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Ecological and genomic characterization of a remarkable natural heritage: a mesophotic ‘giant’ *Paramuricea clavata* forest

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1 Running page head: Characterisation of Mesophotic gorgonian populations

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3 Ecological and genomic characterization of a remarkable natural heritage: a mesophotic
4 'giant' *Paramuricea clavata* forest

5
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21
22 ABSTRACT:

23 *Paramuricea clavata* is an ecosystem engineer, structuring hard bottom communities in
24 the Mediterranean Sea, from 10 to 200m depth. For more than two decades, shallow pop-
25 ulations of *P. clavata* have been impacted by marine heatwaves, resulting in massive mor-
26 tality events. Recently, a new dense population characterised by the tallest colonies ever

27 recorded (up to 1.80m) in the Mediterranean Sea was discovered between 50 and 60m
28 depth. Here, we analyzed the size and genetic structure of this “deep giant population” and
29 conducted a reciprocal transplant experiment with a shallow population inhabiting the
30 same area to test for local adaptation. The experiment showed no significant difference in
31 the survival rate despite the high temperatures registered in the shallow area. Neverthe-
32 less, we observed a significant differentiation by depth in this area, with low estimates of
33 gene flow. The particular local oceanographic conditions could lead to a relative isolation
34 of the “deep giant colony” population. In conclusion, the reduced connectivity of this newly
35 discovered giant populations with shallower ones, question its potential role as a climate
36 refuge. Additionally, this population constitutes a unique natural heritage site that should
37 be effectively protected from physical impacts and other direct consequences of anthro-
38 pogenic activities.

39

40 Key Words: *Paramuricea clavata*, Mediterranean Sea, Climate refugee, Environmental
41 adaptation; transplant experiment; RAD-Seq.

42

43 1. INTRODUCTION

44 Gorgonians are present in the world’s ocean, from the surface to the bathyal zones. These
45 anthozoans are ecosystem engineers, structuring their habitats (Boudouresque et al.
46 2016). Among the gorgonian species present in the Mediterranean Sea, the populations of
47 red gorgonian *Paramuricea clavata* (Risso, 1826) constitute noteworthy submarine land-
48 scapes (Carpine & Grasshoff 1975, Grasshoff 1992, Linares 2006). This Mediterranean
49 endemic species, living from 10m to 200m depth (Boavida et al. 2016; Coelho et al. 2023;
50 Fourt et al. 2017), has a long life span (decades) and a slow growth rate (mean values:
51 from 1.8 to 3 cm/yr in colony height) (Mistri & Cecherelli, 1994; Coma et al. 1998; Coma et
52 al., 2001; Cupido et al., 2012). *Paramuricea clavata* is a gonochoric species with low re-

53 cruitment rates (Coma et al. 1995, 2001). Asexual reproduction is negligible and the main-
54 tenance of the population is based on the recruitment of sexually produced offspring
55 (Coma et al. 1995, Pilczinska et al. 2017). A late first reproductive age depending to
56 Mediterranean region (3 to 13 years old) characterizes this species (Coma et al. 1995; Cu-
57 pido et al., 2012). *Paramuricea clavata* is a suspension feeder, feeding on a large range of
58 particles and this species constitutes a major interface for the transfer of carbon between
59 pelagic and benthic components (Coma et al. 1994, Gili & Coma 1998, Linares et al.
60 2007). The presence of *P. clavata* enhances the hard bottom biodiversity and reduces the
61 sedimentation impacting benthic habitats (Ponti et al. 2016, Valisano et al. 2015).

62 *Paramuricea clavata* is an emblematic species of the coralligenous habitat and its popula-
63 tions are of major interest for recreational scuba divers (Coma et al. 2004, Linares 2006).
64 They can be impacted by different physical pressures (anchoring, SCUBA diving, fishing
65 nets) (Ballesteros 2006, Betti et al. 2020). In addition, shallow populations until 40 to 50
66 meters depth have been affected by several mass mortality events linked to marine heat-
67 waves in recent decades (Perez et al. 2000, Garrabou et al. 2022). These thermal anom-
68 alies, which occur in late summer and autumn periods, are characterized by long periods
69 of high seawater temperatures (Romano et al. 2000, Crisci et al. 2011, Pairaud et al.
70 2014). The consequences are a partial or complete necrosis of living tissues (co-
71 enchyme and polyps) surrounding the skeleton, which can result in the death of gorgoni-
72 ans (Garrabou et al. 2009, 2021). Unfortunately, *P. clavata* has overall low resilience ca-
73 pacity (Garrabou et al. 2001, Cerrano et al. 2005, Linares et al. 2005; Gomez-Gras et al.,
74 2022) even if locally this species seems to recover faster (Cupido et al., 2009; Ruffaldi
75 Santori et al., 2021). Therefore, recurrent marine heat waves are a major threat for the
76 sustainability of shallow gorgonian populations in the Mediterranean Sea (Pairaud et al.
77 2014).

78 Therefore, the study of the genetic diversity of *P. clavata* populations and of their thermo-
79 tolerance is crucial in order to assess: (i) how unimpacted populations can contribute to
80 the resilience of populations affected by mortality events through genetic connectivity and
81 (ii) whether or not the newly established populations are adapted to the local thermal
82 regime, and could cope with warming. These questions started to be addressed focusing
83 on three Mediterranean gorgonians affected by thermal anomalies: the red coral (*Coral-*
84 *lium rubrum*) (Ledoux et al. 2015), the white gorgonian (*Eunicella singularis*) (Pey et al.
85 2013) and the red gorgonian (*Paramuricea clavata*) (Arizmendi-Meija et al. 2015a). Re-
86 garding *P. clavata*, the genetic structure was studied in different regions and depths
87 (Mokhtar-Jamaï et al. 2011, Padrón 2015, Padrón & Guizen 2016, Arizmendi-Meija et al.
88 2015b, Pérez-Portela et al. 2016, Ledoux et al. 2018). It has been shown that significant
89 genetic structure exists at short distances (a few hundred meters) and, occasionally, differ-
90 ences between depths can be observed within the same site (Mokhtar-Jamaï et al. 2011,
91 Pilczynska et al. 2019). However, the limited number of genetic markers used in these
92 studies did not provide a clear understanding of the adaptation of this species to local envi-
93 ronmental conditions (but see Crisci et al. 2017). On the other hand, shallow populations
94 of *P. clavata* (between 20 and 40m depth) have been more extensively studied than
95 deeper ones, which remain poorly understood, apart from the study of Pérez-Portela et al.
96 (2016).

97 In the last decade, new populations of *P. clavata* have been discovered between 50 and
98 60 m depth in the Natura 2000 site "Côte Bleue marine" (north of Marseille) (Astruch et al.
99 2011). These populations settle on rocky outcrops sparsely covering 2300 hectares
100 ("Catchoffs" site). This site is influenced by the flow of the Rhône River and remarkable
101 seasonal upwelling (Frayse 2014). By their exceptional size (up to 1.80m high) and den-
102 sity, the gorgonians that form the Catchoffs site stand out from the colonies usually ob-
103 served (see Results). Such gigantic morphologies could correspond to a phenotypic plas-

104 ticity linked to environmental conditions and/or particular genetic characteristics. Finally,
105 unlike the shallow populations, these deep populations do not appear to be affected by
106 marine heat waves. In this context, the main objective here is to test whether these deep
107 populations of gigantic *P. clavata* constitute potential climatic refuge populations in the
108 face of current global warming. Could they contribute to the resilience of neighboring and
109 shallower populations impacted by mass mortalities? To answer this question, the environ-
110 mental conditions and size structure of *P. clavata* populations in the Catchoffs site were
111 characterized and compared to a shallower population from the same geographical area.
112 Next, we analyzed the differentiation between this deep population and neighboring shal-
113 lower populations at the genomic level using restriction site associated DNA sequencing
114 (RAD-Seq). Finally, the local adaptation signals of the populations to their local environ-
115 ment (especially to the thermal regime) were tested using experimental (reciprocal *in situ*
116 transplantation) and genomic (RAD-Seq) approaches.

117

118 2. MATERIAL AND METHODS

119

120 2.1. Studied area

121 Two populations of *P. clavata* were considered along the “Côte Bleue”, north of Marseille
122 (France), near the Rhône Delta. The first one (Catchoffs - COF) is located two nautical
123 miles south of Carry-le-Rouet (Fig. 1). This population is included in a large Natura 2000
124 site (Leleu et al. 2014). This site is characterized by rocky outcrops emerging from the
125 sediment on a surface covering 2300 ha. Giant colonies of *P. clavata* (between 1.5 and
126 1.8m high) can be observed on these outcrops (Astruch et al. 2011). Other gorgonian
127 species also occur at this site: *Eunicella cavolini* (Koch, 1887), *Eunicella singularis* (Esper,
128 1791), *Eunicella verrucosa* (Pallas, 1766), *Leptogorgia sarmentosa* (Esper, 1791), and
129 *Corallium rubrum* (Linnaeus, 1758). The marine habitat is characterized by a high turbidity

130 of water and by sandy-muddy sediments around rocky outcrops due to the proximity of the
131 Rhône Delta and the impact of associated river plume (Fraysse 2014). In this Natura 2000
132 site, two stations were selected at: (i) 60 m (COF-station A) and (ii) 58 m depth (COF-sta-
133 tion B) (Fig. 1a; Table 1). A third station was studied at 30 m depth (Yeux de chat - ODC),
134 4,500 m away from COF, it is an inshore site characterized by a rocky peak colonized by a
135 dense population of *P. clavata* with some large isolated colonies of *Eunicella cavolini*. As
136 for the previous COF sites, the ODC station is strongly impacted by the Rhône River (Fig.
137 1a; Table 1).

138

139 2.2. Characterization of marine environment and gorgonian populations

140 We monitored the temperature and current regime of both habitats (ODC station and COF-
141 station A) continuously for 13 months between the 1st of July 2019 and the 31st of July
142 2020. Temperature was recorded every 30 minutes with a HOBO water temp pro V2 sen-
143 sor (@Prosensor). A Tilt Current Meter Model 1 (TCM-1) (@Lowell Instruments) was used
144 to characterize the current regime (speed and orientation of current) among the giant
145 colony populations (60 m depth) (Fig. S1). Measurements were also made every 30 min-
146 utes. We also characterized the density and size structure of the *P. clavata* populations
147 studied (COF-site A, B and ODC station) (Table 2). According to Linares et al. (2008), we
148 used 20 open quadrats (50x50 cm) per station (total surface: 5m²) (Fig. S2). In each
149 quadrat, the number of colonies was counted and their height was measured with centime-
150 ter precision. In gorgonians, the characterization of the demographic structure of a popula-
151 tion is challenging. Indeed, the annual growth rate decreases with the age of the consid-
152 ered colonies (Coma et al., 1998; Sartoretto & Francour, 2012; Viladrich et al., 2016). In *P.*
153 *clavata*, annual growth rates values were almost exclusively estimated on small and young
154 colonies (e.g. Mistri & Cecherelli, 1994; Coma et al., 1998; Cupido et al., 2012). In this
155 context and considering the maximal size of *P. clavata* observed in Catchoff site (180cm

156 high), we only focused on the characterization of the size structure of the populations. Fol-
157 lowing Linares et al. (2008), we defined 16 size classes, each corresponding to a 10 cm
158 range.

159

160 2.4. Experimental design

161 To test the potential for local adaptation of *P. clavata* populations according to depth, we
162 performed a reciprocal transplant experiment between the two localities (COF-station A
163 and ODC station) from 1st July 2019 to 3rd June 2020. The transplant experiment included
164 one control (colonies transplanted at their native depth) and one transplant (colonies trans-
165 planted at the foreign depth) in both locations. Sixty 10 cm long apical tips (two per colony)
166 were randomly sampled with scuba diving from each population. For each population, 30
167 fragments were attached to experimental plates (Fig. S2) and installed at their original
168 depth (control transplants). Plates with the remaining 30 fragments were installed at a for-
169 eign depth (reciprocal transplants; i.e. 30 m to 60 m and 60 m to 30 m). Each sampled
170 colony was genotyped as explained below. Photographic monitoring of each transplant
171 was carried out every two months depending on meteorological conditions.

172

173 2.3. Genomic analysis

174 We aimed to characterize the genetic make-up of the COF deep site and to involve these
175 results in a wider context. Therefore, we sampled *P. clavata* colonies in different areas:
176 Northern Marseille Bay (COF station A and ODC), Calanques (Grand Congloue (GOC)
177 and Impérial (IMP) stations) and Porquerolles (Sec du Petit Langoustier (SPL) and Cap
178 d'Armes (CAA) stations), at increasing distance from COF (from 5 km up to 94 km) (Fig.
179 1b). In each area we sampled sites corresponding to different depths: around 30 m deep
180 (hereafter "shallow"), and below 50-55 m ("deep"). Details of the sampling sites are pre-

181 sented in Table 2. It should be noted that we analyzed more individuals from the Northern
182 Bay of Marseille (including the deep COF site) which was our main study area.

183

184

185

186 2.3.1. Library preparation and sequencing

187 DNA from the samples was extracted using the Macherey-Nagel NucleoSpin DNA RapidL-
188 yse extraction kit. After DNA quantification, the extracted DNA samples were sent to the
189 MGX platform (<https://www.mgx.cnrs.fr/>) for RAD library preparation and sequencing. We
190 included in the batch of individuals four replicates with two DNA extractions from the same
191 colony. Library preparation followed the protocol of Baird et al. (2008) with the PstI restric-
192 tion enzyme. The library was sequenced on an Illumina NovaSeq 6000. We obtained a
193 mean of 6,426,012 raw sequences per sample (minimum: 618,725; maximum: 9,181,838;
194 Fig. S3).

195

196 2.3.2. Analysis of RAD sequencing data

197 We checked the quality of sequences with FastQC (Andrews 2019). In a preliminary analy-
198 sis we included an individual of the congeneric species *Paramuricea placomus* (Linnaeus,
199 1758) from Tjärnö (Sweden). A first Principal Component Analysis on this dataset led to
200 the main separation of *P. placomus* and *P. clavata* (Fig. S4). As this analysis did not lead
201 us to suspect the presence of different cryptic lineages among the *P. clavata* samples, we
202 removed the *P. placomus* sample for further analyses. This allowed us to increase the
203 number of SNP loci (from 45,251 to 65,726 SNPs before further filtering), and to improve
204 the characterization of the genetic structure within *P. clavata*. At that stage we also re-
205 moved a *P. clavata* individual with a very low number of reads (618,725). We then re-
206 moved potential contaminant sequences with Kraken 2 (Wood et al. 2019) with the stan-

207 dard database including references from archae, bacteria, human, plasmid, and viral se-
208 quences. The sequences identified by Kraken 2 were filtered with KrakenTools (Lu 2020).
209 The assembly of RAD loci was done with ipyrad 0.9.79 on these filtered sequences (Eaton
210 & Overcast, 2020). We used the genome of *P. clavata* as a reference (Ledoux et al. 2020).
211 We then performed a first PCA which showed the main separation of two samples of COF
212 with high rates of heterozygous loci. The inbreeding coefficient F computed with
213 VCFTOOLS 0.1.15 (Danecek et al. 2011) for these two samples was -0.24 and -0.08,
214 compared to a mean value of 0.13 and a minimum of -0.03 for other samples. We re-
215 moved these two samples for further analyses. We used the output of ipyrad to build a ma-
216 trix of pairwise p-distances among samples with VCF2Dis 1.45 ([https://github.com/BGI-](https://github.com/BGI-shenzhen/VCF2Dis.git)
217 [shenzhen/VCF2Dis.git](https://github.com/BGI-shenzhen/VCF2Dis.git)). We then compared the pairwise distance observed among differ-
218 ent samples with those observed among sequencing replicates. This last analysis led us to
219 identify four sample pairs which showed the same distance than the distance observed be-
220 tween replicates (Table S1). For each pair, we removed the sample with the lowest num-
221 ber of reads, resulting in a total of 82 individuals. We then filtered SNPs with the following
222 filters: two alleles, a maximum of 25% of missing data, in Hardy-Weinberg equilibrium, not
223 in linkage disequilibrium, and one SNP per locus. Filtering on the basis of Hardy-Weinberg
224 equilibrium is useful to remove problematic markers, such as paralogous loci for example.
225 and previous studies based on microsatellites did not suspect any asexual reproduction in
226 this species (Mokhtar-Jamai et al., 2011; 2013). The filter based on linkage disequilibrium
227 aims at retaining only independent loci. The filtering was performed with vcftools 0.1.16
228 and the GBS_SNP_filter 1.17 pipeline (Alexander 2020, Danecek et al. 2011).
229 We used the GENEPOP R package (Rousset 2008) to compute gene diversity within indi-
230 viduals (1-Qintra; corresponding to observed heterozygosity) and among individuals within
231 sampling sites (1-Qinter; corresponding to expected heterozygosity), and F statistics (Weir
232 & Cockerham 1984). We tested the pairwise differentiation among sampling sites with

233 1,000 permutations with Arlequin 3.5 (Excoffier & Lischer 2010). We analysed the genetic
234 structure among samples with a Principal Component Analysis (Jombart et al. 2010), and
235 a clustering analysis followed by a Discriminant Analysis of Principal Components (DAPC;
236 Jombart et al. 2010), with the adegenet 2.1.5 R package (Jombart & Ahmed 2011). We
237 tested for the presence of loci potentially involved in local adaptation with three ap-
238 proaches: Arlequin (Excoffier et al. 2009, Excoffier & Lischer 2010), OUTFLANK (Whitlock
239 & Lotterhos, 2015), and PCADAPT (Luu et al. 2017).

240 We performed demographic inferences to estimate effective size and gene flow among
241 populations in COF and ODC populations for which we obtained the highest sample sizes.
242 We used the dataset obtained from the assembly of these two populations only. We used
243 fastsimcoal2 for demographic inferences (Excoffier et al. 2013, 2021), under a model of di-
244 vergence with gene flow (Fig. S5). The site frequency spectrum (SFS) was computed with
245 easySFS (<https://github.com/isaacovercast/easySFS>). The inference was first performed
246 on the basis of 100 replicated analyses of this initial dataset, and the run with the highest
247 estimated likelihood was retained to estimate demographic parameters. We performed 50
248 non-parametric bootstraps of the original dataset: each bootstrapped dataset was ana-
249 lysed with 10 replicates and we retained the best run to get a confidence interval of the es-
250 timated parameters.

251

252 3. RESULTS

253

254 3.1. Characterization of the marine environment

255 3.1.1. Temperature

256 At the ODC station (-30 m), the range of values of seawater temperature values extended
257 from 23.2°C during autumn 2019 to 13.1°C during winter 2019-2020. In summer and au-
258 tumn, temperature trend showed successions of warm water peaks (21-23°C at 30 m

259 depth). These peaks were observed during short time periods (less than a week) in July
260 and August (Fig. 2). Between September and November 2019, two longer periods (two
261 and three weeks) were observed with temperatures reaching 20°C and 23°C. In the COF
262 station (-60 m), temperature values ranged from 22.54°C in autumn 2019 to 13.40°C in
263 winter 2019-2020. During the summer, the same sequence of temperature increases as at
264 the ODC station was observed with lower maximum values (16-17°C). During the autumn,
265 the warm water periods were also the same as at the ODC station with the same maxi-
266 mum values (20°C to 23°C) but of a shorter duration (two weeks) (Fig. 2).

267

268 3.1.2. Current regime

269 The current regime in the COF station is characterized by low speed values ($< 0.09 \text{ m.s}^{-1}$).
270 During spring and summer, we observed a maximal period of time with a current speed of
271 less than 0.03 to 0.04 m.s^{-1} . (Fig. 3A). During autumn and winter, the current speed values
272 are more unstable, ranging from 0.01 to 0.09 m.s^{-1} . The current orientation shows a uni-
273 modal pattern in spring and summer with a predominance of the southeast direction (bear-
274 ing: 220°). In autumn and winter, this pattern is bimodal with: (i) southeast predominance
275 (bearing: 230°) and (ii) to a lesser extent northeast predominance (bearing: 50°) (Fig. 3B).

276

277 3.2. Size structure

278 The shallow population studied (ODC station, -30m) is characterized by a density of $26 \pm$
279 $7.3 \text{ colonies.m}^{-2}$. The size structure of this population shows a unimodal distribution of size
280 classes. The small (10 to 20 cm) and average sized gorgonians (20 to 50 cm) represent 67
281 % of the total (Fig. 4). The tallest colonies (50-110 cm) represent 23 % with only 1 % of the
282 colonies belonging to the class size 110-120 cm.

283 Compared to the ODC station, the COF-station A (-60m) shows a lower value for density
284 with $18.05 \pm 7.29 \text{ colonies.m}^{-2}$. The gorgonian population is characterized by a bimodal

285 size structure with a predominance of average sized colonies (20 to 50 cm) representing
286 50 % of total and high colonies (100-130 cm), representing 23 % of the colonies. Tall
287 colonies (130 to 150 cm) and giant (>150 cm with a maximum of 180 cm) represent re-
288 spectively 9 % and 6 % of the total (Fig. 4). In the COF-station B (-58m), the density value
289 is 23.6 ± 7.4 colonies.m⁻², with small (10-20 cm) and average sized colonies (20 to 50 cm)
290 representing 17% and 39% of the total number of colonies. Tall colonies (130-150 cm) and
291 giant (>150 cm with a maximum of 160 cm) represent 13 % and 2 % of the observed
292 colonies.

293

294 3.3. Transplantation experiments and genomic analysis

295 3.3.1. Monitoring of transplants

296 At 60 m depth (COF-Station A), 24 fragments from the control transplant (60 to 60 m) died
297 one month after their installation. Ten months later, all fragments were dead. Regarding
298 the reciprocal transplants from ODC (30 to 60 m), the survival rate was higher than for the
299 control transplant with 11 dead fragments 5 months after the beginning of the experiment.
300 One year later, 14 fragments were dead (47 %) and the remaining ones showed between
301 25 % and 75 % of tissue necrosis. At 30 m depth (ODC station), after four months the sur-
302 vival rate reached 96.67 % for the control transplants (30 to 30 m), and 83.33 % for the re-
303 ciprocal transplants from COF (60 to 30 m). After 12 months, these values respectively
304 reached 60 % and 40 % (Fig. 5). At the end of the experiment, no significant differences
305 (Wilconson Rank Sum Test, $p = 1$) in final necrosis levels was observed between control
306 transplants and reciprocal transplants coming from COF. The majority of colonies pre-
307 sented a mean necrosis level lower or equal to 50 %. In June 2020 (end of experiment), 90
308 % of COF transplants and 92 % ODC transplants presented fertile polyps. Finally, the ke-
309 toparasitic annelid *Haplosyllis chamaeleon* (Pola et al. 2020) was observed on 28.6 % of
310 the reciprocal transplants from COF and 22 % of the control transplants (ODC).

311

312 3.3.1. Genetic diversity and genetic structure

313 After the different filtering steps, statistical analyses were performed with 82 individuals
314 and 49,215 SNPs. The number of loci retained at each stage of the analysis is shown in
315 Tables S2 and S3. The levels of diversity were roughly similar between samples, with $1-$
316 Q_{intra} around 0.06 and $1-Q_{inter}$ around 0.07 (see Table 2). We did not observe any regu-
317 lar increase or decrease of genetic diversity along depth. The F_{IS} estimates indicated a sig-
318 nificant heterozygous deficit for all populations, varying from 0.08 for SPL to 0.13 for CAA.
319 When computed over all sites and loci, the observed F statistics were 0.094 for F_{IS} , 0.044
320 for F_{ST} , and 0.135 for F_{IT} . The pairwise F_{ST} , averaged over all loci, are presented in Table 3.
321 The highest F_{ST} value (0.053) was observed for the comparison between the two sites in
322 the northern bay of Marseille, Catchoffs (COF) and Yeux de Chat (ODC), and between
323 COF and GCO (different depths, Marseille North and Calanques). The mean F_{ST} value for
324 the comparisons between depths within a given area was 0.032. Between areas, the mean
325 F_{ST} value was 0.038, 0.044 and 0.030 considering all sites, shallow sites and deep sites,
326 respectively. All pairwise differentiation tests were significant according to the permutation
327 tests (highest p-value: 0.014 for the CAA/IMP comparison).

328 The result of the PCA analysis on all loci is presented in Fig. 6A. The first axis mainly sep-
329 arated populations COF and ODC (2.1 % of variance), while the second axis was driven
330 by a few individuals from SPL (2 % of variance). The DAPC analysis did not indicate a
331 clear cut-off for the choice of the number K of clusters (Fig. S6). The clustering at $K= 2$
332 separated ODC from other populations, and the clustering at $K= 3$ further separated COF
333 from ODC and other populations (Fig. S7). The clustering at $K= 4$ separated COF, ODC,
334 the two Calanques populations (GCO and IMP), and the two Porquerolles populations
335 (SPL and CAA; Fig. 7) with high membership probabilities (near 1 in all cases). One can

336 note that one individual from Porquerolles was assigned to the Calanques cluster, and one
337 individual from Calanques was assigned to the Porquerolles cluster.

338 We identified 267 potentially selected outlier loci with PCADAPT, 25 with Arlequin and
339 none with OUTFLANK. None of the outliers has been identified with both methods simulta-
340 neously.

341 We performed a separate PCA analysis with the outlier loci identified by each method.
342 With PCADAPT, the first axis of this last PCA separated a small group of individuals from
343 various populations, whereas the second axis mainly separated ODC from other popula-
344 tions (Fig. 6B). The third axis separated the COF population, and the fourth axis mainly
345 separated the two Porquerolles populations (CAA and SPL; Fig. 6C). With the Arlequin
346 outliers, there was no clear signal of differentiation in the PCA (results not shown).

347 The results of demographic inferences are presented in Table S4. Estimates of effective
348 size indicate a much higher population size for the 30 m population (ODC) compared to
349 the 58 m population (COF), with non-overlapping distributions based on bootstraps. Gene
350 flow estimates indicate very low levels of connectivity between these two populations, but
351 gene flow from ODC to COF appears higher than in the reverse direction (0.0041 com-
352 pared to less than 0.0001; non-overlapping distributions).

353

354 4. DISCUSSION

355

356 4.1. Size structure

357 At the two stations of COF site, mean values for colony height of *Paramuricea clavata*
358 reached 71.08 ± 47.9 cm (site A) and 57.39 ± 39.1 cm (site B), respectively. These values
359 are higher than those reported in the ODC station (32.44 ± 22.54 cm), and, more gener-
360 ally, higher than those reported from the same depth in the northwestern Mediterranean
361 basin (Linares et al. 2008, Pérez-Portela et al. 2016). Surprisingly, the presence of tall

362 (1.25-1.50 m) and giant colonies (>1.50 m) is associated with density values close to those
363 noted in shallower sites with smaller colonies (Harmelin & Garrabou 2005, Linares 2008,
364 Iborra et al. 2022). By referring to the growth rate value estimated by Mistri & Ceccherelli
365 (1994), Cerrano et al. (2005) and Cupido et al. (2012) on small colonies (2.7 to 3.7 cm.yr⁻¹),
366 the highest *P. clavata* (1.8 m) could be 50 to 70 years old. Nevertheless, the smallest
367 (and youngest) gorgonians usually show high values of annual growth rate (Coma et al.,
368 1998; Viladrich et al., 2016). Based on the growth rate value calculated by Coma et al.
369 (1998) on higher colonies (from 3 to 55cm), they could be around 100 years, old even
370 though the authors underline the great variability of the growth rate within and between the
371 colonies of *P. clavata*. This age is well above the upper limit of this gorgonian's previously
372 estimated life span (50 years). Nevertheless, this astonishing size could be also due to a
373 growth rate boosted by environmental conditions. Indeed, the Catchesoff study area is char-
374 acterized by a low current and the proximity of the Rhône River induces high input of or-
375 ganic matter with a high productivity (chlorophyll a) potentially beneficial to the growth of
376 colonies (Cocito et al. 1997, Linares 2008, Fraysse 2014). Further studies are needed to
377 formally estimate the age of the highest colonies of *P. clavata*. To date, it should be noted
378 that these giant deep-sea populations of *P. clavata* are not only unique but also constitute
379 a natural heritage in the north-western Mediterranean basin deserving special attention in
380 terms of conservation and management.

381

382 4.2. Transplant experimentation

383 At 30 m, the survival rate of transplants was similar to the percentage obtained in other ex-
384 periments with different methods and gorgonian species (Weinberg 1979, Fava et al.
385 2010, Villechanoux et al. 2022). The presence of the kleptoparasite *Haplosyllis*
386 *chamaeleon* after one year did not cause injuries or any malformation on transplants as
387 usually observed on colonies of *P. clavata* (Pola et al. 2020). A majority of fertile polyps at

388 the end of the experiment was a sign of a good adaptation of reciprocal and control trans-
389 plants to the 30 m habitat. On the contrary, the high mortality rate at 60 m was surprising.
390 The factors explaining this mortality are probably of different origins such as handling dur-
391 ing experimental set up or environmental conditions. At 60 m, the high level of sediments
392 falling on the experimental disposal could strongly impact transplants (Cocito et al. 1995,
393 Rowley 2014). Identifying their relative impacts on the mortality rates is challenging, yet
394 the high level of sediments on experimental disposal observed at 60 but not at 30 m may
395 be a prominent factor.

396

397 4.3. Genetic originality of the deep population of *Paramuricea clavata*

398 With nearly 50,000 SNPs genotyped, our results confirm the interest of RAD-sequencing
399 for population genetics in non-model species. This number of loci is comparable to results
400 with the same restriction enzyme by Quattrini *et al.* (2022) on different *Paramuricea*
401 species (almost 30,000 SNPs), and by Pratlong *et al.* (2021) on *C. rubrum* with more dis-
402 tant populations (more than 25,000 SNPs). Within *P. clavata*, we observed significant dif-
403 ferentiation between sampling sites. When considering our three replicate comparisons
404 between depths, clustering analysis indicated grouping first by sampling area and then by
405 depth. This is consistent with the results obtained with microsatellites by Pérez-Portela et
406 al. (2016) focusing on populations around 50-60 m depth, and by Mokhtar-Jamaï et al.
407 (2011) for shallower populations (mainly above 40 m). There is then a local differentiation
408 along depth, rather than the presence of deep and shallow lineages, which would be
409 shared among sites. The highest F_{ST} value (0.053) was observed for the comparison be-
410 tween the deep population of giant colonies and the nearest population at around 30 m
411 depth (30 m). This differentiation also corresponded to the first axis of the PCA. It can be
412 noted that with microsatellite loci, Mokhtar-Jamaï et al. (2011) also observed a clear differ-
413 entiation with a shallow population from the Côte Bleue where the ODC site is located. The

414 particular oceanographic conditions of the Côte Bleue (Frayssé 2014) could lead to a rela-
415 tive isolation of this area explaining our results. The deep population of giant colonies
416 (COF) therefore corresponds to a unique population well differentiated from shallower pop-
417 ulations from the same area, as well as from the populations of the Southern Calanques
418 area. The results of demographic inferences support this distinction with very low gene
419 flow between COF and ODC, but higher from COF and ODC. Indeed, these populations
420 are 4,500 m apart and currents are very low ($<0.1 \text{ m}\cdot\text{s}^{-1}$), limiting the dispersal of planula
421 with a short life span before their transformation into new colonies (around 48h, see
422 Linares et al. 2008, Coma et al. 1995). This may explain the relatively high F_{ST} observed
423 between these two spatially close sites. The observed F_{ST} between COF and ODC is also
424 similar to the F_{ST} estimated between *P. clavata* populations below 50 m and above 30 m
425 with microsatellites by Perez-Portela et al. (2016; F_{ST} 0.049-0.066). The F_{ST} observed here
426 is nevertheless lower than most pairwise F_{ST} observed for *C. rubrum* in the Marseille area
427 using RAD-sequencing (variation between 0.03 and 0.10; Pralong et al. 2021): this would
428 indicate either lower gene flow or higher drift for *C. rubrum* compared to *P. clavata*. For *P.*
429 *clavata*, with respect to effective population size, the estimated value with RAD-Seq, is
430 much higher for the shallow ODC population compared to the deep COF population. This
431 result is in contradiction with the analyses of Pilczynska et al. (2019), who observed an in-
432 crease of genetic diversity with depth, a pattern not observed here. To take demographic
433 inference analyses further, it would be necessary to test the impact of additional connectiv-
434 ity with other neighboring populations, and of variations in census population size on the
435 inferred patterns of effective population size.

436

437 4.4. Local adaptation to depth

438 The *P. clavata* populations from COF and ODC occur under contrasting ecological condi-
439 tions, including different thermal regimes with higher and more variable temperatures in

440 ODC compared to COF. Nevertheless, it can be noted that the deep population in COF
441 was exposed to temperatures above 22°C during our survey. We could not formally test
442 the hypothesis of local adaptation in our reciprocal transplant experiment due to the loss of
443 the samples at the COF site. Indeed, a full test of local adaptation would require a compar-
444 ison of fitness in both habitats (Kawecki & Ebert 2004, Ledoux et al. 2015). Nevertheless,
445 the treatment at 30 m depth including reciprocal transplantation (from COF) and control
446 transplantation (ODC) can be considered as a common garden experiment. Interestingly,
447 we did not observe any significant difference in necrosis rates between colonies from COF
448 and ODC, despite the high temperatures in this shallower habitat (especially in July-Au-
449 gust 2019). This result would indicate a lack of local adaptation, which is at odds with the
450 differences in tolerance capacity towards warm water, observed between 20 and 40 m
451 depth in *C. rubrum* (Oriol Torrent 2007, Ledoux et al. 2015) and *E. cavolini* (Pivotto et al.
452 2015). In an *ex-situ* common garden, Crisci et al. (2017) observed no difference in thermo-
453 tolerance between *P. clavata* colonies of different depths (20 m vs 40 m) from the Mar-
454 seille area (Calanques). The same lack of phenotypic differences was observed in Corsica
455 and Catalonia when comparing gorgonians populations along a depth gradient. This result
456 could be the consequence of genetic drift blurring the result of local selection (Crisci et al.
457 2017). In line with this apparent lack of local adaptation at the phenotypic level, the search
458 for outlier loci has identified loci that confirm the geographical separation of populations,
459 but without a clear link to environmental variables and local adaptation. Such a RAD-se-
460 quencing based approach may miss locally selected alleles (e.g., due to reduced genome
461 representation), or may be limited especially when local adaptation is based on a combina-
462 tion of loci with small effect (Hoban et al. 2016).

463

464 4.4. Conservation aspects

465 The results of demographic inferences indicate that the deep population of giant *P. clavata*
466 is isolated and unique with a reduced effective size compared to the shallower popula-
467 tions. Our results, and previous ones on such deep populations (Pérez-Portela et al. 2016)
468 do not support the hypothesis of deep refugia for *P. clavata*, at least for the studied areas.
469 This also strengthens the need to protect such a deep population which is original, both
470 from a genetic and demographic point of view. This need is reinforced by the major impact
471 of anchoring and use of fishnets on the giant populations of *P. clavata* in a Marine Pro-
472 tected Area, with up to 100 boats per day (Leleu et al. 2014, Charbonnel et al. 2020,
473 PMCB 2022) (Fig. S8). In this, the Marine Park of the 'Côte Bleue' (manager of the Natura
474 2000 site) has proposed a new technical disposal to the recreational fishermen in order to
475 prevent the impact of anchoring (Fig. S8). Despite the fact that the deeper populations are
476 less impacted by warming (Cupido et al. 2008), proper management of this human activity
477 is strongly needed to help preserve these populations (Betti et al. 2020). Indeed, gor-
478 gonian forests enhance α and β diversity, and their loss replaces a structurally complex
479 habitat dominated by long-lived species with a simplified habitat (turf forming species) with
480 a loss of biodiversity (Verdura et al. 2019, Piazzini et al. 2021).

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 770 *Genome Biol* 20(1), 257. DOI: 10.1186/s13059-019-1891-0

772 TABLES

773

774 Table 1. Studied sites with tasks performed. TM: temperature monitoring, CM: current
 775 monitoring, TRE: Transplant experimentation, DS: Density of colonies and size structure,
 776 G: Genomic analysis.

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Area	Station	Geographical coordinates	Depth	Task
Marseille north	Catchoff – Station A	43°17.640 N/05 11.151 E	60m	TM, CM, DS, TRE, G
Marseille north	Catchoff – Station B	43°17.840 N/05 11.009 E	58m	DS
Marseille north	Yeux de Chat	43°11.640 N/05°11.151 E	30m	TM, CM, DS, TRE, G
Calanques	Grand Congloue	43°10.582 N/05°24.185 E	33m	G
Calanques	Impérial du large	43°10.177 N/05°23.694 E	54m	G
Porquerolles	Sec Petit Langoustier	42°59.895 N/06°09.612 E	30m	G
Porquerolles	Cap d'Arme	42°58.692 N/06°12.250 E	54m	G

778 Table 2. Characteristics of the sampling sites for the genetic analyses. N initial, N all and N Marseille North indicate the initial number of
 779 samples, the number of samples retained for the complete analysis and the number of samples for the analysis focused on the two sites
 780 in the North of the Bay of Marseille respectively. The last columns present the estimates of gene diversity within ($1-Q_{intra}$) and among in-
 781 dividuals ($1-Q_{inter}$), and of F_{IS} computed with all samples and averaged over 49 215 loci. The lines with a grey background indicate the
 782 populations around 30 m depth.

783

Station	Code	Sampling date	N initial	N all	N Marseille North	$1-Q_{intra}$	$1-Q_{inter}$	F_{IS}
Yeux de chat	ODC	01/07/19	32	27	27	0.060	0.066	0.091
Catchoff - Station A	COF	01/07/19	32	28	28	0.061	0.067	0.087
Grand Congloue	GCO	30/04/19	7	6	-	0.058	0.064	0.099
Impérial du large	IMP	30/04/19	7	6	-	0.059	0.067	0.115
Sec Petit Langoustier	SPL	22/05/19	8	8	-	0.063	0.068	0.080
Cap d'Arme	CAA	22/05/19	8	7	-	0.058	0.066	0.127

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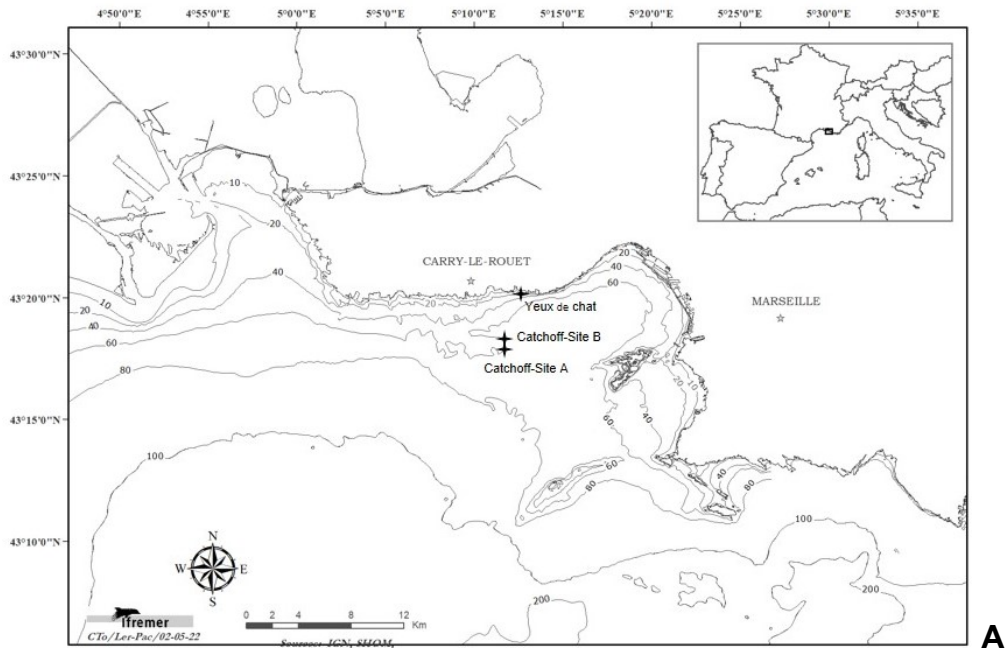
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790 Table 3. Pairwise F_{ST} for the whole dataset averaged over all loci. Grey areas highlight the comparisons between depths in the same
791 area. ODC: Yeux de chat; COF: Catchoff – Station A; GCO: Grand Congloue; IMP: Imperial du large, SPL: Sec Petit Langoustier; CAA:
792 Cap d'Arme.

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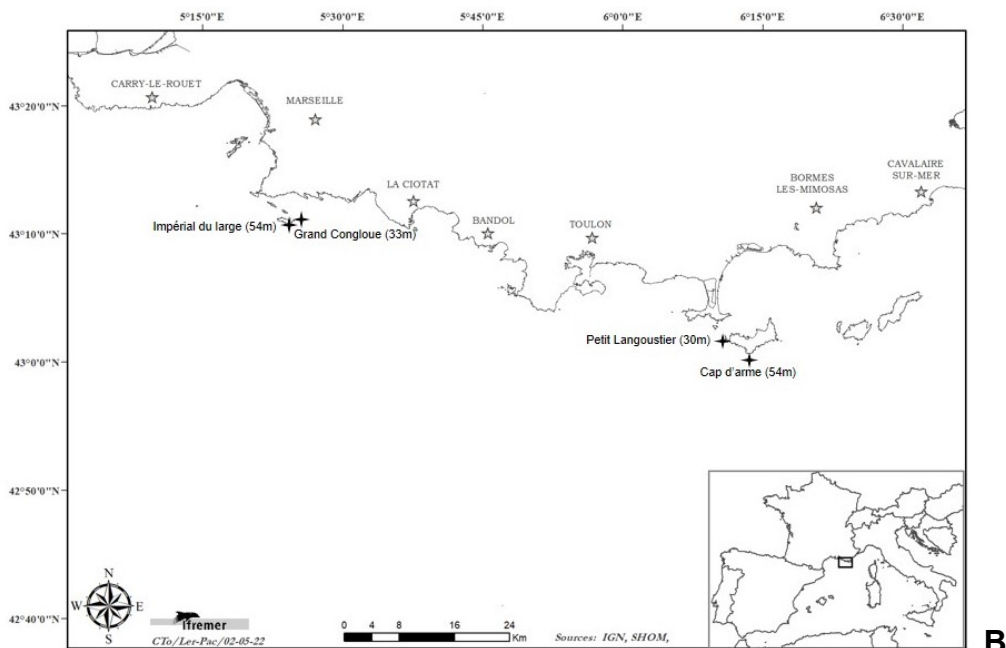
	ODC	COF	GCO	IMP	SPL	CAA
ODC	-					
COF	0.053	-				
GCO	0.046	0.053	-			
IMP	0.039	0.030	0.024	-		
SPL	0.044	0.041	0.043	0.027	-	
CAA	0.050	0.039	0.023	0.020	0.020	-

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A

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B

797 Fig. 1. Location of studied *Paramuricea clavata* populations. A: Catchoff-station A, Yeux
 798 de Chat (temperature and current monitoring, transplant experiment, density and size
 799 structure) and Catchoff-station B (density and size structure). B: Additional sites selected
 800 for the genomic analysis of *Paramuricea clavata* populations.

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Catchoff-Station A (-60m)

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Yeux de Chat (-30m)

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806 Fig. 2. Temperature of sea water surrounding *Paramuricea clavata* populations studied.

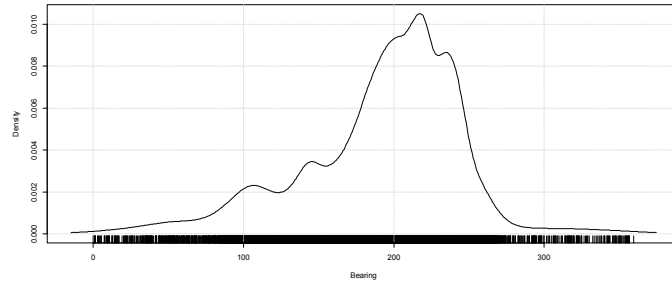
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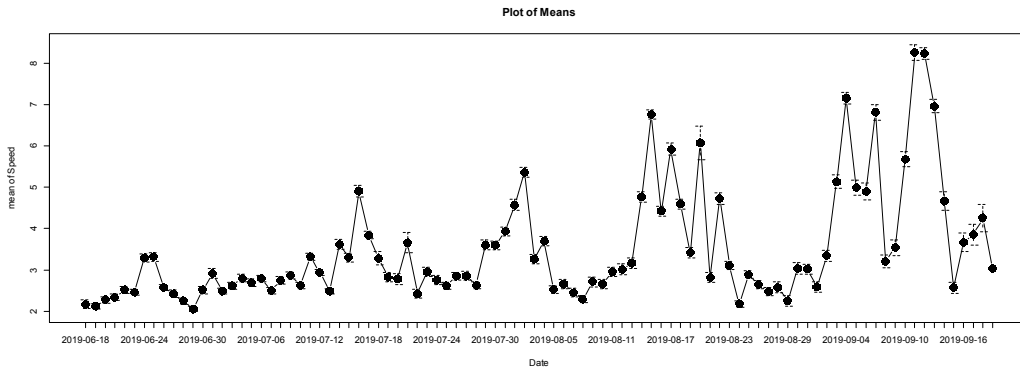
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809 **A**

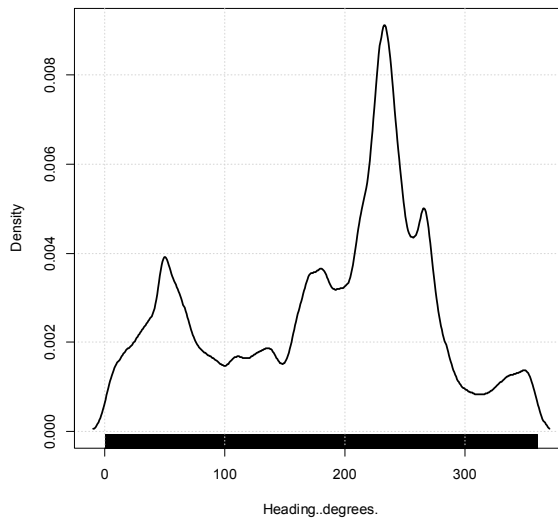


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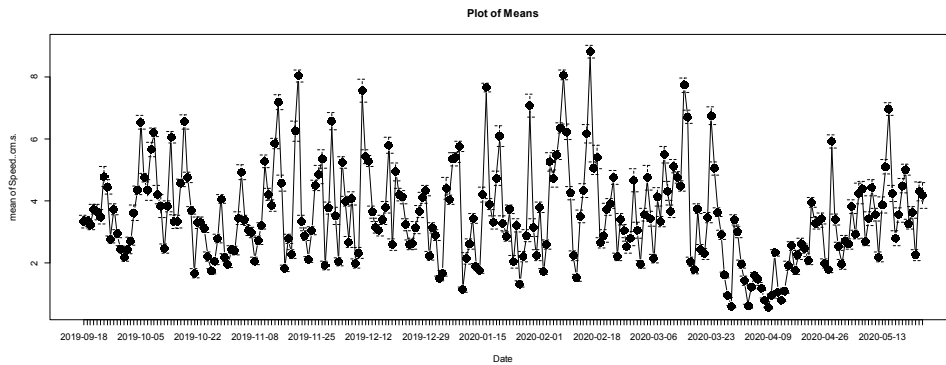


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812 **B**



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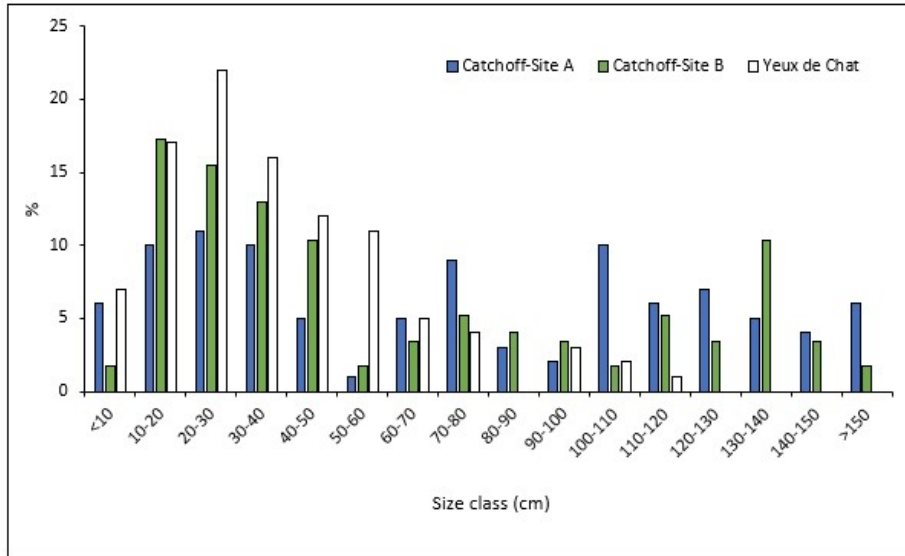
815 Fig. 3. Characterisation of the courantology in Catchoff-Station A (High: bearing in degree,

816 Low: speed in cm.s⁻¹). A: summer period; B: winter period.

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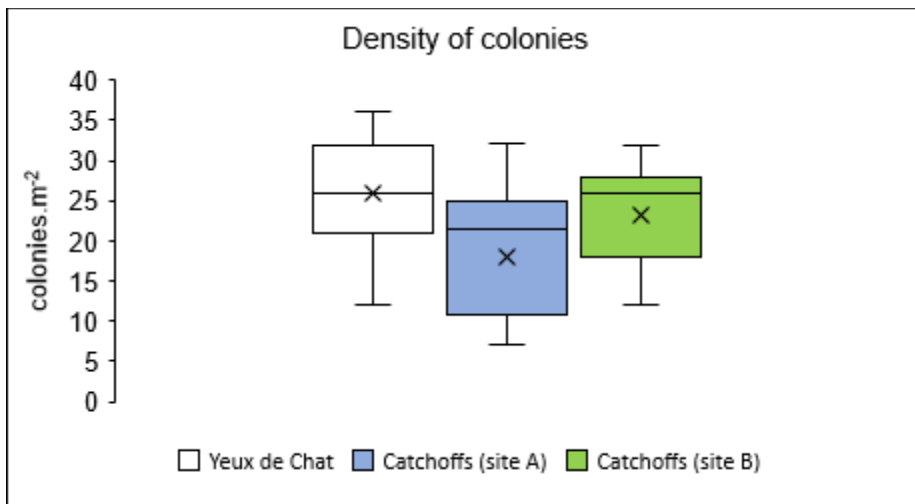
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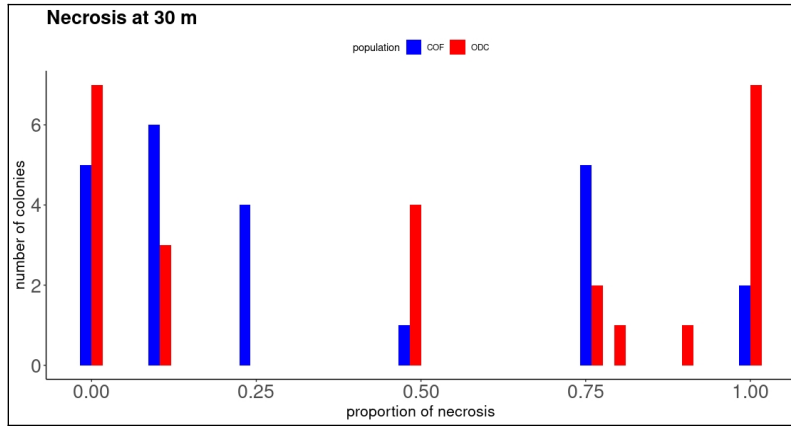
822 Fig. 4. Characterisation of *Paramuricea clavata* populations: size structure (up) and den-
823 sity of colonies (down).

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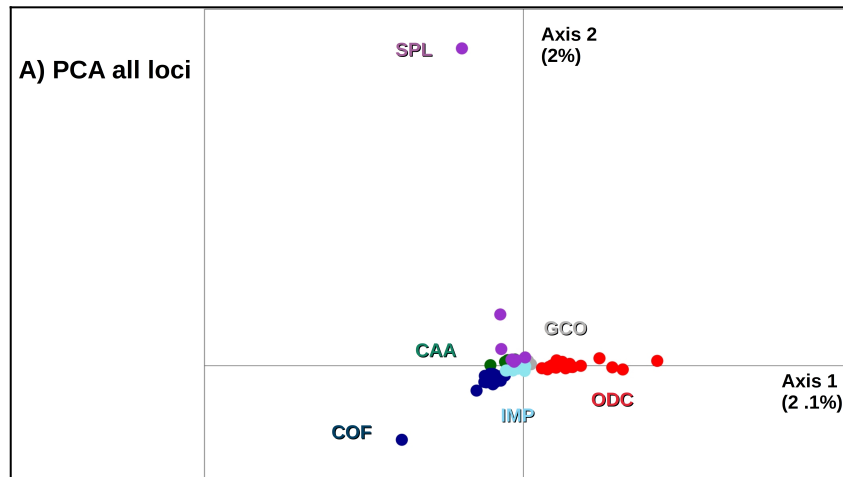


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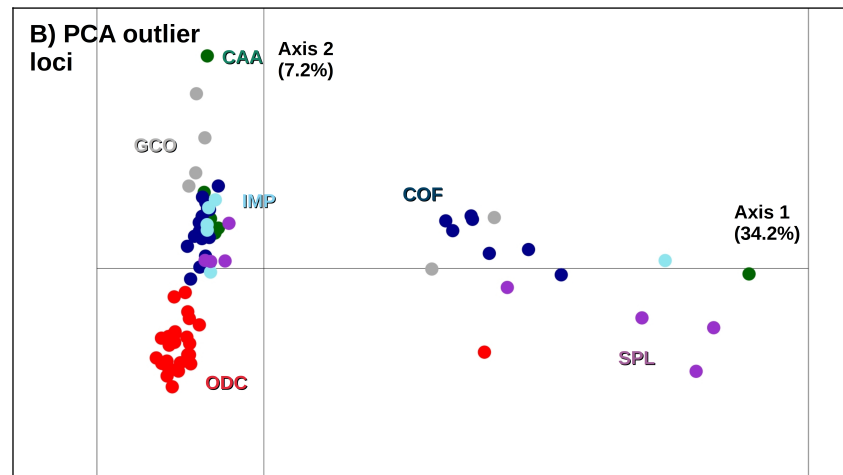
827 Fig. 5. Survival rate of *Paramuricea clavata* transplants after one year of experiment. COF:

828 Catchoff-Station A; ODC: Yeux de Chat station.

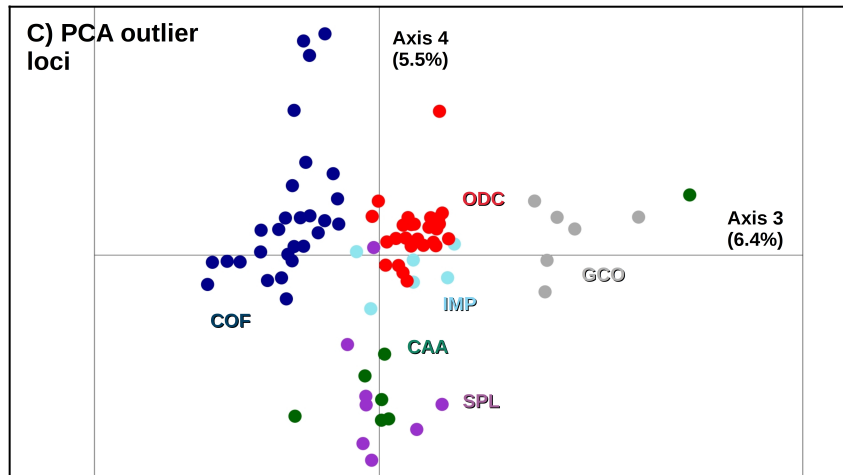
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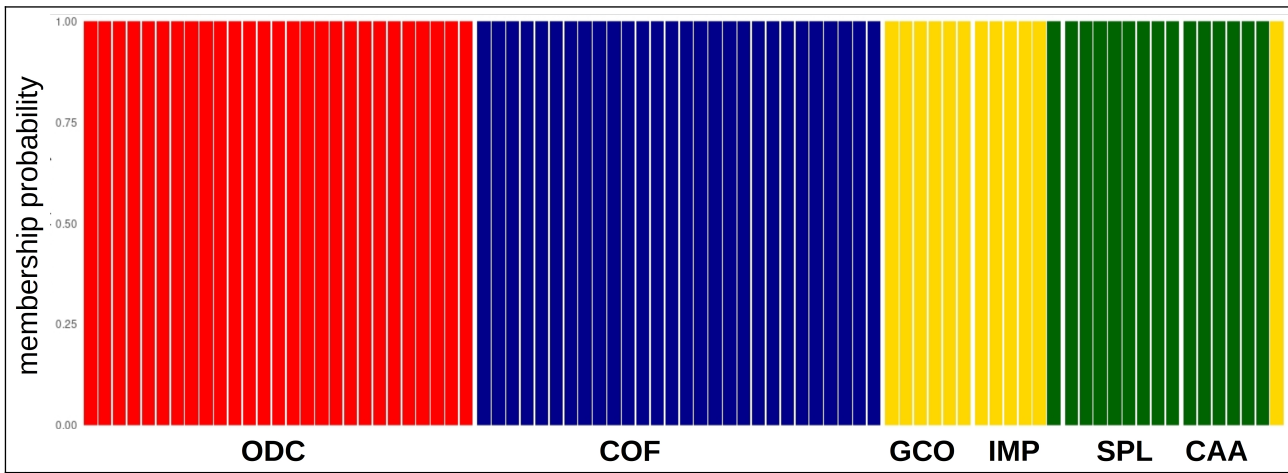
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833 Fig. 6. Plots of individual colonies with the PCA analysis. The numbers in brackets indicate
 834 the percentages of inertia for the corresponding axes. A) PCA on all 49 215 loci; B) PCA
 835 on the 267 outlier loci identified with padapt; C) PCA on the 267 outlier loci identified with
 836 padapt. COF: Catchoff – Station A; GCO: Grand Congloue; IMP: Impérial du large; SPL:
 837 Sec du Petit Langoustier; CAA: Cap d'Arme.

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839 Fig. 7. Barplot of the results of the DPAC analysis for K= 4 clusters. ODC: Yeux de Chat;
 840 COF: Catchoff – Station A; GCO: Grand Congloue; IMP: Impérial du large; SPL: Sec du
 841 petit langoustier; CAA: Cap d’Arme.

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1 SUPPLEMENTARY TABLES

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3 Table S1. Pairs of sequencing replicates (with grey background) and of samples separated
 4 by *p distance* similar or lower than distances observed for replicates (on the basis of
 5 51 439 RAD loci obtained with ipyrad; see table S3). The read numbers correspond to the
 6 number of reads after the Kraken analysis. For each sample pair, we retained the sample
 7 with the highest number of reads for further analyses. See main text for details. PCCOF:
 8 Catchoff – Station A; PCODF: Yeux de chat; PCIMP: Impérial du large; PCGCO: Grand
 9 Congloue.

Sample 1	Reads	Sample 2	Reads	<i>p distance</i>
PCCOF58-17	7708166	PCCOF58-17-2	6,380,908	0.018
PCCOF58-8	6733912	PCCOF58-8-2	9,117,315	0.022
PCODC30-25	5057861	PCODC30-25-2	4,444,312	0.027
PCODC30-9	6613213	PCODC30-9-2	4,153,968	0.022
PCODC30-21-2	4365254	PCODC30-5	6,556,789	0.020
PCODC30-18	9148556	PCODC30-20-2	5,220,776	0.018
PCIMP54-18	6264317	PCIMP54-13	5,090,699	0.020
PCGCO33-8	6548623	PCGCO33-4	6,513,661	0.025

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12 Table S2. Number of loci retained at each filtering step for all populations, with the soft-
13 ware used at each step. The final dataset included 49,215 SNPs for 82 samples.

	retained loci	software
total_prefiltered_loci	109,1960	ipyrad
filtered_by_rm_duplicates	109,1960	ipyrad
filtered_by_max_indels	109,1960	ipyrad
filtered_by_max_SNPs	109,1081	ipyrad
filtered_by_max_shared_het	108,7331	ipyrad
filtered_by_min_sample	51,439	ipyrad
max 75 % of missing data, 2 alleles per SNP, no LD, one SNP per locus	49,215	vcftools and GBS_SNP_filter

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16 Table S3. Number of loci retained at each filtering step for the analysis of the two sites in
17 the North of the Bay of Marseille, with the software used at each step. The last two lines
18 correspond to the dataset Mars_1 and Mars_2 respectively, with 55 samples in both
19 cases.

	retained loci	software
total_prefiltered_loci	757,308	ipyrad
filtered_by_rm_duplicates	757,308	ipyrad
filtered_by_max_indels	757,308	ipyrad
filtered_by_max_SNPs	756,695	ipyrad
filtered_by_max_shared_het	751,168	ipyrad
filtered_by_min_sample	62,313	ipyrad
max 75% missing data per locus, 2 alleles per SNP, no LD, one SNP per locus	49,215	vcftools and GBS_SNP_filter
no missing data per locus, 2 alleles perSNP, no LD, one SNP per locus	7,653	Vcftools and GBS_SNP_filter

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21 Table S4. Demographic inferences for the ODC (Yeux de Chat) and COF (Catchoffs – Sta-
22 tion A) populations. The model used for inferences is presented in Figure S2. The esti-
23 mated parameters are effective sizes N_{COF} and N_{ODC} for COF and ODC respectively,
24 the gene flows $M_{\text{ODC_COF}}$ (from ODC to COF in forward time) and $M_{\text{COF_ODC}}$ (from
25 COF to ODC), and the divergence time (TDIV in generations). The first line presents the
26 value estimated for the best run (over 100 replicates) for the analysis of observed data.
27 The following lines indicate the statistics describing the distribution of the parameters over
28 50 non-parametric bootstraps: median, standard deviation, minimum and maximum val-
29 ues. The computation was performed with a mutation rate of 2.9×10^{-8} / site / generation
30 as estimated in *Acropora* corals by Mao et al. (2018).

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	N_{COF}	N_{ODC}	$M_{\text{ODC_COF}}$	$M_{\text{COF_ODC}}$	TDIV
Best run	5,378	1,247,133	0.0041	< 0.0001	1987
Median	12,507	1,710,848	0.0018	< 0.0001	5004
Standard deviation	5,879	714,299	0.0053	< 0.0001	2161
Minimum	954	183,719	0.0010	< 0.0001	384
Maximun	20,015	2,651,810	0.0251	< 0.0001	7815

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36 SUPPLEMENTARY FIGURES

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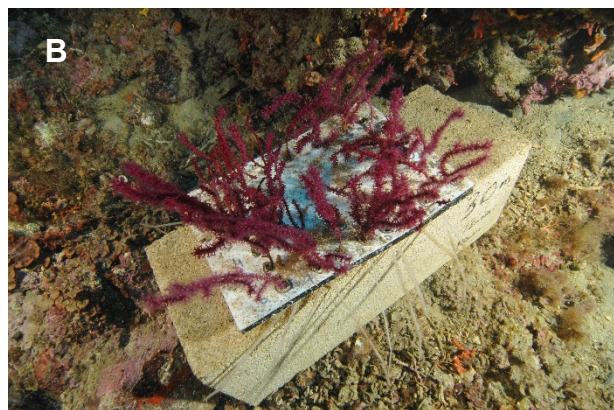


40 Fig. S1. Temperature sensor (left) and current meter (right) used to characterize the envi-
41 ronment in the Catchoff site (Annex).

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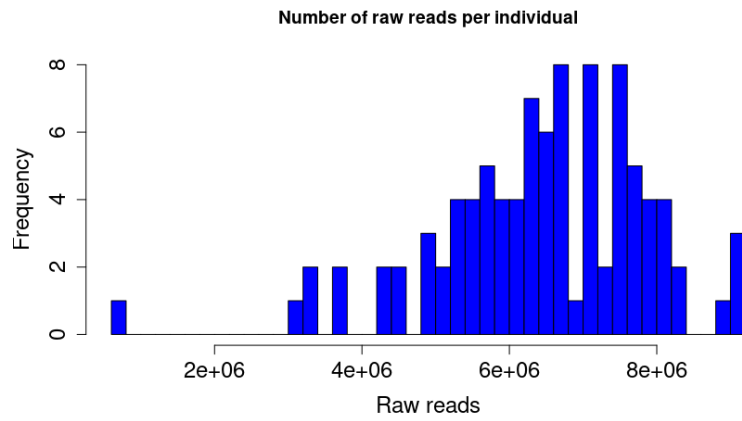
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45 Fig. S2. Open quadrat used to characterize the size structure (50x50cm) (A) and Experi-
46 ment design for the transplantation of *Paramuricea clavata* colonies (samples of colonies
47 are fixed on a plastic plate and numbered) (B).

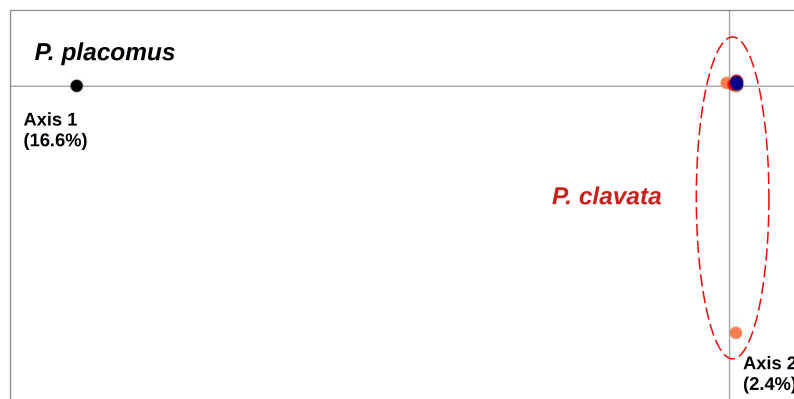
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51 Fig. S3. Distribution of the number of raw reads per individuals obtained with RAD-se-
52 quencing.



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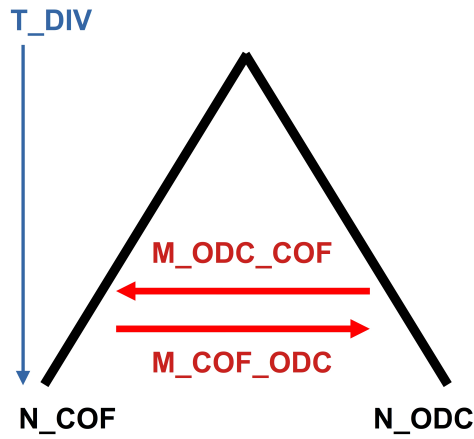
54 Fig. S4. Results of the preliminary PCA including *P. clavata* and *P. placomus* (one individ-
55 ual). The analysis is based on 45 251 SNPs.

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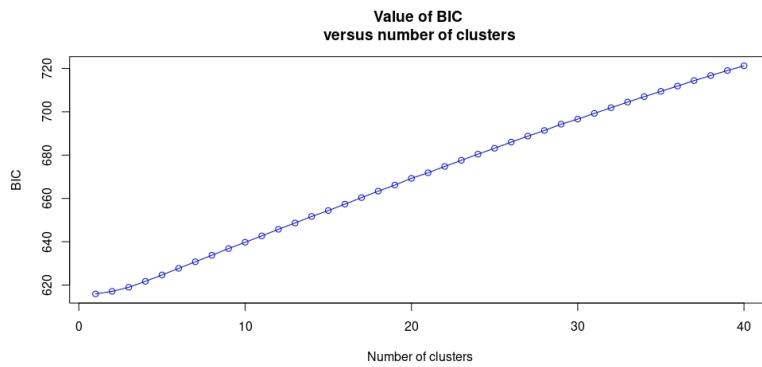
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60 Fig. S5. Model of evolution used for demographic inferences with fastsimcoal2. This is a
61 model of divergence with gene flow. T_{DIV} indicates the time of divergence,
62 M_{ODC_COF} and M_{COF_ODC} the gene flow (forward in time) between the two popula-
63 tions, N_{COF} and N_{ODC} the effective size of populations COF and ODC respectively.

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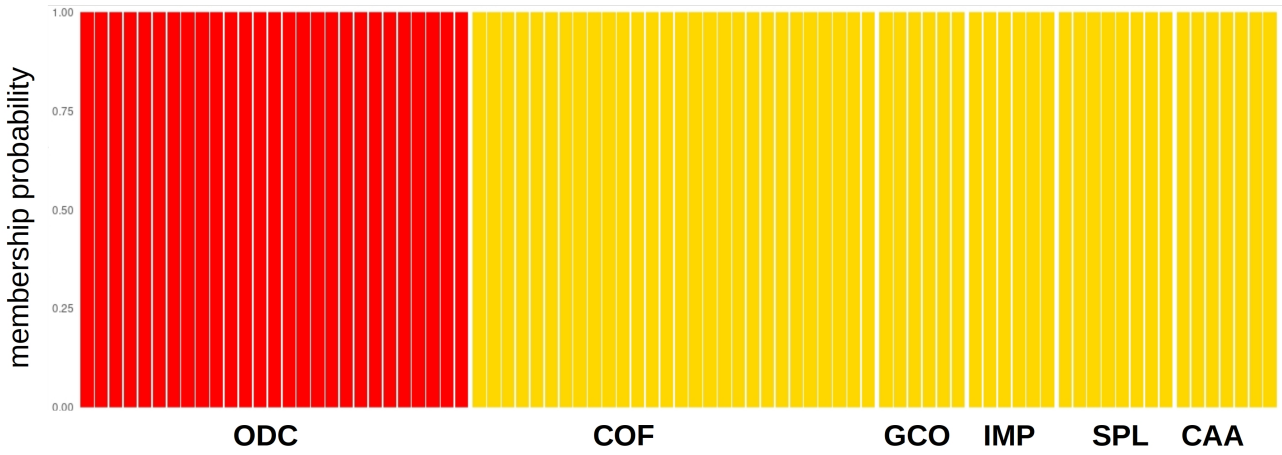
66 Fig. S6. Evolution of the BIC parameter according to the number of clusters for the DAPC
67 analysis.

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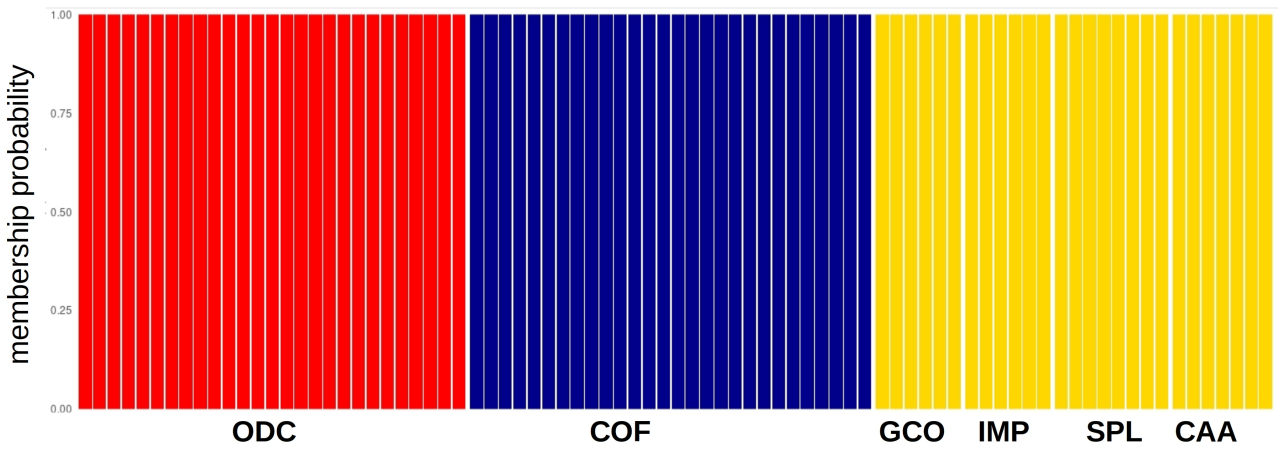
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72 **B)**



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74 Fig. S7. Barplot of the results of the DPAC analysis for A) K= 2, and B) K = 3 clusters.

75 ODC: Yeux de Chat; COF: Catchoff – Station A; GCO: Grand Congloue; IMP: Impérial du

76 large; SPL: Sec du petit langoustier; CAA: Cap d'Arme.

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**NOTE D'UTILISATION DU BLOQUEUR
POUR LE SYSTEME DE MOUILLAGE
AU FLOTTEUR COULISSANT**

→ Qu'est-ce que le bloqueur ?



Le bloqueur proposé par le Parc Marin de la Côte Bleue est une plaque en bois renforcée permettant de bloquer le flotteur coulissant pour que l'ancre ne touche plus le fond afin de tirer l'ensemble du mouillage au mouleur.

Cette plaque est conçue pour être manipulable par une seule personne lorsque que le mouillage est suspendu. En effet, elle se fixe sur la ligne de mouillage avec une seule main pendant que l'autre main maintient le mouillage à la verticale.

→ Comment on l'utilise ?



Étape 1 - Le mouillage est mis à l'eau.



Étape 2 - Le ligne de mouillage est suspendu à la verticale et que l'ensemble du mouillage est tiré à la verticale.



Étape 3 - Le bloqueur est mis au bloc à l'ancre.



Étape 4 - Une fois installé, le bloqueur empêche que le ligne de mouillage ne retombe au fond.



Étape 5 - Le mouillage est tiré jusqu'à la surface du flotteur, ce qui permet d'arrêter le mouillage et de le laisser en place.



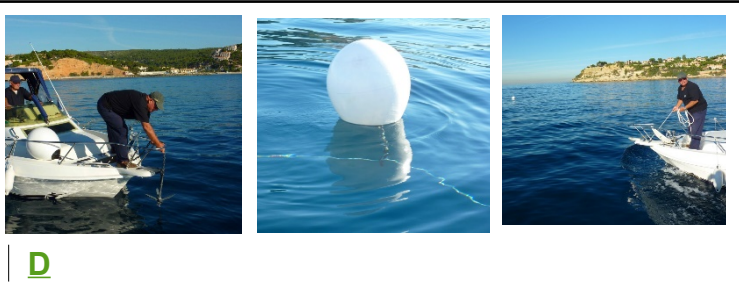
Étape 6 - Le mouillage est tiré jusqu'à la surface du flotteur et le mouillage est en place.

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Fig. S8. Impact of anchoring on giant *Paramuricea clavata* populations. A: Giant colony of *Paramuricea clavata* (h: 170cm) ripped apart by an anchor belonging to a small fishing boat; B: Giant colony of *P. clavata* (h: 152cm) brought to the Marine Park of the 'Côte Bleue' by a recreational fisherman; C: Group of fishing boats anchored on gorgonian population (15th November 2016); D: Mooring dropped with a sliding buoy on the Catchoff site by a recreational boat. When the fisherman uses his boat to pull it, the buoy stop the anchor at the surface. E: User instructions for the blocker used for a mooring with a sliding buoy (disposal implemented by the Marine Park of the 'Côte Bleue' to prevent the damage on the giant gorgonians). What is a blocker ? this is a reinforced wooden plate which can block the sliding buoy in order to keep straight the rope and the chain. How to use it ? the

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104 blocker can be installed by a person. In a first step, the mooring with the sliding buoy is
105 dropped until the anchor touch the bottom. In the next step, the mooring is pulled. When the
106 anchor begins to take off from the bottom, the blocker is fixed on the rope keeping away
107 the chain from the rocky substrate.

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