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1 **Community composition predicts photogrammetry-based structural**
2 **complexity on coral reefs**

3

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17

18 **Keywords**

19 Coral Complexity – Rugosity measures – Photogrammetry – Reef ecology – Modeling

20

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28 **Abstract**

29 The capacity of coral reefs to provide ecosystem services, to keep their diversity and
30 their productivity are related to their three-dimensional structural complexity. This parameter
31 is also correlated to total fish biomass, to the general reef resilience to external stresses and to
32 their ability to dissipate wave energy. However, information on structural complexity (also
33 defined as reef rugosity) has been uncommonly assessed in historical monitoring programs,
34 with the result that the long-term trend of this variable is generally unavailable. In this study,
35 we show that it is possible to predict and hindcast the three-dimensional complexity of coral
36 reefs by combining photogrammetry, statistical modeling and historical benthic community
37 data. We calibrated a lasso generalized linear model to predict structural complexity obtained
38 by 57 photogrammetry transects recorded at 13 sites around the island of Moorea (French
39 Polynesia). Our model was able to predict structural complexity with high accuracy (cross-
40 validated $R^2 = 0.81 \pm 0.12$). We then used our model to hindcast historical trends in 3D
41 structural complexity using community composition data collected in Moorea from 2004 to
42 2017. The temporal analysis highlighted the dramatic effect of a crown-of-thorns outbreak in
43 2006-2009 and Cyclone Oli in 2010. These two events together reduce coral cover from $\approx 50\%$
44 to almost zero. Our model captured these effects, confirming the possibility to predict structural
45 complexity on the basis of assemblage composition.

46 **Introduction**

47 Global concerns are emerging about the increasing frequency of mass mortality of
48 corals associated to coral bleaching events (Van Oppen and Lough 2009; Heron et al. 2016;
49 Hughes et al. 2017). These disturbances are associated to severe habitat destruction that reduces
50 the structural complexity (i.e., flattening) of coral reefs (Newman et al. 2015). Structural
51 complexity is the three-dimensional spatial arrangement of an ecosystem (McCormick 1994;
52 Chazdon 2014), which is largely due to the growth form and distribution of hard coral.
53 According to the habitat heterogeneity hypothesis (MacArthur and Wilson 1967), the more
54 complex the structure of an ecosystem, the greater the diversity and abundance of associated
55 organisms. On coral reefs, the 3D structural complexity of the habitat is correlated to the
56 biomass and diversity of fish (Willis and Anderson 2003; Gratwicke and Speight 2005;
57 Alvarez-Filip et al. 2009; Rogers et al. 2014), to the reef capacity to recover from disturbance
58 (Graham et al. 2015), but also to the reef ability to dissipate wave energy, thus protecting the
59 shoreline from extreme inundations (Harris et al. 2018). Broad-scale declines in the complexity
60 of coral reefs have been observed both in the Caribbean and the Pacific as a result of both human
61 impacts and climate changes (Hoegh-Guldberg 1999; Hughes et al. 2003; Hoegh-Guldberg et
62 al. 2007; Perry et al. 2018). Despite the well-known important relationship between structural
63 complexity, ecological diversity, abundance and biomass, information on structural complexity
64 is sparse in monitoring programs with the result that long-term trends for this variable are
65 virtually unknown (Graham et al. 2015).

66 Methods to measure structural complexity (often referred as rugosity, in particular in
67 older literature) on coral reefs first arose in the 70' in articles by Risk (1972) and Hobson
68 (1972). These authors defined three criteria for measuring complexity: 1) the measure had to
69 be easily understandable, 2) it had to be measurable during the fieldwork and, 3) it should be
70 comparable. In early studies, it was proposed that rugosity could be recorded by draping a steel
71 chain over the reef surface, and then measuring the ratio between the total length of the chain

72 and the planar distance between the ends of the chain. The higher the ratio, the more complex
73 the substratum (Hill and Wilkinson 2004; Graham and Nash 2013). Despite the ease of use of
74 such metric, laying a chain represents a bi-dimensional measure which does not capture the full
75 complexity of complex three-dimensional (3D) habitats such as coral reefs. Although some
76 time-consuming 3D metrics have been proposed in the past (e.g. Parravicini et al. 2006), the
77 recent progress in underwater photogrammetry are finally affording researchers the opportunity
78 to capture the three-dimensionality of coral reefs. For example, Friedman et al. (2012) started
79 to use a georeferenced survey work and each includes a downward-looking camera pair with a
80 baseline of approximately 7cm, pixel resolution of 1360×1024 to define rugosity. Others
81 authors like Burns et al. (2015) were using these new advances for defining the rugosity about
82 a transect and extract a complexity index at the species level for 6 species. Leon et al. (2015),
83 defined three roughness parameters, namely the root means square height, tortuosity (i.e.
84 rugosity) and fractal dimension, and were derived and compared in order to asses which one
85 better characterizes reef flat roughness. Naughton et al. (2015) succeed with an accuracy never
86 equaled to define maps of community structures between taxa. Some writers have even pushed
87 the boundaries to measure the small-scale three-dimensional features of a shallow-water coral
88 reef thanks to drone (Casella et al. 2017). Thus, a plethora of works have emerged asking
89 several authors about the chain-tape future (Storlazzi et al. 2016). However, whatever the metric
90 employed (chain-tape or photogrammetry methods), there is still no clear evidence concerning
91 what is driving structural complexity. Some authors claim that it is driven by the presence of
92 some branching species like the *Acropora* spp. and thus the overall coral cover would not matter
93 (Aronson and Precht 2006; Alvarez-Filip et al. 2009, 2011). Others have found that coral cover
94 is significantly and highly correlated to the rugosity (Halford et al. 2004; Graham and Nash
95 2013) or species composition (Richardson et al. 2017). But in both cases, there is a common
96 consensus for admitting coral drives complexity which could be used for rebuilding past
97 rugosities.

98 In this study, we combined statistical modeling to 3D reef transects reconstructed using
99 photogrammetry in order to test the potential to predict coral reef structural complexity on the
100 basis of benthic community composition. We study the reefs of Moorea (French Polynesia)
101 where, using benthic communities time series we back-calculate reef structural complexity. We
102 were able to retrace two relevant episodes of habitat destruction: the *Acanthaster planci*
103 outbreak of 2006-2009 and cyclone Oli of 2010.

104

105 **Material and Methods**

106 **1. Study area**

107 Moorea is a tropical volcanic island of volcanic origin, located in the Pacific Ocean
108 between 17.4714° and 17.6058° South and 149.7522° and 149.9269° West. The island is
109 shaped as a triangle with a perimeter of 61 km and coastlines facing north, southwest and
110 southeast (**Fig. 1**). The island is encircled by a coral reef, that is 500 to 700 m wide; the only
111 exception to this pattern is the Northeast extremity where the lagoon width is limited to few
112 tens of meters. Moorea is exposed to Northwest winds from January to March. Tides are
113 semidiurnal with an amplitude of less than 0.3 m (Chazottes et al. 1995; Leichter et al. 2013).
114 The swell direction is from southwest to northeast during the whole year.

115 The reefs of Moorea are threatened by several disturbances of biotic and abiotic origin
116 (Adjeroud et al. 2018). The most devastating biotic disturbances were the 1979 and 2006
117 *Acanthaster planci* outbreak, which reduced coral cover from 50% to 10% (in 1979; Berumen
118 and Pratchett 2006) and from 50% to less than 10% (in 2006; Lamy et al. 2016). Abiotic
119 disturbances also impacted Moorea island, with main cyclones recorded in 1991 (Wasa) and
120 2010 (Oli). The impact of Wasa reduced the coral cover by 5% to over 20% across all the island.
121 In contrast, coral cover was reduced to lower than 5% by Cyclone Oli (Lamy et al. 2016;
122 Adjeroud et al. 2018) (**Fig. 2**).

123

124 **2. Rugosity measures**

125 In Moorea, a total of 57 photogrammetric transects were surveyed in end-of-2015 –
126 beginning-of-2016, at three different sites: Tiahura (North Coast, 21 transects); Haapiti
127 (Southwest coast, 20 transects) and Temae (Southeast coast, 16 transects) (**Fig. 1**). Each transect
128 consisted of swaths of 20m length and 2m width and all transects were carried out in the outer
129 reef, between 5 and 8m depth. Each transect was set up fixing on the bottom a 2m-long chain
130 and, perpendicularly to it, a 20m-long metered tape. A diver swam ≈ 2 m above the sea-bottom,
131 maintaining the swimming speed as constant as possible and collecting images with a GoPro
132 Hero camera pointed towards the sea-bottom. The camera was set to collect photos (12
133 megapixels) in time-lapse mode (2 pictures per second). For each transect, we collected
134 approximately 200 photos with a forward overlap of $\approx 90\%$, with the diver swimming over the
135 length of the entire transect four times to allow optimal side overlap. After the collection of the
136 photos, the diver noted the depth of each extremity of the chain and metered tape to use them
137 in the photogrammetric process as Ground Control Points (GCPs). In the case of an on-the-job
138 self-calibration, the camera calibration is derived from image coordinates measured in the
139 mapping photography and including the camera calibration parameters as unknowns in a self-
140 calibrating bundle adjustment (Harwin et al. 2015).

141 The set of photos and the GCPs collected were then used as input to Agisoft Photoscan
142 (www.agisoft.com), a photogrammetry software based on the Structure from Motion (SfM)
143 method (Ullman 1979; Westoby et al. 2012). We used Agisoft to build the orthophotomosaic
144 and the Digital Elevation Model (DEM) of each transect, with the same procedure explained
145 by Storlazzi et al. (2016). Details of the photogrammetric process are shown in the **Annex S1**.
146 Subsequently, we imported the DEM in ArcGIS v10.2 and calculated the reef rugosity by
147 dividing the surface of the DEM area by the area of its planar projection (approximately 40m^2)
148 (**Fig. 3**). For the 57 transects, we estimated an average horizontal error of $0.1\pm 0.06\text{m}$ and
149 average vertical error of $0.04\pm 0.04\text{m}$, internal to the reconstructed model. Only the vertical error

150 had an influence on the estimation of rugosity, but given the range of the error, it was considered
151 negligible.

152

153 **3. Benthic community description and assessment**

154 The orthophotomosaics were imported into Coral Point Count, which was used
155 with an Excel extension v4.1 (Kohler and Gill 2006). We assessed the benthic cover placing
156 100 random points on the photomosaic and described 8 distinct benthic cover categories (**Table**
157 **1**). A second dataset was used according to the CRIOBE surveys from 2004 to nowadays and
158 consists of 25m point intercept transects data collected at 13 sites around the island across three
159 habitats (fringing reef, back reef, outer reef) and using the same benthic categories (**Fig. 1**).
160 This classification is based on the guideline of the monitoring program created by SO CORAIL
161 (<http://observatoire.criobe.pf/CRIOBEData/>), the coral reef observation program of the French
162 National Institute for Earth Sciences and Astronomy (INSU). These categories enabled us to
163 back-calculate structural complexity on time series data from Moorea. For matching both
164 datasets according to the habitat, only the outer reef was selected.

165

166 **4. Statistical analysis**

167 Our main goal was to calibrate a model that predicts structural complexity according to
168 the benthic community composition. Since benthic community cover is expressed as
169 percentages, we preferred not to use them as predictor variables as they are heavily correlated,
170 and collinearity would have been high. We preferred to build a database that include the time
171 series data and our photogrammetry transects without transforming the data to perform
172 multivariate analysis. Thus, the Euclidean distance could be used to conduce a Principal
173 Component Analyses (PCA). The first five orthogonal axes (accounted for more than 75% of
174 the variance) were then extracted to be used as predictor variables in the model. A lasso
175 generalized linear model has been conducted to predict coral reef structural complexity

176 according to the 5 PCA axes. A 10-Fold cross validation was done and a step AIC procedure
177 defining the best model was applied. Because the 57 transects were measured at the same depth,
178 those transects were pooled together rather to apply a mixed model due to the lack of the data,
179 making us benefit from a solid robustness. The best model selected kept only 3 PCA
180 dimensions. According to the k-fold analysis, $k R^2$ were obtained giving a necessary uncertainty
181 for the model. This method appears more meaningful estimate than classical R^2 when the model
182 has to be used for predictions. The lasso generalized linear model was then applied to time
183 series data to back-calculate structural complexity and to test whether our model was able to
184 detect drops of structural complexity due to the major perturbations.

185 The PCA data for the time series in Moorea were used to produce PCA plots and define
186 the long-term tendencies in order to descriptively assess the entity of the effect of the
187 *Acanthaster planci* outbreak (2006-2009) and the Oli cyclone (2010) on benthic communities.
188 An ANOVA was then applied with the aim to define several bunches of similar years according
189 to the PCA axes. To match those years with each other, a Tukey post-hoc analysis was
190 conducted and a matrix of results was elaborated. Finally, special attention has been given about
191 the *Acropora* spp. cover, *Pocillopora* spp. cover and rugosity index in 2004 (pre-disturbance
192 year, with the high percent cover of corals) and 2017 (post-disturbance year, with the high
193 percent cover of corals) to define a potential resilience or recovery (**Table S1**).

194

195 **Results**

196 The analysis of time series revealed that coral diversity was higher in 2004 with a
197 percent cover of corals (CC) of 44.08% (**Fig. 4**). The CC decreased from 2004 to 2010 down
198 to a minimum of 3.62%, which corresponds to the event of Cyclone Oli. After the cyclone
199 passed, the coral cover increased over time until the end of the series (2017) with a final value
200 of 42.77%. In 2004 the coral reefs of Moorea also showed a greater diversity of coral
201 morphology (massive, branching in general, columns and encrusting). The assemblages

202 remained fairly stable despite a slow decline of the CC the first 2 years ($CC_{2004} = 44.08\%$ to
203 $CC_{2006} = 40.62\%$). Then, a first Crown-Of-Thorns Starfish (COTS) outbreak was reported in
204 early 2006 (Kayal et al. 2012) and continued until 2009. The following year, cyclone Oli hit the
205 island further decreasing the CC. After these events and until 2014, the substrate consisted of
206 rubble and cobbles. From 2015, the CC recovered to a state similar to that of 2004. However,
207 compared to 2004, the coral cover in 2017 was dominated by *Pocillopora* spp. ($20.10 \pm 6.78\%$
208 in 2004 vs $26.61 \pm 14.52\%$ in 2017) instead of a more diverse assemblage with a high abundance
209 of *Acropora* spp ($9.76 \pm 5.61\%$ vs $2.53 \pm 1.90\%$ in 2017).

210 The cross-validated R^2 (CV- R^2) from our model reaches 0.81 ± 0.12 . The 3 dimensions
211 used were all significant and non-correlate (**Table 2, Fig S1**). The back calculation of structural
212 complexity captured these major shifts in community structure. High structural complexity was
213 observed in 2005 and 2006. All sites were then predicted to lose complexity corresponding to
214 the timing of COTS outbreak models present patterns of decrease and increase in rugosity,
215 matching with the biotic and abiotic changes like the COTS outbreak and the Cyclone Oli, as
216 discussed above (**Fig. 5**). The model also exemplifies that the resilience of structural
217 complexity differs among the thirteen reefs studied around Moorea island. In 2004, the
218 highest values of structural complexity were measured respectively at Pihaena (North),
219 Motu Ahi (East) and Haapiti (Northwest) (3.86, 3.51 and 2.92 respectively) while the
220 lowest were recorded in Maatea (Southeast), Tiahura (North) and Aroa (North) (2.26,
221 2.07 and 1.81 respectively). After the disturbances in 2010, the higher values were
222 defined in Taotaha (Northwest), Afareaitu (Southeast) and Entre 2 Baies (North) (2.08,
223 2.10 and 2.10 respectively) while the lowest values were documented at Haapiti
224 (Northwest), Tiahura (North) and Maatea (Southeast) (1.84, 1.66 and 1.15 respectively).
225 Finally, in 2017, the 3 lowest values were measured on the East coast (Motu Ahi, Maatea
226 and Temae with rugosity values of 2.35, 2.12 and 1.98 respectively) while the sites located

227 on the northwest side (Entre 2 Baies, Tiahura and Gendron) presented the 3 higher
228 rugosity scores (4.36, 4.31 and 3.53 respectively).

229 Finally, rugosity values rise to values equivalent to the first year of monitoring, during
230 the last year of monitoring in 2017. The presence of *Acropora* spp. shows a significant
231 difference between 2004 and 2017. However, no significant difference could be observed in
232 either the *Pocillopora* spp. presence or the rugosity score (**Fig. 6**). In addition, the ANOVA
233 followed by the post-hoc analysis confirmed a difference between two bunches of years
234 according to the complexity around the island. Indeed, two profiles were highlighted: 1)
235 one from 2004 to 2007 and 2016 to 2017 and 2) one from 2008 to 2015. These results
236 support that the 3D complexity came back to an equilibrium four years after the Oli
237 cyclone (**Table S1**).

238

239 **Discussion**

240 In this study we used a combination of methods – coral reef photogrammetry and
241 statistical models – to test the potential to use species composition data to predict the structural
242 complexity of coral reef assemblages. The use of the photogrammetry allowed us to obtain a
243 three-dimensional metric of structural complexity, compared to linear metrics classically used
244 such as the chain transect (Burns et al. 2015). Photogrammetry permits us to cover 40m² of the
245 reef in one dive of about 90 minutes, whereas the chain method usually requires
246 approximatively 15 minutes for a simple 20m transect. However, even if the pixel size of 1.73
247 × 1.73 μm - used for defining the complexity - is higher resolution than what is achieved using
248 chain and tape, the results have to be interpreted with cautious. Indeed, a number of studies
249 have shown photogrammetry to be error prone in a number of different ways. Lavy et al. (2015)
250 and Figueira et al. (2015) both found that branching corals and other complex growth forms
251 produce more error in photogrammetry-based estimates of complexity compared to in situ
252 methods. Furthermore, Bryson et al. (2017) found that environmental conditions,

253 postprocessing, and even taking photos underwater can impact the accuracy of 3D structure
254 estimates using photogrammetry. In addition, this model is relevant for planar parts of the
255 reef, however, facing dropoff would be challenging. This technique requires swimming
256 over the bottom, nevertheless, as the more the distance you add between you and the
257 bottom, the worst the reconstruction will be. Finally, all the hidden part (not present in
258 the photos) are not reconstructed (e.g. what is inside a hole). The latter limit causes
259 relatively heavy consequences to define an accurate measure of the rugosity in those
260 conditions. From a statistical point of view, Carroll et al. (2006) defined 3 different regimes of
261 swell in Moorea which could altered the benthic composition, according to the exposure due to
262 the side of the island. Even if these affirmations are directly observable concerning the rugosity
263 in 2017 with our current model (lowest values on the east coast and higher values on the north
264 coast) a mixed model would have been more relevant. Unfortunately, only 16 transects were
265 done on the southeast side of Moorea which is not allowed us for using a mixed model. The
266 robustness of the model would have been directly impacted by the lack of residuals (rugosity
267 values sometimes lower than 1; Launer & Wilkinson, 2014). As per any statistical model, the
268 accuracy of prediction will increase with the size of the calibrating dataset. In that context, more
269 data will likely be needed to accurately capture spatial variation.

270 Despite these limits, we have found a significant relationship between reef structural
271 complexity and the composition of the benthic assemblages. Indeed 3 PCA axes were enough
272 to accurately predict complexity with a high accuracy ($CV-R^2 = 0.81 \pm 0.12$). To validate our
273 model, we compared our values to (Kayal et al. 2017). These authors have found values at 12m-
274 depth of 1.44 ± 0.08 , 1.41 ± 0.05 and 1.70 ± 0.03 for Haapiti, Tiahura and Entre 2 Baies
275 respectively. Our model suggests values for these locations of 1.75 ± 0.50 , 1.68 ± 0.47 and 1.70
276 ± 0.60 respectively. Thus, even according the huge range of the uncertainties, our results
277 highlight the potential to use statistical modeling to predict structural complexity when this
278 information is lacking. Given the importance of structural complexity in ecological functioning

279 of coral reefs, the reconstruction of structural complexity is critical from long-term benthic
280 historical data, if we want to better understand and predict changes in coral reefs. For example,
281 Graham and Nash (2013) reviewed 20 studies using chain method to measure coral reef rugosity
282 in the Caribbean and found a strong negative relationship between structural complexity and
283 algal cover, a positive relationship between the structural complexity and the coral cover, and
284 a strong positive relationship between structural complexity and fish density and biomass.
285 Later, Graham et al. (2015) demonstrated that structural complexity is the main predictor of
286 coral reef recovery capacity after acute disturbance. This metric represents thus a key variable
287 of coral reef status, and apodictically exists also regarding the present day flattening of coral
288 reefs under the influence of climate change and human impacts. Back-calculating structural
289 complexity, with due caution, may be important to infer present coral reef status compared to
290 historical or quasi-pristine conditions.

291 Here, we have documented major changes in benthic assemblages across Moorea's coral
292 reefs (Berumen and Pratchett 2006; Adjeroud et al. 2018). *Acropora* spp. and *Pocillopora* spp.
293 were dominant species in 2003 (Berumen and Pratchett 2006) and this was still the case in 2004.
294 *Pocillopora* spp. then, *Acropora* spp. were affected by both COTS outbreak and the Oli cyclone
295 more than any other taxon (Kayal et al. 2012). Branching and table-shaped species belonging
296 to the genus *Acropora* were affected first and most heavily. Then, it was followed by those of
297 sub-branching *Pocillopora*. Finally, Populations of encrusting *Montipora*, massive *Porites*, and
298 other hard-coral assemblages also declined, showing a synchronized collapse with the entire
299 coral communities. From 2011 onward, benthic assemblages started to recover mainly thanks
300 to encrusting coral forms and *Pocillopora* spp. that is presently the dominating coral form in
301 Moorea. The current *Pocillopora*-dominated state may be a transitional phase, indicative of
302 either continuing degradation or recovery (Aronson et al. 2004). Our back-calculated structural
303 complexity was able to capture major changes due to COTS outbreak and Cyclone Oli, thus
304 attesting the potential to use statistical modeling when the rugosity has not been empirically

305 collected. However, the status of coral reefs in 2004 when *Acropora* spp. was on average $\approx 10\%$
306 and the present status (average *Acropora* cover $\approx 2\%$) was not enough to distinguish difference
307 in back-calculated structural complexity. There are two proposed explanations for this
308 observation: (a) our model is calibrated with present-day data. Only two transects in 2017 had
309 assemblages with an *Acropora* cover higher than 5% which is a consequent statistic assumption
310 according to the *Acropora* cover in 2004 ($9.76 \pm 5.61\%$ in 2004 vs $2.53 \pm 1.90\%$ in 2017). This
311 again results in an extremely cautious interpretation of the results due to a possible
312 underestimation of *Acropora* spp. in the past years (Aronson and Precht 2006; Alvarez-Filip et
313 al. 2009, 2011). And/or (b) *Acropora* and *Pocillopora* taxa harbored branching form and
314 similarly contribute to the complexity (Reichert et al. 2017). Thus, the complexity could be
315 rebuilt according to the coral cover underlying the different coral morphologies (Halford et al.
316 2004; Graham and Nash 2013; Richardson et al. 2017). In order to sharp our hindcasting, the
317 reproducibility of this method could allow us to find a new area with the needed information
318 (i.e. past *Acropora* and *Pocillopora* cover vs post *Acropora* and *Pocillopora* cover and past and
319 post rugosity) and to test our model. Waiting for this improvement, the CC could be enough
320 accurate to rebuild the past and to predict the complexity for the coming years. Indeed, today
321 more than ever, global coral reefs are witnessing the effects of climate changes, local impacts
322 and natural stressors. Coral bleaching is affecting global coral reefs with an unprecedented
323 frequency and intensity and the future structural complexity of coral reefs is expected to be
324 reduced by these repeated perturbations (Hughes et al. 2018; Lough et al. 2018). As a
325 consequence a loss of ecological diversity productivity is likely (Alvarez-Filip et al. 2009).

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333 **Conflict of interest:** On behalf of all authors, the corresponding author states that there
334 is no conflict of interest.

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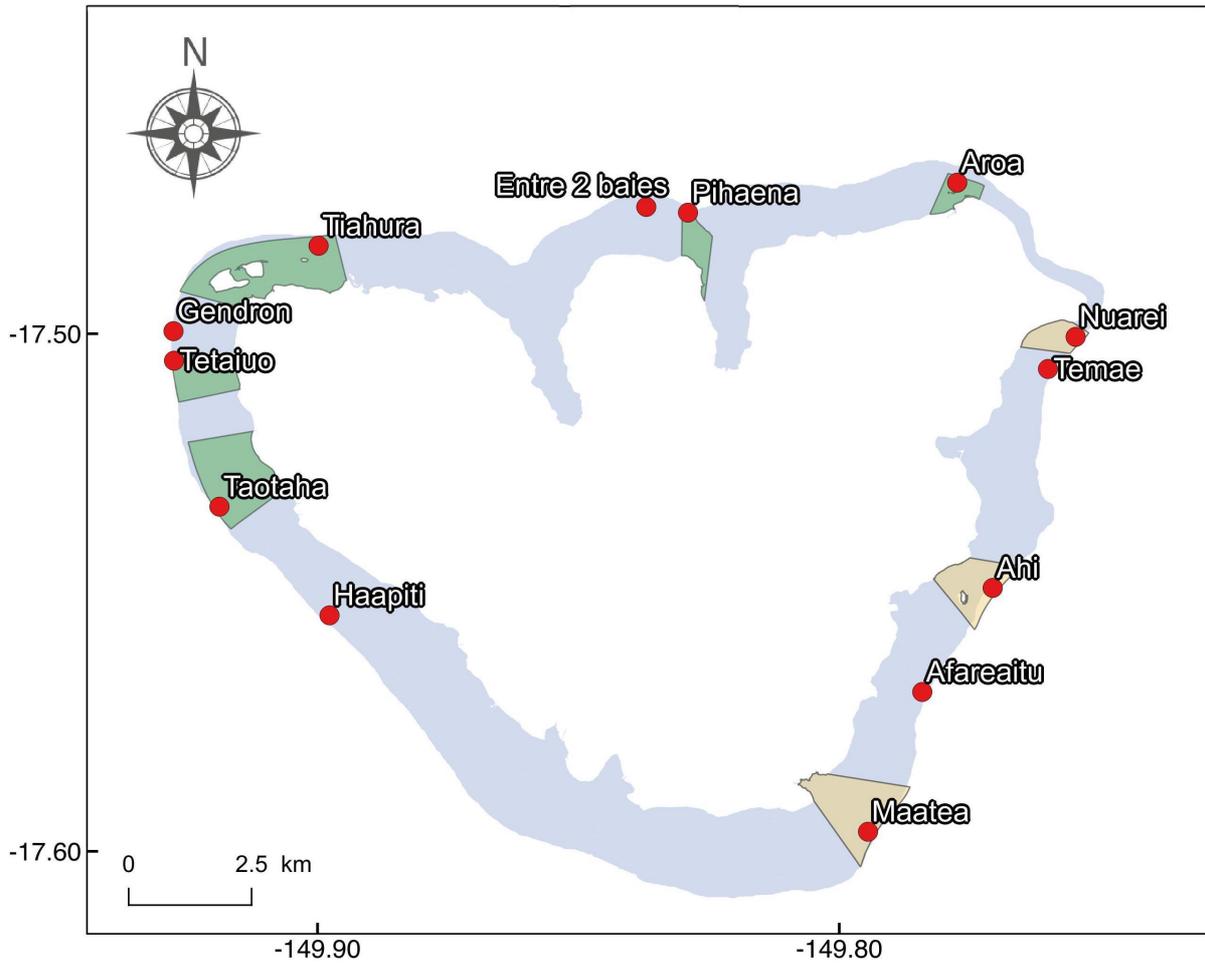
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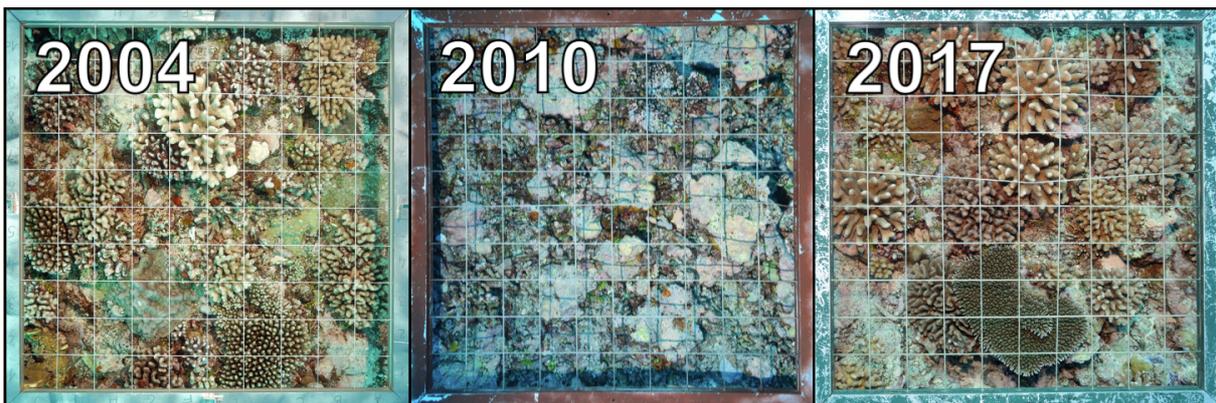
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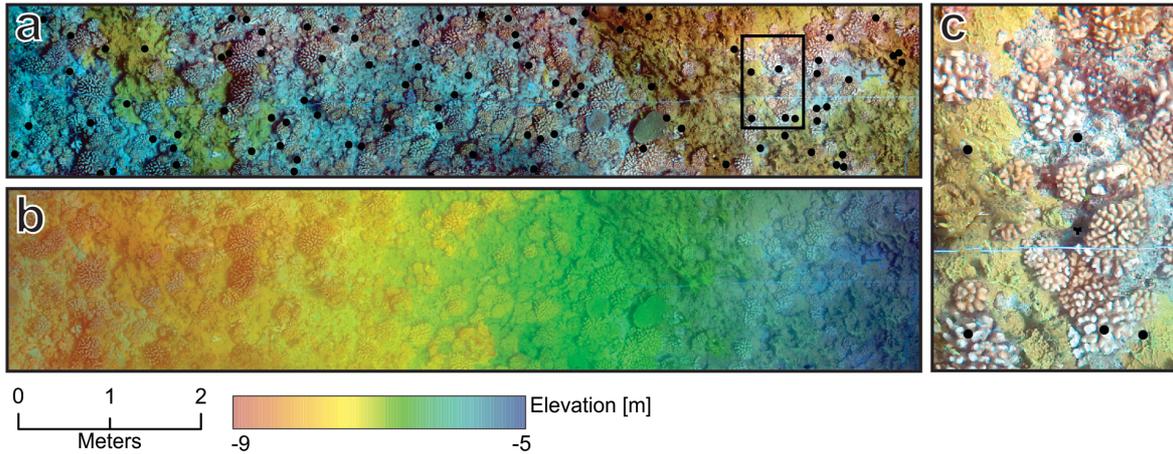
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484
485 **Fig. 1** Location of the 13 sites sampled each year since 2004 from 2017 of the MPA monitoring
486 (red dots) around the island of Moorea. The 5 fully protected MPAs are highlighted in green
487 and the restricted MPAs are highlighted in yellow. The 5 sites outside of the MPAs are controls.
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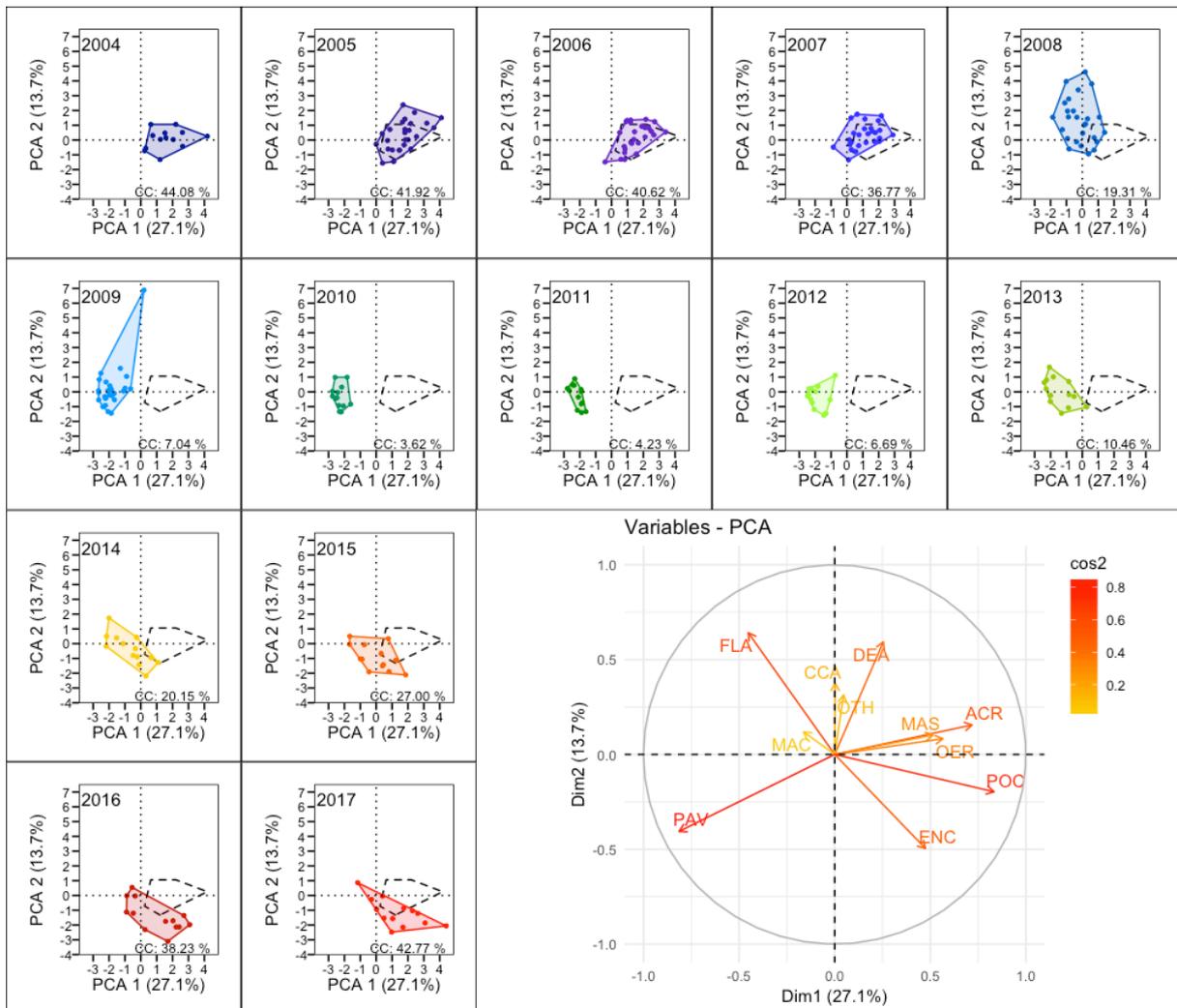


489
490 **Fig. 2** Evolution of one of the twenty quadrats used to define the coral cover in Haapiti (South
491 West of the island) before (in 2004), during (in 2010) and after (in 2017) Cyclone Oli.
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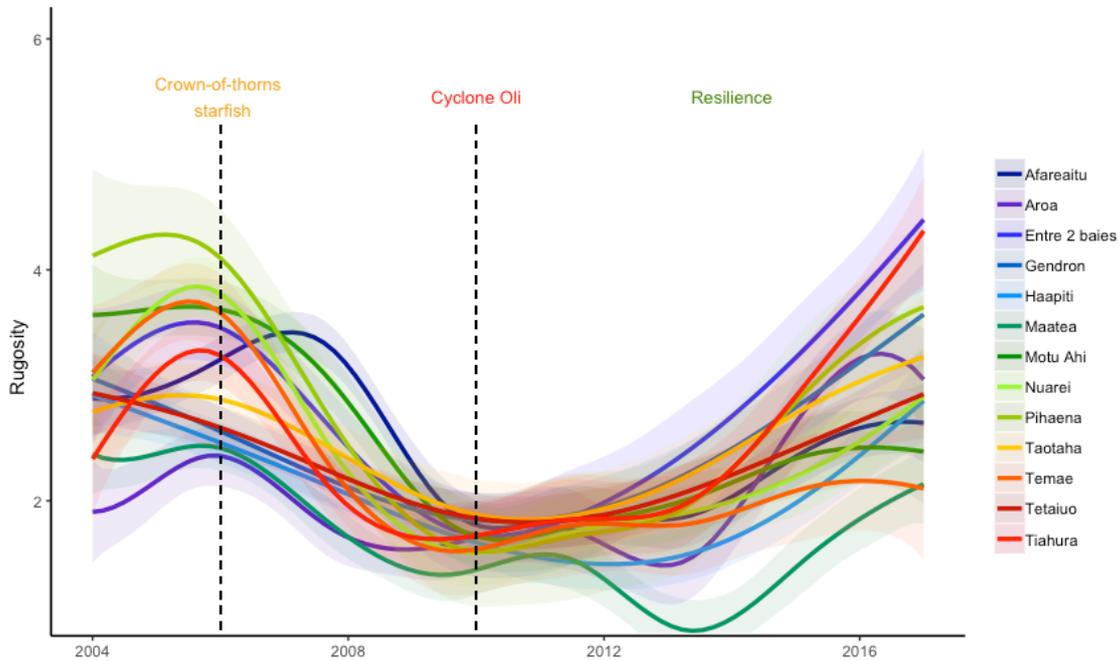
Fig. 3 Example of results from underwater photogrammetry. a) Orthorectified photomosaic. The black dots indicate the random points where the shape classification has been carried out. b) Digital Elevation Model representing depth values (the photomosaic is kept in transparency in the background). c) Detail of the photomosaic.



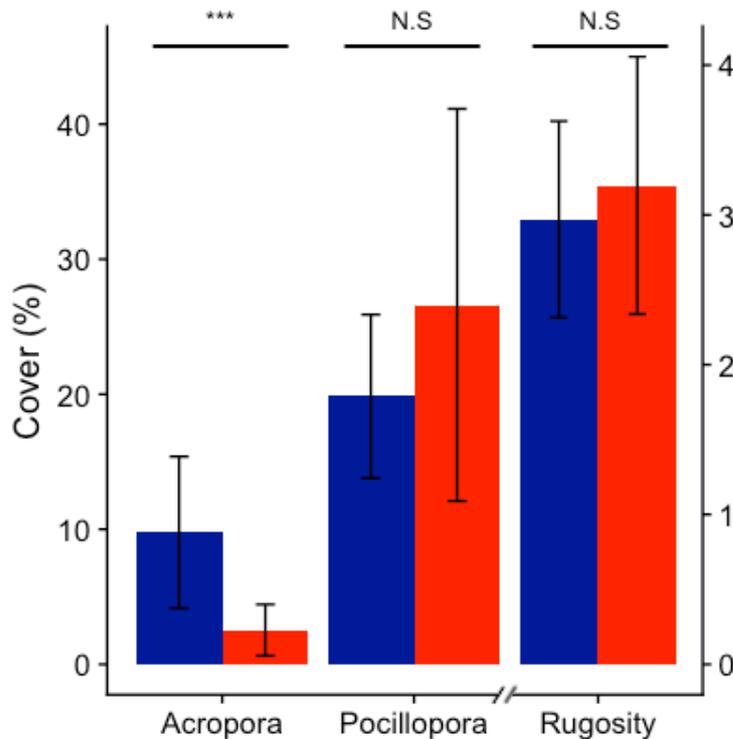
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Fig. 4 Principal Components Analysis (PCA) using the 11 morpho-species respecting the code as follows: ACR - Acropora spp; CCA - Crustose Coralline Algae; DEA - Dead Coral; ENC - Encrusting Corals; FLA - Flat (Sand or Mud); MAC - Macroalgae; MAS - Massive corals; OER

510 - Other Erects Forms; OTH - Others (Sponges or benthic species); PAV - Pavement; and POC
 511 - Pocillopora spp. The PCA was used year by year from 2004 to 2017 and the coral cover (CC)
 512 is written at the bottom right of each box. The coral community in 2004 is referred as model in
 513 black dashed lines each year.



514
 515 **Fig. 5** Rugosity reconstruction from 2004 to 2017 according to the average model and according
 516 to the 13 sites around the island of Moorea. Both biologic invasion and extreme climatic
 517 weather events are shown for respectively 2006 and 2010.
 518



519
 520 **Fig. 6** Difference between the Acropora and the Pocillopora cover (%) on the left, and the
 521 difference in rugosity (index) on the right. The dark blue color represents 2004 instead of 2017
 522 is representing in red. The p-value is represented on the top of each barplot according to the

523 significant R code (*** highly significant (<0.001), **very significant (<0.01), * significant
 524 (<0.05), . almost significant (<0.1), N.S non-significant; threshold: p-value = 0.05)
 525

526 **Tab. 1** Categories of shape classification defined and used to rebuild the rugosity these last 14
 527 years. 9 variables are morphologic instead a distinction at the genus level is done for *Acropora*
 528 spp. and *Pocillopora* spp. The CCA was differentiated from the pavement according to their
 529 extension: when this later was higher than 100 cm², which corresponds to a projected surface
 530 of a circle of radius of 5-6 cm it was considered as CCA rather than pavement. The dead corals
 531 category understands rubbles and cobbles. The flattening category represents sand or mud
 532 substrate. The categories Encrusting, Other Erect Forms and Massive represent different coral
 533 morphologies. Finally, the others category represents mostly benthic organism like echinoid or
 534 even sponges.
 535

ACR	<i>Acropora</i> spp.
CCA	Coralline Crustose Algae
DEA	Dead corals
ENC	Encrusting corals
FLA	Flat (Mud, Sand)
MAC	Macroalgae
MAS	Massive corals
OER	Corals with other erects forms
OTH	Other (like echinoid)
PAV	Pavement
POC	<i>Pocillopora</i> spp.

536
 537 **Tab. 2** Coefficients and standard error for each parameter according to best model defined:
 538 **Rugosity ~ Dim 1 + Dim 3 + Dim 5** (AIC = 71.776 and R² = 0.81 ± 0.12). The p-value
 539 represents the significance of each parameters according to the R code (*** highly significant
 540 (<0.001), **very significant (<0.01), * significant (<0.05), . almost significant (<0.1), N.S non-
 541 significant; threshold: p-value = 0.05)
 542

	Estimate	Standard Error	p-value
Intercept	1.65970	0.14616	1.08e-15 (***)
Dimension 1	0.53283	0.08602	9.48e-08 (***)
Dimension 3	0.41917	0.07003	2.03e-07 (***)
Dimension 5	-0.15003	0.06090	1.71e-02 (*)

543
 544

545 **Appendix**

546

547 **Tab. S1** Post Hoc (Tukey HSD) matrix for testing the rugosity difference according to each
 548 year combination. The P-value (threshold: 0.05) for each combination is written in the matrix
 549 data as follows. The red values are significantly different and the blue values are not.

550

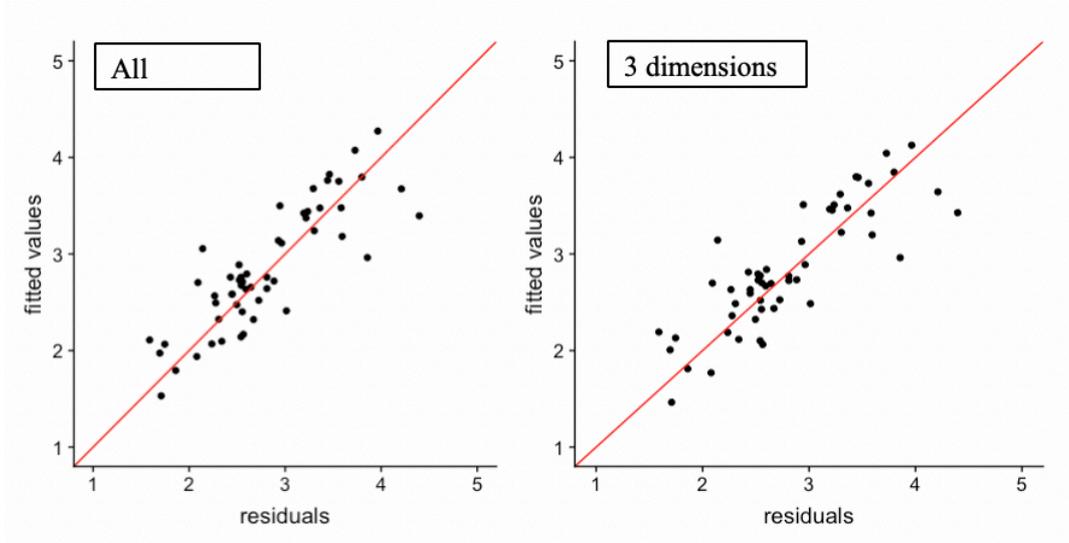
	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017
2004	1.00													
2005	0.98	1.00												
2006	0.96	1.00	1.00											
2007	1.00	0.87	0.80	1.00										
2008	0.04	0.00	0.00	0.00	1.00									
2009	0.00	0.00	0.00	0.00	0.93	1.00								
2010	0.00	0.00	0.00	0.00	0.96	1.00	1.00							
2011	0.00	0.00	0.00	0.00	0.95	1.00	1.00	1.00						
2012	0.00	0.00	0.00	0.00	0.98	1.00	1.00	1.00	1.00					
2013	0.01	0.00	0.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00				
2014	0.11	0.00	0.00	0.03	1.00	1.00	0.99	0.99	1.00	1.00	1.00			
2015	0.91	0.05	0.04	0.81	1.00	0.20	0.31	0.30	0.35	0.51	0.98	1.00		
2016	1.00	1.00	0.99	1.00	0.01	0.00	0.00	0.00	0.00	0.00	0.05	0.80	1.00	
2017	1.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.34	1.00	1.00

551

552

553 **Fig. S1** Analysis of the residuals (fitted values vs observations) from the total model: Rugosity
 554 ~ Dim 1 + Dim 2 + Dim 3 + Dim 4 + Dim 5 (AIC = 71.8, $R^2 = 0.78 \pm 0.08$) on the left and the
 555 best model Rugosity ~ Dim 1 + Dim 3 + Dim 5 (AIC = 73.6, $R^2 = 0.81 \pm 0.12$) on the right.

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559 **Annex**

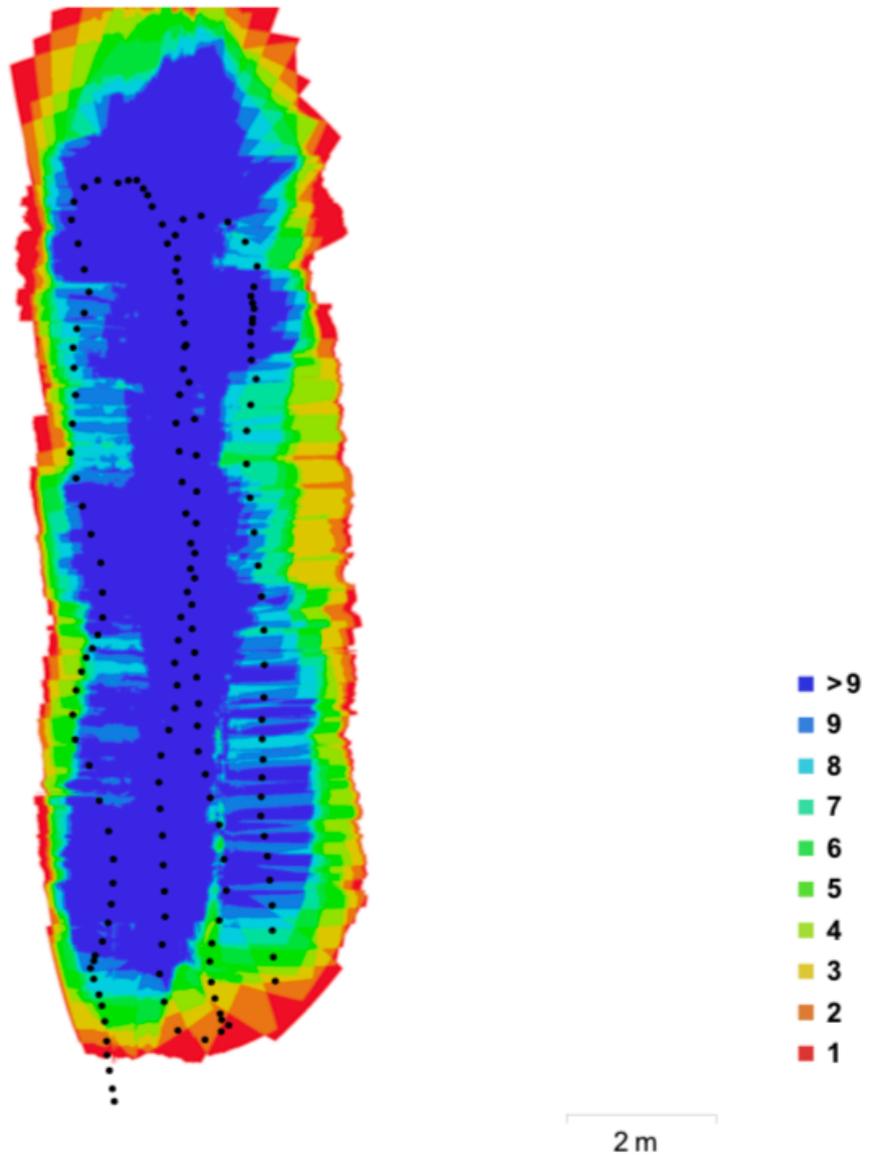
560

561 **Annex S1** Report from Agisoft Photoscan for one site, detailing the settings used for the
 562 processing of underwater photos.

563

564 **1. Survey Data**

565



566

567 **Fig. 1** Camera locations and image overlap

568

Number of images:	157	Camera stations:	157
Flying attitude:	2.56m	Tie points:	139.838
Ground resolution:	0.53 mm/pix	Projections:	383.598
Coverage area:	56.3 sq m	Reprojection error:	1.88 pix

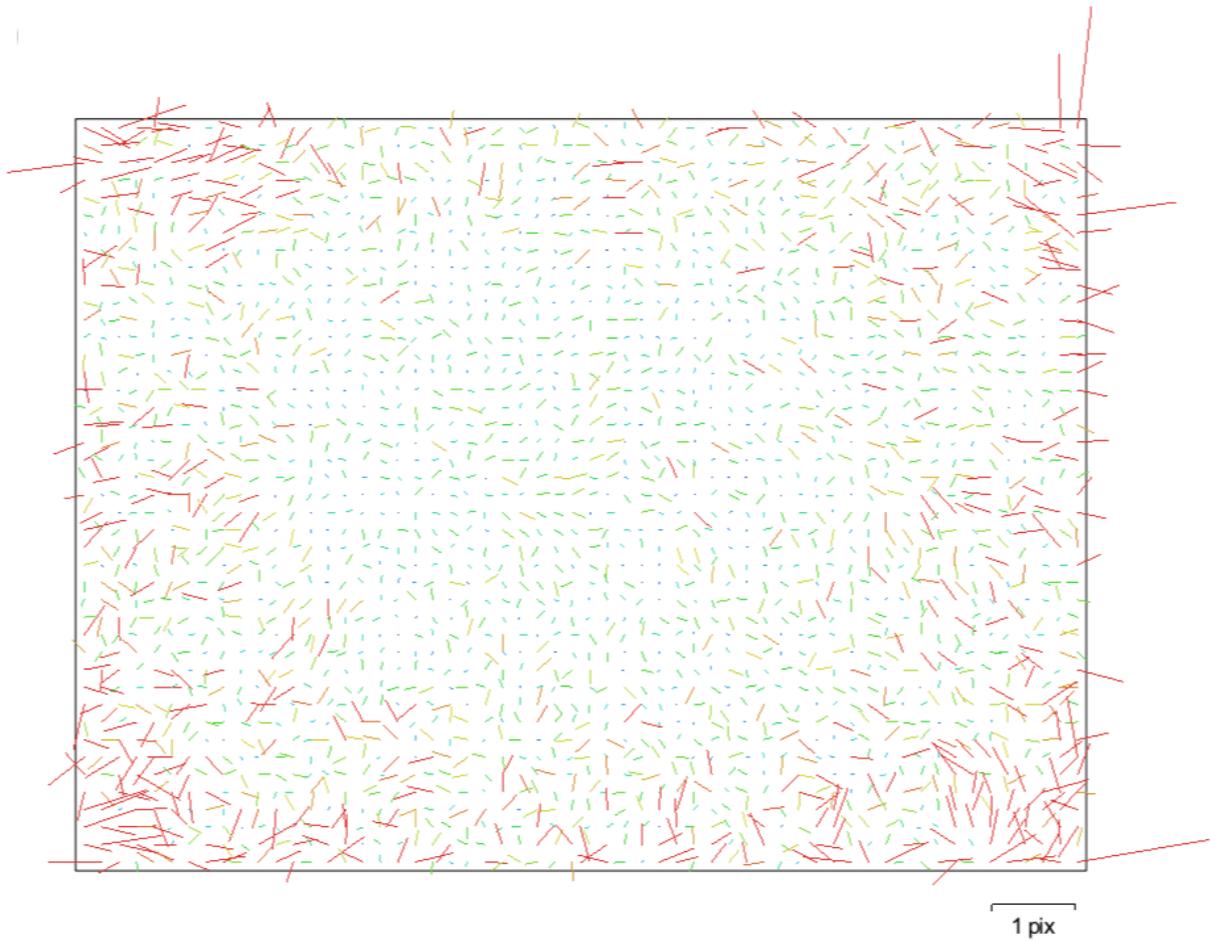
569

570 **Tab. 1** Cameras

Camera Model	Resolution	Focal Length	Pixel Size
HERO4 Black (3 mm)	4000 x 3000	3mm	1.73 x 1.73 um

571

572 **2. Camera calibration**



574 **Fig. 2** Image residuals for HERO4 Black (3 mm).
 575

576
 577
 578

HERO4 Black (3mm)

157 images

Resolution	Focal length	Pixel size	Precalibrated
4000x3000	3 mm	1.73 x 1.73 μm	No
Type:	Frame	Skew:	0
Fx:	4666.42	Cx:	2005.25
Fy:	4666.42	Cy:	1486.48
K1:	0.223613	P1:	0.00194777
K2:	0.373779	P2:	-0.00200162
K3:	1.24196	P3:	0
K4:	0	P4:	0

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3. Ground Control Points



2 m

586
587 **Fig. 3** GCP locations

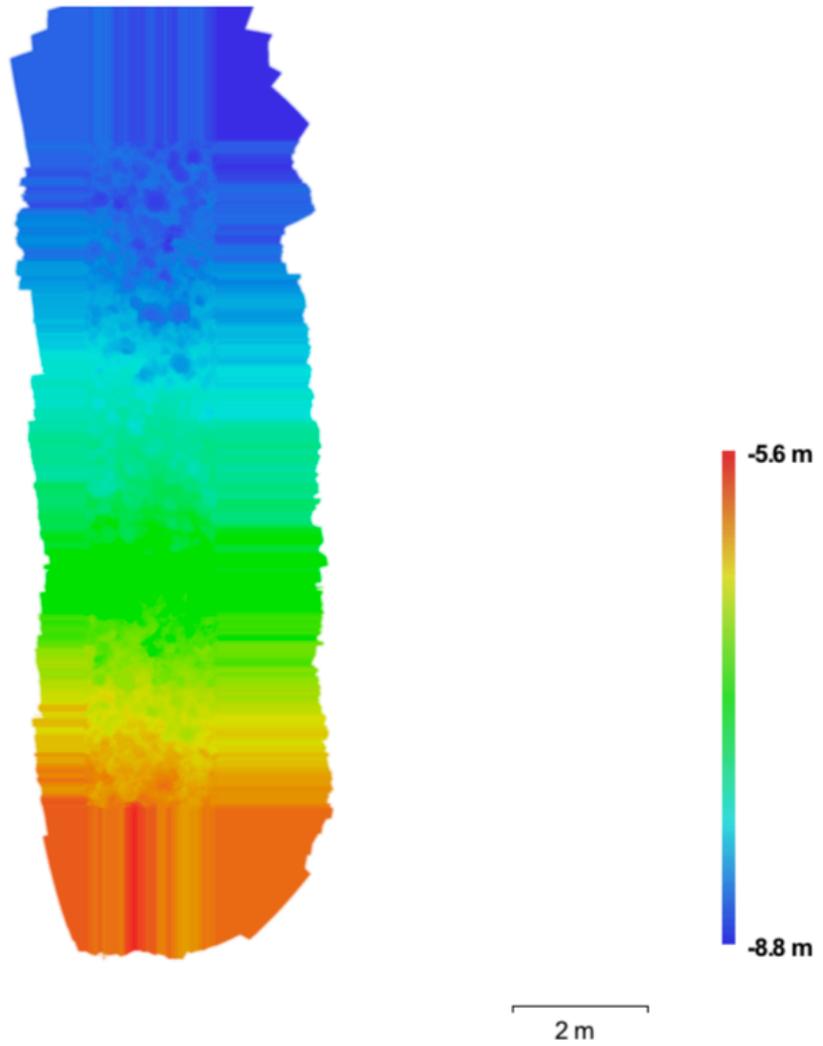
588
589 **Tab. 2** Control points

Label	XY error(m)	Z error (m)	Error (m)	Projections	Error (pix)
point1	0.206298	-0.0677987	0.217153	13	1.992
point2	0.0963633	0.0426041	0.105361	16	1.153
point3	0.039409	3.96756e-05	0.039409	17	0.051
point4	0.205045	0.0251539	0.206582	9	0.044
Total	0.154468	0.0419657	0.160067		1.151

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4. Digital Elevation Model



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Fig. 4 Reconstructed digital elevation model.

Resolution: 1.06 mm/pix
Point density: 889956 points per sq m

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598

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600

5. Processing parameters

General

Cameras	157
Aligned cameras	157
Markers	4
Coordinate system	Local Coordinates

Point Cloud

Points	139,838 of 221,231
RMS reprojection error	0.382302 (1.88392 pix)
Max reprojection error	6.30304 (30.1948 pix)
Mean key point size	5.32459 pix
Effective overlap	2.94411

Alignment parameters

Accuracy	High
Pair preselection	Disabled
Key point limit	40,000
Tie point limit	4,000
Constrain features by mask	No
Matching time	17 minutes 46 seconds
Alignment time	3 minutes 10 seconds

Optimization parameters

Parameters	f, cx, cy, k1-k3, p1, p2
Optimization time	5 seconds

Dense Point Cloud

Points	72,229,238
--------	------------

Reconstruction parameters

Quality	High
Depth filtering	Aggressive
Processing time	8 minutes 29 seconds

Model

Faces	4,815,282
Vertices	2,417,898

Reconstruction parameters

Surface type	Arbitrary
Source data	Dense
Interpolation	Enabled
Quality	High
Depth filtering	Aggressive
Face count	4,815,282
Processing time	4 hours 29 minutes

DEM

Size	1,886 x 9,433
Coordinate system	Local Coordinates

Reconstruction parameters

Source data	Dense cloud
Interpolation	Enabled

Orthomosaic

Size	3,773 x 18,867
Coordinate system	Local Coordinates
Channels	3, unit8
Blending mode	Mosaic

Reconstruction parameters

Surface	Mesh
Enable color correction	No

601