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Recovery of hydrothermal vent communities in response to an induced disturbance at the Lucky Strike vent field (Mid-Atlantic Ridge)

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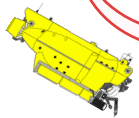
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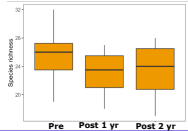
Graphical Abstract

Vent communities of
Bathymodiolus azoricus
Lucky Strike vent field
MAR, 1700 m

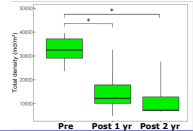
Experimental disturbance
by removing faunal
assemblages



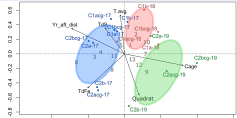
High recovery in taxonomic richness



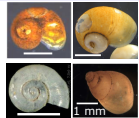
Incomplete recovery in faunal density



Assess the recovery and follow the recolonisation process within 2 years



Significant difference in faunal composition in **pre-disturbed**, **1** and **2** years after disturbance



Gastropod species pioneer colonists

1 **Recovery of hydrothermal vent communities in response to**
2 **an induced disturbance at the Lucky Strike vent field (Mid-**
3 **Atlantic Ridge)**

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20

21 Abstract

22 So far, the natural recovery of vent communities at large scales has only been evaluated at
23 fast spreading centres, by monitoring faunal recolonisation after volcanic eruptions. However,
24 at slow spreading ridges, opportunities to observe natural disturbances are rare, the overall
25 hydrothermal system being more stable. In this study, we implemented a novel experimental
26 approach by inducing a small-scale disturbance to assess the recovery potential of vent
27 communities along the slow-spreading northern Mid-Atlantic Ridge (nMAR). We followed the
28 recovery patterns of thirteen *Bathymodiolus azoricus* mussel assemblages colonising an active
29 vent edifice at the Lucky Strike vent field, in relation to environmental conditions and assessed
30 the role of biotic interactions in recolonisation dynamics. Within 2 years after the disturbance,
31 almost all taxonomic richness had recovered, with the exception of a few low occurrence
32 species. However, we observed only a partial recovery of faunal densities and a major change
33 in faunal composition characterised by an increase in abundance of gastropod species, which
34 are hypothesised to be the pioneer colonists of these habitats. Although not significant, our
35 results suggest a potential role of mobile predators in early-colonisation stages. A model of
36 post-disturbance succession for nMAR vent communities from habitat opening to climax
37 assemblages is proposed, also highlighting numerous knowledge gaps. This type of
38 experimental approach, combined with dispersal and connectivity analyses, will contribute to
39 fully assess the resilience of active vent communities after a major disturbance, especially
40 along slow spreading centres targeted for seafloor massive sulphide extraction.

41

42 **Key words:** Hydrothermal vent; *Bathymodiolus azoricus*; Disturbance; Colonisation; Recovery;
43 Deep-sea mining; Ecological succession; Benthic ecology; Mid-Atlantic Ridge

1. Introduction

Deep-sea hydrothermal vents are mainly distributed along mid-ocean ridges and back-arc basins. Vent communities are considered as productivity hotspots with a high level of endemic fauna (Tunnicliffe, 1991) that thrives mainly on chemoautotrophic primary production (Childress and Fisher, 1992). Faunal assemblages are often dominated by symbiotic foundation species such as siboglinid tubeworms, mytilid mussels, large provannid gastropods or alvinocaridid shrimps, which promote local diversity by providing 3D structures and enhancing habitat heterogeneity (Dreyer et al., 2005; Govenar and Fisher, 2007). At the edifice scale, faunal distribution consists in a mosaic of assemblages mainly influenced by environmental conditions and patchiness of fluid emissions (Sarrazin et al., 1997; Sarrazin and Juniper, 1999; Luther et al., 2001; Gollner et al., 2010; Marsh et al., 2012; Husson et al. 2017). Indeed, species colonise the mixing gradient depending on their physiological tolerance to environmental conditions, nutritional requirements and biotic interactions (e.g. predation, facilitation; Levesque et al. 2003, Mullineaux et al. 2003, Sancho et al. 2005). Biotic interactions were suggested to prevail in high diffuse-flow areas where the resources are not limited, while facilitation will predominate in habitats with lower fluid input (Mullineaux et al. 2003). As observed in coastal hard substrate communities, mosaics are highly dynamic and patches size and boundaries amongst the patches may change through time (Connell and Keough, 1985). At large spatial scale, the patchiness of vent habitat results in a network of metacommunities and population connectivity is insured by dispersal of planktonic larvae (Mullineaux et al., 2018).

Hydrothermal vents are naturally subject to stochastic major disturbance such as volcanic eruptions that may eradicate faunal assemblages at the vent-field scale. On the other hand, since the first discovery of hydrothermal vents and associated seafloor massive sulphide (SMS) deposits, more than 40 years ago, the interest of mining companies for commercial exploitation of their high metal content has been increasing (Corliss et al., 1979; Spiess et al., 1980; Van Dover, 2011). These industrial activity has not yet started, but it is predicted that they may induce different levels of impacts (Boschen et al., 2013; Cuvelier et al., 2018; Orcutt et al., 2020), including physical destruction of habitats and the complete eradication of their faunal communities within the mining site (Van Dover 2007). The creation of a sediment plume may also affect different biological processes, such as reproduction, dispersal, mobility

76 and feeding strategies at larger scale (Van Dover, 2010; Boschen et al., 2013; Gollner et al.,
77 2017; Suzuki et al., 2018; Washburn et al., 2019). However, there are still many uncertainties
78 about community resilience, and the time-scale needed for a possible recovery of the
79 impacted ecosystems (Cuvelier et al., 2018).

80 Disturbance in mosaic habitats such as active vents may play an important role in
81 initiating, maintaining or enlarging patches within established assemblages (Sousa 1985;
82 Denny 1987). The fundamental question of recolonisation and recovery of vent assemblages
83 after a disturbance can be studied in a metacommunity framework, using a patch dynamics
84 approach in which the colonisation and persistence of impacted area is highly dependent on
85 dispersal across vent fields and local disturbance regimes (Leibold et al., 2004; Mullineaux et
86 al., 2018). At local scale, the settlement of post-larvae is influenced by environmental
87 conditions and habitat suitability and recolonisation dynamics are also dependent on biotic
88 interactions that may induce facilitation or competitive exclusion (Mullineaux et al., 2003;
89 Sancho et al., 2005). Understanding processes acting at small scales are paramount in
90 evaluating mechanisms controlling successional dynamics after recolonisation by species from
91 afar.

92 At active vents, the few examples of recovery are based on studies linked to large-scale
93 natural disturbances caused by volcanic and tectonic activities (Butterfield et al., 1997;
94 Tunnicliffe et al., 1997; Shank et al., 1998; Marcus et al., 2009; Gollner et al., 2015a). The
95 frequency of such disturbances is highly variable among vent systems, depending on their
96 geological settings. At fast-spreading ridges, where vent sites are separated by a few
97 kilometers, volcanic eruptions occurs with time intervals of a decade (Tolstoy et al. 2006) and
98 macrofaunal communities show a fairly good recovery of diversity and densities within few
99 years following the various eruptions (Tunnicliffe et al. 1997; Shank et al. 1998; Marcus et al.
100 2009; Gollner et al. 2015a, 2017, 2020). However, differences in the sampling methodology
101 between these studies (e.g. some used visual surveys while others sampled faunal
102 assemblages) and the faunal compartment considered lead to differences in the estimation of
103 recovery rates. Moreover, little information about the pre-disturbed baseline communities
104 was available, making the comparison with post-disturbance communities difficult.
105 Differences in community composition after re-colonisation were also observed (Mullineaux
106 et al., 2020, 2012) and the prolonged monitoring of diversity showed that community
107 composition was still changing ten years after the disturbance, suggesting that the disturbed

108 assemblages did not reach a climax stage during this time period (Mullineaux et al., 2020).
109 Conversely, at slow spreading ridges, vent sites are separated by hundreds of kilometers
110 (Beaulieu et al., 2015) and opportunities to observe natural disturbances are rare. Therefore,
111 assessing the recovery ability of communities requires the use of alternative indirect
112 approaches. One way is to use population connectivity data to estimate the recolonisation
113 potential of key species, and thus infer vent community recovery rates (Baco et al., 2016;
114 Breusing et al., 2016) as it was done by Suzuki et al. (2018). Their dispersal network analysis
115 on species from 131 vent fields of the western Pacific Ocean estimated that a full recovery to
116 original communities would take from 6 to 130 years. The slow recovery rate estimated in
117 comparison to fast-spreading centers may notably be due in part to differences in topography
118 that may reduce horizontal dispersal and connectivity (Mullineaux et al. 2018). However, this
119 approach based on dispersal ability does not take into account the local factors influencing
120 faunal establishment and many uncertainties remain regarding the role of biotic and abiotic
121 conditions in recolonisation dynamics and ecological succession once the larvae reach the
122 disturbed area.

123 In the present study, we provide an early evaluation of the recovery potential of active
124 vent communities to a small-scale (< 1 m²) disturbance experiment initiated in 2017 on the
125 Lucky Strike (LS) vent field, northern Mid-Atlantic Ridge (nMAR). After removing the fauna, we
126 followed during 2 years the recolonisation dynamics of *Bathymodiolus azoricus* mussel
127 assemblages and their habitats on a series of experimental quadrats. This experimental setting
128 allowed us to describe the pre-disturbed structure of vent communities on the Montségur
129 edifice (LS) and to monitor the recolonisation of benthic communities after the disturbance.
130 The main objective of this work is to identify the role of biotic and abiotic conditions on
131 recolonisation dynamics at the edifice scale, through the use of cages and measurements of
132 environmental conditions. We expected that microbial communities would first colonise the
133 bare substratum, followed by grazers (including several species of gastropods) that may feed
134 on microbial mats. The engineer species *B. azoricus* would take more time to fully occupy the
135 space, its presence facilitating the establishment of associated taxa and contributing to
136 increasing diversity. We anticipated that mobile predators (e.g. shrimps, crabs or fishes) would
137 play a major role in patch colonisation, influencing the first step of recovery. Although the
138 scale and target of this experiment strongly differ from large-scale disturbance, our results

139 provide fundamental knowledge on recolonisation patterns of active hydrothermal vent
140 habitats at the edifice scale.

141 2. Material and methods

142

143 2.1. Study site

144 The Lucky Strike (LS) vent field is a basalt-hosted vent field situated close to the Azores Triple
145 Junction on the northern part of the Mid Atlantic Ridge (MAR) (Langmuir et al., 1997) (Fig. 1A).
146 LS contains over twenty active hydrothermal edifices distributed around a circular fossilised
147 lava lake at an average depth of 1700 m (Ondreas et al., 2009). Montségur is a small active
148 sulphide edifice that extends over a surface of 24 m x 16 m. It is located on a flat hydrothermal
149 slab at the south-east of LS (Fig. 1B). At least seven black smokers have been identified on the
150 edifice, in addition to the extensive diffuse low-temperature discharges through cracks at its
151 base and on its flanks (Barreyre et al., 2014). Montségur is covered by dense mussel
152 assemblages of the engineer species *Bathymodiolus azoricus*. Vent faunal communities
153 inhabiting diffuse flow areas on and around the edifice are characterised by high-density
154 populations of gastropods (*Protolira valvatoides*, *Lepetodrilus atlanticus*, *Pseudorimula*
155 *midatlantica*), polychaetes (*Branchiopolynoe seepensis*, *Amphisamytha lutzi*) and shrimps
156 (*Mirocaris fortunata*) (Sarrazin et al. 2020).

157 2.2. Experimental setup

158 In July 2017, an experimental setup was deployed during the Momarsat cruise on board the
159 R/V “*Pourquoi pas ?*” using the Remotely Operated Vehicle (ROV) *Victor6000*. Thirteen
160 stainless steel quadrats (50 x 50 cm), equipped with pyramidal structures on top, were
161 installed over *Bathymodiolus azoricus* assemblages (Fig. 2), on the steep walls of the
162 Montségur edifice or in cracks at its base (Fig. 1C), to account for spatial variability of vent
163 assemblages. Eight of them, named “experimental quadrats”, were devoted to the study of
164 recolonisation processes following faunal clearance after 1 (C1) and 2 (C2) years (August 2018
165 and June 2019 respectively). Replicate samples for each year were denoted as “a” or “b” (Fig.
166 1C). In addition to the experimental quadrats, five “reference” quadrats (R) were deployed
167 and sampled in 2017 (R0a, R0b), 2018 (R1) and 2019 (R2, R2cg) to characterise the natural
168 dynamics of faunal communities on Montségur throughout the experiment. The role of large
169 mobile predators (crabs, shrimp or fish) on local recolonisation was examined by covering

170 some of the pyramidal structures with a 1 cm plastic mesh. These specific quadrats were
171 denoted as "cg" for caged (Fig. 2C). This experimental design is summarised in Figure 3.

172

173 2.3. Environmental characterisation

174 Temperature and key chemical parameters were assessed from *in situ* measurements on all
175 quadrats before and after faunal sampling and this, for each year of the study (2017 to 2019).
176 Our objectives were to identify the spatial and temporal variability of these factors and
177 evaluate their role in the recolonisation processes. The *in situ* chemical analysers CHEMINI
178 (Vuillemin et al., 2009) were used on three replicate points in each quadrat to measure
179 dissolved concentration of total sulphides [TdS : $\text{H}_2\text{S} + \text{HS}^- + \text{S}_2$] and total dissolved iron [TdFe :
180 Fe (II)]. To complete the chemical characterisation, water samples were collected with the
181 PEPITO water sampler at each quadrat prior to faunal sampling (Sarradin et al., 2009). Oxygen
182 concentrations were measured using an Aanderaa optode probe (Tengberg et al. 2006)
183 connected to the outlet of the PEPITO sampler. Methane [CH_4], was analysed back in the
184 laboratory by GC-FID and HID (Donval et al. 2008). In addition to this one-time yearly
185 characterisation, temperature was monitored every 2 hours over the deployment period using
186 two iButtons™ probes attached to each quadrat and deployed directly on the mussel
187 assemblages with a measurement resolution of 0.5 °C.

188

189 2.4. Faunal sampling and identification

190 During the Momarsat 2017 cruise, eight experimental quadrats -noted "C"- were cleared of
191 their fauna using both the suction sampler and the claw of the ROV *Victor6000* mechanical
192 arm (Fig. 2A, 2B). The same year, R0a and R0b reference quadrats were also sampled, leading
193 to a total of 10 quadrats used to describe the pre-disturbed vent community of Montségur
194 (Fig. 3). During Momarsat 2018, the four experimental quadrats dedicated to the "one-year
195 after disturbance recolonisation study" -noted "C1"- and reference quadrat R1 were sampled
196 (5 quadrats in total; Fig. 3). During the Momarsat 2019 cruise, the four experimental quadrats
197 dedicated to the "two-year after disturbance recolonisation study" noted "C2"-and reference
198 quadrats R2 and R2-cg were sampled (6 quadrats, Fig. 3). The surface area of each quadrat
199 was filmed before and after faunal sampling with the ROV high definition cameras to estimate

200 the sampled surfaces using imagery analysis (Fig. 2A, 2B). A target with 7 mm checkerboard
201 squares was fixed on each quadrat, providing scaling in the field of view (Fig. 2B).

202 In this study, fauna will include macrofauna and any meiofauna taxa larger than 250 μm
203 (nematodes, copepods and ostracods). We also include species often considered as
204 megafauna (shrimp, mussels) recovered within the quadrats. The faunal samples were
205 preserved in 96% ethanol. All individuals collected were identified to the lowest possible
206 taxonomic level under a stereomicroscope and counted.

207 2.5. Population size structure

208 Size-frequency distributions of the six most dominant species were analysed for each sample
209 of the Montségur edifice. Each individual was measured, using different measurements
210 depending on the species (see details in Table S1). The biggest individuals were measured
211 using a caliper while small individuals were measured on screen to the nearest 0.001 mm,
212 using the Leica Application Suite software. Measurement error was calculated as the
213 maximum difference among 10 measurements of the same individual on 10 specimens
214 comprising a range of all sizes for each species (Table S1). For each assemblage sampled,
215 length-frequency distribution was plotted for the six species. Size class intervals were chosen
216 according to three criteria: i) most size-classes must have at least five individuals; ii) the
217 number of adjacent empty classes must be minimised; and iii) the interval has to be greater
218 than the measurement error (see Jollivet et al. 2000). Size-frequency distributions were
219 compared to a normal distribution using a one-sample Kolmogorov-Smirnov test and
220 differences between the pre-disturbed and post-disturbance communities were identified
221 using a pairwise Kolmogorov-Smirnov test. Non-parametric Wilcoxon-Mann-Whitney tests
222 were performed to identify differences in mean individual size between the pre-disturbed
223 community and the novel one, after the recolonisation processes in each location.

224 2.6. Data analyses

225 All analyses were computed in R environment (R Core Team, 2018). Species rarefaction curves
226 were computed for each sample, habitat and year to verify the robustness of the sampling
227 effort and characterise the overall diversity. Local diversity was estimated for each assemblage
228 by computing α -diversity indices such as species richness (S), Shannon entropy (H) and the
229 Pielou's evenness index (J') using the vegan package in R (Oksanen et al., 2019). Contingency

230 tables were weighted by the sampling surface for each quadrat for comparison purposes. The
231 resulting density data were used for all subsequent analyses.

232 **Environmental conditions** – The temperatures measured by the iButtons™ probes were used
233 to characterise each assemblage/quadrat. Four temperature parameters were compiled,
234 including the average (T.avg), minimum (T.min), maximum (T.max) and standard deviation
235 (T.sd). In addition, average concentrations of oxygen (O₂), methane (CH₄), total dissolved iron
236 (TdFe) and sulphides (TdS) as well as standard deviations of TdFe and TdS were used to
237 characterise the spatial variability of abiotic factors among the different Montségur quadrats.
238 A principal component analysis (PCA) was built with all environmental variables (packages
239 FactoMineR and factoextra - Kassambara and Mundt 2019) to identify patterns in
240 environmental conditions among quadrats and determine which variables accounted for most
241 of the observed variance. Finally, Whittaker-Robinson periodograms, programmed in the R
242 package adespatial (Dray et al., 2020) were used to screen for significant periodicities in
243 temperature time series.

244 **Community structure** – A canonical redundancy analysis (RDA) was performed on Hellinger-
245 transformed densities and environmental variables retained by a forward selection (vegan
246 package - Oksanen et al. 2019) to evaluate the spatial variability of community composition in
247 relation to abiotic factors in the baseline communities on the Montségur edifice. This allows
248 us to evaluate the representativeness of baseline communities in Montségur in comparison
249 with faunal assemblages already described on other active edifices of the Lucky Strike vent
250 field.

251 **Recovery patterns** – Faunal recovery patterns were assessed from experimental quadrats.
252 Differences in faunal composition among quadrats along the recolonisation processes were
253 tested using a non-parametric analysis of similarity (ANOSIM; Anderson 2001). The ANOSIM R
254 value is based on differences in average ranking of dissimilarity indices (i.e. Bray-Curtis
255 dissimilarity matrix) between and within the different predefined groups (here each recovery
256 stage, i.e.: pre-disturbed state, one year and two years after disturbance). A RDA on Hellinger-
257 transformed densities data was also used to identify the role of environmental conditions and
258 biotic interactions (i.e. by testing the cage effect) on the structure of macrofaunal assemblages
259 during the recolonisation processes. A variable named “quadrat” was used to evaluate the
260 independence of the samples from the same quadrat over the years in the explanatory

261 environmental matrix. Moreover, to test for the effect of time after disturbance, we coded a
262 quantitative variable named “Yr-aft-dist” (i.e. year after disturbance). In this framework, pre-
263 disturbed reference samples were considered as baseline communities at an equilibrium state
264 and thus were coded with a value greater than 2 years. As the age of the natural community
265 is unknown, analyses were run with different values [3 years, 10 years and 100 years] but they
266 all yielded to similar results. Based on previous studies about the temporal stability of these
267 communities (more than 14 years on Eiffel Tower, Cuvelier et al. 2011b) and data about
268 recovery time in other vent system after a major disturbance (4-5 years, Gollner et al. 2017),
269 we considered 10 years as a good compromise to be used for the analysis.

270

271 3. Results

272 3.1. Environmental conditions

273 Mean temperature among the different quadrats of Montségur varied between 5.2 °C and 9.5
274 °C (Table 1). R1 and C2a exhibited the highest maximum temperatures (with maximum of 16.1
275 °C and 22.1 °C respectively), but also higher concentrations in TdFe and CH₄ associated with a
276 more acidic pH (Table 1, Fig. S1).

277 The two temperature probes separated by ~ 10 cm deployed on each quadrat were used to
278 characterise the spatial variability of abiotic conditions at fine scales. While homogeneous
279 temperatures are observed within some quadrats (e.g. C1a, C1bcg, C2b, C2bcg), others
280 showed a high variability of temperatures in the narrow spatial gradient (few centimetres, e.g.
281 C1b, C2acg); (Fig. S2).

282 Notable differences in temperature on single quadrats between the two years were observed.
283 C1b, C1acg and C2a quadrats showed a sharp decrease in mean and variability of
284 temperatures at different times during the first year of deployment (Fig. S2). Periodogram
285 analyses carried out on temperature time series revealed significant periods of 12 h for most
286 quadrats. In addition, significant periods of 24 h were also identified on all quadrats except
287 C1acg. Additional periodic signals, possibly harmonics related to the tidal signal, with periods
288 of 36 h and 48 h, were also revealed for C1a, C1acg and C1bcg.

289 3.2. Pre-disturbed communities

290 The rarefaction curves built for each pre-disturbed sample of Montségur (Fig. S3) nearly
291 reached an asymptote showing that the sampling effort was sufficient to capture the overall
292 taxonomic diversity of macrofaunal benthic communities of active vent habitats. In total, 43
293 taxa were identified among a total of 34 158 individuals in the different samples. Most
294 assemblages were characterised by a taxonomic richness varying between 19 and 28 (Table
295 S2). The C1a sample, which is the only quadrat located on the west side of the edifice,
296 displayed the highest taxonomic richness with the occurrence of 32 taxa, while R2 showed
297 only 12 taxa among 133 identified specimens (Fig. 4; Table S2). Macrofaunal communities
298 were dominated by six taxa: the engineer species *Bathymodiolus azoricus* and its commensal
299 worm *Branchipolynoe seepensis*, the polychaete *Amphisamytha lutzi* and three species of
300 gastropods *Lepetodrilus atlanticus*, *Protolira valvatoides* and *Pseudorimula midatlantica*.
301 Together, they accounted for $68.3 \pm 15.7\%$ of the total abundance. The nematode
302 *Oncholaimus dyvae* and copepod *Aphotopontius sp.*, which are typical meiofaunal species,
303 were also abundant in the $> 250 \mu\text{m}$ fraction of most samples. In the pre-disturbed
304 community, $\sim 74\%$ of taxa (e.g. 29 taxa over 43) showed low occurrence and abundance (i.e.
305 below 1% frequency) in the different samples (Table S3).

306 A RDA has been performed to identify the role of environmental conditions on faunal
307 distribution and verify the temporal stability of baseline communities. The RDA model
308 performed on Hellinger-transformed species densities accounted for 49.6% (adjusted R^2 :
309 25.1%, $p = 0.008$) of the total inertia in macrofaunal species assemblage structure (Fig. 5). The
310 overall RDA model was significant (p -value = 0.004) and only the first axis was significant ($p =$
311 0.05), accounting for 20% of the variation in community structure. Maximum temperature
312 (T.max) and total dissolved sulphide concentrations (TdS) were the significant environmental
313 factors influencing macrofaunal composition ($p = 0.009$ and 0.021, respectively). The years at
314 which the samples were collected did not explain the differences between quadrats. R2cg
315 sample stood out from the other sampling locations and was characterised by a high relative
316 density of the gastropod *Lurifax vitreus*, contrasting with a low density of *B. azoricus* (Fig. 5).
317 Moreover, the C2acg and R0b samples, characterised by a high density of amphipods (*Luckia*
318 *striki*), formed a distinct group (Fig. 5). All other samples showed a quite homogeneous faunal
319 composition.

3.3. Recovery patterns of benthic communities

320 **Recolonisation dynamics of the foundation species** – The recovery rate of *Bathymodiolus*
321 *azoricus*, in terms of density, varied between 9.7% and 37.6% on the different quadrats one
322 year after disturbance, and from 1.9% to 33% two years after disturbance (Fig. 6). No
323 significant difference can be noticed between the mean recovery rate after 1 year ($19.8 \pm 13\%$)
324 and 2 years of recolonisation ($14.4 \pm 13.5\%$) (Student test: $t = 0.59$, $p\text{-value} = 0.58$). However,
325 with the exception of the C2bcg quadrat, the percentage of recovery was slightly higher in the
326 quadrats that were caged during the recolonisation process ($>20\%$) compared to the uncaged
327 quadrats ($<15\%$) (Fig. 6). The size population structure analyses of *B. azoricus* showed
328 individuals ranging from 251 μm to 8.5 cm length within the different assemblages (Fig. 6).
329 The pre-disturbed structure of the population on Montségur showed a polymodal size
330 distribution dominated by a large proportion (i.e. 52% of the overall population) of small
331 individuals below 5 mm in shell-length and a tail of distribution in larger sizes containing
332 several cohorts (Fig. 6). Pairwise Kolmogorov-Smirnov distribution tests showed significant
333 differences in population size structure between the pre-disturbed and post-disturbance
334 communities in all samples ($p\text{-value} < 0.001$), except C2b ($D = 0.10$, $p\text{-value} = 0.13$) (Fig. 6).
335 Furthermore, Wilcoxon-Mann-Whitney tests highlighted that the mean shell length of *B.*
336 *azoricus* was smaller 1 and 2 years after the disturbance compared to that of the pre-disturbed
337 community for all samples except C1a and C2b (Fig. 6). Furthermore, the proportion of
338 juveniles of *B. azoricus* (< 5 mm) in the overall population was higher in assemblages sampled
339 1 year (67%) and two years (70%) after the disturbance in comparison to pre-disturbed
340 populations (52%) (Table S3).
341

342 **Recolonisation dynamics of active vent communities** – The rarefaction curves did not level
343 off for most of the post-disturbance samples on Montségur, but they show similar trends than
344 that of pre-disturbed communities (Fig. S3). The shape of the curves indicate that they should
345 reach a plateau earlier, highlighting a higher evenness in the recovering communities. Species
346 richness (S) is lower (from 1 to 6 less species) in the post-disturbance assemblages compared
347 to the pre-disturbed communities 1 year after the induced disturbance (Fig. 4A, Table S2). On
348 the other hand, two years after, the C2a and C2acg quadrats showed a higher species richness
349 than pre-disturbed quadrats, while C2b and C2bcg exhibited lower values after the
350 disturbance (Fig. 4A, Table S2). Overall, species richness was homogeneous between all
351 samples and was not significantly different along the recolonisation process (Kruskal-Wallis

352 test: $P = 1.17$, $p\text{-value} = 0.56$, Fig. 4A). However, macrofaunal densities were significantly lower
353 after 1 year ($15\,768 \pm 12\,487 \text{ ind.m}^{-2}$) and 2 years ($11\,190 \pm 8\,270 \text{ ind.m}^{-2}$) after the
354 disturbance, in comparison to the pre-disturbed community ($34\,402 \pm 7\,590 \text{ ind.m}^{-2}$) (Kruskal-
355 Wallis test: $P = 7.65$, $p\text{-value} = 0.021$ and Post hoc Dunn test: $p\text{-value} < 0.05$, Fig. 4A) with a
356 density recovery rate ranging from 15.7% on C1b after 1 year to 79.6% on C2acg 2 years after
357 the disturbance (Fig. 6, Table S2). The Shannon index and Pielou's evenness were highly
358 variable across samples in the pre-disturbed communities, but higher 1 year and 2 years after
359 the disturbance (Fig. 4C and 4D, Table S2). Overall Pielou's evenness index is significantly
360 higher in post-disturbance communities compared to pre-disturbed communities (Kruskal-
361 Wallis test: $P = 7.34$, $p\text{-value} = 0.026$ and Post hoc Dunn test: $p\text{-value} < 0.05$, Fig. 4D). In the
362 same way, the proportion of low occurrence species is lower in post-disturbance communities
363 (60% after 1 year and 58% after 2 years) than prior to the induced disturbance (74%) (Table
364 S2).

365 The output of the RDA computed on Hellinger-transformed densities of the different species
366 along the recolonisation process showed a significant difference in faunal composition
367 between the pre-disturbed communities and post-disturbance communities at Montségur
368 (Fig. 7). The RDA model explained 42% (Adjusted $R^2 = 20.5\%$) of the total inertia in species
369 assemblage structure ($p\text{-value} = 0.006$). The main driver of this observed difference is time
370 after the induced disturbance ($p\text{-value} = 0.001$), whereas no significant cage effect or
371 dependence between sites were observed ($p\text{-values} = 0.300$ and 0.262 , respectively). The
372 analysis of similarity (ANOSIM) on Bray-Curtis dissimilarity matrix suggests a major change in
373 macrofaunal composition between pre-disturbed communities and those after 1 and 2 years
374 of recolonisation ($R = 0.712$, $p\text{-value} = 0.001$). However, no significant difference in faunal
375 composition was identified between the assemblages collected 1 year and those collected 2
376 years after the disturbance.

377 Some species appeared to play a major role in the observed differences along the
378 recolonisation process (Fig. 8). Indeed, a decrease in the abundance of the typical vent species
379 (*Bathymodiolus azoricus*, *Branchipolynoe seepensis*, *Amphisamytha lutzi* and *Lepetodrilus*
380 *atlanticus*) was observed in the post-disturbance communities, while small gastropod species
381 (i.e. *Lurifax vitreus*, *Protolira valvatoides*, *Laeviphitus desbruyeresi*, *Xylodiscula analoga*) and
382 nematodes (*Oncholaimus dyvae*) showed a significant increase in the post-disturbance

383 communities (Fig. 8, Fig. S4). *Pseudorimula midatlantica* and the copepod *Aphotopontius sp.*
384 displayed higher relative abundances in the first year after the disturbance in comparison to
385 the pre-disturbed community and returned to lower values 2 years after the disturbance. As
386 observed for *B. azoricus*, the other dominant species displayed a polymodal structure of size
387 distribution and differences have been identified between the pre-disturbed community and
388 post disturbance state (pairwise Kolmogorov-Smirnov test) (Fig. S4). Furthermore, individuals
389 of *A. lutzii*, *B. seepensis*, *L. lepetodrilus* and *P. valvatooides* were overall smaller within the
390 communities after disturbance in comparison to those of the pre-disturbed community in
391 most quadrats (Fig. S4). For *P. midatlantica*, only 1 quadrat showed significant differences in
392 population size structure (Fig. S4).

393 4. Discussion

394 In this study, we provide an early evaluation of the recovery of deep-sea benthic communities
395 to a small-scale (<1 m²) disturbance experiment at an active hydrothermal edifice located on
396 the Lucky Strike vent field. The structure of pre-disturbed communities and their recovery
397 patterns were characterised through the analysis of faunal composition, diversity, population
398 size structure in relation to biotic and abiotic factors at the Montségur edifice. This
399 experimental design represents an innovative approach to assess the recovery of vent
400 communities in areas where opportunities to observe natural disturbances are rare. It
401 provides useful insights about local recolonisation drivers at hydrothermal vents, data that
402 can contribute to the elaboration of conservation strategies in the context of potential deep-
403 sea mining activities on seafloor massive sulphides.

404

405 4.1. Habitat characterisation

406 In active vent ecosystems, environmental factors are strongly linked to the output flux and
407 chemistry of hydrothermal fluids and the resulting physico-chemical conditions along the
408 mixing gradient between vent fluids and surrounding sea water. Within the active habitats
409 sampled in this study, mean temperature among *Bathymodiolus azoricus* faunal assemblages
410 varied from 5.2 to 9.5 °C with a maximum of 22.1 °C, which corresponds to the temperature
411 ranges of Eiffel Tower habitats (Husson et al. 2017, Sarrazin et al. 2020). We identified two
412 microhabitats hosting *B. azoricus* assemblages, which have previously been described as cold
413 and warm habitats in Sarrazin et al. (2015). However, while in our study these habitats are

414 colonised by mussels, in the previous study warm habitats were rather reported to be
415 associated with shrimp assemblages. This discrepancy could be related to temperature
416 measurements: in the present study, temperature was measured using iButtons™ deployed
417 on or within the mussels while most measurements reported previously were conducted using
418 the ROV probe placed a few millimeters above the faunal assemblages (Cuvelier et al. 2014a,
419 Husson et al. 2017, Sarrazin et al. 2015, 2020). The rapid mixing of the warm fluids with the
420 above cold seawater can account for these differences. Similar to previous studies, most
421 samples belonging to the cold habitat showed small variability in environmental conditions
422 and were associated with low temperature, low concentrations of iron and sulphides, high pH
423 and high concentrations of dissolved oxygen (Cuvelier et al. 2011a; Sarrazin et al. 2015).
424 However, a few quadrats (R1, C2a and R0b) were characterised by higher temperatures, total
425 dissolved sulphide and iron concentrations as well as lower dissolved oxygen concentrations
426 with acidic pH, which are more representative of warm habitats.

427

428 The continuous bi-hourly monitoring of temperature revealed a high spatial variability in
429 temperature regime (up to 3°C across 10 cm), suggesting the occurrence of multiple
430 microhabitats within a single quadrat. This was supported by high standard deviation values
431 of replicate measurements for sulphides and iron concentrations performed every year. This
432 small-scale temporal variability of temperature can be a result of several processes, including
433 the interplay between sulphide and oxygen biological uptake (Johnson et al., 1988), the
434 formation of diffuse fluids in the subsurface, the chemical reactivity of the mixing zone, the
435 porosity of the substratum in active habitats on the East Pacific Rise (Butterfield et al. 1990;
436 Sarrazin et al. 2002, Le Bris et al. 2006) or tidal oscillations (Barreyre et al. 2014). Our results
437 show significant semi-diurnal and diurnal periods and harmonics, supporting the presence of
438 periodic oscillations related to tidal processes. Tidal modulation of diffused-flow has been
439 reported in many vent systems (Cuvelier et al., 2014b; Sarrazin et al., 2014; Scheirer et al.,
440 2006). These variations are mainly caused by tidally induced currents (Barreyre et al., 2014;
441 Khripounoff et al., 2008) and changes in hydrostatic pressure on the seafloor (Davis and
442 Becker, 1999). This periodicity could be beneficial for symbiotic sessile species that need
443 alternative inputs of reduced compounds and oxygen to ensure chemosynthesis (Scheirer et
444 al. 2006, Mat et al. 2020) but can also influence the behaviour of mobile species (Lelièvre et
445 al., 2017).

446

447

4.2. Pre-disturbed communities and natural variability

448

449 On the active Montségur edifice, all experimental quadrats were visually dominated by
450 medium-sized *B. azoricus* mussels from 5.2 ± 8.8 mm to 24.4 ± 14.3 mm. These sizes are
451 consistent with the mean lengths reported by Comtet and Desbruyères (1998) on different
452 edifices of Lucky Strike (between 5.63 ± 5.67 mm and 49.63 ± 31.41 mm), but smaller than
453 those measured by Sarrazin et al. (2015) on the nearby Eiffel Tower edifice (between $22.7 \pm$
454 18.07 and 74.7 ± 2.57 mm). Indeed, we observed a high proportion (between 52 and 96%) of
455 very small individuals -below 3 mm- in each sample, sizes that correspond to post larval and
456 juvenile stages. The presence of several successive cohorts suggests the occurrence of a
457 massive recruitment event around June, just before sampling. These results are consistent
458 with the lifecycle of *B. azoricus*, with an annual spawning event in January followed by a
459 planktotrophic larval development and the settlement of post-larvae in May-June (Colaço et
460 al., 2006; Comtet and Desbruyères, 1998; Dixon et al., 2006). Furthermore, differences in
461 mean shell length of *B. azoricus* observed among samples on pre-disturbed communities may
462 be due to spatial segregation of sizes related to environmental factors (Sarrazin et al., 2015;
463 Husson et al., 2017) or to biotic interactions (e.g. competition, predation) that may play an
464 important role in recruitment success and survival of post-larvae (Lenihan et al., 2008; Sancho
465 et al., 2005).

466

467 All samples collected at the active Montségur edifice were dominated by the same
468 macrofaunal species (e.g. *B. azoricus*, *B. seepensis*, *A. lutzi*, *P. valvatooides* and *L. atlanticus*),
469 which have been previously described as indicator species of cold microhabitats on the Eiffel
470 Tower edifice situated ~ 50 m from Montségur (Sarrazin et al., 2015b). The high similarity
471 between the fauna from the two edifices may be related to their belonging to the same
472 chemistry domain (Chavagnac et al. 2018, Sarrazin et al. 2020). Among the 43 macrofaunal
473 species identified on Montségur, approximately 74% exhibit a low frequency of abundance
474 ($<1\%$). Total densities of organisms in the pre-disturbed communities ranged from 3 330 to 68
475 960 ind.m⁻² across the different samples, and is much lower than the values reported by
476 Sarrazin et al. (2020) on the same edifice (between 62 253 and 126 437 ind.m⁻²). In several
477 studies, small mussel assemblages, inhabiting cold microhabitats, harbour higher density and

478 diversity of associated species than large mussel assemblages, found in warmer microhabitats
479 (Cuvelier et al., 2009; Dreyer et al., 2005; Sarrazin et al., 2015). Surprisingly, in this study the
480 highest densities of organisms have been observed in the warmest and more variable habitats.
481 This result may be linked to the differences in the method for assessing temperature as
482 mentioned above. Indeed, temperature values obtained by probes deployed directly on the
483 substratum are expected to be higher than the ones obtained with the ROV probe a few
484 millimeters above faunal assemblages.

485

486 As expected, macrofaunal distribution was significantly influenced by environmental
487 conditions, especially by mean temperature and mean concentrations in total sulphides and
488 methane, in addition to slightly acidic conditions (pH <7.3). However, biotic factors such as
489 competition for space and food resource, but also predation or facilitation, may also play an
490 important role in faunal distribution in diffuse flow habitats (Sarrazin et al. 1997, Sen et al.
491 2013; Gollner et al. 2015b; Husson et al. 2017). On the other hand, faunal composition within
492 reference quadrats did not differ over the three years of the experiment, suggesting a relative
493 stability of the community over time. This supports the observed high stability of mussel
494 communities on the nearby Eiffel Tower edifice, which led to the assumption that *B. azoricus*
495 assemblages at Lucky Strike can be considered as a “climax” community (Cuvelier et al.,
496 2011b). The absence of natural changes in faunal assemblages, at the edifice scale, during the
497 experiment allows us to use them as a baseline to test the effect of the induced disturbance
498 on benthic communities.

499

500 4.3. Recolonisation processes and recovery

501

502 In Figure 9, we propose a succession model of nMAR vent communities based on the present
503 experiment at the Lucky Strike vent field and from previous studies conducted after natural
504 disturbances at vents. The first step after the disturbance relies on the release of an ecological
505 niche induced by the removing of faunal assemblages. Then, the stabilisation of
506 environmental conditions, especially of temperature and reduced compounds, would allow
507 chemoautotrophic primary production and proliferation of microbial mats, as observed in
508 studies from vents in the Pacific Ocean (Marcus et al., 2009; Shank et al., 1998; Tunnicliffe et
509 al., 1997). This is followed, within one year, by the arrival of mobile opportunistic species,

510 including shrimps and copepod species. Although not significant, our results suggest that
511 these predator species may slow down the settlement of associated species, resulting in a
512 poor recovery of faunal densities despite a good species richness recovery. Two years after
513 the disturbance, the settlement of several gastropod species grazing on free-living microbial
514 mats have been observed. At this stage, the higher Pielou's evenness compared to baseline
515 communities suggests that biotic interactions are not yet fully effective within assemblages.
516 Gastropods have already been described as main pioneer colonists at 9°N EPR after the 2006
517 volcanic eruption (Mullineaux et al., 2012, 2010). Indeed, despite contrasting reproductive
518 characteristics, some of them are able to maintain an important effective population size and
519 support high abundances, especially through an early maturity and continuous gametogenesis
520 (Marticorena et al., 2020). Thereafter, we hypothesise a later settlement of the foundation
521 species *B. azoricus* due to its seasonal reproduction, which leads to a single recruitment event
522 in June (Colaço et al., 2006; Dixon et al., 2006). The recolonisation of *B. azoricus* can occur
523 through recruitment events and settlement of post-larvae and juveniles or by immigration of
524 mobile adults from nearby assemblages (Comtet and Desbruyères, 1998). Indeed,
525 observations made on imagery on the Eiffel Tower edifice showed that *B. azoricus* is able to
526 move several centimetres a day (Matabos, Sarrazin, unpublished data). Since the growth rate
527 of *B. azoricus* juveniles has been estimated to reach ~ 2 mm per year on the Eiffel Tower edifice
528 (from imagery analysis, Sarrazin and Matabos unpublished data), we can assume that the
529 presence of mussels larger than 1 cm after 1 and 2 years of recolonisation is most probably a
530 result of adult migration. On the other hand, the mean shell length of *B. azoricus* was
531 significantly lower and a higher proportion of juveniles were observed on post-disturbance
532 assemblages compared to pre-disturbed communities. This suggests that within our study, the
533 recruitment and settlement of young mussels were the main drivers of recolonisation after
534 the disturbance, rather than migration. Moreover, the results of the predator exclusion
535 experiment suggest that the recruitment success of *B. azoricus* might depend on predation
536 pressure on post-larval individuals by large mobile predators (e.g. shrimp, crabs, fishes). The
537 impact of predation on the entire benthic community could be even more significant when
538 predators specifically feed on taxa that play a key role in the community and interact widely
539 with other species (Paine, 1966). We also observed that the cages led to the formation of thick
540 microbial mats on their surfaces, implying that the presence of the plastic mesh and its size
541 may have modified the input of hydrothermal fluids. The deployment of additional "true" cage

542 control quadrats would be necessary to dissociate the role of predator exclusion and
543 potentially other effects of the mesh such as hydrodynamic modifications. The establishment
544 and growth of *B. azoricus* may then promote the settlement of low occurrence species and a
545 rapid recovery of faunal densities through the creation of a three dimensional habitat that
546 contributes to reduce fluid flux, making the habitat more suitable for other species (Johnson
547 et al. 1988; Sarrazin et al. 1997, Shank et al. 1998). Finally, biotic interactions including
548 predation, competition for space and nutritional resources and facilitation may lead to
549 changes in faunal relative abundance and dominance before reaching an equilibrium. All these
550 mechanisms contribute to reducing the evenness among assemblages and enhance the
551 dominance of a few taxa (Fig. 9). Once this equilibrium is achieved, we can consider that these
552 assemblages reach their climax. The climax community of Montségur appears to be similar to
553 that of the neighbouring Eiffel Tower edifice (Cuvelier et al., 2011a) and some other active
554 edifices of the Lucky Strike vent field (Sarrazin et al. 2020). These communities are
555 characterised by the dominance of a few vent taxa and a high proportion of low occurrence
556 species. Natural or anthropogenic disturbance events, which can occur at each step of this
557 successional model, may lead to significant changes in faunal assemblages and even provoke
558 community collapse, depending on their spatial breadth as proposed in different vent
559 successional models (Sarrazin et al. 1997, Shank et al. 1998).

560 Several factors can come into play in recolonisation and ecological succession following a
561 disturbance, and their relative importance changes according to the scale of disturbance
562 (Zajac et al. 1998, Benedetti 2000). After a small-scale disturbance, recovery of vent
563 assemblages are strongly affected by the spatio-temporal variability of environmental
564 conditions, which may lead to local extinction or creation of new suitable habitats (Sarrazin et
565 al. 1997; Shank et al. 1998, Marcus et al. 2009; Sen et al. 2014). Feeding strategies (Lelièvre et
566 al. 2018; Van Audenhaege et al., 2019) and biotic interactions (i.e. competition for space,
567 facilitation or predation) have also been identified as important drivers of faunal succession
568 at the edifice scale (Sarrazin et al. 1997, Micheli et al. 2002; Hunt et al. 2004; Govenar and
569 Fisher 2007; Cuvelier et al. 2014a). In this study, we showed that, at this small-scale, biological
570 interactions are more likely to play a predominant role in faunal succession rather than
571 environmental conditions. The same observations have been noticed on vents at back-arc
572 basins and may be due to the high stability of environmental conditions, typical of slow-
573 spreading centers (Sen et al., 2014). Furthermore, in mosaic habitats, the diversity and species

574 composition at the boundary of disturbed patches might modulate biotic interactions and
575 migrations of individuals, influencing early stages of recovery (Bulleri et al. 2006). However,
576 diversity descriptors and faunal composition were relatively homogeneous between the
577 different quadrats at each step of the recolonisation process, suggesting that succession after
578 small-scale disturbance at Lucky Strike can be described as a deterministic sequence of species
579 replacement. As observed on rocky-shore habitats, the timing of disturbance might also affect
580 recolonisation patterns (Sousa 1985, Benedetti and Cinelli 1996). For example, *B. azoricus*
581 have been described to recruit seasonally around the month of June (Dixon et al. 2006; Colaço
582 et al. 2006) and the occurrence of disturbance in spring might result in a faster recovery of
583 assemblages and less importance of gastropods in the first stage of recolonisation.

584

585 5. Conclusion

586 We designed a novel *in situ* experimental approach to identify biotic and abiotic factors driving
587 the recolonisation and succession of vent communities after a small-scale disturbance.
588 Recolonisation dynamics was strongly affected by species composition of the neighbouring
589 faunal assemblages. Biotic interactions were predominant and highly influenced the slow
590 recovery of vent assemblages, while environmental factors remained stable. Our results,
591 coupled with observations from literature data, lead to a first conceptual model of
592 colonisation and ecological succession for northern Mid-Atlantic communities.

593

594 At regional scales (i.e. vent field), life-history traits including reproduction (Kelly and Metaxas,
595 2007), larval dispersal modes and recruitment abilities (Levin et al., 1996; Levin, 2006;
596 Mullineaux et al., 2003, 2012) constitute additional key factors that influence faunal
597 colonisation processes and subsequent successional patterns (Zajac et al., 1998; Adams et al.,
598 2012; Nakamura et al., 2014). While the recolonisation of areas following large-scale
599 disturbance relies on dispersal across vent fields, at local scale the successful settlement of
600 post-larvae depends on habitat suitability, environmental conditions and biotic interactions.
601 Understanding the processes acting at small scales are paramount in evaluating mechanisms
602 controlling successional dynamics after recolonisation by species from afar. In addition, recent
603 workshops and working groups, emerging from the development of mining regulations and
604 the necessity to inform industries and policy makers, stressed the urgent need to address

605 knowledge gaps in vent species biology and ecology (Collins et al. 2013; Levin et al. 2016; Dunn
606 et al. 2018, ISA REMPS, SEMPIA). This study is one of the first to assess natural recovery of
607 communities on a slow-spreading ridge and provide data that are essential to elaborate and
608 develop conservation strategies and mitigate long-term harmful effects of anthropogenic
609 activities on hydrothermal vent ecosystems.

610

611 DOI of cruises involved

612 SARRADIN Pierre-Marie, CANNAT Mathilde (2017) MOMARSAT2017 cruise, RV Pourquoi pas
613 ?, <https://doi.org/10.17600/17000500>

614 CANNAT Mathilde (2018) MOMARSAT2018 cruise, RV L'Atalante,
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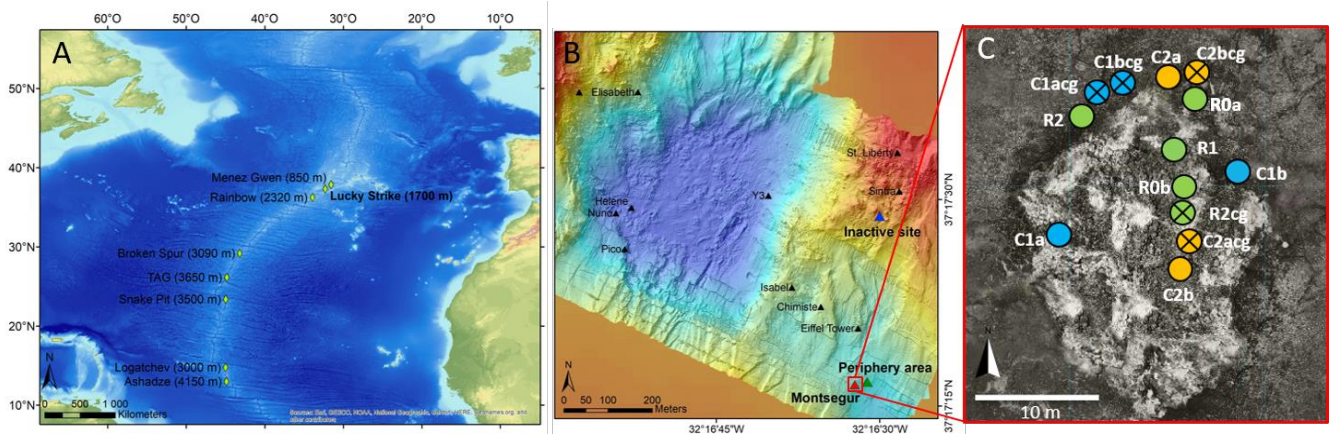


Figure 1. **A.** Location of the Lucky Strike (LS) vent field along the Mid-Atlantic Ridge. **B.** Bathymetric chart of LS and location of the Montségur edifice. **C.** Position of the experimental and reference quadrats on and around the Montségur edifice. Green circles represent the reference quadrats, blue circles represent the experimental quadrats used to study the recolonisation 1 year after the disturbance, and orange circles represent the experimental quadrats used to study the recolonisation 2 years after the disturbance. Crossed off circles represent "caged" quadrats while empty circles represent quadrats without a cage.



Figure 2. The C1a-cg experimental quadrat in 2017, **(A)** before faunal clearance (baseline community) and ; **(B)** after the induced disturbance. Red arrow highlights the check-board used to calibrate imagery analysis and estimate the sampling surface area (red dotted line). **(C)** The C1bcg “caged” experimental quadrat used to exclude large mobile predators. A 1 cm mesh grid was adjusted on the pyramidal structure on top of the quadrat (in black on the picture) and a grey fabric sleeve was attached to the edge of the caged quadrat to avoid colonisation of crawlers. A camera was deployed at the top of the pyramidal structure and connected to a battery on the side (yellow cables).

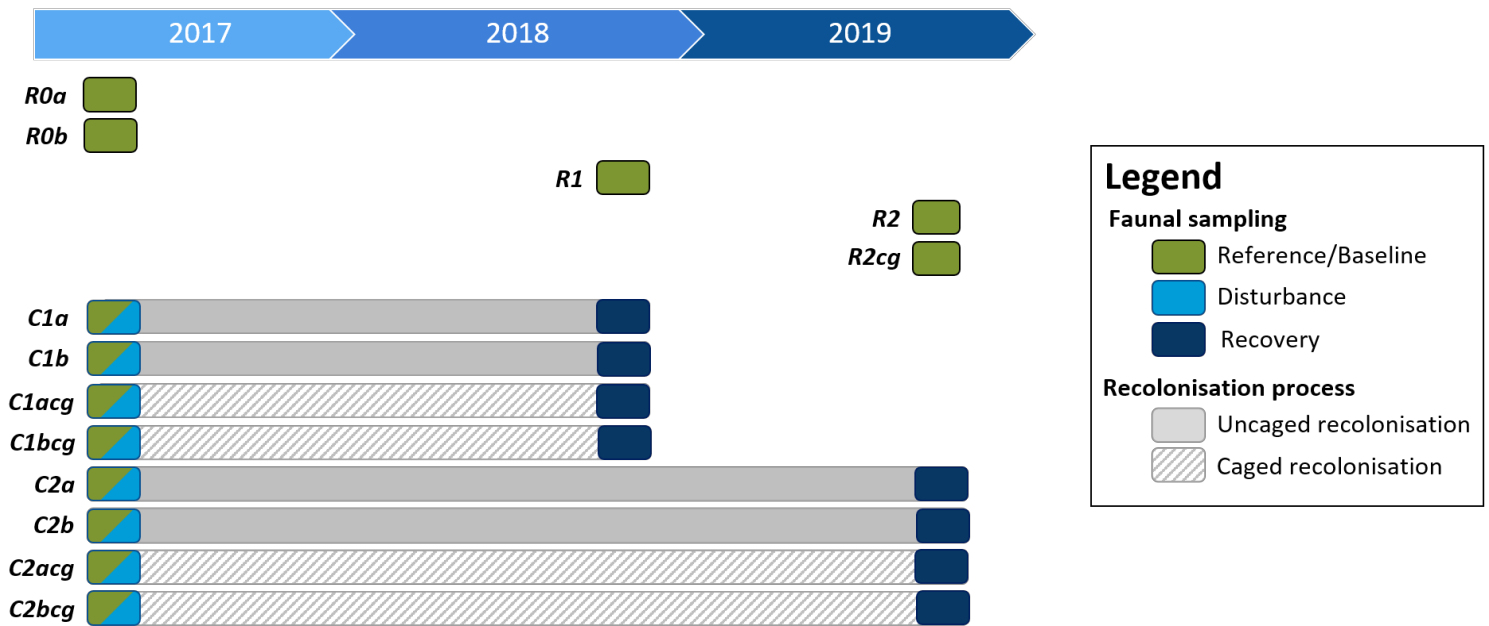


Figure 3. Experimental design of the disturbance experiment deployed between 2017 and 2019 on the Montségur edifice, Lucky Strike vent field (Mid-Atlantic Ridge). Small rectangles represent faunal sampling and their color indicates the nature of the operation: green, sampling of baseline communities; light blue, induction of disturbance by clearing faunal assemblages; dark blue, sampling after recolonisation to evaluate the recovery. Grey segments represent the recolonisation period studied for each quadrat. Hatched segments indicate the presence of caged during the recolonisation period.

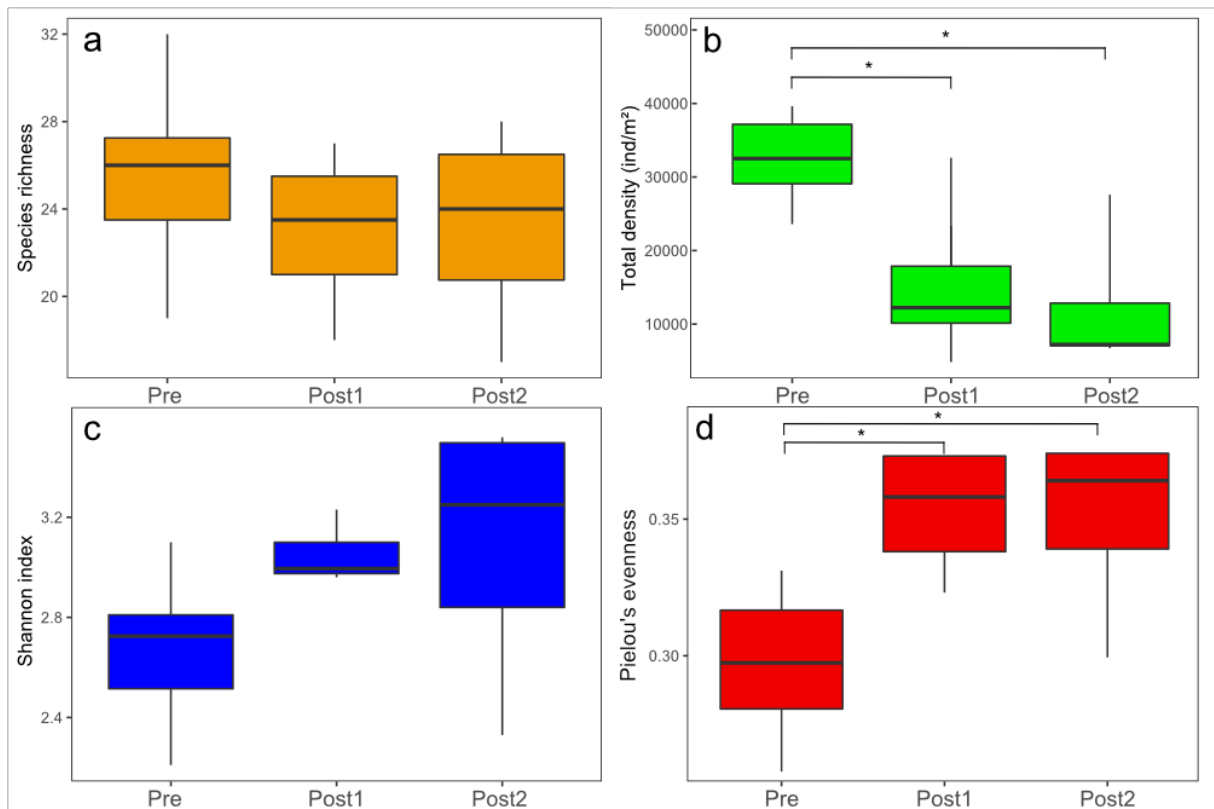


Figure 4. Species richness (a), total density (b), Shannon index (c) and Pielou's evenness index (d) of macrofaunal communities on the baseline communities and during the recolonisation process on the active Montségur edifice. Pre: assemblages sampled before the disturbance; Post1: assemblages sampled 1 year after the disturbance; Post2: assemblages sampled 2 years after the disturbance. Significance of Kruskal-Wallis multisample tests and post-hoc Dunn's tests are represented on the top of the boxplots.

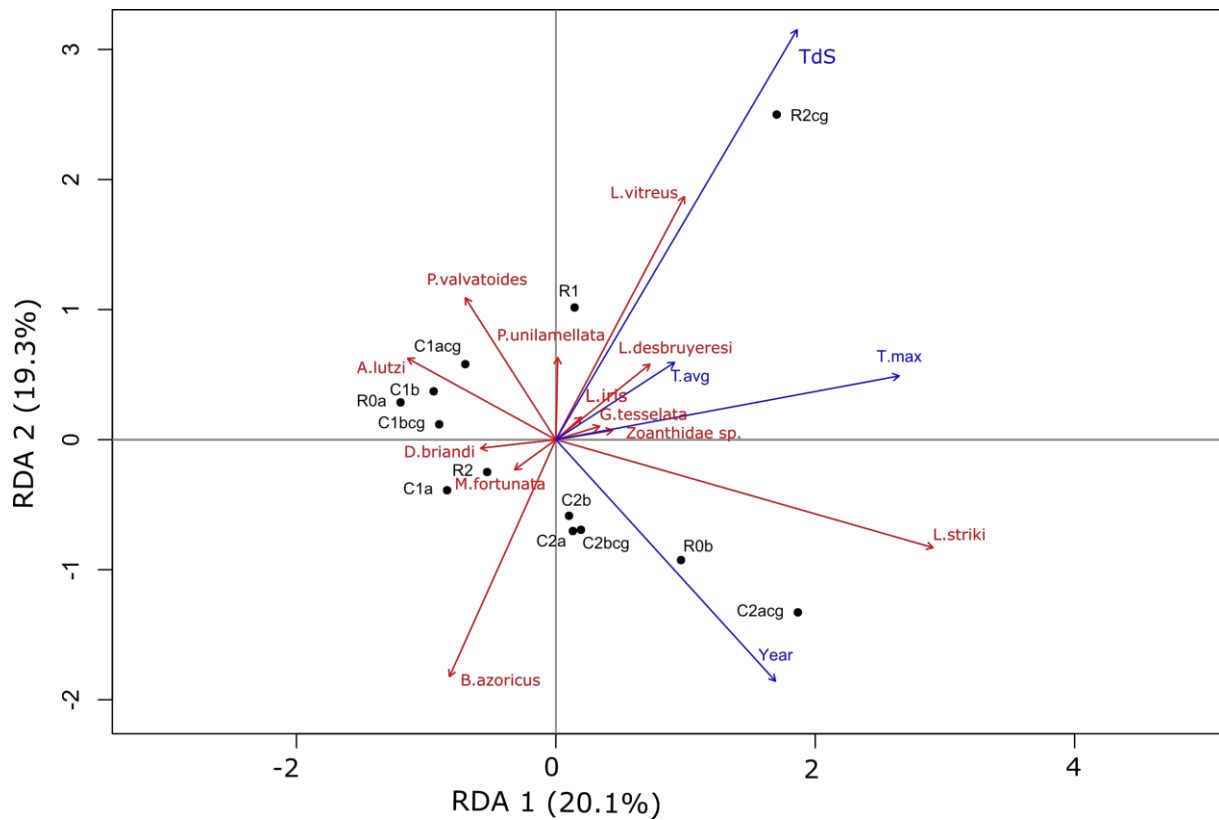


Figure 5. Canonical redundancy analysis (RDA, scaling 2) of Hellinger-transformed macrofaunal densities observed in the baseline community of the Montségur active edifice at the Lucky Strike vent field (Mid-Atlantic Ridge). The first canonical axis represents 20.1 % of the total variance in macrofaunal densities while the second axis represents 19.3% ($\text{adj } R^2 = 25.1\%$, $p = 0.004$). The first axis is significant ($p = 0.05$). Only species that accounted for more than 50% of cumulative inertia on the two first axes are represented.

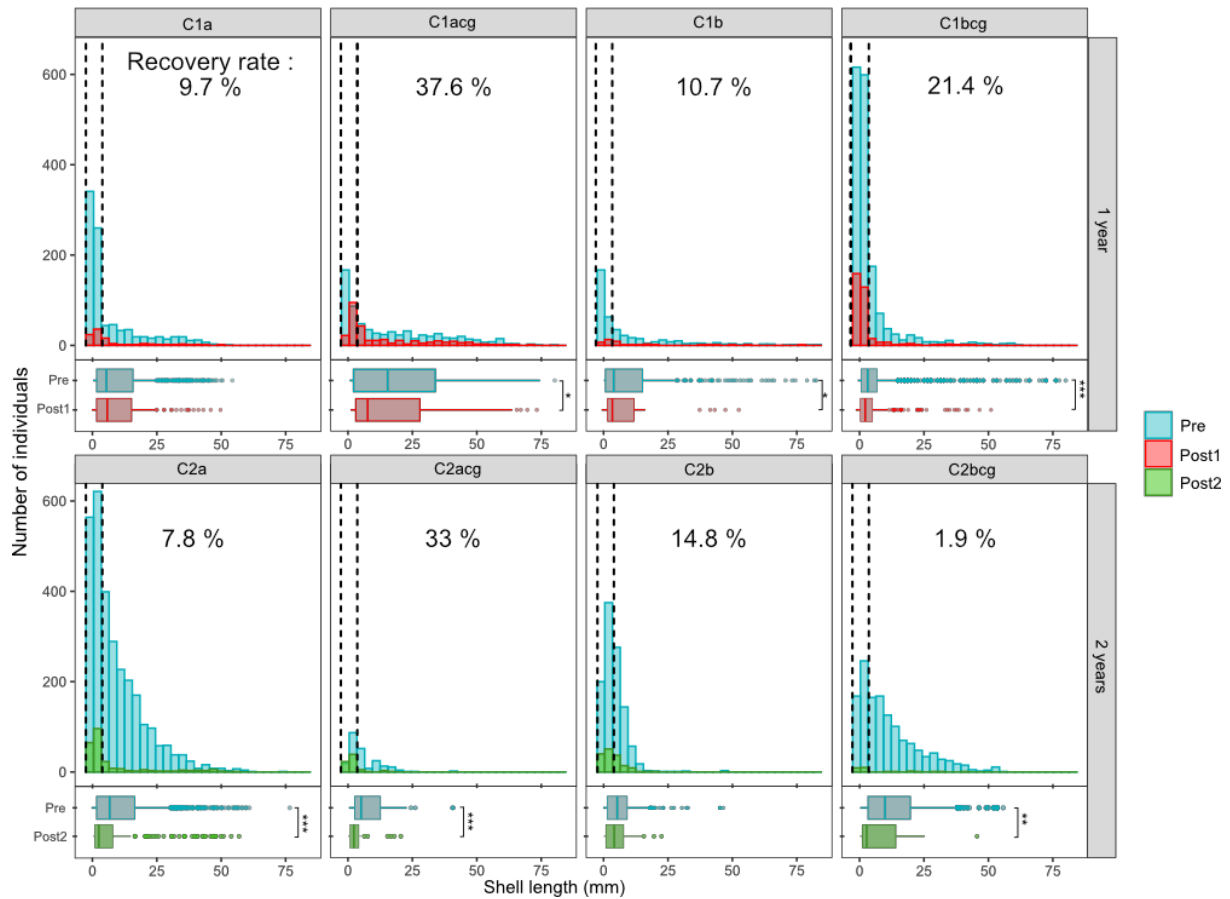


Figure 6. Histograms and boxplots of size frequency distribution of *Bathymodiolus azoricus* for each quadrat sampled at the Montségur edifice at the Lucky Strike vent field (Mid-Atlantic Ridge) including the pre-disturbed community (blue) and the communities one (red) and 2 (green) years after disturbance. Wilcoxon-Mann-Whitney tests were performed to identify differences in mean individual size between the baseline and post-disturbance communities. Asterisks indicate significant differences in mean shell length (*p-value<0.05; ** p-value <0.01; *** p-value <0.001). The interval between dotted lines represents the range of size at recruitment. The percentages represent the proportion of *B. azoricus* density which recovered in comparison of the pre-disturbed value in each quadrat.

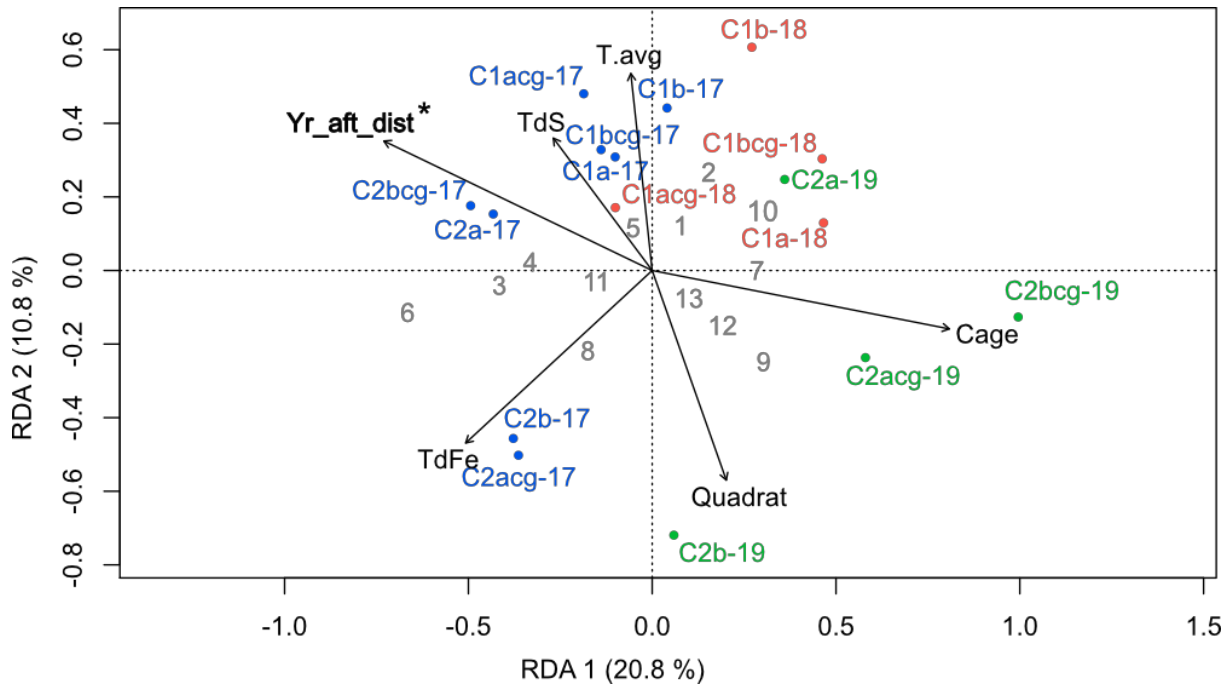


Figure 7. Canonical redundancy analysis (RDA, scaling 2) of Hellinger-transformed macrofaunal densities observed in the different assemblages during the recolonization process at the Montségur active edifice (Lucky Strike vent field, Mid-Atlantic Ridge). The first canonical axis represents 20.8% of the total variance in macrofaunal densities while the second axis represents 10.8% (with an adjusted R^2 of 20.5%). The RDA and the first axis are significant (p -values = 0.006 and 0.023, respectively). Only species showing good fit with the first two canonical axes are represented. Colors refer to the time after disturbance: baseline communities (blue); 1 year after disturbance (red); two years after disturbance (green). Explanatory variables: Years after disturbance (*Yr_aft_dist*), average temperature measured before sampling (*T.avg*), mean concentration of total dissolved sulphides (*TdS*), mean concentration of total dissolved iron (*TdFe*), if quadrats are caged or uncaged (*Cage*), identification of quadrats to test the dependence of the same location over the time of the experiment (*Quadrat*). Response variables, each species is designated by a number: 1 – *Amphisamytha lutzii*; 2 – *Aphotopontius* sp.; 3 – *Bathymodiolus azoricus*; 4 – *Branchipolynoe seepensis*; 5 – *Lepetodrilus atlanticus*; 6 – *Lirapex costellata*; 7 – *Laeviphitus desbruyeresi*; 8 – *Luckia striki*; 9 – *Lurifax vitreus*; 10 – *Oncholaimus dyvae*; 11 – *Paralepetopsis ferrugivora*; 12 – *Protolira valvatoides*; 13 – *Xylodiscula analoga*.

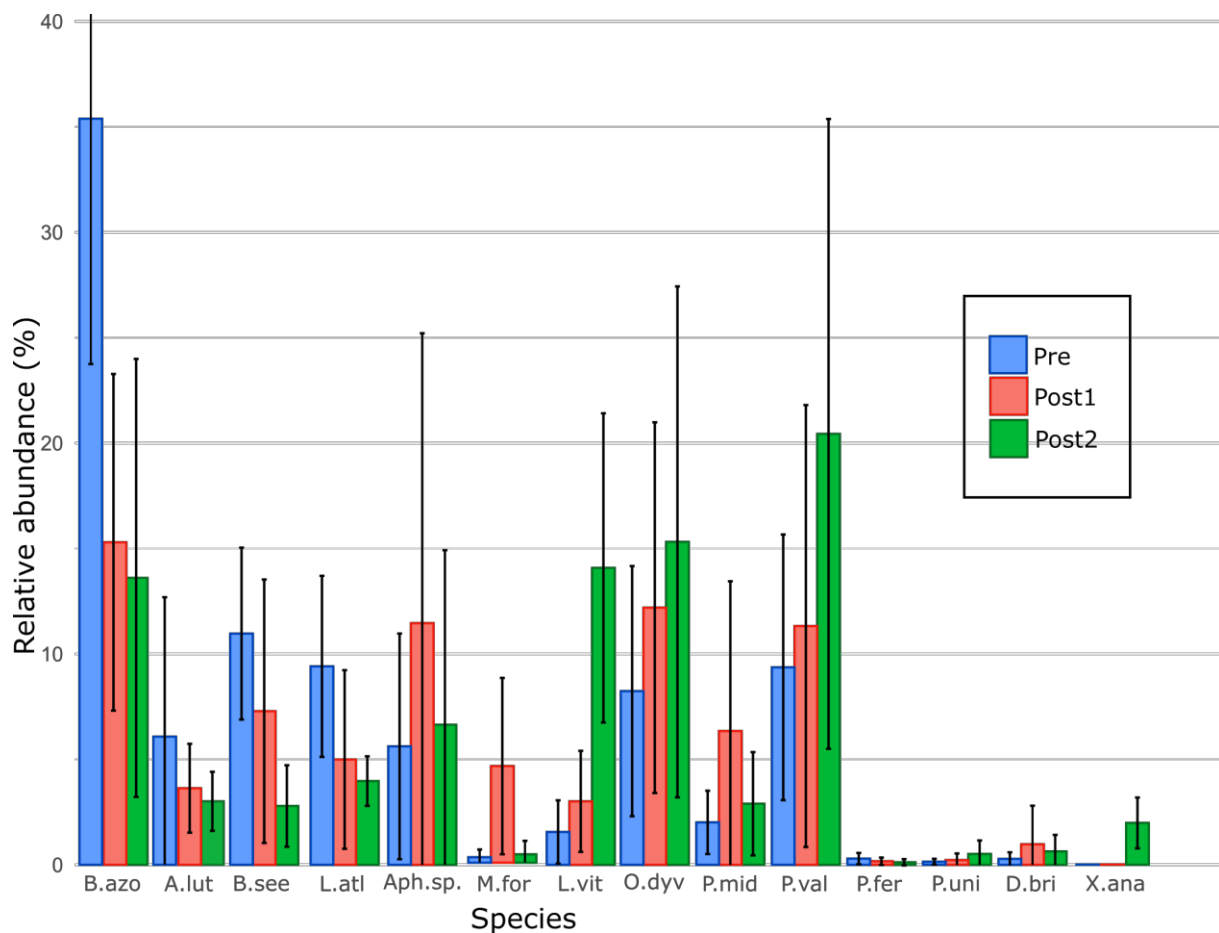


Figure 8. Mean and standard deviations of densities for the most abundant species among the experimental quadrats on the active Montségur edifice before the disturbance (Pre) and one/two years after the disturbance (Post1 and Post2). Species acronyms: B.azo – *Bathymodiolus azoricus*; A.lut – *Amphisamya lutzi*; B.see – *Branchipolynoe seepensis*; L.atl – *Lepetodrilus atlanticus*; Aph.sp. – *Aphotopontius sp.*; M.for – *Mirocaris fortunata*; L.vit – *Lurifax vitreus*; O.dyv – *Oncholaimus dyvae*; P.mid – *Pseudorimula midatlantica*; P.val – *Protolira valvatoides*; P.uni – *Prionospio unilamellata*; D.bri – *Divia briandi*; X.ana – *Xylodiscula analoga*.

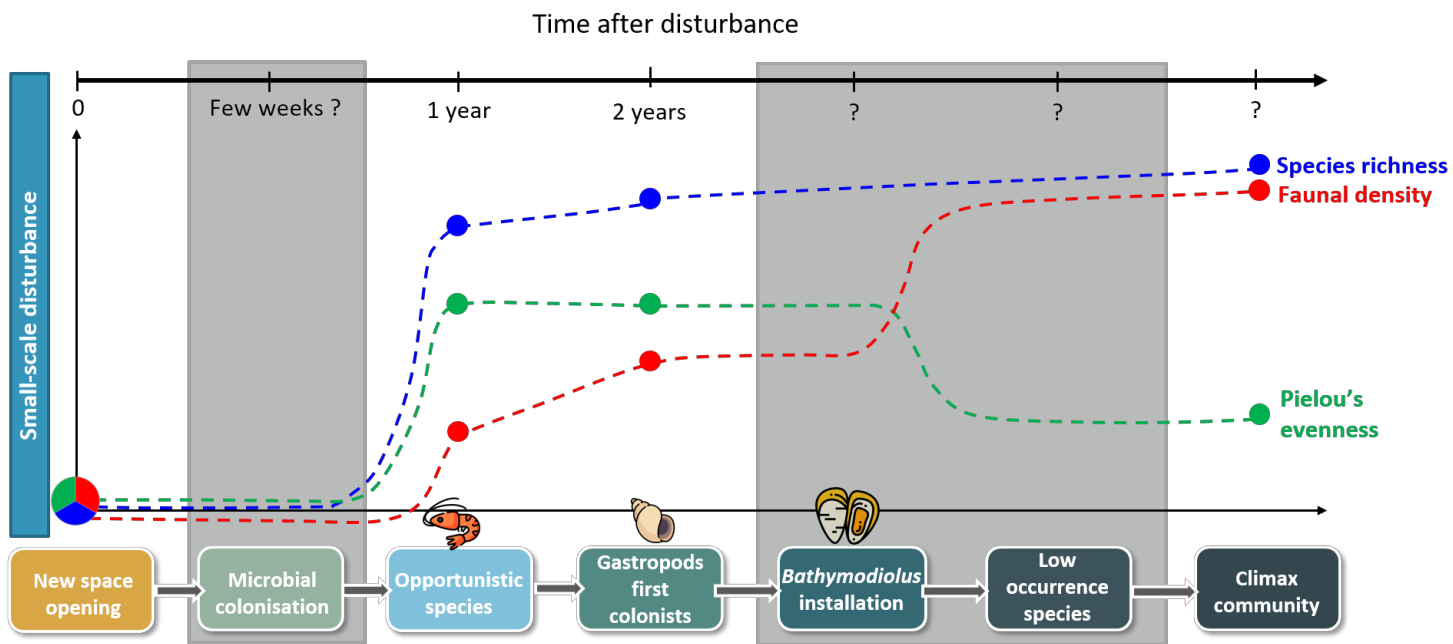


Figure 9. Conceptual model of colonisation and ecological succession until climax after a small-scale disturbance on the Lucky Strike vent assemblages (MAR). Evolution of species richness, faunal densities and Pielou's evenness index during the recovery process, based on the main results of our disturbance experiment (solid dots) and inferred from the literature (grey boxes).

Table 1. Environmental conditions on the baseline communities of the different quadrats deployed on the Montségur edifice (Lucky Strike vent field, Mid-Atlantic Ridge). Temperature: average: T.avg., standard deviation: T.std. maximum: T.max and minimum: T.min. from iButtons™. Oxygen (O₂). Total dissolved sulphide (TdS) and Total dissolved iron (TdFe) measured with the *in situ* analysers CHEMINI. Methane (CH₄) and pH were measured through quantitative analyses from samples collected with the PEPITO water sampler (Sarradin et al. 2009). Highest values are highlighted in bold and lowest values in grey.

Quadrat	T.avg	T.std	T.min	T.max	O ₂ (μM)	TdS (μM)	TdFe (μM)	CH ₄ (μM)	pH
Montségur									
R0a	5.2	0.2	4.6	6.1	208.2 ± 0.1	2.7 ± 0.2	0.2 ± 0.1	0.4	7.8
R0b	6.9	0.8	5.1	11.5	207.2 ± 0.4	3.1 ± 1.0	1.1 ± 0.3	0.5	7.6
R1	9.5	2.7	6.1	22.1	206.1 ± 1.1	2.3 ± 0.2	2.2 ± 0.2	2.1	7.2
R2	5.5	0.4	5.1	11.4	206.9 ± 1.3	3.2 ± 2.7	0.2 ± 0.1	0.9	7.5
R2cg	5.3	0.2	4.6	7.1	205.6 ± 0.6	0.9 ± 0.2	0.6 ± 1.1	0.2	7.9
C1a	6.1	0.3	5.1	7.1	207.4 ± 0.1	3.2 ± 0.8	0.2 ± 0.1	0.7	7.6
C1acg	5.8	1.2	4.6	12.1	204.3 ± 1.5	3.9 ± 2.6	0.3 ± 0.1	2.1	7.2
C1b	6.4	0.4	4.6	10.6	206.2 ± 1	10.8 ± 14.7	0.3 ± 0.3	1.1	7.4
C1bcg	5.7	0.42	4.6	8.1	207.9 ± 0.4	2.5 ± 0.6	0.2 ± 0.1	0.8	7.7
C2a	7.6	1.12	6.1	16.1	203.8 ± 2.1	23.2 ± 26.3	1.1 ± 0.3	15.2	6.1
C2acg	6.3	0.5	5	8.6	207.4 ± 0.8	1.3 ± 0.1	0.9 ± 0.8	0.7	7.7
C2b	5.3	0.2	5	6.1	205.2 ± 0.5	3.8 ± 3.8	0.9 ± 0.4	0.4	7.8
C2bcg	5.3	0.3	4.6	6.6	206.6 ± 0.3	5.6 ± 1.2	0.2 ± 0.1	2.0	7.2



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Declaration of interest

The authors declare no competing interests.

Author Statement

JM, MM and JS conceived the ideas and designed the methodology. JM, MM, JS, ALH and CC collected the samples on board during oceanographic cruises. JM, MM, JS, ALH, CC, JPD and SH processed and analysed the data. JM and RL did the statistical analyses. JM, MM, ERL and JS discussed and interpreted the results. JM wrote the first draft of the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.