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1 **Long term monitoring of cold-water coral growth shows response to**
2 **episodic meteorological events in the NW Mediterranean**

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9
10 **Abstract**

11 *Lophelia pertusa* and *Madrepora oculata*, two cosmopolitan coral species of the deep
12 ocean, build reef-like structures that provide ecological niches and nurseries for many
13 species. These cold-water corals (CWCs) are thought to grow slowly making associated
14 communities vulnerable to disturbance. However, *in situ* growth dynamics remains
15 poorly known. The aim of this study was thus to quantify the growth rates of *L. pertusa*
16 and *M. oculata* and their variability in relation to environmental conditions that are
17 expected to influence their physiological functions. Such data can be useful to ground-
18 truth physiological rates and improve the prediction of their sensitivity to global change.
19 As part of a long-term monitoring programme of the Lacaze-Duthiers canyon in the
20 Northwestern Mediterranean Sea, fragments of the two species were repeatedly
21 sampled and redeployed at 530 m depth, from November 2010 to May 2018. Budding
22 rates and linear extensions of *L. pertusa* and *M. oculata* were hence quantified and their
23 inter-annual variability documented. The data were analyzed in relation to *in situ*
24 monitoring of water temperature, current speed and turbidity.

25 This study presents the longest *in situ* survey of the growth patterns of *L. pertusa*
26 and *M. oculata*. The observations revealed a strong inter-annual variability in growth
27 rates, both for *L. pertusa* and *M. oculata*, and suggest an influence of hydrological
28 conditions on the growth dynamics. Particularly, as regard to episodic water plumes
29 events such as NW wind-induced dense water shelf cascades and E-SE storm-induced
30 downwellings in autumn-winter. In this study, three types of responses were observed:
31 (i) high budding rates but low colony linear extension for strong water plume events
32 periods (ii) low budding rates, low linear extension and high mortality due to high
33 sedimentation rates in the absence of water plumes event, and (iii) high budding rates
34 and high linear extension associated to organic matter supply during medium intensity
35 water plume events. *Lophelia pertusa* appears to be more resilient to these hydrological
36 changes. Disturbance of the regional circulation patterns, in addition to longer-term
37 change in water mass properties such as warming, deoxygenation and acidification, are
38 thus important parameters to consider for CWC reef stability. This is particularly
39 important since increased storminess, and decreased cascading/downwelling intensities,
40 are predicted to occur within the next century.

41

42 Keywords: *Lophelia pertusa*, *Madrepora oculata*, Lacaze Duthiers submarine canyon, *in*
43 *situ*, skeletal growth, dense-water cascading

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50 **1. Introduction**

51

52 Engineer species forming three-dimensional structures, such as scleractinian cold-water
53 corals (CWCs), provide ecological niches for a number of associated species ([Buhl-](#)
54 [Mortensen et al., 2010](#)). These habitat-building species that support deep-sea
55 biodiversity, have a great ecological value and are listed in the CITES convention
56 (Appendix II) ([Foley and Armstrong, 2010](#)). In the last thirty years, significant research
57 efforts by the scientific community have been dedicated to characterize their physiology
58 and ecology, including feeding, reproduction, growth and the associated microbiome
59 ([Waller and Tyler, 2005](#); [Roberts, 2009](#); [Lartaud et al., 2014](#); [Lunden et al., 2014](#);
60 [Meistertzheim et al., 2016](#)). However, understanding of the CWC ecology still display
61 important knowledge gaps due to the difficulty of studying these species in their natural
62 environment.

63 Calcification is one of the key physiological indicators of calcifying organism
64 fitness. During the last decades, a number of studies have been dedicated to characterize
65 the growth patterns of CWCs with the aim of establishing adequate conservation
66 strategies (see details in [Lartaud et al., in press.](#)). Among all known CWC species, the
67 emblematic *Lophelia pertusa* exhibits the highest growth rates, but with a high
68 variability, ranging from 0.01 to 38.1 mm y⁻¹ ([Lartaud et al., 2014](#); [2017](#)). This range
69 contrasts with the growth rate of another deep-sea coral species, *Solenosmilia variabilis*
70 that exhibits the smallest skeletal growth for scleractinian (~1 mm y⁻¹) (at 750m depth
71 on SW Pacific seamounts observed in [Fallon et al., 2014](#)). Differences in growth patterns
72 are also observed for *M. oculata*, another common reef-building species, with growth
73 rates ranging from 0.01 to 18 mm y⁻¹ ([Lartaud et al., 2017](#)). The growth rate variability
74 among studies can be partly explained by the use of different measurement methods,

75 such as budding rates analysis, sclerochronology, buoyant weight, alkalinity anomaly or
76 radioisotopic technics. The differences could also be due to the comparison of values
77 originating from different geographic locations, depths, and related environmental
78 conditions (e.g. Gulf of Mexico, Mediterranean Sea, Norway) (Lartaud et al., *in press*).
79 Growth rates using the same measurement method for one species like *L. pertusa* can
80 range from 34 mm y⁻¹ (the North Sea) to 6 mm y⁻¹ (Rockall Bank, North Atlantic) (Gass
81 and Roberts, 2006; Wilson, 1979; Lartaud et al., *in press*). Strong regional variability is
82 also observed like in the Gulf of Mexico where *L. pertusa* exhibits growth rates varied
83 from 3.8 mm y⁻¹ (Brooke and Young, 2009) to 32.3 mm y⁻¹ (Larcom et al., 2014), but for
84 different time period and habitat conditions. Growth rate variability for this coral
85 species was also observed in the Western Mediterranean Sea for different time periods
86 at the same location, with a maximum of 38.1 mm y⁻¹ (Lartaud et al., 2014; 2017). This
87 limited set of growth rate measurements at different locations using different methods
88 prevents robust assessment of CWC growth patterns in their natural habitat, and
89 highlights the need for longer-term monitoring efforts of growth rates with respect to
90 the local environmental variability.

91 Experimental studies have led to identify a series of factors that influence the
92 growth patterns of cold water corals. Temperature can influence primary physiological
93 processes like respiration and calcification (Naumann et al., 2014). The seawater pH can
94 also impact these biological parameters (Gori et al., 2016; Hennige et al., 2014). In
95 addition, nutrients, salinity, dissolved oxygen and current speed could affect coral
96 calcification (Cairns and Macintyre, 1992; Thiem et al., 2006; Guinotte et al., 2006
97 Roberts, 2009; Purser et al., 2010; Lunden et al., 2014). Lartaud et al. (2014) showed
98 through *in situ* experiments a seasonal difference in growth rates of *M. oculata*, which
99 was suggested to reflect differences food supplies induced by meteorological events.

100 Coral growth rates likely respond differently to the combination of these factors in their
101 environment. Available data furthermore suggests that CWC growth might be directly
102 modulated by environmental changes. Understanding the growth dynamic of these
103 species, and assessing response to change in habitat conditions, should take into account
104 this variability while defining monitoring strategies.

105 Understanding the drivers of growth dynamics of CWCs under various
106 environmental conditions is essential to predict their fate in a changing ocean under
107 anthropogenic perturbations (Maier et al., 2012; Hennige et al., 2014; IPCC, 2014; Levin
108 and Le Bris, 2015). In an effort to document the impacts of climate change and other
109 anthropogenic disturbances on a Mediterranean submarine canyon ecosystem hosting
110 abundant colonies of *L. pertusa* and *M. oculata* (Gori et al., 2013), we have set up a long-
111 term *in situ* monitoring programme focusing on key ecological functions. These
112 functions include coral growth, for which data have been lacking so far on multiannual
113 time-scale. Growth rate can furthermore be used as an assessment tool to determine the
114 health and conservation status of deep-sea reef-building corals in marine protected
115 areas (Davies et al., 2008; Vad et al., 2017; Boolukos et al., 2019).

116 The aim of this study was to investigate the growth patterns of *L. pertusa* and *M.*
117 *oculata* over time, to determine their inter-annual temporal dynamics in a region of the
118 Mediterranean where hydrodynamic conditions are seasonally contrasted, with episodic
119 extreme events characterizing winter conditions. These events transporting water
120 masses and particles from the shelf down to the bathyal and abyssal regions vary
121 interannually in frequency and intensity (Béthoux et al., 2002; Canals et al., 2006;
122 Heussner et al., 2006; Durrieu de Madron et al., 2013). The *in situ* experimental
123 approach implemented to study coral growth was based on yearly deployment and
124 recovery of small coral fragments in a study site located at 530 m depth in the Lacaze-

125 Duthiers canyon (LDC), Gulf of Lion, in an area where these two species are naturally
126 abundant. To avoid methodological bias, the growth of *L. pertusa* and *M. oculata* was
127 measured using the same method over eight years (as described in [Lartaud et al., 2017](#)).

128

129 **2. Material and methods**

130

131 2.1. Study site and sampling

132 The Lacaze-Duthiers submarine canyon, 23 km long, is located in the northwestern part
133 of the Mediterranean Sea, in the Gulf of Lion. This canyon is located in the Gulf of Lion
134 Marine Nature Park, a Marine Protected Area that harbour abundant populations of
135 CWCs, particularly the stony corals *L. pertusa* and *M. oculata* between 300 and 600 m
136 depth ([Fig 1-A-B](#)), which have been explored during the MEDSEACAN cruise of the
137 Marine Protected area agency.

138 Previous publications have described the experimental site for coral growth
139 experiments, called site A (42°32.43N, 03°25.26E), located at 530 m depth in the canyon
140 and characterized by large structures of mixed *L. pertusa*, *M. oculata* and *D. Dianthus*
141 ([Lartaud et al., 2014, 2017](#)). Coral collections for this study were obtained during eight
142 distinct cruises lead under the LECOB programme 'Biodiversity, extreme environment
143 and global change' ,using the Remotely Operated Vehicle (ROV) Super Achille on the R/V
144 Minibex or the R/V Janus II from COMEX S.A.. Coral samples were expected to belong to
145 the same genetic population considering that they came from the same small area (<50
146 m²). Colony fragments of *L. pertusa* and *M. oculata* were collected and then transported
147 to the surface using thermally insulated polypropylene boxes that maintain the ambient
148 temperature of deep seawater (i.e., 13°C). On board, the collected corals were
149 transferred into aerated 30 L seawater tanks maintained at 13°C using a chiller. The

150 apical part of corals was cut into small nubbins (called NS and corresponding to ~5
151 polyps for *L. pertusa* and ~8 polyps for *M. oculata*) and/or into longer branches (called
152 BS, with ~15 polyps for *L. pertusa* and ~20 polyps for *M. oculata*). The use of different
153 types of transplant unit (i.e., NS or BS) was previously shown to have no impact on the
154 growth parameters studied (Lartaud et al., 2017). Both types of fragments were glued
155 with an aquatic epoxy resin on transplant units following the protocols described in
156 Lartaud et al (2014) (Fig 1- C). Following years, different deployment conditions were
157 used. First, different nubbins were placed in different orientations on a cobblestone, but
158 no statistical differences were observed in growth rates and polyp mortality between
159 orientations (Lartaud et al., 2014). Also, the deployments on cobblestone directly on the
160 sediment or on a platform about 50 cm above show no impact on cold water corals
161 growth and mortality (Kruskal-Wallis test, p-value > 0.05).

162

163 To measure coral growth rates a catch-recapture approach was used during 6 periods of
164 12 ± 2 months from November 2010 to May 2018 (Table 1). Thirty-seven transplant units
165 were used for *L. pertusa*, which corresponded to 22 nubbins (NS) and 15 branches (BS).
166 Fifty-one transplants units were used for *M. oculata*, which corresponded to 32 nubbins
167 and 19 branches. Also, we performed a temporal monitoring of *L. pertusa* and *M. oculata*
168 growth rates of the same colonies between 2015 and 2018 to exclude genetic factors.

169

170 2.4. Growth measurements

171 Each living and dead polyps of the coral nubbins and branches were counted and
172 photographed before and after deployment with the same orientation for comparison.
173 The use of a scale bar on the pictures allows to measure the linear extension of the coral
174 fragments, which corresponds to the calcification between the last polyp observed

175 before deployment to the summit of the calix of the last polyp observed after recapture.
176 For each year, the maximal linear extension of each BS/NS, which represents the growth
177 capability along a maximum growth direction, were measured using the software ImageJ
178 (Fig 2) (Strömberg et al., 2010; Lartaud et al., 2017). As the growth of *L. pertusa* and *M.*
179 *oculata* colonies is driven by the successive addition of new polyps, growing on top of
180 previous generation of polyps, following a longitudinal axis, the addition of new polyps
181 was counted and measured using the protocol established by Lartaud et al. (2014) to
182 determine the budding rates. The budding rate corresponds to the percentage of new
183 polyp added per polyp initially present per year, and thus reflects the density
184 development of polyps within the colony.

185

186 2.2. Hydrological parameters

187 To monitor hydrological parameters of the Lacaze Duthiers canyon, a Nortek Aquadopp
188 single-point acoustic current meter was installed on the experiment platforms from
189 2015. The probe provided measurements every half hour of the current speed and
190 direction, temperature and acoustic echo intensity in the habitat surrounding the CWCs
191 (~530 m depth in the Lacaze Duthier canyon). Acoustic echo intensity records were
192 converted into suspended particle concentration using an empirical linear equation
193 between the logarithm of concentration (C) and echo intensity (EI) (Gartner, 2004). The
194 equation found using simple regression between concomitant backscatter data and
195 direct sampling concentration in the Gulf of Lions was $10 \times \log(C_{mg/L}) = 0.407 * EI_{dB} -$
196 22.55 ($r^2 = 0.94$, $N = 66$) (Durrieu de Madron et al., 2017).

197 In addition, significant wave height data series were also used to identify eastern storm
198 periods that generate plateau water export and downwelling in the Lacaze-Duthiers

199 canyon (Palanques et al., 2006; Ulses et al., 2008a). They were measured at the Leucate
200 houlograph located about 40 km northwest to the experimental site.

201 From 2010, *in situ* temperature was also monitored in the water column of the Lacaze
202 Duthiers at 500 and 1000 m depth using a Nortek Aquadopp single-point acoustic
203 current meter.

204

205 2.5. Statistical analyses

206 Statistical analyses were conducted using R software and tests for normality and
207 homoscedasticity were performed using the Shapiro-Wilk test ($p < 0.05$). Considering
208 that the distribution was not normal for either budding rates, linear extension and
209 mortality, multiple comparison non-parametric tests were used to assess growth
210 differences between years: a Friedman test for the monitoring on the same colony and a
211 multiple Kruskal-Wallis test for the monitoring on different colonies.

212

213 3. Results

214

215 3.1. Coral survival

216 There was no significant difference between the survival of the two species (Friedman
217 test, $n=11$, $p < 0.05$, Fig. 3 and Table S1), with the exception of the period 2017-2018,
218 where *M. oculata* exhibited higher mortality than *L. pertusa* (average of 70 ± 40 % vs 17
219 ± 27 % respectively).

220 The mortality of *L. pertusa* polyps was generally low ($< 25\%$) except for 2013-
221 2014 (100%), which exhibited significant higher mortalities (K-W test, $n=37$, $p < 0.05$,
222 Table S1). Also, there was a high mortality observed for *L. pertusa* polyps for 2015-2016

223 (71 ± 46 %), which was significantly different from 2010-2011 (0%) and 2017-2018 (17
224 ± 27 %) (K-W test, n=37, p<0.05, Table S1).

225 For *M. oculata*, the percentages of dead polyps were more variables. As for *L.*
226 *pertusa*, the lowest value observed was for 2010-2011 (0 %) and the highest for 2013-
227 2014 (98 ± 11 %), which were statistically different compared to the other periods (K-W
228 test, n=51, p<0.05, Table S1). The periods 2015-2016 (71 ± 35 %) and 2017-2018 (70 ±
229 40 %) were also characterized by high polyp mortality.

230

231 3.2. Budding rates

232 There was no statistical difference in budding rates between *L. pertusa* and *M. oculata*
233 except for the 2016-2017 and 2017-2018 periods, with significantly higher values for *L.*
234 *pertusa* (Friedman test, n=11, p<0.05, Fig. 4 and Table S2).

235 *Lophelia pertusa* exhibited high budding rates (means ranging from 41 to 69 %),
236 excepted for 2013-2014 (1 ± 3 %) and 2015-2016 (22 ± 34 %). Specifically, budding
237 rates for 2013-2014 were statistically lower compared to the other periods (K-W test,
238 n=37, p<0.05, Table S2).

239 For *M. oculata*, the budding rates were variable with significantly higher rates
240 observed in 2010-2011 (54 ± 22 %) and 2016-2017 (28 ± 17 %). For the other time
241 periods, the mean budding rates were below 25%.

242

243 3.3. Linear extension

244 There was no statistical difference between *L. pertusa* and *M. oculata* for the linear
245 extensions except for the 2016-2017 and 2017-2018 periods, with significantly higher
246 growth rates for *L. pertusa* (Friedman test, n=11, p<0.05, Fig. 5 and Table S3).

247 The mean linear extensions of *L. pertusa* were significantly higher during 2016-
248 2017 (24 ± 7 mm y^{-1}) and 2017-2018 (26 ± 9 mm y^{-1}) compared to the other periods
249 (mean values ranging from 1 to 5 mm y^{-1}) (K-W test, $n=88$, $p<0.05$, [Table S3](#)). The
250 highest values were recorded for coral fragments deployed during the 2016-2017
251 period (40.2 mm y^{-1}).

252 For *M. oculata*, the average linear extension was low (≤ 4 mm y^{-1}) except for
253 2016-2017, which displayed a significantly higher growth rate (9 ± 6 mm. y^{-1}).

254

255 3.4. Hydrological parameters from 2015 to 2018

256 The monitoring of temperature, current and suspended particles matter (SPM)
257 concentration conducted at 530 m depth in the Lacaze Duthiers canyon revealed a
258 significant seasonal and interannual variation of the bottom hydrological and current
259 conditions in the canyon head ([Fig. 6](#)). First, these parameters were stable during most
260 of the year except during winter (January-March), which exhibited a period
261 characterized by intermittent temperature drops concurrent with increases in current
262 speed and SPM concentration.

263 The bottom currents during these episodes are directed down-canyon. In 2016-2017
264 ([Fig. 6-B](#)) and 2017-2018 ([Fig 6-C](#)), these episodic signals are often concomitant with
265 high significant wave heights ($> 2-3$ m) recorded at the coast. They are therefore the
266 signature of a water export from the continental shelf to the head of the canyon linked to
267 downwellings induced by easterly winds (as shown by [Palanques et al., 2006](#) and [Ulses
268 et al., 2008a](#)). The lower temperature of the shelf waters compared to the slope waters
269 resulted from the formation of cold and dense water along the coast, which can be
270 rapidly exported to the slope during this eastern storms (as observed in winter 2013,
271 [Fig S1](#)) ([Ulses et al., 2008b](#)). However, some episodes such as those in March 2015 and

272 January 2018 (Fig. 6-A and C) also indicate that there are periods of export and dense
273 shelf water cascading in the canyon independently of these eastern storms. This export
274 is possible under the effect of strong northward winds that are at the origin of the
275 formation by evaporation of cold and dense water at the coast (as observed in winter
276 2012, Fig S1) (Ulses et al., 2008c).

277 In all cases, the increase in SPM concentration could result both from the bottom
278 transport of fine sediment from the shelf and from the local resuspension of sediment in
279 the canyon head. The intensity of the currents during these brief events, between 20 and
280 70 cm/s is sufficient to erode and resuspend fine (clayey and silty) sediments.

281

282 **4. Discussion**

283

284 4.1. Interannual variation in the growth of *Lophelia pertusa*

285 The growth patterns of *L. pertusa* (linear extension and rate of new polyp addition)
286 varied between years. Based on the monitored parameters (mortality, budding rate and
287 linear extension), three main response type can be described for *L. pertusa*: (i) high
288 budding rate but low linear extension (2010-2011 and 2011-2012), (ii) low budding
289 rate, low linear extension and high mortality (2013-2014 and 2015-2016), and (iii) high
290 budding rate and high linear extension (2016-2017 and 2017-2018). Since the corals
291 were deployed at the same location, their growth responses are likely primarily
292 controlled by the surrounding environmental conditions. Particularly for the periods of
293 survey of the same colonies.

294 In the Mediterranean Sea, CWCs are found in submarine canyons where the
295 environmental conditions can vary between years because of episodic dense shelf water
296 events (Canals et al., 2006). Three different types of water plumes are described,

297 corresponding to autumnal storm events (stratified water masses with low intensity),
298 winter storm events (large amount of particles) and winter cascading events (non-
299 stratified water masses with high intensity) (Canals et al., 2006). These events lead to
300 ventilation, changes in the temperature, current speed and transport of material such as
301 organic matter and sediments (Canals et al., 2006; Bonnin et al., 2008; Durrieu de
302 Madron et al., 2013). The input in organic matter is essential to CWCs that are
303 considered to feed primarily on zooplankton and phytodetritus with a preference for
304 living food (Houlbrèque et al., 2004; Kiriakoulakis et al., 2005; Duineveld et al., 2007;
305 Becker et al., 2009; Purser et al., 2010; Tsounis et al., 2010). The change in intensity of
306 these events from year to year, strongly associated with the local meteorological
307 conditions at the surface (Heussner et al., 2006), should impact the growth of *L. pertusa*.

308 The periods 2013-2014 and 2015-2016 (Fig. S1) showed the lowest budding
309 rates and linear extensions combined with the highest *L. pertusa* mortality. The present
310 and earlier *in situ* observations (Lartaud et al., 2017) revealed a high sedimentation rate
311 during these periods, which led to the partial burial of the coral colonies deployed.
312 Sediment exposure leads to physical abrasions of the coral tissues and to a depletion in
313 oxygen for the polyps (Larsson and Purser, 2011). Moreover, the accumulation of
314 sediment particles on the tissues (e.g. coenosarc) can limit food access for the polyps.
315 Sediment cleaning by tentacle movements, tissue distension and mucus secretion also
316 has an energy cost for the coral (Rogers, 1999). Even though moderate concentrations of
317 suspended particles used as nutritional sources can be beneficial, a high sediment
318 concentration leads to coral mortality (Mortensen, 2001). The corals' energy budget are
319 altered by sediment particles that lead to a higher metabolic activity (represented by
320 respiration rates) (Larsson et al., 2013). It has also been reported that stress induced by
321 sediment particles limits the tissues and skeleton growth of scleractinian corals

322 (Anthony et al., 2002). Thus, in a highly turbid environment, the CWCs need to maintain
323 their essential physiological functions (e.g. respiration, remove particles) by allocating
324 their energy away from secondary functions such as biomineralization.

325 In contrast, the periods 2016-2017 and 2017-2018 showed the highest budding
326 rates and linear extension with low mortalities for *L. pertusa*. *In situ* observations
327 showed low sedimentation coupled with winter storm events with comparable
328 moderate intensities for both periods (Fig. 6). Laboratory studies suggest that the
329 increase in food supply, rather than temperature, may control growth rates of CWCs
330 (Mortensen, 2001; Roberts and Anderson, 2002; Orejas et al., 2011b). A reduction in
331 food supply caused a significant decline in the calcification of CWCs (Naumann et al.,
332 2011). Thus, the rapid transport of fresh and labile organic matter during downwelling
333 and cascading events observed during these periods may promote physiological
334 processes, as biomineralization, which is directly positively linked to their ability to
335 catch suspended prey from the water column (van Oevelen et al., 2009). Optimal growth
336 conditions for *L. pertusa* in the Lacaze Duthiers canyon are thus suggested to be strongly
337 influenced by the occurrence of dense shelf water cascades or storm-induced
338 downwelling as suggested (Lartaud et al., 2014), a major driver being the prevention of
339 excessive sedimentation on coral surfaces.

340 However, strong hydrological events can reduce growth patterns as observed for
341 the 2010-2011 and 2011-2012 periods. The combination of a high addition of new
342 polyps together with low linear extension observed for *L. pertusa* suggests that the
343 energy budget was allocated to the production of small polyps and not to the linear
344 growth of the colony. This process may thicken the colony that will better resist to
345 strong water current. It could promote an increase in number of polyp mouths to catch
346 and ingest more food resources from the water column (Musco et al., 2018). Contrary to

347 2016-2017 and 2017-2018, the 2010-2011 and 2011-2012 episodic water plumes were
348 characterized by stronger intensities. The winter 2012 exhibited one of the strongest
349 cascade event recorded in the Gulf of Lion (Durrieu de Madron et al., 2013, Fig S1), and
350 several strong winter storms in the Lacaze Duthiers canyon occurred in 2011 (Puig et al.,
351 2013, Fig S1). Thus, the optimal growth for *L. pertusa* in the Lacaze Duthiers canyon
352 seems to be favored by episodic winter downwelling events of moderate intensity. It
353 shows that cascading events can have antagonist effects on CWCs with the positive effect
354 of food supply in one hand, and on the other hand, the negative effect of currents that
355 are too strong to allow cold water coral polyps to catch preys (Pusceddu et al., 2013;
356 Orejas et al., 2016). This argument should, however, be considered with caution as the
357 importance of these events, lasting only a few weeks, in the annual nutritional budget of
358 corals that is still poorly known.

359

360 4.2. Interannual variation in the growth of *Madrepora oculata*

361 *Madrepora oculata* also displayed high variability in the growth patterns between years.
362 The growth responses scenarios were: (i) high budding rates but low linear extension
363 (2010-2011), (ii) low budding rates, low linear extension and high mortality (2011-
364 2012, 2013-2014, 2015-2016 and 2017-2018) and (iii) high budding rates and high
365 linear extension (2016-2017).

366 The scenario (ii) appeared more frequently for *M. oculata* than *L. pertusa*. As for *L.*
367 *pertusa*, the unfavorable growth conditions in 2013-2014 and 2015-2016 might
368 correspond to high sediment concentrations in the coral habitat. It has been shown that
369 sediment cover must be considered as a fundamental limiting factor for various CWC
370 species, and could be considered to describe the health status of deep-water coral reefs
371 (Lartaud et al., 2017). The period 2011-2012, associated to a strong cascading event

372 during winter 2012 (Durrieu de Madron et al., 2013, Fig S1), suggests that *M. oculata* is
373 more sensitive to strong currents than *L. pertusa*. The high current velocities associated
374 with cascading events may not be optimal for *M. oculata* prey capture rates, or the
375 energy budget may not be sufficient to allow biomineralization under these
376 environmental conditions. However, in the 2017-2018 period that was characterized by
377 an episode of dense water plumes of moderate intensity, both the linear extension and
378 budding rates remain low. Thus, *M. oculata* appear to be more sensitive than *L. pertusa*
379 to environmental variations.

380 The scenario (i) for *M. oculata* follows the same pattern as for *L. pertusa* for 2010-
381 2011 characterized by an intense winter storm (Puig et al., 2013, Fig S1). It suggests that
382 high intensity hydrological events may have a negative impact on *M. oculata*
383 biomineralization, although this species, similarly to *L. pertusa*, can display an increase
384 in polyp density rather than the colony extension as a response to such events. In
385 opposition, the optimal growth rates observed for *M. oculata* were in 2016-2017, which
386 was characterized by a moderate winter storm (Fig. 6). Thus, the scenario (iii) should
387 represent median to favorable environmental conditions for this species. Moreover, the
388 difference between 2016-2017 and 2017-2018 are characterized by hydrological events
389 of similar intensities but not occurring at the same period of the year (Fig. 6). The export
390 of nutrients from surface waters to deeper water layers in the canyon are likely different
391 in both quantity and quality considering the seasonality in phytoplankton blooms in late
392 winter to early spring (Heussner et al., 2006).

393

394 4.3. Distinct responses of *L. pertusa* and *M. oculata* to environmental conditions

395 It was previously shown that *L. pertusa* has a higher growth rate than *M. oculata*
396 (Lartaud et al., 2014; 2017), particularly at the studied location in the Lacaze-Duthiers

397 canyon where *L. pertusa* dominates the assemblages (Gori et al., 2013; Fabri et al., 2014).
398 This study highlights the different growth dynamics between the two species in
399 response to local environment within a shared habitat. Both species feed primarily on
400 zooplankton and phytodetritus (Duineveld et al., 2007; Carlier et al., 2009). *Lophelia*
401 *pertusa* is, however, a more opportunistic feeder (Dodds et al., 2009) and has a higher
402 prey capture rate (Kiriakoulakis et al., 2005; Tsounis et al., 2010). As a consequence, *L.*
403 *pertusa* should be less impacted by changes in food type, likely associated to the
404 intensity and period of occurrence of water plumes. Other factors such as the
405 reproduction strategy (Waller and Tyler, 2005) and the microbiome (Meistertzheim et
406 al., 2016) suggest more plasticity in the behavior of *L. pertusa* and could partly explain a
407 higher resilience to environmental changes compared to *M. oculata*. In the NE Atlantic
408 Ocean, *L. pertusa*'s seasonal reproductive strategy involves the spawning of a high
409 quantity of small oocytes for a maximal dispersion, contrary to *M. oculata* that spawns a
410 smaller quantity of bigger oocytes. This suggests that *M. oculata* may produce and
411 spawn gametes only during optimal conditions for reproduction (Waller and Tyler,
412 2005). In addition, *M. oculata* is more sensitive to thermal stress compared to *L. pertusa*
413 (Naumann et al., 2014; Brooke et al., 2013) which suggests that *L. pertusa* is more plastic
414 in term of temperature variations. At the level of the microbiome, the difference in
415 associated bacterial community composition could also reflect different ecological
416 strategies. *Madrepora oculata* has a very specific microbiome in contrast with the more
417 versatile microbiome for *L. pertusa*, suggesting again that this species is more plastic to
418 environmental variations (Meistertzheim et al., 2016).

419 It is thus essential to incorporate the inter species responses to forecast future
420 changes of deep sea reefs and establish efficient conservation measures for these critical
421 habitats, particularly considering that CWCs are at their upper thermal tolerance in the

422 Mediterranean region (Freiwald et al., 2004). In this region, predictive models using the
423 IPCC A2 scenario indicate less precipitation and river runoff in the coming century, with
424 higher temperatures suggesting that dense water shelf cascade to the deep basin in the
425 Gulf of Lion could disappear by 2100 (Somot et al., 2006; Herrmann et al., 2008).

426

427 4.4. Are cold-water corals slow-growing species?

428 Scleractinian cold-water corals have long been considered as slow-growing species with
429 growth rates below 1 cm y⁻¹ (Wilson, 1979; Freiwald and Roberts, 2006), much lower
430 than zooxanthellate scleractinian coral growth that can exceed 15 cm y⁻¹ for some
431 species (Dullo, 2005). This study highlights that *in situ* CWCs biomineralization can be
432 much higher and comparable to some of their shallow water analogues. Some studies
433 already showed that scleractinian cold water corals could exceed 3 cm y⁻¹ in the
434 Mediterranean Sea and the Gulf of Mexico (Lartaud et al., 2017; Larcom et al., 2014), but
435 here we report growth rates reaching 4 cm y⁻¹. The growth of CWCs is strongly
436 influenced by biotic and abiotic factors such as food supply, hydrography and
437 temperature (Cairns and Macintyre, 1992; Thiem et al., 2006; Guinotte et al., 2006;
438 Roberts, 2009; Purser et al., 2010). Temperature increase can improve physiological
439 processes such as growth rates due to increase metabolism efficiency (Dodds et al.,
440 2007). However, the thermal optimum and the potential for adaptation to temperature
441 variations are still unknown for CWCs. Although in the Mediterranean Sea, CWCs are
442 thought to reach their upper ecological thermic limit (i.e., 14°C) (Freiwald et al., 2004),
443 the high growth rates could reflect present particular favorable conditions compared to
444 other coral areas, likely due to the supply of food from peculiar hydrological conditions.

445

446 5. Conclusion

447 This first long-term *in situ* study conducted on CWCs highlights growth rate variations
448 associated with inter-annual changes in environmental conditions driven by
449 hydrological processes. In the Lacaze Duthiers canyon, episodic hydrologic events (e.g.
450 downwelling, cascading, storms) transport surface waters drive organic particles from
451 surface production inside the canyon and are likely to modulate the quality and quantity
452 of food available for CWCs. Consistent with these irregular inputs, the growth of CWCs
453 differs from year to year depending on the type of dense water shelf event: (i) strong
454 water plume events cause high budding rates but low colony linear extension by limiting
455 prey capture rates with high current speed, (ii) the absence of water plume events cause
456 low budding rates, low linear extension and high mortality due to high sedimentation
457 rates, and (iii) median water plume events cause high budding rates and high linear
458 extension associated with higher organic matter supply. Furthermore, we observed an
459 inter-specific variability in mortality, growth rates and linear extension between *L.*
460 *pertusa* and *M. oculata*. *Lophelia pertusa* appears more plastic to environmental
461 variation as compared to *M. oculata*. Finally, we demonstrated for the first time that *L.*
462 *pertusa* could reach linear extension comparable to their shallow water counterparts.

463 In the context of the ongoing global change, an increase of the stratification is
464 expected in the Mediterranean Sea, which will reduce the supply of fresh oxygenated
465 water containing organic matter from the surface to the deep ocean. The resilience of
466 cold-water corals in the future Mediterranean Sea is threatened, particularly considering
467 that CWCs are supposed at their upper thermal tolerance. It is essential to incorporate
468 the inter species responses to establish efficient conservation strategies for these critical
469 habitats.

470

471 **Author contributions**

472 LC, FL, NLB and PG designed the study. LC, NLB, XDDM, EP, PG and FL conducted the
473 study, analyzed the data and wrote the paper.

474

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482

483 **Additional information**

484 Supplementary information accompanies this paper.

485 Competing Interests: The authors declare no competing interests.

486

487 **Figure and table captions**

488

489 Figure 1: Cold-water coral reefs with (A) *Lophelia pertusa*, and (B) *Madrepora oculata* in
490 the Lacaze-Duthiers canyon (C) where branches and nubbins has been deployed on
491 transplant units fixed to a deep-sea experimentation platform (© UPMC-Fondation
492 TOTAL).

493

494 Figure 2: The pictures represent the same replicate of *L. pertusa* during four years (in
495 purple, the first linear extension during 2015-2016, the second in green during 2016-
496 2017 and the third in red during 2017-2018).

497

498 Figure 3: Polyp mortality of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010
499 and 2018. All the values represented the median and quartiles.

500

501 Figure 4: Budding rates (%) of *L. pertusa* (grey) and *M. oculata* (white bars) between
502 2010 and 2018. All the values represented the median and quartiles.

503

504 Figure 5: Linear extension (mm.y^{-1}) of *L. pertusa* (grey) and *M. oculata* (white bars)
505 between 2010 and 2018. All the values represented the median and quartiles.

506

507 Figure 6: Time series of significant wave height at the Leucate site, near-bottom
508 temperature, near-bottom current speed component along the canyon axis, and near-
509 bottom suspended particle matter concentration, at 530 m depth in the Lacaze-Duthiers
510 canyon for the (A) 2015-2016, (B) 2016-2017 and (C) 2017-2018.

511

512 Table 1: Characteristics of the transplant units used for each time period for *L. pertusa*
513 and *M. oculata*. The mean \pm SD is shown for the polyp mortality.

514

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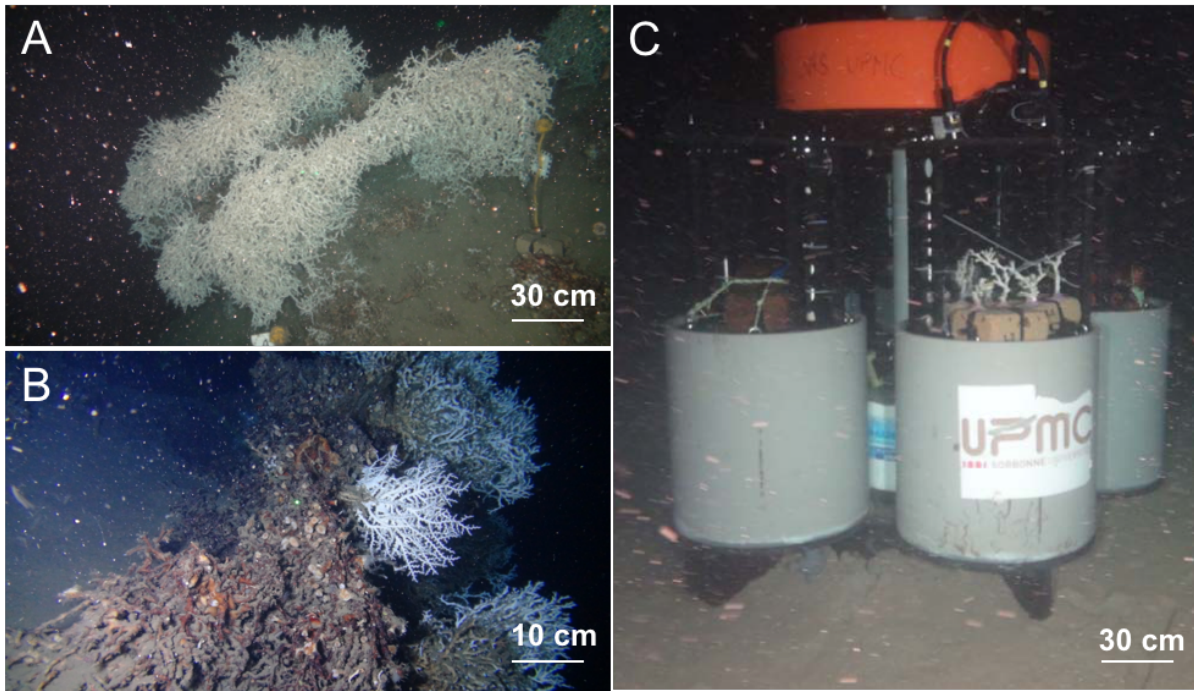
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767 Table 1: Characteristics of the transplant units used for each time period for *L. pertusa*
 768 and *M. oculata*. The mean \pm SD is shown for the polyp mortality.

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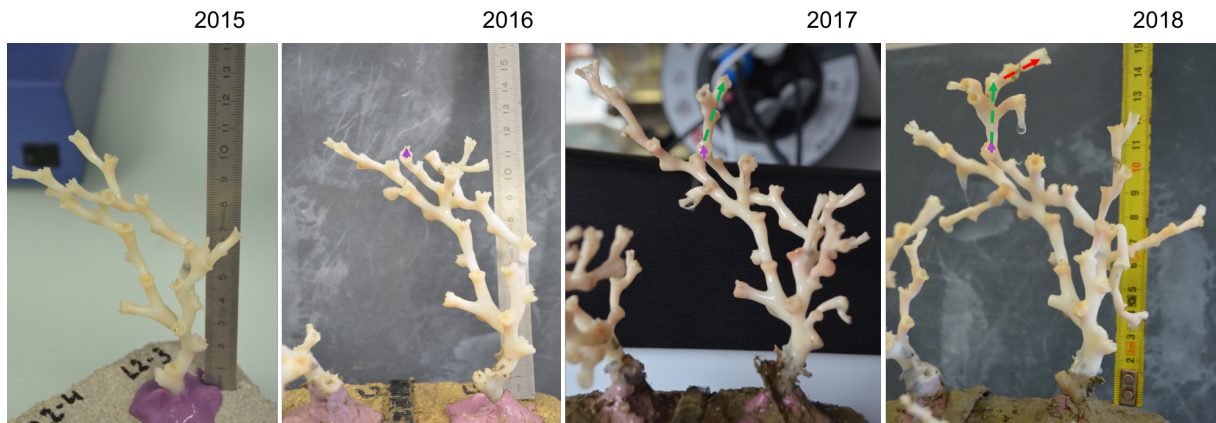
Species	Time period	Transplant unit	Number of colonies	Number of replicates	Initial number of polyps	Number of new polyps	Breakage (%)	Mortality (%)
<i>L. pertusa</i>	Nov2010-Sep2011	NS	2	4	12	6	8	0 \pm 0
	Sep2011-Jul2012	NS	2	6	20	9	5	18 \pm 36
	Jul2013-Oct2014	NS	1	4	13	0	8	100 \pm 0
		BS	2	2	20	1	13	100 \pm 0
	Jun2015-Jun2016	NS	2	7	31	6	9	87 \pm 34
		BS	1	3	61	13	24	34 \pm 57
	Jun2016-Jun2017	BS	2	5	96	66	3	15 \pm 12
	Jun2017-May2018	BS	2	5	130	54	1	17 \pm 27
<i>M. oculata</i>	Nov2010-Sep2011	NS	2	5	38	16	0	0 \pm 0
	Sep2011-Jul2012	NS	2	7	76	11	0	48 \pm 43
	Jul2013-Oct2014	NS	3	12	118	7	5	96 \pm 13
		BS	3	6	141	10	51	100 \pm 0
	Jun2015-Jun2016	NS	1	8	81	2	10	67 \pm 38
		BS	1	2	39	0	34	86 \pm 19
	Jun2016-Jun2017	BS	1	5	229	63	6	23 \pm 12
	Jun2017-May2018	BS	1	6	226	9	0	70 \pm 40

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Figure 1: (A-B) Cold-water coral reefs with (A) *Lophelia pertusa* and (B) *Madrepora oculata* in the Lacaze-Duthiers canyon, (C) where branches and nubbins has been deployed on transplant units fixed to the deep-sea experimentation platform.



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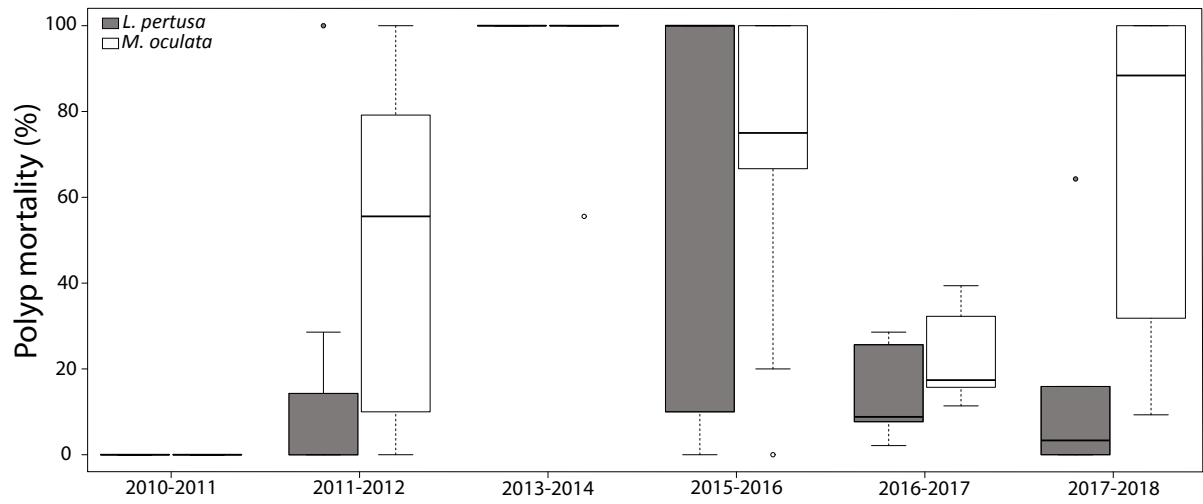
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780 Figure 2: The pictures represent the same replicate of *L. pertusa* during four years (in

781 purple, the first linear extension during 2015-2016, the second in green during 2016-

782 2017 and the third in red during 2017-2018).

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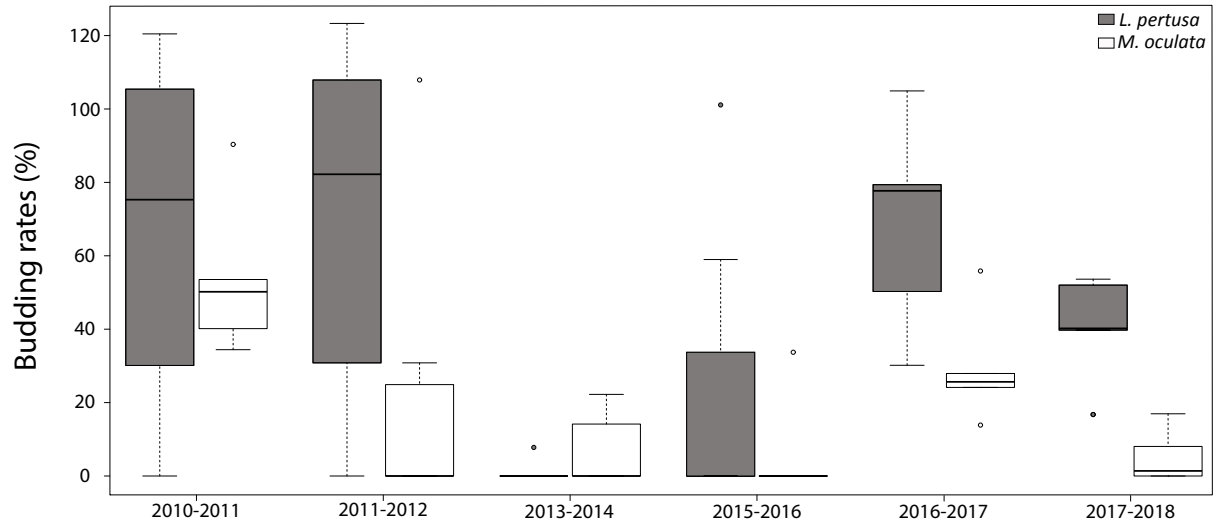
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786 Figure 3: Polyp mortality of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010

787 and 2018. All the values represented the median, quartiles and extrema.

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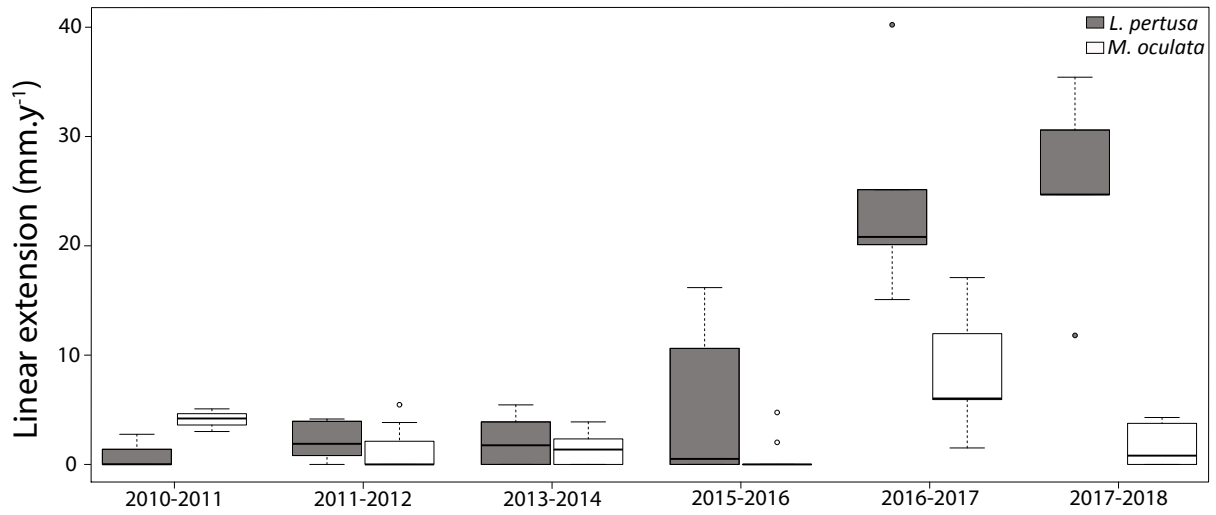
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792 Figure 4: Budding rates (%) of *L. pertusa* (grey) and *M. oculata* (white bars) between

793 2010 and 2018. All the values represented the median, quartiles and extrema.

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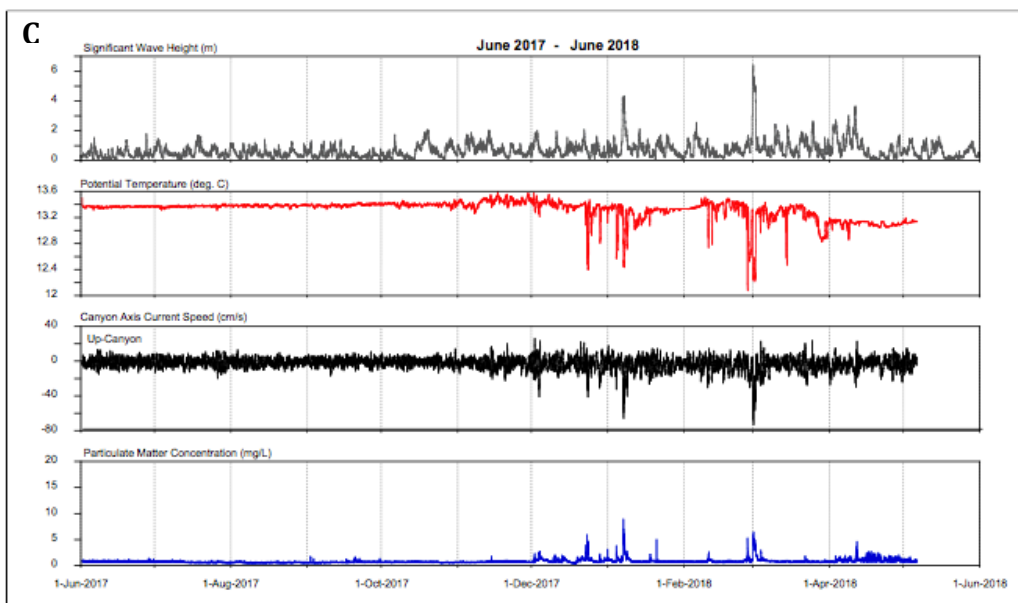
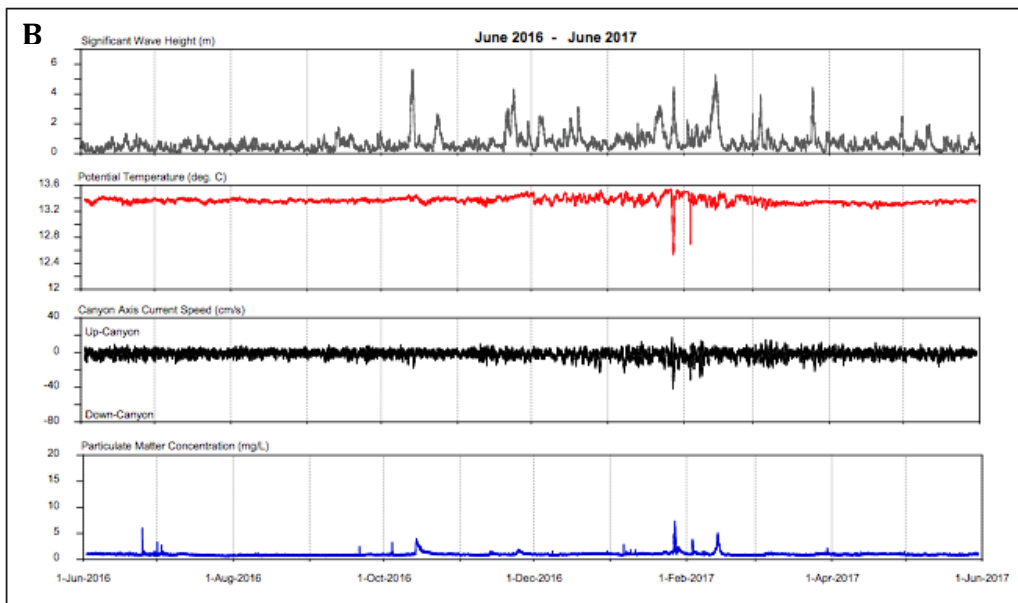
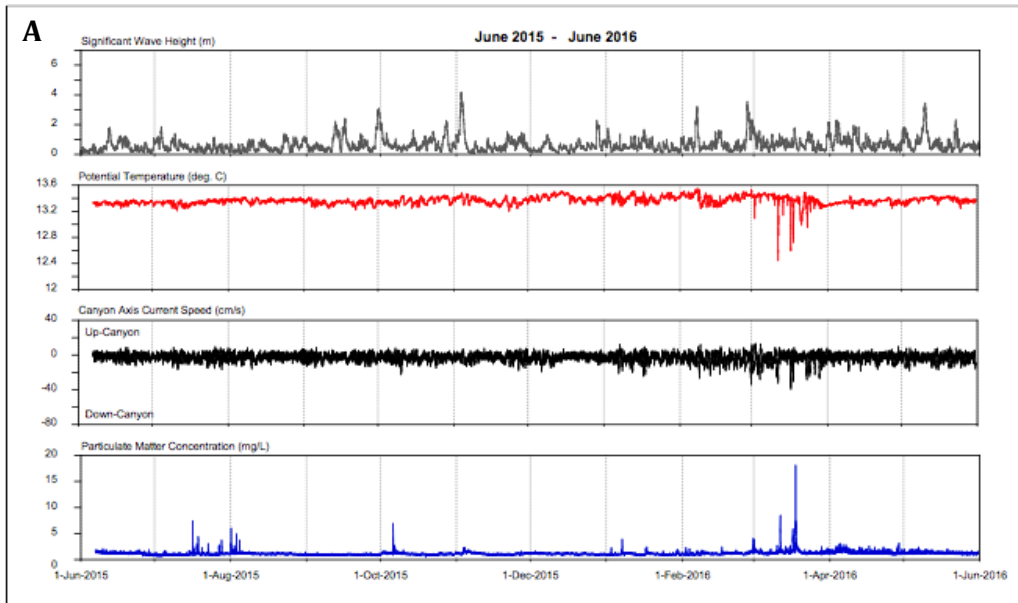
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798 Figure 5: Linear extension (mm.y⁻¹) of *L. pertusa* (grey) and *M. oculata* (white bars)

799 between 2010 and 2018. All the values represented the median, quartiles and extrema.

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803 Figure 6: Time series of significant wave height at the Leucate site, near-bottom

804 temperature, near-bottom current speed component along the canyon axis, and near-

805 bottom suspended particle matter concentration, at 530 m depth in the Lacaze-Duthiers

806 canyon for the (A) 2015-2016, (B) 2016-2017 and (C) 2017-2018.

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