fig. 1). Given such persistent occurrence of CWC, it has been argued that the
49 117 Mediterranean basin may have acted as a CWC glacial refugium during range contractions in the
50 118 North Atlantic Ocean during Pleistocene glaciations (De Mol *et al.*, 2002; Henry *et al.*, 2014). Such a
51 119 refugium may have constituted the source for the Atlantic northward recolonisation of CWC at the end
52 120 of the LGM by larvae, transported with intense flows of Mediterranean Outflow Water (MOW) since
53 121 50 ka (Fig. 1; Voelker *et al.*, 2006; Stumpf *et al.*, 2010).

1
2
3 122 Sympatric paleo-coral occurrence suggests a common history in terms of range contraction and
4 123 expansion for *Lophelia pertusa* and *Madrepora oculata*. Such a common response to past-
5 124 environmental change may not hold true in light of recent studies (Lartaud *et al.*, 2014, 2017) pointing
6 125 to physiological differences between both species, particularly in terms of optimal growth
7 126 temperatures. Dissimilar ecological strategies between the two CWC are possible. *Lophelia pertusa*
8 127 presents potential for widespread larval dispersal (Strömberg and Larsson, 2017), high fecundity
9 128 (Waller & Tyler, 2005) and a variable microbiome composition (Meistertzheim *et al.*, 2016).
10 129 *Madrepora oculata* presents a different reproductive strategy, having much lower fecundity (Waller &
11 130 Tyler, 2005) and a resilient microbiome (Meistertzheim *et al.*, 2016; and unknown larval
12 131 characteristics). Although reduced genetic connectivity has been demonstrated for *L. pertusa* at an
13 132 inter-basin scale along with moderate to high gene flow within regions (Morrison *et al.*, 2011; Dahl *et al.*,
14 133 2012; Flot *et al.*, 2013), the extent of CWC connectivity along the European margins and the role
15 134 that extant populations had in the past remain to be tested. Here we investigate the population genetic
16 135 diversity and structure of *L. pertusa* and *M. oculata* along the deep margins of the NE Atlantic, using
17 136 nuclear data (microsatellites and sequences). We discuss how past environmental variations related to
18 137 the LGM may have affected genetic diversity and structure of the two CWC species across this wide
19 138 geographic region. We hypothesise that distinct ecological requirements in the deep-sea influence
20 139 population structure and the distribution of genetic diversity within species. In particular, we expected
21 140 that *L. pertusa* would present low levels of population differentiation across the NE Atlantic margins,
22 141 consistent with a post-LGM northward expansion from southern refugia, and maintained by present-
23 142 day connectivity. We expected *M. oculata* to present stronger population differentiation, consistent
24 143 with lower fecundity. To these aims, we examined the genetic structure and diversity of *L. pertusa* and
25 144 *M. oculata* within and among the principal biogeographic provinces of the NE Atlantic and the
26 145 Mediterranean Sea where CWC are known to occur.

146 2. Materials and methods

147 2.1 Field collections

148 Two-hundred and seventy samples of *Lophelia pertusa* and 260 of *Madrepora oculata* were collected
149 from six regions between 250 and 1,170 m-depth: the eastern Mediterranean basin (Ionian Sea, south-
150 eastern Adriatic Sea); western Mediterranean basin (Gulf of Lions); Mid-Atlantic region (Azores);
151 Bay of Biscay; Rockall Bank (off western Ireland); and the High latitudes (Iceland) (Fig. 1; Appendix
152 Table S1). In one canyon of the Bay of Biscay, Petite Sole, two sample collections were made at
153 different sections of the canyon. Samples were stored in 96% ethanol and stored frozen at -20 or -80°C
154 prior to DNA extraction. *Lophelia pertusa* DNA was extracted aboard using the Fast DNA®SPIN for
155 soil kit, according to the manufacturer protocol (MP Biomedicals, France); for *M. oculata* we used
156 cetyl trimethyl ammonium bromide (Doyle & Doyle, 1988).

157 2.2 Core collection and dating

158 Within the Guilvinec Canyon (Bay of Biscay), a 1.2 m-length sediment core (BBCO-CS01) was
159 collected (N46°56,045'; W005°21,642') at 815 m-depth. The core is representative of the superficial
160 layers of the Armorican margin. Remains of coral skeleton were dated using the U/Th method at the
161 Institute for Environmental Physics at Heidelberg University (Schröder-Ritzrau *et al.*, 2003).
162 Foraminifera from nearby sediments were ¹⁴C-dated. Corals and foraminifera were subsequently
163 calibrated to absolute ages using Intcal13 (Reimer *et al.*, 2013).

164 2.3 DNA amplification and sequencing

165 The Internal Transcribed Spacer (ITS) ribosomal sequence was amplified using primers developed by
166 Diekmann *et al.* (2001). ITS-sequences (262 samples of *L. pertusa* 1130 base pair, bp, 200 samples of

167 *M. oculata* 1124 bp) were proof-read and aligned using GENEIOUS v6.1 (Kearse *et al.*, 2012). Nine
 168 *L. pertusa* (Morrison *et al.*, 2008; Becheler *et al.*, 2017) and six *M. oculata* microsatellite markers
 169 were amplified following Becheler *et al.* (2017). Products were scored using GENEIOUS v5.6.4. One *L.*
 170 *pertusa* locus was discarded due to high frequency of null alleles (>30%). Clones were removed from
 171 each dataset (ITS and microsatellites). Statistical power was assessed for the two coral species
 172 (Appendix Supplementary methods S2). Only sites with five or more samples were kept for analyses.

173 2.4 Phylogeographic patterns and genetic diversity

174 Population genetic differentiation for ITS-sequences was assessed with pairwise haplotype F_{ST} -statistic
 175 (Weir & Cockerham, 1984) in ARLEQUIN v3 (Excoffier *et al.*, 2005). The distribution of genetic
 176 variability within and among groups was estimated with an Analysis of Molecular Variance
 177 (AMOVA) with ARLEQUIN on four groups for *L. pertusa*, and five for *M. oculata* (1. Mediterranean,
 178 2. Bay of Biscay, 3. Rockall Bank and 4. High Latitudes, and 5. Mid Atlantic). Population genetic
 179 diversity was estimated with: i. the number of distinct and private haplotypes, ii. number of
 180 polymorphic sites, iii. haplotypic diversity (Nei, 1987), and iv. the mean number of pairwise
 181 differences (Tajima, 1983). Haplotype relationships were visualized with statistical parsimony
 182 networks, on TCS v1.21 (Clement *et al.*, 2000)

183 Microsatellite genetic diversity and structure were estimated with GENETIX v4.05 (Belkhir K., Borsa
 184 P., Chikhi L., 2004). The mean number of alleles per locus standardized to the lowest number of
 185 samples collected; estimates of observed (H_O) and unbiased (H_E) multi-locus heterozygosity (Nei,
 186 1978); the F_{IS} -statistic and its significance (tested with 1000 permutations); and linkage
 187 disequilibrium, assessed through the index \hat{r}_d with MULTILOCUS v1.3
 188 (<http://www.bio.ic.ac.uk/evolve/software/multilocus/>) were calculated. Genetic structure (pairwise
 189 F_{ST}) was estimated with θ (Weir & Cockerham, 1984). Inference of spatial population structure with
 190 Bayesian clustering was done with TESS v2.3 (François *et al.*, 2006; Chen *et al.*, 2007) via the *tess3r* R
 191 package (The R Foundation for Statistical Computing, 2018).

192 We used Discriminant Analysis of Principle Components (DAPC; Jombart *et al.*, 2010)
 193 implemented in the R package *adegenet* (Jombart, 2008), to determine whether the genotypes of *L.*
 194 *pertusa* and *M. oculata* were distinct between different sampling sites. We used k-means clustering
 195 (k=2 to maximum number of sampling sites) with the Bayesian Information Criterion (BIC) to
 196 identify an optimal number of genetic clusters that describe the data, as well as the α -score
 197 optimisation procedure to identify the optimal number of principal components (PCs) to retain
 198 (retaining too many PCs can lead to overfitting the discriminant functions). The α -score optimisation
 199 showed that approximately 25 PCs needed to be retained for *M. oculata* (>69.3% of the total
 200 variance), and 60 PCs for *L. pertusa* (28.9%). Next we used DAPC to derive membership
 201 probabilities for each individual in each of the groups using location priors (see Appendix
 202 Supplementary methods S2).

203 2.5 Demographic inferences

204 Historical fluctuations in population size for each sampled site were detected using Fu's F_s (Fu, 1996)
 205 and Tajima's D (Tajima, 1989) on ITS data from *L. pertusa* and *M. oculata*. Departures from mutation-
 206 drift equilibrium were tested under the null hypothesis of no significant change of effective population
 207 size, with ARLEQUIN. A negative value significantly different from constant population size is
 208 interpreted as a signature of population expansion; the significance of F_s and D values was determined
 209 by randomization.

210 The evolutionary and demographic histories of NE Atlantic and Mediterranean CWC (*L. pertusa* and
 211 *M. oculata*) were further reconstructed using Approximate Bayesian Computations (ABC) as
 212 implemented in DIYABC v2.1.0 (Cornuet *et al.*, 2014). We used microsatellite and ITS sequence data
 213 for *M. oculata* and microsatellite only for *L. pertusa*. *Lophelia pertusa* populations were grouped
 214 according to the microsatellite Bayesian clustering (cluster 1 - Eastern Mediterranean, cluster 2 -
 215 Western Mediterranean, cluster 3 - Bay of Biscay and High latitudes, cluster 4 - Rockall bank) and for

216 *M. oculata* we used the geography-based population grouping. We compared competing scenarios in
 217 order to identify the patterns of post-LGM CWC range expansion along the NE Atlantic margins.
 218 Scenarios 1, 2 and 4 determine the pattern of colonisation of the northern edge of the NE Atlantic
 219 range, comparing models of stepping-stone colonization from the Mediterranean Sea to the Bay of
 220 Biscay and then further north (Scenario 1 - Stepwise range expansion), and models of admixture:
 221 between the Bay of Biscay, High latitudes and the west Mediterranean to produce the Rockall bank
 222 population (Scenario 2), between the High latitudes and Rockall bank to produce the Mid Atlantic
 223 population (Scenario 2 *M. oculata*), between the Bay of Biscay and Rockall bank to produce the Mid
 224 Atlantic population (Scenario 4 *M. oculata*), and between the Mediterranean Sea and the Bay of
 225 Biscay to produce the Mid Atlantic population (Scenario 5 *M. oculata*). Scenario 3 examined the
 226 demographic history of the NE Atlantic and Mediterranean populations with changes in population
 227 size since colonisation. We compared a null model of no change in population size (Scenarios 1 and 2)
 228 to a model of a short bottleneck (10 generations) during colonisation followed by population
 229 expansion (Scenario 3). In this scenario, at each split, there is an initial reduction of the population size
 230 of the newly formed population, because the expansion is assumed to start with few immigrants. For
 231 *L. pertusa* we used the known time of Rockall bank colonisation (approx. 9 ka; Frank et al., 2009) to
 232 calibrate divergence times (mode and 95% confidence interval) from the estimated ABC number of
 233 generations; we then assumed the same generation time (est. approx. 3 years) for *M. oculata*.

234 We generated 3 to 5×10^6 simulations for each scenario tested using the combined microsatellite and
 235 ITS datasets for *M. oculata* and the microsatellite dataset for *L. pertusa* (Appendix Supplementary
 236 methods S2) to produce a set of pseudo-observed datasets (PODs). Effective population sizes and
 237 parameters for the Generalized Stepwise Mutation and Kimura two parameter models were set to
 238 default values, while time of population divergence (in generations) was defined as uniform within
 239 post-LGM periods (for model parameters see Appendix S2). The posterior probability of each scenario
 240 was inferred with a logistic regression performed on the 1% of PODs closest to the empirical data. We
 241 empirically evaluated the power of the model to discriminate among scenarios using a Monte Carlo
 242 estimation of false allocation rates (type 1 and 2 errors) resulting from ABC posterior probabilities-
 243 based model selection.

244 Supplementary methods can be found in the Appendix (S2).

245 3. Results

246 3.1 Core collection and dating

247 Fossils of *Lophelia pertusa* and *Madrepora oculata* were found in the gravity core. The dating of
 248 CWC remains revealed ages ranging from present to $6,959 \pm 169$ years (U/Th corrected age).

249 3.2 Phylogeographic patterns and genetic diversity

250 *Lophelia pertusa* showed four genetically distinct groups: the eastern and the western Mediterranean
 251 Sea, the Rockall bank and the remaining NE Atlantic populations (Bay of Biscay and High latitudes)
 252 (Fig. 2a right). Within *L. pertusa*, the Mediterranean genetic ancestry, and in particular the west
 253 Mediterranean ancestry (blue) can be seen in low proportions across all NE Atlantic sites. The green
 254 genetic ancestry is maximized in Bay of Biscay and High latitudes populations, while the grey genetic
 255 ancestry (found in the Bay of Biscay and High latitudes sites) is maximized in the Rockall bank
 256 population. The grey ancestry component is present in high proportion in the High latitudes
 257 populations, particularly in Hafadsjup (HAF), which comprises over half of *L. pertusa* ancestry.
 258 Genetic differentiation was strong between east and west Mediterranean populations and weak across
 259 the NE Atlantic samples, with nearly all values not significantly different from zero. The Rockall bank
 260 population was differentiated from over half of the Bay of Biscay locations but not with the High
 261 latitudes populations (Appendix Table S4.1). Clustering analyses showed that *M. oculata* was also
 262 structured in four genetic clusters, but with a different organisation (Fig. 2a). The Mediterranean Sea
 263 and the High Latitudes formed two distinct clusters (displayed in red and grey on Fig. 2a left). The
 264 next two clusters are not so geographically coherent: The Bay of Biscay genetic ancestry (blue; third

265 cluster) is nearly absent from the Lampaul canyon, as well as from the Rockall bank and Mid Atlantic
 266 populations (which together form the fourth cluster). *M. oculata* populations from the Bay of Biscay
 267 harbour a strong Mediterranean genetic component (red) maximized in the northern Bay of Biscay
 268 canyons (Morgat, Crozon and Petite Sole), which is absent from most individuals in the Mid Atlantic,
 269 Lampaul canyon (in the Bay of Biscay) and Rockall bank populations. The NE Atlantic genetic
 270 ancestry (green) is well represented in all NE Atlantic populations and in smaller proportion in some
 271 Mediterranean individuals. The High latitudes genetic ancestry (grey) is found in high proportion in
 272 Rockall and Mid Atlantic populations. Mean pairwise F_{ST} between regions was high, up to 0.5
 273 between the eastern Mediterranean Sea and the High Latitudes, but not significantly different from
 274 zero between eastern and western Mediterranean Sea populations, while nearly all pairwise F_{ST} values
 275 were significantly different from zero. Lack of population differentiation was observed between two
 276 Bay of Biscay canyons (CRZ-LMP), within one canyon (PS1-PS2), between High latitudes locations,
 277 and between Rockall bank and its closest High latitudes site, Londsjud (Appendix Table S4.2).
 278 Regional F_{ST} was significantly different from zero for all pairwise comparisons for the two coral
 279 species: Mediterranean Sea, Mid-Atlantic, Bay of Biscay, Rockall bank and High latitudes. The lowest
 280 regional F_{ST} for *M. oculata* was between the High latitudes and Rockall bank populations (0.051) and
 281 for *L. pertusa* between the High latitudes and Bay of Biscay populations (0.004).

282 The genetic affinities of the sampled individual corals were projected onto principal components
 283 (DAPC). As expected, the first axis of *L. pertusa* separates Mediterranean and NE Atlantic
 284 populations. Within each group, genetic variability is spread across the second axis: The Eastern
 285 Mediterranean samples at one end and the Western Mediterranean samples at the other end, a
 286 separation that is also clearly visible in the group membership probabilities on the bottom of figure 3b.
 287 The NE Atlantic genetic group along PC2 spans samples from the Bay of Biscay to the High latitudes,
 288 including Rockall bank (Fig. 3b). The most important *M. oculata* genetic affinities show a cline on the
 289 first axis, spanning samples from the lower (Mediterranean) to the higher latitudes. The gradient is
 290 visible in the group membership proportions shown on the bottom of figure 3a, particularly along the
 291 Bay of Biscay canyons and along Rockall-High latitudes populations.

292 Gene diversity and the average number of alleles per locus for *L. pertusa* and *M. oculata* samples
 293 were high (*L. pertusa* H_E 0.90 +/- 0.08, and 30.4 alleles per locus; *M. oculata* H_E 0.53 +/- 0.23 and 12.3
 294 alleles per locus; Tables 1 and 2). Regionally, average allelic richness was higher at intermediate
 295 latitudes for both species (Mediterranean 7 for *L. pertusa* and 3 for *M. oculata*, Bay of Biscay 16 and
 296 5, Rockall Bank 15 and 6, and High Latitudes 12 and 4, for *L. pertusa* and *M. oculata* respectively, and
 297 Mid Atlantic, where only *M. oculata* was sampled, 3). Private alleles were present in all sampled
 298 *L. pertusa* sites, while they were rarely present in *M. oculata* populations. *Madrepora oculata*
 299 presented higher private allelic richness in the Mediterranean basin (2-4). An excess of homozygotes
 300 was observed in all *L. pertusa* populations and in half of the *M. oculata* sites, particularly along the
 301 NE Atlantic populations.

302 The patterns of genetic structure inferred with ITS were generally concordant with those of
 303 microsatellites. Based on statistic parsimony, a haplotype network was constructed for *L. pertusa*, with
 304 one main ITS lineage inferred as the most likely ancestral haplotype (from a total of 39 haplotypes),
 305 which possibly radiated from lower to higher latitudes (>60% of samples), and many rare haplotypes
 306 (over 20 unique). The ancestral haplotype is nearly absent from Rockall bank *L. pertusa*, supporting
 307 the Bayesian clustering, where High latitudes and Bay of Biscay share a genetic ancestry (green)
 308 almost absent from Rockall bank samples. Two other well-represented haplotypes were restricted to: i)
 309 the Bay of Biscay, High Latitudes and Mediterranean Sea, and ii) mostly the Rockall Bank with few
 310 Bay of Biscay samples (Fig. 2b), supporting the Rockall bank genetic ancestry (grey) as distinct from
 311 relatively close populations (Bay of Biscay and High latitudes). The Atlantic sites harbour the majority
 312 of sequence variation. The Bay of Biscay has the highest number of haplotypes (24), with 12
 313 haplotypes unique to this region, but the highest haplotype diversity ($H=0.7$) was found in the west
 314 Mediterranean Sea (Table 3). Ten haplotypes were observed in the Mediterranean Sea with two unique
 315 to the western Mediterranean. Iceland, regardless of the high latitude and recent CWC fossil ages (8.3
 316 Ka, Fig. 1), harbours the second highest number of *L. pertusa* haplotypes (14; Appendix Table S7),

with two haplotypes exclusive to its CWC reefs. *L. pertusa* haplotypes are not particularly clustered and, except for the inferred ancestral haplotype, most haplotypes are found in moderate to low frequency at each site (Appendix Table S7). There are no *L. pertusa* region-specific haplotypes in the Bay of Biscay or the west Mediterranean Sea.

There was some phylogeographic clustering for the *M. oculata* haplotype network, with one lineage dominant in the Higher latitudes and Rockall bank, modestly present in distant, southern, geographic locations (e.g., one samples from the Mediterranean Sea), and absent from the Bay of Biscay. A quarter of all haplotypes are shared across distant geographic regions (i.e. High Latitudes and Mediterranean Sea). Haplotypes found in Mid-Atlantic *M. oculata* are also found in all other regions (one haplotype) or are restricted to the Bay of Biscay and Rockall bank (two haplotypes), with one haplotype unique to the Mid Atlantic site. Private (unique) haplotypes were observed in all regions where *M. oculata* was sampled but not at all sites. Seven haplotypes were well represented, and there was no obvious sign of haplotype radiation (Fig. 2b). Similarly to *L. pertusa*, the majority of ITS sequence variation for *M. oculata* occurred in Atlantic sites. The Bay of Biscay and Rockall bank presented the highest number of haplotypes (15 and 11, respectively) and the only region-specific haplotype (Appendix table S7). Nonetheless, the highest haplotype diversity ($H=0.9$) was observed in *M. oculata* from the Mid Atlantic.

Along the NE Atlantic *L. pertusa*, populations were little differentiated while within the Bay of Biscay genetic structure was weak for *M. oculata* (nearly all pairwise F_{ST} not significantly different from zero; Appendix Tables S2-S3). *Madrepora oculata* showed a regional pattern of population genetic structure concordant with microsatellite analyses (high F_{ST} between populations from distinct regions). Overall, 5% of *L. pertusa* and nearly 40% of *M. oculata* genetic variation occurred among regions (AMOVA; Appendix Table S5).

Haplotypic and molecular diversities varied among locations (Tables 3 and 4). For *L. pertusa*, haplotypic diversity was high (up to 0.6 in the NE Atlantic and up to 0.7 in the Mediterranean Sea) due to haplotype radiations. Haplotypic diversity was also high in *M. oculata* populations (0.3-0.7 in High Latitudes, 0.9 in the Mid Atlantic site, where there were four haplotypes for five individuals). A comparable pattern of variation of molecular diversity was observed for both species. In the NE Atlantic, nucleotide diversity was lower than in the Mediterranean Sea sites for *L. pertusa*. For *M. oculata*, nucleotide diversity was higher in the west Mediterranean and Mid Atlantic populations.

Demographic inferences

The tests of conformity to selective neutrality suggest different demographic histories for *L. pertusa* and *M. oculata*. The Mediterranean populations of *L. pertusa* did not produce significant departures from mutation-drift equilibrium (Fu, 1996), while most populations in the Bay of Biscay showed negative F_s values significantly departing from mutation-drift equilibrium. This is consistent with the network and indicates a demographic expansion of Atlantic populations. Only two *M. oculata* sites showed Tajima D values significantly departing from constant effective population size that would indicate a demographic expansion: one in the east Mediterranean and one in the Bay of Biscay (Crozon canyon; Tables 3 and 4).

Model-based inference pointed to an ancient (up to 30 ka; Appendix Table S2) divergence of *L. pertusa* east and west Mediterranean Sea populations, in agreement with DAPC. The west Mediterranean population was identified as the source from which all other NE Atlantic populations emerged, either directly (Bay of Biscay and High latitudes; approx. 21 ka) or through admixture (Rockall bank; much later at 9 ka), agreeing with the Bayesian clustering, where the west Mediterranean ancestry (blue) is found throughout the Atlantic sites, and with ITS network, where most Mediterranean haplotypes are shared with Bay of Biscay corals. The shared Rockall genetic ancestry (grey) between Biscay and the High latitudes populations identified with Bayesian clustering agrees with the admixed origin for Rockall *L. pertusa* found with ABC. Population size estimates were much smaller for Mediterranean populations ($N=2,500$ to $7,000$) than NE Atlantic ones ($N=70,000$ - $85,000$). The Bay of Biscay demographic expansion scenario with admixture was supported with high

367 probability relative to around 0.2 support for scenarios including stepping-stone colonisation and
368 changes in population sizes (Appendix Figs. S3-S4). Confidence in scenario choice was high, with low
369 error rates (posterior predictive error = 0.29). Post-LGM range colonisation followed a long-range
370 model of northern range colonisation, whereby Bay of Biscay and High latitudes were colonised
371 directly from the west Mediterranean Sea populations, while at a later stage the Rockall bank was
372 colonised from admixture between Bay of Biscay, High latitudes and west Mediterranean populations
373 (Fig. 1 bottom inset).

374 Analyses with ABC pointed to the Mediterranean Sea *M. oculata* populations being the main source
375 population (N=8,600) from which all other NE Atlantic populations emerged. The Mediterranean
376 source population scenario, with colonisation of the Atlantic margins via Bay of Biscay agrees with
377 Bayesian clustering, where the Mediterranean genetic ancestry (red) is found in moderate proportions
378 in Bay of Biscay populations and is absent from the Mid Atlantic and Rockall populations. The
379 scenario of a Mediterranean source population with colonisation of the NE Atlantic and admixture was
380 supported with high probability (0.9) relative to low support for scenarios including changes in
381 population sizes or competing admixture scenarios (Appendix Figs. S3-S4). Confidence in scenario
382 choice was high, with low error rates (0.3). Post-LGM range colonisation along the European margins
383 followed a stepping-stone model of northern range colonisation, whereby Bay of Biscay was colonised
384 directly from Mediterranean Sea populations (22 ka), while the Bay of Biscay *M. oculata* later
385 colonised the Rockall bank (7 ka). The Rockall bank populations then originated other NE Atlantic *M*
386 *oculata* populations. That happened either through admixture with the Bay of Biscay (Mid Atlantic)
387 only about 2 ka, or directly (High latitudes) much more recently (0.3 ka; Fig. 1 top inset). The genetic
388 footprint of those events are seen on the main haplotype shared between High latitudes and Rockall
389 but absent from Bay of Biscay corals, by a haplotype restricted to the Bay of Biscay, Rockall bank and
390 Mid Atlantic (haplotype V in Appendix Figure S6), and by the position of Mid Atlantic samples in the
391 DAPC between Rockall and Biscay samples.

392 Discussion

393 In terms of molecular analyses, Cold-Water corals (CWC) in NE Europe have been understudied. In
394 this study we extend the available information from this area considerably, and present the first
395 inferences and empirical analyses of deep-sea coral phylogeography in the area. While the Bay of
396 Biscay genetic component presented here has been previously described in extant populations from the
397 region (Morrison et al., 2011; Becheler et al., 2017), we gain further insights into its temporal depth.
398 Given their recurrent association and similarities (Arnaud-Haond et al., 2017), the two main CWC reef
399 building species in the North Atlantic, *Lophelia pertusa* and *Madrepora oculata*, have been
400 hypothesised to share similar phylogeographic histories (De Mol et al., 2002; Henry et al., 2014). Yet,
401 our results depart from that expectation. Far-reaching gene flow along the European margin results in
402 a poor genetic differentiation in distant NE Atlantic *L. pertusa* populations (Bay of Biscay and High
403 latitudes), while high differentiation characterizes populations of *M. oculata*. We hypothesize that both
404 species were affected by glacial events differently, and/or that the geographic location of the source
405 and date of post-glacial expansion of NE Atlantic reefs differed. Verifying such hypotheses is
406 important if we are to forecast the responses of CWC facing on-going climate changes.

407 Despite the deep-sea being considered as relatively environmentally stable over time, there is evidence
408 that CWC undergo demographic changes similarly to those experienced by their coastal water
409 counterparts (Wilson & Eigenmann Veraguth, 2010; Sabelli & Taviani, 2014; Vertino et al., 2014;
410 Quattrini et al., 2015). Here we focused on the LGM, and explored two scenarios that could explain
411 the observed patterns of genetic diversity and structure for *L. pertusa* and *M. oculata*, respectively:

- 412 i) Before the LGM (and to about 50 ka, which is the oldest period accounted for by existing
413 data), NE Atlantic populations were absent from the current northern range of their modern
414 distribution and present-day patterns of genetic variation were caused by expansion
415 northwards, originated most likely from the west Mediterranean Sea and/or adjacent NW coast
416 of Africa, and a later Mediterranean-NE Atlantic admixture;

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3 417 ii) Before the LGM, NE Atlantic populations were absent from the current northern range of their
4 418 modern distribution and present-day patterns of genetic variation were caused by "stepping-
5 419 stone" northwards colonisation with modest demographic expansions and by a much later
6 420 admixture between NE Atlantic populations with possible contribution from other unsampled
7 421 populations.
8

9 422 **Scenario i)**

11 423 Geological studies report the absence of deep CWC reef growth in the NE Atlantic during glaciations
12 424 of the Late Pleistocene (approx. 126 - 12 ka; with the Last Glacial Maximum approx. 26.5-19 ka;
13 425 Clark et al., 2009; Frank *et al.*, 2009). Contrastingly, between 50-12 ka, *L. pertusa* reefs flourished in
14 426 the Mediterranean Sea (Appendix Supplementary Paleo-History). The Mediterranean Outflow Water
15 427 (MOW 800-1300 m depth; Price et al., 1993) volumes were smaller than at present (Rogerson *et al.*,
16 428 2004) but concentrated in channels with high local flow (Zahn *et al.*, 1997). In the Gulf of Cadiz and
17 429 on the Moroccan shelf, reef growth was estimated to have started around 40-50 ka (Fig. 1) when
18 430 glacial conditions there were particularly favourable for coral growth, unlike in the NE Atlantic
19 431 (Schröder-Ritzrau *et al.*, 2005; Eisele *et al.*, 2011; Ramos *et al.*, 2017; Weinberg *et al.*, 2018). The
20 432 rapid increase in post-glacial Atlantic Meridional Overturning Circulation resulted in increased
21 433 transport of suspended particles and is speculated to have boosted the expansion of *L. pertusa* from
22 434 these southern locations (Mediterranean Sea and/or adjacent NW coast of Africa) into the NE Atlantic
23 435 (Eisele *et al.*, 2011; Fink *et al.*, 2013; Henry *et al.*, 2014).

26 436 Continuous and vertical growth of CWC reefs occurred in the Bay of Biscay area during at least the
27 437 past 7,000 years, shown by geological analyses of the core. Genetic evidence of recent *L. pertusa*
28 438 demographic expansions in the Bay of Biscay, at the end of the LGM (approx. 21 ka), is substantiated
29 439 by Internal Transcribed Spacer sequences with haplotype network and conformity tests, attributed to a
30 440 founder event, i.e. a dominant haplotype found in all regions (from the Mediterranean Sea to the High
31 441 Latitudes). Such demographic expansion would have produced satellite haplotypes with low genetic
32 442 distance, as observed in *L. pertusa*. The vast nearly-panmictic ensemble occurring along the NE
33 443 Atlantic indicates a recent common history for Atlantic *L. pertusa* reefs. This is supported by studies
34 444 of reproduction and larval development that indicate that *L. pertusa* larvae have high dispersal
35 445 potential (Waller & Tyler, 2005; Larsson *et al.*, 2014; Strömberg & Larsson, 2017). Despite these
36 446 experiments in aquaria with *L. pertusa* that have shown larvae swimming towards the surface, it
37 447 remains unknown whether larvae are neutrally buoyant and if in their natural environment remain at
38 448 spawning depth, concurrent with the depth of North Atlantic currents in figure 1. Larval dispersal
39 449 trajectories may have evolved to track specific water masses (Dullo *et al.*, 2008), occurring at
40 450 intermediate depths with potential settling sites. Such high larval dispersal ability favours large-scale
41 451 expansion and shared genetic ancestry, such as that between Bay of Biscay and High latitudes *L.*
42 452 *pertusa*.
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45 453 The genetic distinctiveness of Rockall bank *L. pertusa* (seen on microsatellites and ITS loci) indicates
46 454 a more complicated history. The rarity of the dominant haplotype in Rockall bank suggests either
47 455 another source for colonisation, strong post-colonisation drift or local adaptation. Approximate
48 456 Bayesian Computation favours an evolutionary scenario whereby the Rockall population is colonised
49 457 via admixture of the Bay of Biscay group and west Mediterranean corals, around the time of the onset
50 458 of the modern Atlantic Meridional Overturning Circulation (AMOC; Repschläger *et al.*, 2017). The
51 459 Mediterranean Water traveling northwards along the Iberian Peninsula and Bay of Biscay does not
52 460 reach the Rockall bank (Frank *et al.*, 2009). Instead, Rockall hydrodynamics are more influenced by
53 461 northward moving Atlantic waters, including the rich North Atlantic Current (NAC). The NAC is part
54 462 of the Gulf Stream, which may promote occasional genetic material from the West North Atlantic *L.*
55 463 *pertusa* reefs (Morrison *et al.*, 2011). Analyses encompassing the full distributional range of *L. pertusa*
56 464 are essential to clarify missing links in population relatedness at trans-Atlantic scales.
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59 465 The ancient divergence of Mediterranean *L. pertusa* populations from the eastern and western basins
60 466 estimated by the ABC model to have taken place during the Last Glacial Maximum (around 24 ka) is

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3 467 reasonable. In the temperate Eastern Atlantic, including the Mediterranean Sea, CWC growth
4 468 sustained glacial-interglacial cycles (Frank et al., 2011). Such a steady allopatry may have been
5 469 maintained by vicariance driven by ocean currents acting upon the earliest life stage of *L. pertusa* or
6 470 by local adaptation. Finer-scale analyses are needed to identify and quantify the importance of such
7 471 variables. All together, the data support a post-glacial recolonisation of the NE Atlantic by *L. pertusa*.
8 472 Mediterranean *L. pertusa* are divergent from most NE Atlantic populations (ITS, microsatellites).
9 473 Given that sampling is at best partial, it is difficult to speculate about the precise origin of NE Atlantic
10 474 populations. The Mediterranean lineages and genotypes found in low proportion across the NE
11 475 Atlantic reefs, the high haplotypic diversity mainly in the western basin of the Mediterranean Sea,
12 476 concur with ABC analyses that the glacial refugia for NE Atlantic *L. pertusa* colonisation may have
13 477 been located in the west Mediterranean Sea or in adjacent regions (e.g. the coral mounds in the Gulf of
14 478 Cadiz and NW Africa; Eisele et al., 2011). *Lophelia pertusa* populations in this region thrived during
15 479 glacial periods and might have provided larvae dispersing in Mediterranean Water northwards towards
16 480 the Bay of Biscay (Fig. 1).

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19 481 Contrastingly, *M. oculata* populations are more strongly structured and there is no evidence of a large
20 482 demographic expansion.

21 22 483 **Scenario ii)**

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24 484 Concurrent to *L. pertusa*, Mediterranean Sea *M. oculata* populations were the main source from which
25 485 all other NE Atlantic populations emerged around the end of the LGM, as estimated by model-based
26 486 inference (Fig. 1 top inset). Mediterranean *M. oculata* thus represent the putative LGM refugium,
27 487 which may have included other unsampled adjacent populations present during glacial periods (Gulf
28 488 of Cadiz, NW Africa). As for *L. pertusa*, absence of samples from the NW coast of Africa meant that
29 489 inference regarding the role of this potential refugium could not be made. The estimated time for NE
30 490 Atlantic colonisation, approx. 21 ka, suggests that Mediterranean *M. oculata* represent a "stable rear-
31 491 edge" population (Hampe & Petit 2005). Mediterranean harbours high levels of DNA diversity and the
32 492 greatest number of unique haplotypes and private alleles, a testament to the long-term stability of
33 493 Mediterranean populations (Hewitt 2000). But unlike *L. pertusa*, there is no substantial differentiation
34 494 of east and west Mediterranean *M. oculata*, possibly linked to differences in reproductive or early life
35 495 traits. Information on reproduction and early life history is much needed to reduce model uncertainty
36 496 and allow a better understanding of CWC past and present connectivity.

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39 497 Analyses identified that *M. oculata*'s northern range edge was colonised in a stepping-stone manner
40 498 (Bay of Biscay, followed by Rockall and later the High latitudes) instead of long-range colonisation
41 499 directly from glacial refugia as in *L. pertusa* northern populations. Unique haplotypes were almost
42 500 evenly spread across the distribution range, indicating that *M. oculata* maintained other glacial
43 501 (cryptic) refugia throughout its current range and underwent only localized, modest, postglacial
44 502 expansions. The result is the co-existence of divergent genetic lineages across the NE Atlantic, one
45 503 dominating the higher latitudes and another in the Bay of Biscay, both with lower frequency in other
46 504 regions. Such pattern is consistent with distinct areas of persistence for *M. oculata*, locally or
47 505 regionally, followed by a redistribution of divergent lineages after periods of allopatry (Petit et al.,
48 506 2003). The low occurrence of unique haplotypes and alleles found in *M. oculata* is a result of the more
49 507 recent admixture and colonisation events (Mid Atlantic, High latitudes), estimated by ABC to have
50 508 taken place during the late Holocene. The large-scale spatial genetic structure was shaped by the
51 509 refugium-driven vicariance. Long-distance dispersal and gene flow that may disturb this pattern of
52 510 population structure may be unlikely in *M. oculata*, if this CWC presents different reproduction and
53 511 dispersal modes to those of *L. pertusa*, for instance, lower pelagic larval duration, brooding. A
54 512 hypothetical poorer ability to disperse associated with the complex geomorphology (canyons,
55 513 seamounts) along with extreme depth gradient present in habitats along the North East Atlantic
56 514 (hundreds to thousands of meters), has probably caused fragmentation, reduced gene flow and further
57 515 reinforced the large-scale pattern of NE Atlantic population structure in *M. oculata*. For instance, the
58 516 Lampaul canyon has the highest composition of soft substrate and near absence coral framework
59 517 compared to the other Bay of Biscay canyons studied here (van den Beld et al., 2017). Such

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3 518 differences may have created (past) barriers to gene flow. However, separating the exact effects of
4 519 geography and the environment on population structure is difficult. Finer-scale analyses are needed to
5 520 estimate the contribution of such variables and putative allopatric refugia.
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7 521 The formation of the admixed Mid Atlantic population was dated to c. 2 ka (0.7–11 ka); even
8 522 accounting for wide confidence interval of the estimated time, it is well within the Holocene. During
9 523 this period, the modern AMOC was established and can have contributed to colonisation of deep coral
10 524 habitat along the Mid Atlantic Ridge and to admixture with older populations either from the
11 525 European margins (Rockall bank, Bay of Biscay canyons) or from the NW Atlantic (which we did not
12 526 sample here). The southward branch of the vigorous NAC may have favoured the link between
13 527 European margins and Mid Atlantic. The absence of Mediterranean ancestry together with the
14 528 substantial presence of High latitudes ancestry in Mid Atlantic and Rockall *M. oculata* substantiates a
15 529 less important connection with Mediterranean populations via the weak flow of Mediterranean Water.
16 530 The fact that the European margins genetic components and haplotypes are consistently shared among
17 531 Mid Atlantic *M. oculata* makes it tempting to equate this genetic component with the colonisation or
18 532 at least the spread of *M. oculata* in the Mid Atlantic. However, such a model may be overly simplistic.
19 533 As shown in our analyses, the admixture patterns found in *M. oculata* are complex and more than a
20 534 single admixture event is possible, with sources on both sides of the N Atlantic. The lower coral
21 535 abundance and available habitat as compared to the NE Atlantic margins, may have further contributed
22 536 to post-colonisation drift. More detailed analyses of Mid Atlantic CWC are needed to clarify the N
23 537 Atlantic phylogeography of the deep-sea.
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26 538 The colonisation of higher latitudes much more recently (c. 0.3 ka, 0.07–3 ka) from Rockall
27 539 populations left genetic footprints; main *M. oculata* haplotype shared between High latitudes and
28 540 Rockall but absent from Bay of Biscay. The timing difference of High latitudes colonisation among *L.*
29 541 *pertusa* and *M. oculata* suggests that differences in environmental tolerance exist: *L. pertusa* reached
30 542 the High latitudes at the end of the LGM (c. 21 ka; 9–29 ka). In fact, *L. pertusa* has thermal
31 543 acclimation in respiration and calcification mechanisms that mechanisms are absent in *M. oculata*
32 544 (Nauman et al., 2014). The Holocene colonisation of the higher latitudes of Europe (e.g., Norway; Fig.
33 545 1) is well documented (Schröder-Ritzrau et al., 2005). Although reassuring for interpreting our
34 546 findings, ABC model-based inferences rely on assumptions that cannot easily be controlled in natural
35 547 populations. Our findings should be interpreted as probable hypotheses rather than clear proof of past
36 548 demographic events. Further theoretical and experimental work are needed that can contribute to a
37 549 better understanding of CWC phylogeography and connectivity (e.g., early life history traits).
38 549 Analyses making use of high-density data will allow reconstructing the phylogeographic history of
39 550 CWC with more precision. Moreover, our study highlights the need to explore the genetic nature of
40 551 CWC found in the Western Mediterranean (Alboran Sea) and the Gulf of Cadiz to determine their
41 552 contribution to larval connectivity and past re-colonisation of the NE Atlantic.
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44 554 **Conclusion** The novel genetic data presented here from deep-sea corals from European margins opens
45 555 new insights into Cold-Water coral population history. Our results show a northward post-LGM
46 556 expansion of *Lophelia pertusa* and *M. oculata* from the west Mediterranean Sea into the NE Atlantic
47 557 margin. While *L. pertusa* moderate to high gene flow homogenized nearly the whole Atlantic genetic
48 558 pool, *M. oculata* progressed slower, particularly in High latitudes. *Lophelia pertusa* expanded swiftly
49 559 along the NE Atlantic at a rate of 0.7 to 2 km per year (considering 4,000 km in the past 10 to 30 ka).
50 560 The period of Atlantic-Mediterranean separation led to a strong genetic differentiation between extant
51 561 coral populations in the respective regions. This differentiation can be explained either by a founder
52 562 effect at the NE Atlantic, or an unsampled genetic source in the Mediterranean Sea or around NW
53 563 Africa. The remarkable mosaic of distinct genotypes of *M. oculata* supports the existence of a more
54 564 complex history, shaped by putative cryptic refugia, admixture and possible different dispersal ability.
55 565 With current data limitations, it is not yet possible to determine the most important factor underlying
56 566 the apparent lack of gene flow along the European margin for *M. oculata* populations. Further CWC
57 567 from the North Atlantic are needed in order to conclude, to what extent these signals of migration and
58 568 admixture are representative of N Atlantic CWC as a whole. Nonetheless, the contrasting patterns of
59 569 genetic diversity observed here strongly support the existence of a different influence of past
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3 570 environmental changes and differing present-day dispersal of *L. oculata* and *M. oculata*. Our study
4 571 provides an important warning for managers that even taxa with seemingly similar ecological roles
5 572 and tolerances may well differ in their response to global change. Therefore, multi-species models are
6 573 required to ensure conservation measures such as truly representative and connected networks of
7 574 Marine Protected Areas.

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9 575 Author contributions:

10
11 576 Designed research RB, SAH,

12
13 577 Performed research RB, SAH, JB, A-L C, OM, MC

14
15 578 Contributed new reagents or analytic tools SAH, JFB, NF, MT, AS, AG, JB

16
17 579 Analysed data RB, JB, SAH

18
19 580 Wrote the paper JB, RB, SAH

20
21 581 **Data Accessibility Statement**

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23 582 Microsatellite data are accessible online at GenBank under accession numbers: KF944311, KF944317,
24 583 KF944323, KF944330, KF944331 and KF944344.

584 **viii. Tables and captions**

585 Table 1 - Genetic diversity at microsatellite loci for *Lophelia pertusa*. n - sample size; $\hat{A}r$ - allelic richness; $\hat{A}r(5)$ - standardized allelic richness to the lowest
 586 sample size (N=5); $\hat{A}p$ - private allelic richness; He and Ho - expected and observed heterozygosity respectively; Fis - departure from HWE. P-values below
 587 0.05, 0.01 and 0.001 are respectively represented by *, ** and ***.

Region	Site	n	$\hat{A}r$	$\hat{A}r(5)$	$\hat{A}p$	He	Ho	Fis
Eastern Mediterranean Sea	Santa Maria di Leuca (SML)	12	8.1	6.0 ± 0.2	4	0.80 ± 0.06	0.71 ± 0.31	0.15***
Western Mediterranean Sea	Lacaze-Duthiers canyon (LCD)	7	4.9	4.9 ± 0.00	2	0.72 ± 0.13	0.84 ± 0.19	-0.10
Bay of Biscay	Croisic canyon (CRS)	30	18.9	8.8 ± 0.12	5	0.89 ± 0.07	0.80 ± 0.14	0.12***
Bay of Biscay	Guilvinec canyon (GUI)	34	18.3	8.7 ± 0.12	4	0.89 ± 0.08	0.86 ± 0.04	0.05**
Bay of Biscay	Lampaul canyon (LMP)	7	8.8	8.8 ± 0.00	2	0.83 ± 0.09	0.80 ± 0.19	0.11**
Bay of Biscay	Crozon canyon (CRZ)	12	11.0	8.0 ± 0.13	2	0.84 ± 0.09	0.74 ± 0.14	0.16***
Bay of Biscay	Morgat-Douarnez canyon (MRG)	20	16.4	8.6 ± 0.16	4	0.87 ± 0.09	0.83 ± 0.20	0.07**
Bay of Biscay	Petite Sole 1 canyon (PS1)	26	17.4	8.7 ± 0.12	5	0.88 ± 0.09	0.83 ± 0.11	0.07***
Bay of Biscay	Petite Sole 2 canyon (PS2)	27	17.5	8.9 ± 0.10	4	0.90 ± 0.06	0.85 ± 0.09	0.07***
Rockall bank	Logachev Mounds (LOG)	22	14.8	8.1 ± 0.12	2	0.87 ± 0.07	0.77 ± 0.13	0.14***
High latitudes	Londsjud 1 (LON1)	7	8.5	8.5 ± 0.00	1	0.82 ± 0.09	0.77 ± 0.15	0.14**
High latitudes	Londsjud 2 (LON2)	20	14.5	8.2 ± 0.12	4	0.86 ± 0.10	0.74 ± 0.16	0.17***
High latitudes	Hafadsjud (HAF)	16	13.6	8.5 ± 0.12	1	0.89 ± 0.05	0.70 ± 0.22	0.25***

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589 Table 2 - Genetic diversity at microsatellite loci for *Madrepora oculata*. n - sample size; $\hat{A}r$ - allelic richness; $\hat{A}r(5)$ - standardized allelic richness to the
 590 lowest sample size (N=5); $\hat{A}p$ - private allelic richness; He and Ho - expected and observed heterozygosity respectively; Fis - departure from HWE. P-values
 591 below 0.05, 0.01 and 0.001 are respectively represented by *, ** and ***.

Region	Site	n	$\hat{A}r$	$\hat{A}r(5)$	$\hat{A}p$	He	Ho	Fis
Eastern Mediterranean Sea	Montenegro (MNG)	5	2.3	2.3 ± 0.0	2	0.31 ± 0.34	0.27 ± 0.39	0.26
Western Mediterranean Sea	Lacaze-Duthiers canyon (LCD)	6	3.5	3.3 ± 0.04	4	0.45 ± 0.32	0.56 ± 0.40	-0.16
Mid Atlantic Ocean	Azores (AZO)	5	2.7	2.7 ± 0.0	0	0.38 ± 0.27	0.47 ± 0.39	-0.12
Bay of Biscay	Croisic canyon (CRS)	39	6.3	3.7 ± 0.06	1	0.66 ± 0.10	0.67 ± 0.13	0.00
Bay of Biscay	Guilvinec canyon (GUI)	42	5.5	3.7 ± 0.06	0	0.67 ± 0.15	0.60 ± 0.28	0.12***
Bay of Biscay	Lampaul canyon (LMP)	11	3.8	3.2 ± 0.03	1	0.56 ± 0.28	0.58 ± 0.31	0.02
Bay of Biscay	Morgat-Douarnez canyon (MRG)	29	4.8	3.5 ± 0.05	0	0.61 ± 0.16	0.56 ± 0.23	0.10*
Bay of Biscay	Crozon canyon (CRZ)	23	5.5	3.5 ± 0.06	1	0.59 ± 0.24	0.52 ± 0.27	0.14**

Bay of Biscay	Petite Sole 1 canyon (PS1)	23	5.2	3.6 ± 0.05	0	0.63 ± 0.16	0.65 ± 0.21	-0.01
Bay of Biscay	Petite Sole 2 canyon (PS2)	32	6.2	3.7 ± 0.08	0	0.65 ± 0.14	0.59 ± 0.19	0.10*
Rockall bank	Logachev Mounds (LOG)	24	6.0	3.5 ± 0.07	0	0.54 ± 0.30	0.49 ± 0.31	0.11*
High latitudes	Londsjud 1 (LON1)	6	3.7	3.3 ± 0.04	0	0.45 ± 0.30	0.39 ± 0.29	0.22*
High latitudes	Londsjud 2 (LON2)	33	4.5	2.5 ± 0.06	2	0.38 ± 0.28	0.31 ± 0.30	0.18**
High latitudes	Hafadsjud (HAF)	17	4.5	3.1 ± 0.06	0	0.46 ± 0.32	0.44 ± 0.34	0.06

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593 Table 3 - Genetic diversity and neutrality tests for ITS at each location of *Lophelia pertusa*. Asterisk (*) - P-values under 0.05. NA - Not applicable (Lampaul
594 canyon had no polymorphic sites).

	No. Samples (n)	No. Haplotypes	No. Private haplotypes	Haplotype diversity (H)	Nucleotide diversity (π)	Tajima's D	FS
East Mediterranean Sea							
Santa Maria di Leuca (SML)	15	4	0	0.4476	0.0011	-0.33	1.52
West Mediterranean Sea							
Lacaze-Duthiers canyon (LCD)	7	6	2	0.7143	0.0028	-0.86	0.75
Bay of Biscay							
Croisic canyon (CRS)	21	6	2	0.2714	0.0003	-1.73*	2.82*
Guilvinec canyon (GUI)	23	7	1	0.249	0.0004	-1.88*	1.75*
Morgat-Douarnes canyon (MRG)	30	10	4	0.2529	0.0003	-2.01*	3.70*
Crozon canyon (CRZ)	11	6	2	0.6182	0.0014	-1.85*	-0.92
Lampaul canyon (LMP)	7	1	0	0	NA	NA	NA
Petite Sole1 (PS1)	28	3	1	0.0909	0.0001	-1.16	-0.96
Petite Sole2 (PS2)	22	5	2	0.2063	0.0004	-1.89*	1.62*
Rockall bank							
Logachev mounds (LOG)	21	5	3	0.4143	0.0006	-1.22	-1.01
High latitudes							
Londsjud1 (LON1)	8	4	2	0.4643	0.0007	-1.45	-0.30
Londsjud2 (LON2)	20	7	2	0.5105	0.0008	-1.41	-1.48

HafadJup (HAF)	16	5	1	0.4417	0.0008	-1.22	-0.37
Mean	14.5	5.5	1.7	0.4	0.0008	-0.78	-1.50
s.d.	8.95	1.90	1.11	0.20	0.00073	0.991	1.594

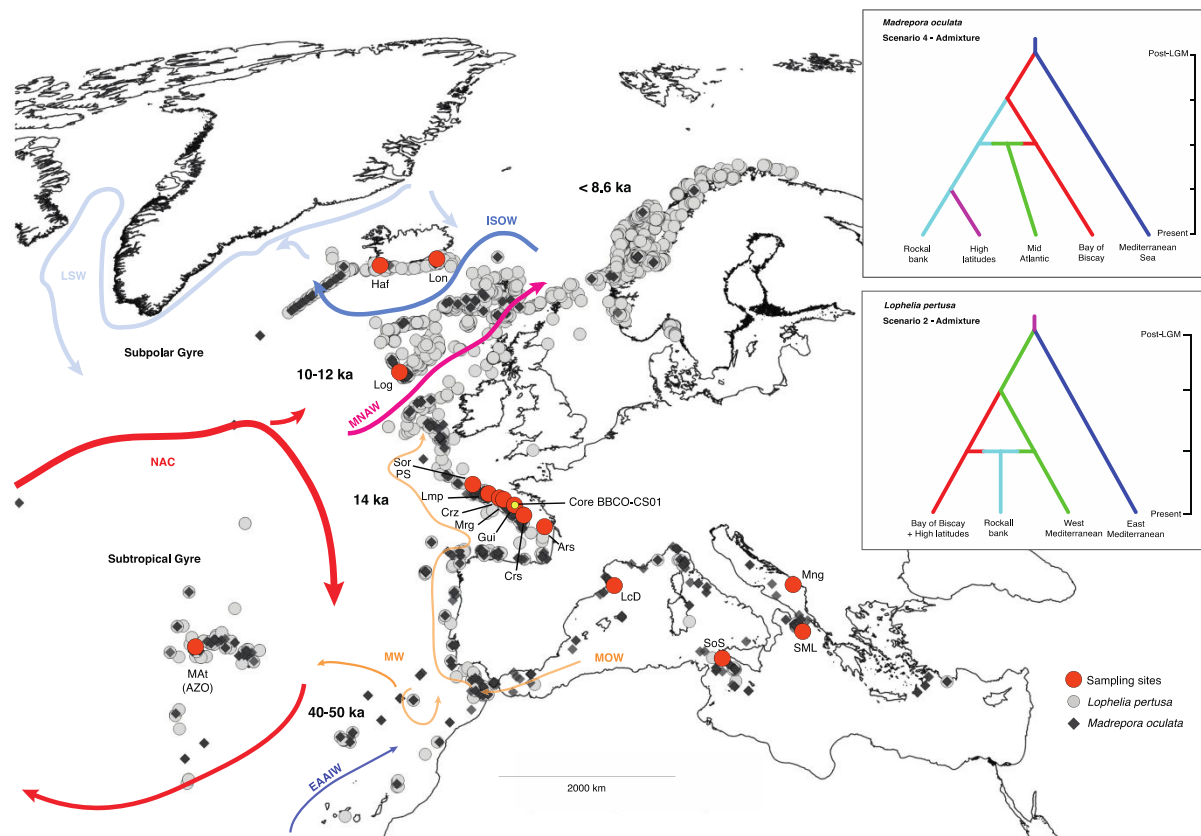
595

596 Table 4 - Genetic diversity and neutrality tests for ITS at each location of *Madrepora oculata*. Asterisk (*) - P-values under 0.05. NA - Not applicable
597 (LondsJup 2 had no polymorphic sites).

	No. Samples (n)	No. Haplotypes	No. Private haplotypes	Haplotype diversity (H)	Nucleotide diversity (π)	Tajima's D	FS
East Mediterranean Sea	5	5	4				
Montenegro (MNG)	5	5	4	0.71	0.0018	-1.55*	-0.13
West Mediterranean Sea	4	4	4				
Lacaze-Duthiers canyon (LCD)	4	4	4	0.83	0.0025	0.37	0.65
Mid Atlantic Ocean	5	4	2				
Azores (AZO)	5	4	2	0.90	0.0020	-0.56	-0.85
Bay of Biscay	91	33	8				
Croisic canyon (CRS)	10	10	0	0.60	0.0011	0.47	0.84
Guilvinec canyon (GUI)	20	16	2	0.68	0.0016	0.25	-0.43
Morgat-Douarnenez canyon (MRG)	10	13	0	0.56	0.0013	0.30	0.17
Crozon canyon (CRZ)	12	8	0	0.14	0.0004	-1.67*	0.90
Lampaul canyon (LMP)	10	10	2	0.47	0.0010	-0.64	0.83
Petite Sole1 (PS1)	7	8	2	0.64	0.0014	0.23	1.23
Petite Sole2 (PS2)	12	12	2	0.42	0.0010	-1.73	-0.16
Rockall bank	27	21	2				
Logachev mounds (LOG)	27	21	2	0.66	0.0014	-0.46	-0.51
High latitudes	63	12	4				
LondsJup1 (LON1)	8	8	2	0.68	0.0018	-0.49	1.65
LondsJup2 (LON2)	34	4	0	NA	NA	N.A.	N.A.
HafadJup (HAF)	21	8	2	0.27	0.0006	-1.02	0.53
Mean	14.1	11.4	2.4	0.58	0.0014	-0.46	0.34
s.d.	8.90	6.82	1.90	0.212	0.00057	0.784	0.722

599 **ix. Figures and captions**

600 Figure 1 - Contemporary distribution of *M. oculata* (black diamonds) and *L. pertusa* (grey circles) in
 601 the NE Atlantic, (2017 UNEP database; <http://data.unep-wcmc.org>) and the path of the main North
 602 East Atlantic Ocean currents (adapted from Montero-Serrano *et al.*, 2011, Somoza *et al.*, 2014 and
 603 Cossa *et al.*, 2018): MOW - Mediterranean Outflow Water; MW - Mediterranean Sea Water; NAC -
 604 North Atlantic Water; MNAW - Modified North Atlantic Water; EAAIW - Eastern Antarctic
 605 Intermediate Water; LSW - Labrador Sea Water; ISOW - Iceland-Scotland Overflow Water. Site
 606 abbreviations as in Table 1. Dates correspond to estimated ages for coral mound growth (adapted from
 607 Schröder-Ritzrau *et al.*, 2005). Insets are the selected demographic history models for each cold-water
 608 coral species. ka - thousand years ago. Map created on QGIS with Mollweide's equal area projection.



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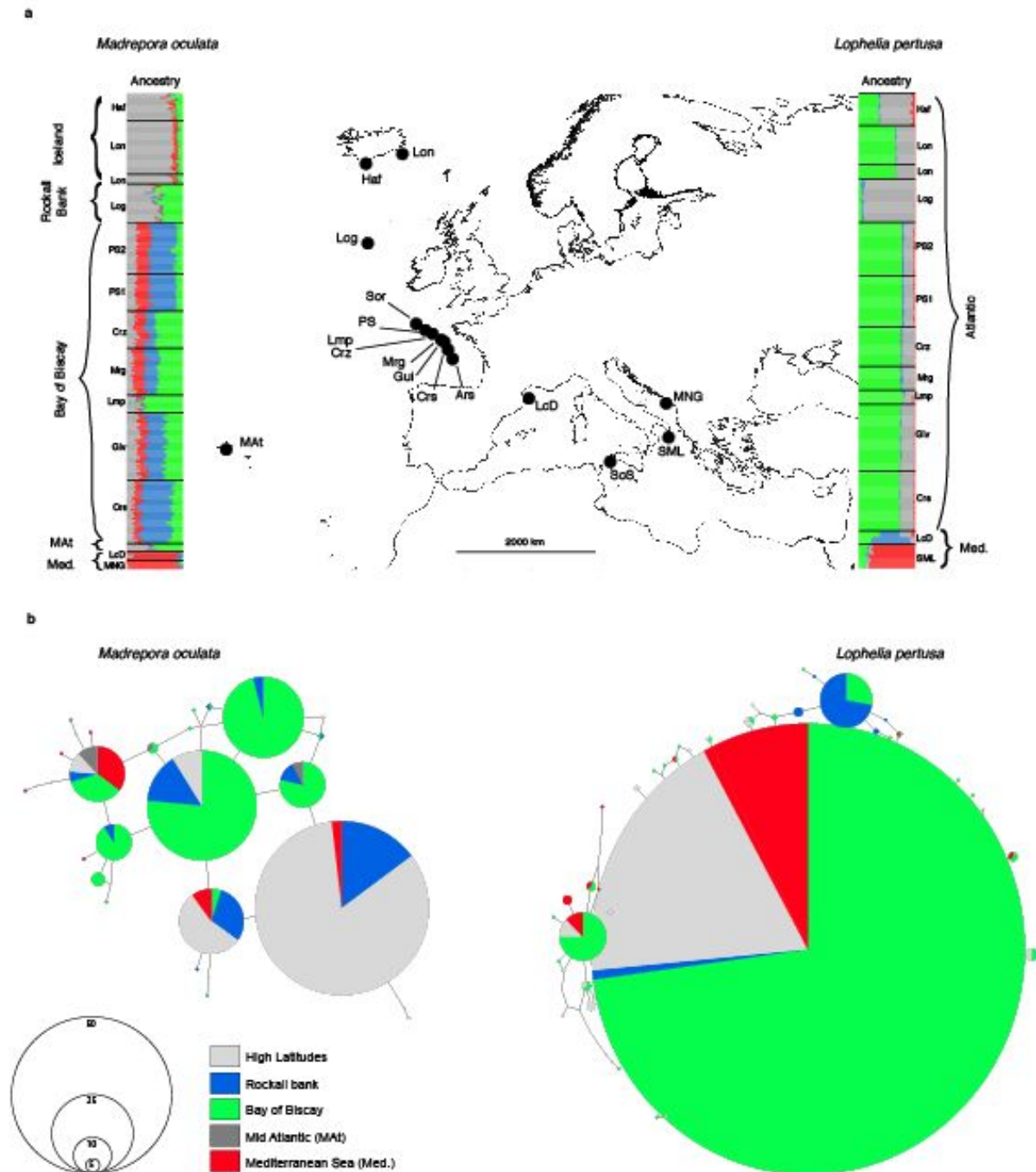
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618 Figure 2 - Genetic subdivision among regional samples. (a) Microsatellites population membership

619 diagrams from TESS displaying the probability of each individual into $K = 4$ clusters for

620 *Madrepora oculata* (left) and *Lophelia pertusa* (right) (denoted by different colours). Each individual

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 3 621 is depicted by a horizontal line partitioned into K coloured sections, with the length of each section
 4 622 proportional to the estimated ancestry proportion to each cluster. Sample names refer to sites indicated
 5 623 in table and Fig. 1. Samples from the Bay of Biscay canyons (left diagram) are geographically ordered
 6 624 from north to south according to what is shown on Fig. 1. Black horizontal lines separate adjacent sites
 7 625 (MAat - Mid Atlantic, Med. - Mediterranean). (b) Parsimony haplotype networks of Internal
 8 626 Transcribed Spacer ribosomal sequences for *M. oculata* (left) and *L. pertusa* (right). The size of the
 9 627 circle is proportional to the observed number of sequences for the corresponding haplotype. Pie charts
 10 628 illustrate the proportion of a haplotype found in each region. The length of links is proportional to the
 11 629 number of mutations separating two haplotypes; the shortest represent a single mutation.
 12 630 Mediterranean includes eastern and western basin samples.

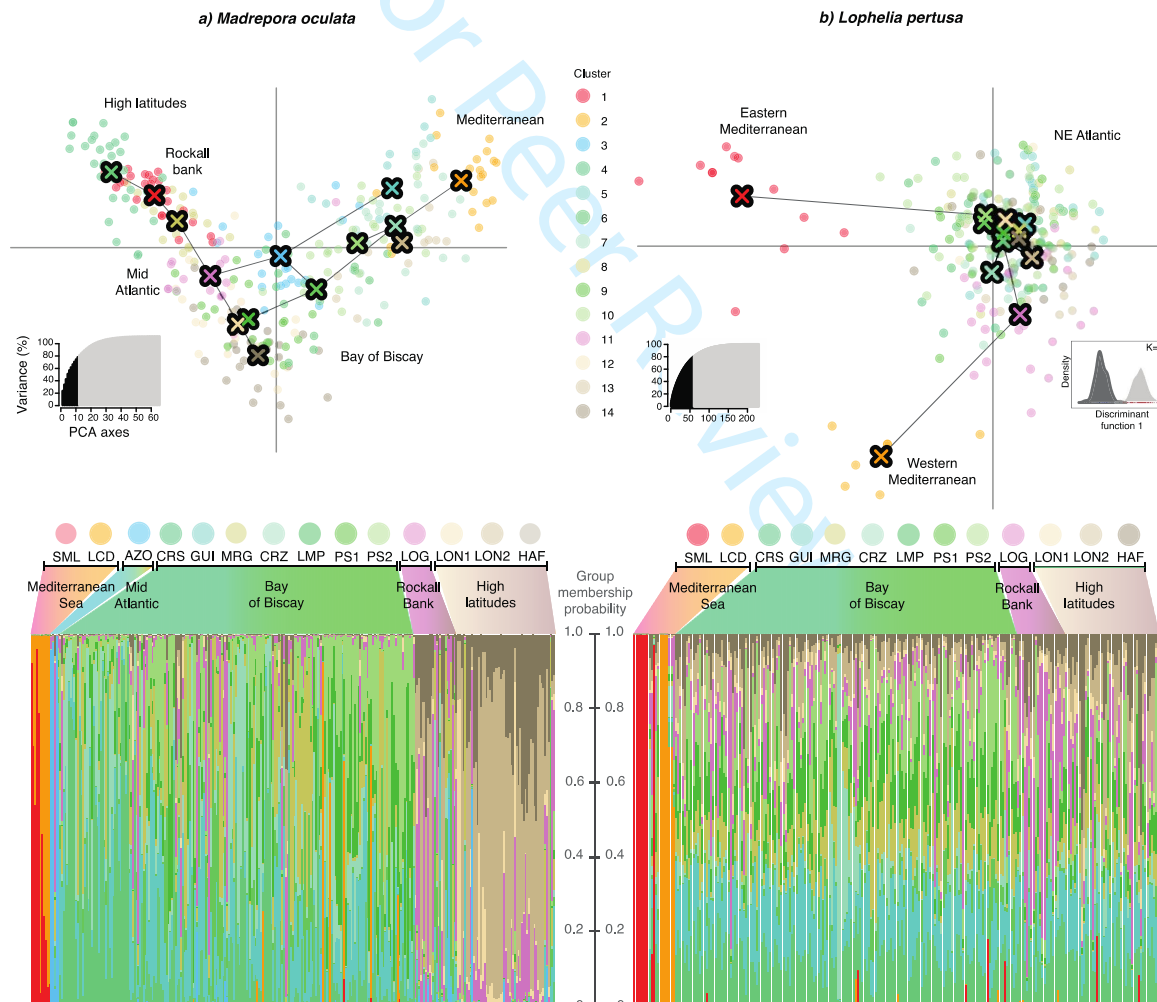


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Figure 3 - Genetic subdivision among regional samples. Top - Discriminant Analyses of Principal Components (DAPC). A minimum-spanning tree based on the squared distances between groups connects group centres (crosses). Insets show the variance explained by the principal components included in the analyses (black). Because the identified optimal number of genetic clusters (K) for *Lophelia pertusa* is K=2 (see additional inset with sample density along the first discriminant function), the DAPC plot for *L. pertusa* shows samples color-coded by sampling site. Bottom - Population membership diagrams displaying the probability of each individual colour-coded by sampling site.



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5 850 **xi. Biosketch**

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7 851 Ronan Becheler is a postdoctoral researcher in evolutionary ecology and population genetics. His
8 852 research interests concern the evolutionary consequences of reproductive systems, with a special
9 853 emphasis on partial clonality. He has worked on the assessment of dispersal in coastal and deep-sea
10 854 species. Currently, he studies the evolution of reproductive strategies and local adaptation in temperate
11 855 macroalgae.

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14 856 Joana Boavida is a postdoctoral researcher interested in biodiversity-related disciplines, from
15 857 taxonomy to biogeography and macroecology, typically using corals as model systems.

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17 858 **xii. Appendices**

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19 859 An appendix shows supporting information

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21 860 **xiii. Supporting information is supplied in a separate file**

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31 865 S2.3 - SPECIES DELIMITATION

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53 876 FIGURE S5 - POWER ANALYSES

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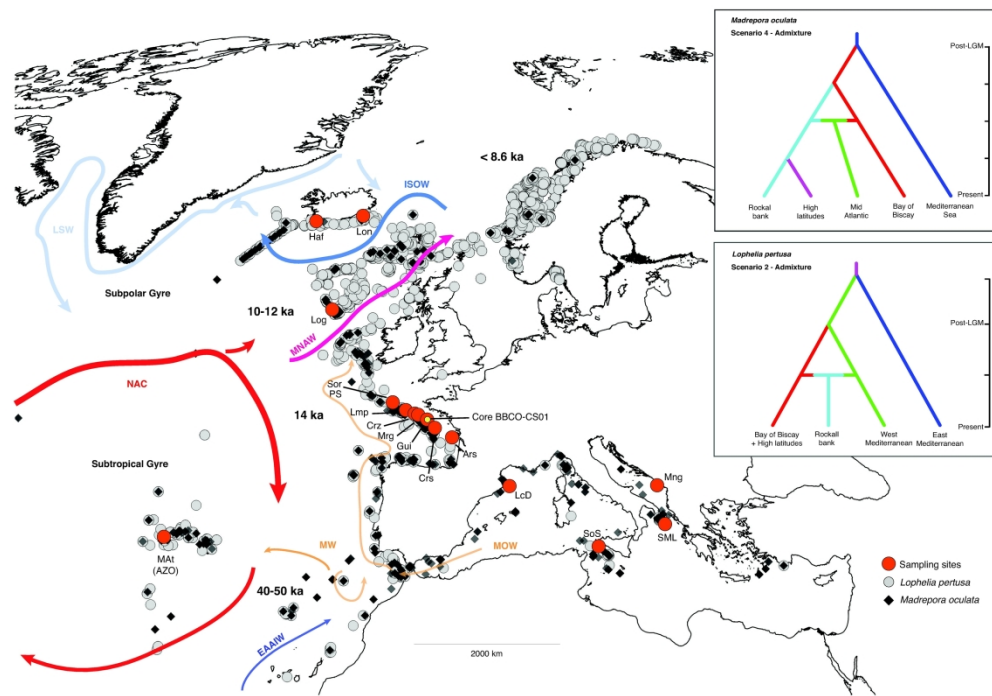


Figure 1 - . Contemporary distribution of *M. oculata* (black diamonds) and *L. pertusa* (grey circles) in the NE Atlantic, (2017 UNEP database; <http://data.unep-wcmc.org>) and the path of the main North East Atlantic Ocean currents (adapted from Montero-Serrano et al., 2011, Somoza et al., 2014 and Cossa et al., 2018): MOW - Mediterranean Outflow Water; MW - Mediterranean Sea Water; NAC - North Atlantic Water; MNAW - Modified North Atlantic Water; EAAIW - Eastern Antarctic Intermediate Water; LSW - Labrador Sea Water; ISOW - Iceland-Scotland Overflow Water. Site abbreviations as in Table 1. Dates correspond to estimated ages for coral mound growth (adapted from Schröder-Ritzrau et al., 2005). Insets are the selected demographic history models for each cold-water coral species. ka - thousand years ago. Map created on QGIS with Mollweide's equal area projection.

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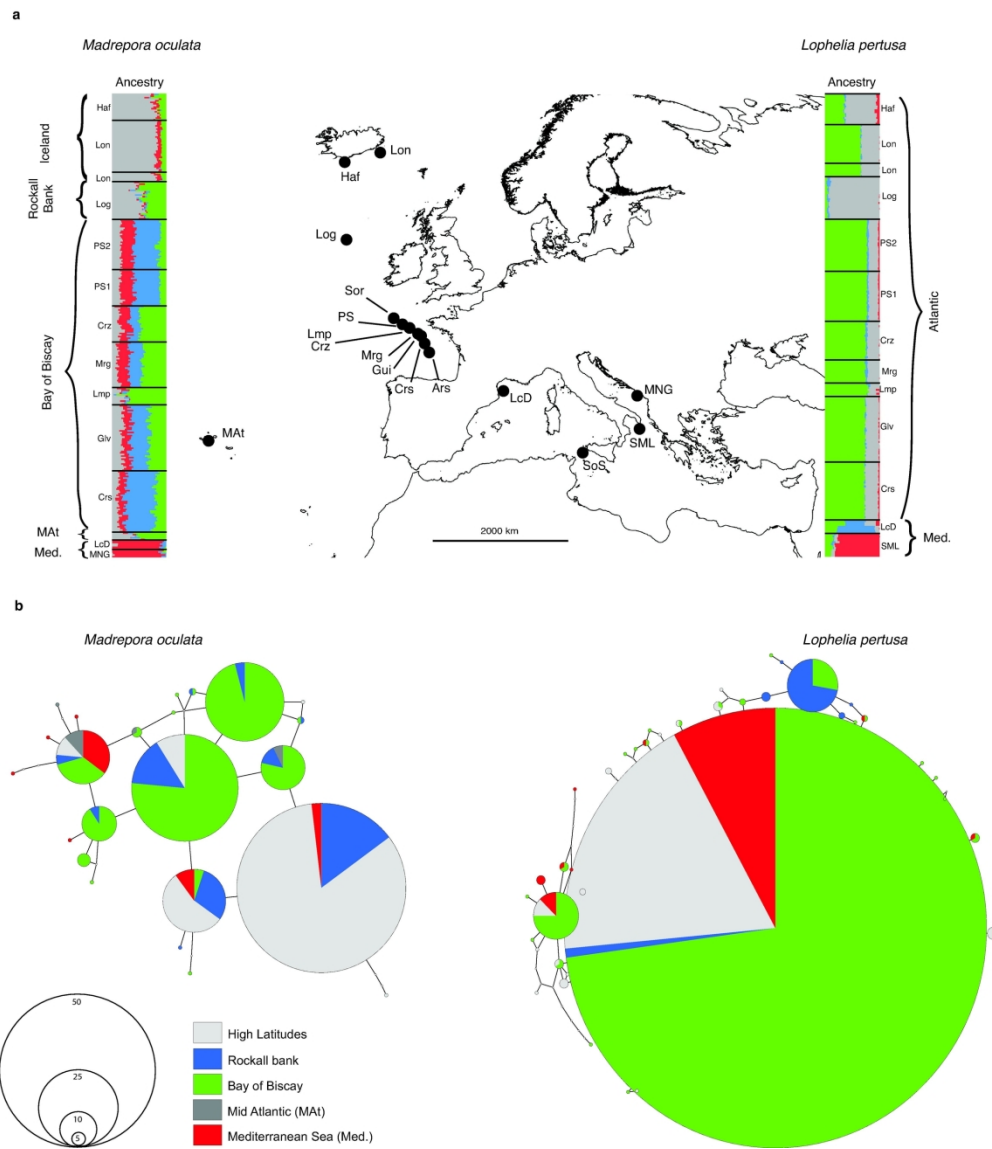


Figure 2 - Genetic subdivision among global regional samples. (a) Population membership diagrams displaying the probability of each individual into $K = 4$ clusters for *Madrepora oculata* (left) and $K = 2$ for *Lophelia pertusa* (right) (denoted by different colours). Each individual is depicted by a horizontal line partitioned into K coloured sections, with the length of each section proportional to the estimated membership ancestry coefficient proportion (Q_{ind}) to each cluster. Sample names refer to sites indicated in table and Fig. 1. Samples from the Bay of Biscay canyons (left diagram) are geographically ordered from north to south according to what is shown on Fig. 1. Black horizontal lines separate adjacent sites (MAT - Mid Atlantic, Med. - Mediterranean). The map shows the distribution of *M. oculata* (black diamonds) and *L. pertusa* (grey circles) known occurrences, according to the 2017 UNEP database (<http://data.unep-wcmc.org>). Map created on QGIS with GDAL bathymetry and the equal area Mollweide projection. (b) Parsimony haplotype networks based on of Internal Transcribed Spacer ribosomal sequences for *M. oculata* (left) and *L. pertusa* (right). The size of the circle is proportional to the observed number of sequences for the corresponding haplotype. Pie charts illustrate the proportion of a haplotype found in each region. The length of links is proportional to the number of mutations separating two haplotypes; the shortest represent a single mutation. Mediterranean includes Ionian Sea eastern and western basin samples.

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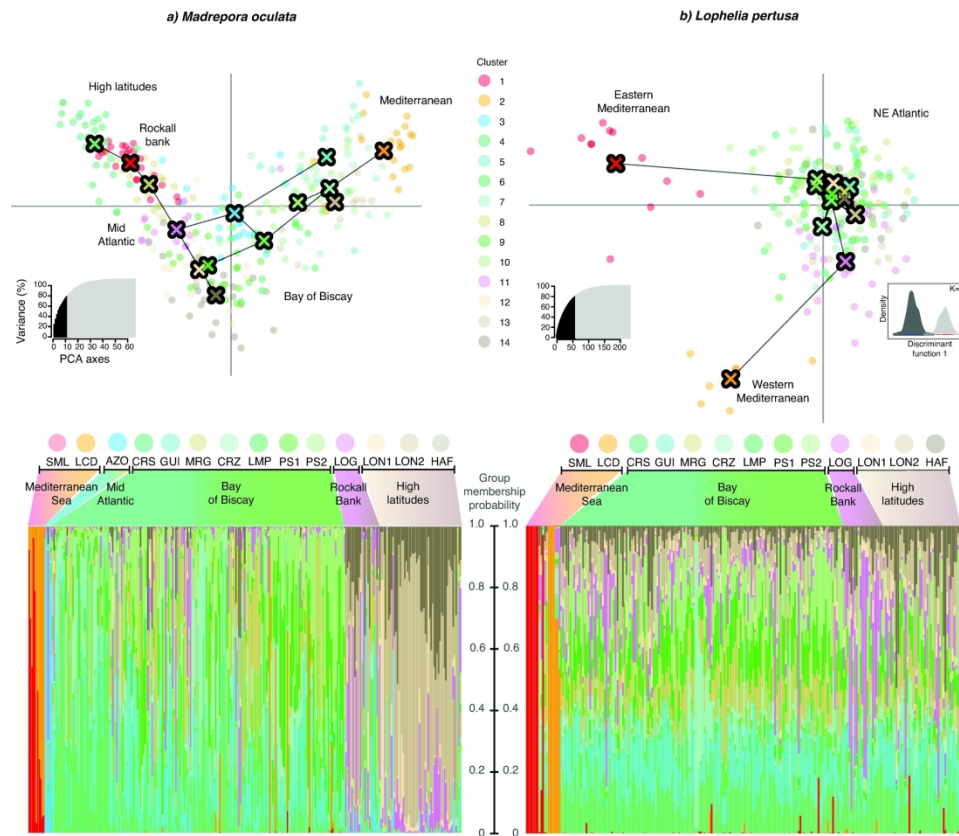


Figure 3 - Genetic subdivision among regional samples. Top - Discriminant Analyses of Principal Components (DAPC). A minimum-spanning tree based on the squared distances between groups connects group centres (crosses). Insets show the variance explained by the principal components included in the analyses (black).

Because the identified optimal number of genetic clusters (K) for *Lophelia pertusa* is K=2 (see additional inset with sample density along the first discriminant function), the DAPC plot for *L. pertusa* shows samples color-coded by sampling site. Bottom - Population membership diagrams displaying the probability of each individual colour-coded by sampling site.

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