

1 **Thirty year ecosystem trajectories in a submerged marine cave under changing pressure**  
2 **regime**

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14 **Abstract**

15 Marine caves are unique and vulnerable habitats exhibiting high biodiversity and heterogeneity,  
16 but threatened by multiple global and local disturbances. Marine caves, although widely  
17 distributed along the Mediterranean coast, suffer for the lack of quantitative data on their  
18 structure and function, which hinder their conservation status assessment. Thanks to the  
19 availability of a nearly 30-year-long series of data (1986 to 2013), we evaluated ecosystem  
20 change in the Bergeggi marine cave (Ligurian Sea, NW Mediterranean), a cave with a complex  
21 shape and high habitat heterogeneity. Non-taxonomic descriptors were adopted, namely growth  
22 forms (GF) and trophic guilds (TG), which are informative about ecosystem structure and  
23 functioning, respectively. The cave experienced a general trend of change during the last three  
24 decades, mainly due to the decline in the cover of sessile organisms (especially 3-dimensional  
25 forms) matched by an increase of turf and sediment, thus causing the structural and functional  
26 homogenization of the cave community. While change before 2004 had been attributed to  
27 climatic factors (especially to the summer heat waves of 1999 and 2003), the most important rate  
28 of change was observed between 2009 and 2013, coinciding with recent major beach  
29 nourishments and the extension of the neighbouring Vado Ligure harbour, thus providing  
30 evidences on the importance of local disturbances deriving from coastal interventions.  
31 Monitoring the status of cave ecosystems is urgently needed, and the use of effective indicators,  
32 such as the specific traits here adopted (morphology and feeding strategy), could provide  
33 effective tools to assist marine cave conservation.

34

35 **Keywords:** marine caves; multiple stressors; climate change; local disturbances; non-taxonomic  
36 descriptors; Mediterranean Sea.

37

## 39 **1. Introduction**

40 A combination of pressures related to human activities at both global and local scales is  
41 threatening marine ecosystems worldwide (Thrush et al., 2008), leading to increasing interest  
42 towards the assessment of the effects of multiple stressors to conciliate conservation targets with  
43 social and economic development (Guarnieri et al., 2016). Local anthropogenic stressors, such as  
44 habitat degradation or destruction, pollution, sedimentation, and overfishing, together with a  
45 gradual history of changes in environmental conditions (climate, habitat quality, resource  
46 availability), can potentially exacerbate biodiversity decline and habitat loss, thus eroding the  
47 ability of ecosystems to absorb and recover from additive or synergic affectors (*sensu*  
48 Montefalcone et al., 2011) of either natural or human origin (Perkol-Finkel and Airoldi, 2010).  
49 Increase in frequency and severity of disturbances, in concert with global change effects related  
50 to climate fluctuations, is thus causing profound changes in the composition of marine  
51 communities over large spatial scales (Bianchi et al., 2014; Defriez et al., 2016), also favouring  
52 the biological invasion by alien species (Montefalcone et al., 2015). Homogenization of habitat  
53 structure has also been suspected to be a major contributor to the sliding baselines that affect our  
54 ability to make ecological assessments of broad-scale change in marine ecosystems (Thrush et al.,  
55 2006).

56 The Mediterranean Sea, a semi-enclosed basin, is a hotspot of biodiversity with a high rate of  
57 endemism (Bianchi and Morri, 2000; Coll et al., 2010), but climate change and heavy human  
58 pressures are giving rise to important shifts in the biota (Cerrano et al., 2000; Lejeusne et al.,  
59 2010; Bianchi et al., 2012a; Di Camillo and Cerrano, 2015), and distinguishing the modifications  
60 caused by climate change from those caused by local human disturbance is often difficult (Morri  
61 and Bianchi, 2001).

62 The rocky coast of the Mediterranean Sea is particularly rich in marine caves (Riedl, 1966;  
63 Cicogna et al., 2003; Giakoumi et al., 2013), which originated from the marine flooding of  
64 limestone karstic networks during the last transgression (Colantoni, 1976; Bianchi et al., 1996).  
65 Composition of benthic sessile communities in a marine cave significantly differs from the  
66 outside littoral zone because of the establishment of a peculiar confined environment that can act  
67 as refuge or ecological island (Gerovasileiou et al., 2015, 2016; Muths et al., 2015; Rastorgueff et  
68 al., 2015; Nepote et al., 2016; Sanfilippo et al., 2017). Marine caves harbour several endemic and  
69 specialized species (Harmelin et al., 1985; Bianchi et al., 1996) and are particularly sensitive to  
70 human impacts as they are naturally fragmented and poorly resilient (Chevaldonné and Lejeusne,  
71 2003; Gerovasileiou and Voultsiadou, 2012; Guarnieri et al., 2012; Nepote et al., 2017); events of  
72 mass mortality linked to positive thermal anomalies due to climate change have already been  
73 reported in marine caves (Parravicini et al., 2010; Zapata-Ramírez et al., 2016 and references  
74 therein). Caves are also ecologically connected with several other marine ecosystems, such as  
75 coralligenous and rocky reefs, seagrass beds and the deep sea, as well as with the pelagic system  
76 due to water movement that brings food and propagules into caves (Rastorgueff et al., 2015).  
77 Marine caves are included in Annex I of the Habitats Directive of the European Community  
78 (1992), which lists those habitats whose conservation requires designation of protected areas, as  
79 they exhibit high aesthetic value and provide important services, such as CO<sub>2</sub> sequestration and  
80 seafloor stability (Martin et al., 2013). Caves are also listed in the Action Plan for the  
81 conservation of habitats and species, and are considered as sensitive “dark habitats” that require  
82 protection (UNEP RAC/SPA, 2015). Because of this, and to avoid degradation of these unique  
83 and vulnerable habitats (Navarro-Barranco et al., 2015), in 2008 about 66% of the Mediterranean  
84 marine protected areas (MPAs) included marine caves (Abdulla et al., 2008); although the  
85 number of MPAs has slightly increased in the last decade, not all of them include marine caves

86 and we do not think therefore that the above proportion has significantly changed.

87 Historical data and long time series are precious to understand magnitude and pattern of change  
88 in the long term evolution of ecosystems (Ellingsen et al., 2017), and provide help to identify  
89 baselines for ecological management (Gatti et al., 2015, 2017). The use of historical information  
90 is also recommended as one of the possible approaches for setting the baselines to restore the  
91 good ecological status of marine ecosystems under the Marine Strategy Framework Directive of  
92 the European Community (Borja et al., 2012). A sufficiently long time sequence of measurements  
93 or observations is essential to provide meaningful information about changes in ecosystem  
94 structure and functioning (Gatti et al., 2017), but available historical data series seldom go back  
95 in the past for more than few decades (Morri and Bianchi, 2001). Quantitative historical  
96 information and proper baselines to which to compare the present situation of marine cave  
97 assemblages are almost inexistent for most of the Mediterranean basin (UNEP RAC/SPA, 2015;  
98 Gerovasileiou et al., 2017), hindering the assessment of potential decline in habitat quality and  
99 thus the implementation of international and European legislations.

100 In this study we explored the long-term (nearly 30 years) change of sessile benthic communities  
101 within the submerged marine cave of Bergeggi (Ligurian Sea, NW Mediterranean). Although  
102 included in a marine protected area (MPA), this cave has been affected by multiple local  
103 (especially the recent extension of a nearby commercial harbour) and global (e.g. thermal  
104 anomalies) stressors. Ecosystem shifts have occurred in the 1980s-90s in the Mediterranean, as  
105 elsewhere, due to major climate anomalies (Conversi et al., 2010; Reid et al., 2016) coupled with  
106 intensified human pressures (Gatti et al., 2015, 2017), which have highly impacted the coastal  
107 marine biota of the whole basin (Bianchi et al., 2014). The marine cave of Bergeggi provides an  
108 extraordinary example of long time series, maybe unique in the Mediterranean Sea (Rastorgueff  
109 et al., 2015), where information about historical condition of the cave communities has been

110 collected since the 1970s (Bianchi et al., 1986; Sgorbini et al., 1988; Morri et al., 1994;  
111 Parravicini et al., 2010), well before the above-mentioned regime shift. In 2013, we re-surveyed a  
112 number of stations where quantitative data on the sessile communities had been taken in 1986,  
113 2004, and 2009 in order to assess whether significant changes, if any, had occurred under the  
114 changing pressure regime. Distribution of sessile biota within a cave is primarily dictated by  
115 gradients of light and water movement (Bianchi and Morri, 1994, 1999). The complex  
116 morphology of the Bergeggi cave, which includes both blind-end and tunnel-shaped portions,  
117 creates different environmental conditions inside the cave, in terms of physical-chemical patterns,  
118 inducing high habitat heterogeneity (Morri et al., 1994). Thus, the analysis of sessile communities  
119 was not designed to conform with the classical zonation scheme that follows the putative major  
120 environmental gradient along the exterior-interior axis (Balduzzi et al., 1989; Morri and Bianchi,  
121 2003), but considering distinct morphological sectors exhibiting comparatively homogeneous  
122 environmental conditions (Alvisi et al., 1994; Ugolini et al., 2003).

123

## 124 **2. Materials and methods**

### 125 *2.1. Study area*

126 The marine cave of Bergeggi (Ligurian Sea, NW Mediterranean) is located in Liguria, an  
127 administrative region in NW Italy (Figure 1). From a geomorphological and genetic point of  
128 view, the marine cave of Bergeggi is a mixed-origin cavity (Colantoni, 1976): the dolomitic-  
129 limestone nature of the area allowed the formation of a karstic system that includes a large  
130 emerged part and whose shape has been subsequently modified by sea ingressions during the  
131 Late Quaternary (Rovere et al., 2010a, 2015). The submerged part of the cave reaches a  
132 maximum depth of 7 m and is divided into two branches, both located under the vault of Remo's  
133 cavern: the eastern branch consists essentially of an isolated "lake" (Lake Through the Hole); the

134 western branch has a more complex shape being composed of a 40 m long Gulley with 2  
135 chambers (First Chamber and Lights' Chamber), a main Hall and an inner lake (Lemons' Lake)  
136 reaching the surface (Figure 1).

137 The peculiar morphology of the cave creates different environmental conditions, as illustrated by  
138 the spatial trends of several physical-chemical variables measured in 1986 (Figure 2). Light  
139 intensity, measured with a diver-held irradiance-meter ( $\mu\text{W}\cdot\text{cm}^{-2}$ ), was zero in most part of the  
140 cave, with the exceptions of the immediate vicinities of the entrances; dim light conditions  
141 characterize the Hall and the initial tract of the Gulley. Current speed was estimated by the  
142 consumption of plaster spheres left in different points of the cave and converted to  $\text{cm}\cdot\text{sec}^{-1}$   
143 through calibration with the data recorded by a magnetic induction field mini-current-meter  
144 (Idromar Sensordata A/S SD-4) contemporaneously placed immediately outside the cave (Morri  
145 et al., 2003): due to the general tunnel-shape of the cavity, water movement remains perceptible  
146 in most parts of the cave but the lakes. Values of pH were electrode-probed with a portable pH-  
147 meter, and showed a progressive reduction entering the cave, with a minimum in the lakes.  
148 Values of suspended organic matter (SOM,  $\text{mg}\cdot\text{l}^{-1}$ ), carbon to nitrogen ratio (C/N), and  
149 chlorophyll *a* ( $\mu\text{g}\cdot\text{l}^{-1}$ ) were determined in water samples collected by means of a 5 l Niskin bottle,  
150 manually operated by the diver; they consistently indicated trophic depletion, in terms of both  
151 reduced quantity and degraded quality of food particles (Bianchi et al., 2003).

152 On the whole, 4 homogeneous sectors can be identified within the submarine cave (Morri et al.,  
153 1994): 1) the Chambers (C), hydrologically confined, completely dark and poor in suspended  
154 organic matter; 2) the Gulley (G), also completely dark but with current speed greater than 10  
155  $\text{cm}\cdot\text{sec}^{-1}$ ; 3) the Hall (H), with dim light (irradiance  $> 0.2 \mu\text{W}\cdot\text{cm}^{-2}$ ), efficient water exchange  
156 (current speed  $> 15 \text{cm}\cdot\text{sec}^{-1}$ ), and chlorophyll content comparable to that of the sea outside; and  
157 4) the inner Lakes (L), confined, dark and with lowered pH ( $< 8.0$ ).

158

159       2.2. *Stressors regime*

160 The marine cave of Bergeggi is under a dual scenario: it is located in a protected area but is very  
161 close to a large commercial harbour. The cave is presently included within the MPA “Bergeggi  
162 Island”, established in 2007, and within a Site of Community Importance (SCI), established in  
163 1995 (Figure 3), and should therefore be safe from direct anthropogenic disturbances. Visitation  
164 by divers is probably negligible, as it is not listed among the diving sites of the MPA, and coastal  
165 water quality is high, according to WFD (Water Framework Directive) standards (Asnaghi et al.,  
166 2009).

167 However, the surrounding coastline has been subjected to high human pressures in the last  
168 decades (Figure 4). The resident population, according to the data provided by the National  
169 Institute of Statistics (ISTAT) exhibited a slight increase, while finfish fishing, date-mussel  
170 harvesting, scuba diving and anchoring have been the major threats affecting this area  
171 (Parravicini et al., 2006, 2008, 2009, 2012; Montefalcone et al., 2009, 2010). Beach nourishments  
172 have been carried out in 1969, 1971, 2005, 2008 and 2011 (<http://geoportale.regione.liguria.it>):  
173 their impact on the local seagrass meadows has been effectively documented (Bianchi and  
174 Peirano, 1995; Peirano and Bianchi, 1997; Vassallo et al., 2013; Oprandi et al., 2014a,b; Paoli et  
175 al., 2016), while the probable siltation within the cave has never been studied.

176 The marine cave is located a few kilometres downstream the important commercial harbour of  
177 Vado Ligure (Figure 4), built in 1987 as an extension of a natural inlet and being extended since  
178 2012, with completion predicted for 2018 (Berriolo, 2017). The project of the harbour extension  
179 implies the construction of a multipurpose platform of 700 m in length with a surface of  
180 210,000 m<sup>2</sup> (for a complete description of the project refers to  
181 <http://www.infrastrutture.regione.liguria.it>). The new harbour will lead to a conspicuous



182 increment in the ship traffic: for instance, the number of containers per year is foreseen to  
183 increase from ca.  $10^5$  containers up to ca.  $10^6$  containers by 2020 (Parravicini et al., 2012). It has  
184 already been shown that the harbour of Vado Ligure has affected important marine key habitats,  
185 such as coralligenous assemblages and seagrass meadows (Parravicini et al., 2007; Rovere et al.,  
186 2010b; Gatti et al., 2012; Ferrari et al., 2013).

187 Along with local stressors, climate change has been shown to cause important modifications to  
188 the coastal ecosystems of the Ligurian Sea (Morri and Bianchi, 2001; Gatti et al., 2015, and  
189 references therein). The trend in sea surface temperature (SST) data was used as a proxy for  
190 climate change (Gatti et al., 2017). Sea surface temperatures from 1985 to 2015 were derived  
191 from NOAA satellite data (freely available at [www.esrl.noaa.gov/psd/cgi-](http://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl)  
192 [bin/data/timeseries/timeseries1.pl](http://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl)), calibrated with the available field measurements (Figure 3). A  
193 general temperature increase with several phases can be distinguished over the last 50 years in the  
194 Mediterranean Sea, stabilizing at about 0.5 °C higher in the 2000s-10s as compared to the 1960s  
195 (Parravicini et al., 2015). The rapid warming phase of the 1980s-90s (culminating with the heat  
196 wave of 1999), with water temperature that increased up to 4 °C above the climatological mean,  
197 caused mass mortalities in many subtidal rocky reef invertebrates (Cerrano et al., 2000; Garrabou  
198 et al., 2009; Rivetti et al., 2014). During the summer heat waves of 2003, necrotic *Agelas oroides*  
199 (Schmidt) and *Chondrosia reniformis* (Nardo) were found at the entrance of the Bergeggi cave, as  
200 well as completely dead *Petrosia ficiformis* (Poiret) in the inner portions (Parravicini et al.,  
201 2010). Although it is untimely to state that the high temperatures measured in the last years could  
202 be indicative of a further phase of rapid warming started in 2013 (Shaltout and Omstedt, 2014;  
203 Bianchi et al., 2017), new events of mass mortality have been observed in the Western  
204 Mediterranean Sea in late summer 2015 (Rubio-Portillo et al., 2016).

205

206        *2.3. Choice of cave ecosystem descriptors*

207 To evaluate structural and functional change in the sessile community of the cave, we used non-  
208 taxonomic descriptors, i.e. growth forms (GF) and trophic guilds (TG). GF are used as  
209 morphological descriptors to assess the strategy of substratum occupation, whilst TG as trophic  
210 descriptors to evaluate the energy sources exploited by sessile organisms (Parravicini et al.,  
211 2010). The same species may exhibit different growth forms in different situations, while  
212 normally does not change feeding guild. Eight GF were identified considering the ratio between  
213 the height (h) and the radius (r) of the organism (Figure 5): runners, determinate sheets,  
214 indeterminate sheets, flattened ( $h < r$ ) mounds, hemispherical ( $h = r$ ) mounds, domed ( $h > r$ )  
215 mounds, vines and threes (Jackson, 1979; Connell and Keough, 1985). Runners and sheets (either  
216 determinate or indeterminate) are 2-dimensional, strictly adhering to the substrate; mounds, vines  
217 and threes are 3-dimensional, projecting to some extent into the water column and producing  
218 higher habitat complexity. Two additional categories were included in the analyses to take into  
219 account the ‘abiotic’ components: bare substrate, algal-turf and sediment considered together  
220 (due to the operational difficulty to separate them during image analysis), both providing an  
221 indication of environmental stress (Nepote et al., 2017).

222 Six TG were defined considering the feeding mechanisms used to get food (Cocito et al., 1997):  
223 autotrophs (i.e. macroalgae), passive filter feeders (e.g. cnidarians), active ciliates (e.g. serpulids  
224 and spirorbids), active ciliates with lophophore (e.g. bryozoans and brachiopods), active pumping  
225 sponges, active pumping ascidians.

226

227        *2.4. Sampling method*

228 Within each of the four sectors, Chambers (C), Gulley (G), Hall (H) and Lakes (L), two random  
229 sampling stations (1 and 2) were chosen (Figure 1). In each station, always on vertical surfaces, 5

230 random replicates of wire-frame photography were collected in 1986, 2004, 2009, and 2013  
231 always at the same depth (Figure 3). The frame allowed a constant sampling of 1200 cm<sup>2</sup>, a  
232 surface that showed effective to study sessile organisms with photographic techniques (Cecchi et  
233 al., 2014). Photos were analysed by superimposing a grid divided into 25 equal squares and the  
234 cover was quantified by giving each descriptor (i.e. growth forms and trophic guilds) a score  
235 ranking from 0 to 4 in each square, and then adding up scores for all squares where the descriptor  
236 was present. An arbitrary value of 0.5 was assigned to descriptors filling less than one fourth of a  
237 square (Bianchi et al., 2004). The height of the organisms was roughly estimated by the length of  
238 their shade (Parravicini et al., 2010).

239

#### 240 *Data analysis*

241 Two multivariate datasets were created for growth forms (GF) and trophic guilds (TG)  
242 descriptors. After an arcsine  $\sqrt{(x/100)}$  transformation of cover data (Legendre and Legendre,  
243 1998), two resemblance similarity matrices based on Bray-Curtis index were constructed  
244 (Anderson, 2001). The multivariate configuration of both GF and TG datasets was visualised  
245 through non-metric multi-dimensional scaling (nMDS). The three-dimensional matrix  
246 descriptors  $\times$  stations  $\times$  years was worked out as a bi-dimensional matrix  
247 descriptors  $\times$  [stations  $\times$  years] or ‘matrix of the states’, as it describes the ‘state’ shown in the  
248 years by individual stations (Fresi and Gambi, 1982) in order to draw their time-trajectories.

249 A permutational analysis of variance (PERMANOVA) was then applied using a three-way model  
250 with year (Y) as a random factor with 4 levels (1986, 2004, 2009 and 2013), topographic sector  
251 (Se) as a fixed factor with 4 levels (C, G, H, and L) and station (St) as a random factor with 2  
252 levels (1 and 2) nested within sectors. Sampling years have been considered formally as  
253 ‘random’, due to the lack of temporal replication. Each analysis used 9999 random permutations

254 and pair-wise tests were used to compare condition levels when significant differences were  
255 detected by PERMANOVA.

256 A SIMPER analysis (Clarke, 1993) was performed to identify percentage contribution of each  
257 descriptor to the Bray-Curtis similarity among stations, with year as a fixed factor. Homogeneity  
258 of multivariate dispersions among years was verified with the permutational test for multivariate  
259 dispersion (PERMDISP, Anderson, 2006), with a lower dispersion indicative of a more  
260 homogeneous assemblage. Following Gatti et al. (2015), the temporal rate of change of the cave  
261 taken as a whole was assessed by computing the average ( $\pm$  se) Bray-Curtis similarity between  
262 the stations of a given year and the centroid of the stations in 1986, taken as the reference  
263 condition.

264

### 265 **3. Results**

#### 266 *3.1. Change in morphologic descriptors (GF)*

267 The ordination model on the matrix of descriptors  $\times$  observations (4 times, 4 sectors) for growth  
268 forms showed two distinct clouds (Figure 6). On the left side of the plot, the stations in the two  
269 Lakes are separated from all the other sectors that are grouped in the right side, reflecting  
270 significant differences among the cave sectors ( $p < 0.001$ , Table 1). Pair-wise comparisons  
271 revealed significant differences between Lakes and all the other sectors (Hall, Gulley and  
272 Chambers).  $Y \times Se$  interaction was not significant, thus highlighting that differences among  
273 sectors were consistent across time. Observation-points also exhibited a vertical arrangement  
274 according to time, from 1986 at the top to 2013 at the bottom, indicative of the significant change  
275 experienced by the sessile communities over the years; however, the sessile communities  
276 displayed significant variability between stations that was not consistent among the 4 times, as  
277 shown by the significant interactions  $Y \times St(Se)$  (Table 1). The time-trajectories of the station

278 centroids were mainly developed along the vertical axis in all the sectors, except in the Lakes  
279 (Figure 7). All stations in Chambers, Gulley and Hall experienced a similar change of path in  
280 time, with increasing distances between each period and especially between the last one (2009 to  
281 2013). The two stations in Chambers and Hall also diverged towards opposite directions during  
282 this last period. On the contrary, the two lakes changed less than the other sectors, and especially  
283 the Lake Through the Hole (L2); this lake, being more isolated, has apparently been less affected  
284 by pressures coming from the outside. Multivariate dispersion within the cave was lower in 2009  
285 than in 1986 ( $20.42 \pm 1.81$  and  $30.87 \pm 1.39$ , respectively;  $p = 0.001$ ), but then recovered in 2013  
286 ( $26.83 \pm 1.27$ ;  $p = 0.018$ ) (Table 2 and Figure 8). The differences observed among years were  
287 mainly due to the increase of indeterminate and determinate sheets (the former increased until  
288 2009), decrease of runners, almost disappearance of vines, and a huge increase of turf and  
289 sediments that covered both the biota and the bare substrate (Table 3). Indeterminate sheets,  
290 determinate sheet and turf and sediment increased their contribution to replicates similarity from  
291 1986 to 2013, and only the former denoting a decrease between 2009 and 2013 (Table 4). On the  
292 contrary, bare substrate, runners and vines decreased their contribution to similarity over time.

293

### 294 3.2. *Change in trophic descriptors (TG)*

295 Although less marked, the spatial gradient along the horizontal axis is still evident in the  
296 ordination model on the matrix of descriptors  $\times$  observations (4 times, 4 sectors) for trophic  
297 guilds (Figure 9), with stations in the two Lakes separated from all the other sectors; however,  
298 differences among the cave sectors were not significant (Table 1). The vertical arrangement  
299 according to time is similarly reduced with respect to that shown by the analysis of growth forms:  
300 the sessile communities changed from 1986 to 2009 but in 2013 they moved towards a new  
301 trajectory on the right side of the plot. As for GF, a significant variability between stations was

302 displayed that was not consistent among the 4 times (Table 1). Looking at the time-trajectories of  
303 the station centroids, the greatest change in TG occurred along the horizontal axis and between  
304 2009 and 2013 in most of the stations (Figure 10). Only in the Hall there were evidences of some  
305 recovery. According to TG, also the two lakes changed with time, notwithstanding their  
306 comparative isolation from the outside. Multivariate dispersion within the cave reduced from  
307 1986 to 2013 (from  $24.96 \pm 1.97$  to  $13.32 \pm 1.41$ ;  $p = 0.001$ ), and the main differences occurred  
308 between 2004 and 2009 (from  $22.83 \pm 1.72$  to  $14.72 \pm 1.20$ ;  $p = 0.002$ ) (Table 2 and Figure 8). Such  
309 differences among years were mainly due to the decrease of active ciliates, increase of active  
310 pumping sponges and near disappearance of active ciliates with lophophore, especially between  
311 2009 and 2013 (Table 3). Notwithstanding some fluctuations, active ciliates (either with or  
312 without lophophore) decreased their contribution to replicates similarity from 1986 to 2013,  
313 whilst active pumping sponges increased their contribution (Table 4).

314

## 315 **Discussion**

316 The analysis of a long time series of quantitative information about the sessile communities  
317 allowed elucidating the evolution of the Bergeggi marine cave ecosystem across nearly 30 years.  
318 Notwithstanding the dearth of long-term ecological studies in the Mediterranean Sea (Bianchi,  
319 2001), the changes that occurred during the last decades are well documented and demonstrate  
320 dramatic modifications in species composition, community structure and trophic organisation in  
321 many marine ecosystems (Parravicini et al., 2010; Bianchi et al., 2014; Gatti et al., 2015, 2017;  
322 Bertolino et al., 2016; Nepote et al., 2016). In the case of marine caves, little research effort has  
323 been invested in comparison to other habitats (Gerovasileiou et al., 2015) and the historical series  
324 of data analysed in the present paper may thus represent a precious and unique baseline for  
325 protecting these fragile ecosystems (Sarà, 1974, 1976; Navarro-Barranco et al., 2015).

326 The Bergeggi marine cave experienced a general trend of change during the last three decades,  
327 highlighted by both growth forms (GF) and trophic guilds (TG), and mainly due to the decline in  
328 the cover of sessile organisms matched by an increase of turf and sediment. First changes in the  
329 cave communities have been reported since the 1990s, which were likely to be due to synergic  
330 effects of both local pressures and climate change (Parravicini et al., 2010). Cover of 2-  
331 dimensional forms, such as sheets (mainly constituted by encrusting sponges), was higher in  
332 2013 than in 1986, while the reverse was true for 3-dimensional forms: vines and mounds, mostly  
333 constituted by serpulids and massive sponges, respectively, almost disappeared from the cave.  
334 Encrusting sponges have already been shown to be winners in stressed environments, being good  
335 competitors for space (Bell and Barnes, 2000; Bell, 2002; Nepote et al., 2017). Appearance of  
336 turf and sediment (Chou et al., 2004; Nepote et al., 2017) can be related to enhanced sediment  
337 arrival to the cave, as its peculiar topography allows circulation and transport through most of the  
338 cave and increased deposit in relatively confined sectors (Morri, 2003). Turf and sediment  
339 covered the 2 and 3-dimensional forms and the bare substrate, thus favouring the structural  
340 homogenization of the cave community, as illustrated by the decline in the multivariate  
341 dispersion until 2009, and the loss of the complex structure of the habitat.

342 The mortalities caused by the thermal events of 1999 and 2003 hit especially massive sponges, as  
343 already observed by Bell et al. (2017b) in other localities: *Petrosia ficiformis*, which was found  
344 dead during the field observations of 2003, used to be the most abundant 3-dimensional species  
345 within the Bergeggi cave in the 1970s and 1980s (Bianchi et al., 1986) but did not recover  
346 anymore. Encrusting sponges were less affected and/or recovered faster to become dominant in  
347 the cave assemblages in 2013. Among encrusting organisms, those displaying an active pumping  
348 trophic strategy were advantaged, thanks to their more efficient filtration capacity, compared with  
349 other small filter feeding organisms such as active ciliates with lophophore (Rastorgueff et al.,

350 2015), which progressively disappeared thus enhancing the trophic homogenization of the cave.  
351 As far as growth forms are concerned, less than five years seem however enough to cave benthic  
352 communities to recover their multivariate dispersion, notwithstanding a steady decline at the  
353 trophic level. As already observed in a stressed marine cave system (Nepote et al., 2017), changes  
354 in morphological strategies are faster than changes in trophic strategies.

355 In spite of some exceptions due to the cave morphology, both GF and TG showed the most  
356 important rate of change during the period 2009-2013, simultaneously to recent major beach  
357 nourishments (occurred in 2005, 2008, 2011) and to Vado Ligure harbour extension (started in  
358 2011). Human activities along the coast may disrupt natural hydrodynamic and sedimentary  
359 regimes, which, in turn, could have detrimental effects on the neighbouring cave assemblages as  
360 a consequence of increased sandy bottom instability, alterations of sedimentation rates, and  
361 increased water turbidity (Ferrari et al., 2013; Guarnieri et al., 2016; Nepote et al., 2017).  
362 Tourism and recreational activities, related to the establishment of the Bergeggi Island MPA (in  
363 2007), when intensive may represent a source of impact on coastal marine communities  
364 (Garrabou et al., 1998; Milazzo et al., 2002; Bianchi et al., 2018). Major thermal events, along  
365 with an increase of about 0.5°C of the surface seawater temperature compared to 1986, took  
366 place in almost the same period and so did the time trajectories of the cave sessile communities,  
367 thus providing suggestive evidence of an ecosystem phase shift in response to a regime shift in  
368 external drivers (Montefalcone et al., 2011), consistently with previous studies in other  
369 Mediterranean habitats and sites (Bianchi et al., 2014, 2017; Gatti et al., 2015, 2017). Global  
370 warming and local human pressures are known to combine their effects on the marine biota, and  
371 identifying the main drivers of the change observed in benthic communities is often difficult  
372 (Morri and Bianchi, 2001). Many clues of the effects of climate change on the benthic  
373 communities of the Bergeggi marine cave have been found, but the reduction in the community



374 complexity and the increased biotic homogenization, mainly due to the large amount of turf and  
375 sediment on the cave walls, provided a striking evidence of the importance of local impacts,  
376 deriving from coastal interventions (Guarnieri et al., 2016). Increased biotic homogenization may  
377 of course suggest a similarly increased homogenization of environmental conditions within the  
378 cave. An array of abiotic data, as complete as that of 1986, is unfortunately not available for  
379 recent years. Apart from the reported increase in sea water temperature (Figure 3), however,  
380 information from other Ligurian Sea coastal localities (Morri and Bianchi, 2001; Parravicini et  
381 al., 2013; Gatti et al., 2015) showed change in water turbidity and suspended particulate matter  
382 between the 1980s-90s and recent years, thus supporting the suspect that abiotic conditions  
383 within the cave may have similarly changed. Establishment of a MPA cannot protect ecosystems  
384 from large-scale stressors originating outside their boundaries (Allison et al., 1998; Montefalcone  
385 et al., 2009; Parravicini et al., 2012; Guidetti et al., 2014). In many cases, exogenous disturbances  
386 have far greater effects on the biodiversity of a MPA than direct activities within the area (Mora  
387 et al., 2006).

388 Submerged marine caves are unique systems and their sessile communities are highly  
389 heterogeneous (Martì et al., 2004), reflecting the cave topography and environmental gradients  
390 (Gerovasileiou et al., 2017). These cave-specific features usually prevents replicated designs to  
391 generalise conclusions (Di Franco et al., 2010), being each cave different from any other.  
392 However, the patterns of change observed in the marine cave of Bergeggi are consistent with  
393 those described in two marine caves located about 80 km to the west (Nepote et al., 2017) and in  
394 other coastal Ligurian Sea ecosystems (Parravicini et al., 2013; Gatti et al., 2015, 2017).  
395 Moreover, finding a cave with a similar topography to the complex one of the Bergeggi cave, in  
396 the same geographical area but unaffected by the same local impacts to be considered as a control  
397 cave, is impossible.

398 Historical information on marine habitats is often sparse and incomplete and our series of data,  
399 although lasting a long period of nearly 30 years and being unique for a submerged marine cave,  
400 lacks information about the status of the cave between 1986 and 2004. The area of Bergeggi, as  
401 well as the whole Ligurian Sea, has been chronically affected by minor local impacts in the last  
402 century (Burgos et al., 2017), which have caused a constant decline in the status of the cave.  
403 However, change between 1986 and 2004 has been mostly correlated to climatic anomalies  
404 (Parravicini et al., 2010). The results of the present paper provide suggestive evidence that  
405 change between 2004 and 2013 is mainly correlated with local impacts, and is greater than the  
406 one previously attributed to climate.

407 Distribution of sessile communities into a cave with complex topography (as the Bergeggi cave)  
408 usually follows a pattern of biotic impoverishment towards the aphotic and/or more confined  
409 sectors (Gerovasileiou et al., 2013). In several cases, the small-scale spatial variability, for  
410 instance between adjacent sectors within the same cave, can be higher than that between caves  
411 (Dimarchopoulou et al., 2017; Gerovasileiou et al., 2017). Differences among the four cave  
412 sectors were evident only for GF and were consistent in all the years examined, suggesting that  
413 morphological and environmental features characterizing the sectors affect the dimensional  
414 structure but not the trophic organisation of communities. When considering GF, Chambers,  
415 Gulley and Hall exhibited similar time trajectories. On the contrary, the Lakes, and especially the  
416 more confined and isolated Lake Through the Hole, exhibited little change, and even some  
417 evidences of recovery in the last period. This result contrasts with the findings by Parravicini et  
418 al. (2010), who stated that size and morphology of individual sectors have a primary influence on  
419 hydrological confinement (Morri, 2003), and hence trophic depletion (Bianchi et al., 2003).  
420 Habitat heterogeneity is a central factor in building models, designing field experiments, and  
421 managing natural resources (García-Charton and Pérez-Ruzafa, 1999). The adoption of a

422 sampling design based on sectors differing in morphology and environmental conditions is thus  
423 recommended to highlight the spatial pattern of sessile communities.

424 Marine cave ecosystems present low recovery potential (Harmelin, 1980; Harmelin et al., 1985)  
425 and it is therefore compulsory to develop innovative non-destructive protocols for monitoring the  
426 status of cave communities and define protective measures (Bianchi et al., 2012b; Zapata-  
427 Ramírez et al., 2016; UNEP-MAP-RAC/SPA, 2017). The use of effective surrogates for taxa,  
428 measured in terms of specific traits such as morphological diversity or feeding strategy  
429 (Cernansky, 2017) could provide effective options to assist in marine cave conservation  
430 (Gerovasileiou et al., 2017). Non-taxonomic descriptors, such as GF and TG, have already been  
431 used to study the structural and functional composition of sessile benthos in several habitat types  
432 (Cocito et al., 1997), marine caves included (Parravicini et al., 2010; Bell et al., 2017a;  
433 Gerovasileiou et al., 2017; Nepote et al., 2017); GF and TG should be concurrently used, as they  
434 may show inconsistent patterns in term of recovery. Clearly, GF and TG cannot provide  
435 information of biodiversity pattern, a major descriptor of ecosystem complexity (Paoli et al.,  
436 2016); sponges, which are usually the dominant and species richest group in caves, have been  
437 suggested as the best proxy to this purpose (Gerovasileiou et al., 2017). The analysis of growth  
438 forms and trophic guilds, however, may represent an efficient complement, or even an alternative,  
439 to taxonomic-based studies when ecosystem structure and function are the focus of the study, as  
440 shown in the present paper.

441

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802

803 **Figure captions and Table headings**

804 Figure 1. Location and plan view morphology of the emerged and submerged parts of the  
805 Bergeggi marine cave, with indication of the four sectors investigated (C = Chambers,  
806 G = Gulley, H = Hall, L = Lakes) and position of the two sampling stations in each sector (1 and  
807 2).

808

809 Figure 2. Spatial distribution of selected physical-chemical variables inside the Bergeggi marine  
810 cave.

811

812 Figure 3. Sampling schedule in the Bergeggi marine cave and change in pressure regime in the  
813 Bergeggi area, 1985 to 2014. Top to bottom: sampling times in 1986, 2004, 2009, 2013; yearly  
814 average of sea surface temperature (SST, from NOAA satellite data), the dotted line depicting the  
815 decadal trend as described by the second degree polynomial  $SST = -0.0003 \cdot \text{year}^2 + 1.3385 \cdot \text{year} -$   
816  $1334.8$ ,  $R^2 = 0.402$ ; phases of the Vado Ligure harbour extension; major beach nourishments at  
817 Bergeggi; resident population in the municipality of Bergeggi; years since the SCI has been  
818 identified and the Marine Protected Area established.

819

820 Figure 4. Top: extension of the Vado Ligure harbour in recent decades. The perimeters of the  
821 existing marine Site of Community Interest (SCI) and Marine Protected Area (MPA) are  
822 indicated by a solid yellow line and a dash-dot light blue line, respectively; the symbol  $\Omega$   
823 indicates the position of the Bergeggi marine cave; the stars indicate the beaches where major  
824 beach nourishments have been carried out. Aerial imagery from Google Earth®. Bottom: photos  
825 of Cape Vado taken from the terrestrial part of the cave, illustrating the impressive increase of  
826 harbour infrastructures in recent decades. Arrows point at an easily recognizable building (left)

827 and the Vado lighthouse (right), which may serve as reference points.

828

829 Figure 5. Eight growth forms adopted as non-taxonomic descriptors to evaluate structural change  
830 in the sessile community of the cave: runners (a), determinate sheets (b), indeterminate sheets (c),  
831 flattened mounds (d), hemispherical mounds (e), domed mounds (f), vines (g), and threes (h).

832

833 Figure 6. Overall nMDS plot, based on the growth forms dataset. In bold are the centroids of  
834 years and sectors. Individual observation points are represented by alphanumeric codes, with year  
835 (1986, 2004, 2009, 2013) followed by sector (C = Chambers, G = Gulley, H = Hall, L = Lakes,  
836 see Figure 1) and station (1, 2).

837

838 Figure 7. Same ordination plane of Figure 5, split for the sake of clarity to show time-trajectories  
839 in the four sectors. Yearly centroids of observation points are indicated by the corresponding year,  
840 polygons depicting the variability among replicates. Arrows show the time-trajectory of the two  
841 stations within each sector. C = Chambers, G = Gulley, H = Hall, L = Lakes; 1 = station 1,  
842 2 = station 2 (see Figure 1).

843

844 Figure 8. Temporal trends of average ( $\pm$  se) Bray-Curtis similarity between all the replicates of  
845 the photostations of a given year and the 1986 centroid, in the sessile communities of the  
846 Bergeggi marine cave from 1986 to 2013.

847

848 Figure 9. Overall nMDS plot, based on the trophic guilds dataset. In bold are the centroids of  
849 years and sectors. Individual observation points are represented by alphanumeric codes, with year  
850 (1986, 2004, 2009, 2013) followed by sector (C = Chambers, G = Gulley, H = Hall, L = Lakes,

851 see Figure 1) and station (1, 2).

852

853 Figure 10. Same ordination plane of Figure 7, split for the sake of clarity to show time-  
854 trajectories in the four sectors. Yearly centroids of observation points are indicated by the  
855 corresponding year, polygons depicting the variability among replicates. Arrows show the time-  
856 trajectory of the two stations within each sector. C = Chambers, G = Gulley, H = Hall, L = Lakes;  
857 1 = station 1, 2 = station 2 (see Figure 1).

858

859 Table 1. Results of PERMANOVA performed on growth forms and trophic guilds datasets.  
860 Y = years; Se = sectors; St = stations. Bold characters indicate significant values.

861

862 Table 2. Homogeneity of the multivariate dispersions among years resulting from PERMDISP  
863 analysis performed on growth forms (GF) and trophic guilds (TG). Bold characters indicate  
864 significant values.

865

866 Table 3. Mean values of the percent cover ( $\pm$ s.e.) of the non-taxonomic descriptors in the two  
867 stations within each sector of the cave from 1986 to 2013. C = Chambers, G = Gulley, H = Hall,  
868 L = Lakes; 1 = station 1, 2 = station 2; R = runners, DS = determinate sheets, IS = indeterminate  
869 sheets, FM = flattened mounds, HM = hemispherical mounds, DM = domed mounds, V = vines,  
870 T = threes, BS = bare substrate, TS = turf and sediment, A = autotrophs, PF = passive filter  
871 feeders, AC = active ciliates, ACL = active ciliates with lophophore, APS = active pumping  
872 sponges, APA = active pumping ascidians.

873

874 Table 4. Percentage contribution of each descriptor to the Bray-Curtis similarity among stations

875 in each sampling year, as depicted by the SIMPER analysis on growth forms (GF) and trophic  
876 guilds (TG). Only descriptors that contributed more than 1% are reported.

877

878 Table 1.

<b>Source</b>	<b>df</b>	<b>SS</b>	<b>MS</b>	<b>Pseudo-F</b>	<b>P(perm)</b>
<i>Growth forms</i>					
Y	3	23588	7862.8	7.0692	<b>0.001</b>
Se	3	51099	17033	3.6054	<b>0.001</b>
St(Se)	4	15377	3844.2	3.4562	<b>0.008</b>
Y×Se	9	10697	1188.6	1.0686	0.417
Y×St(Se)	12	13347	1112.3	3.5755	<b>0.001</b>
Residuals	128	39819	311.08		
Total	159	1.5393E5			
<i>Trophic guilds</i>					
Y	3	27777	9259	8.923	<b>0.001</b>
Se	3	21503	7167.5	1.9472	0.060
St(Se)	4	12500	3125	3.0116	<b>0.014</b>
Y×Se	9	9799.1	1088.8	1.0493	0.451
Y×St(Se)	12	12452	1037.7	6.2393	<b>0.001</b>
Res	128	21288	166.3		
Total	159	1.0532E5			

879

880 Table 2.

<b>Years</b>	<b>P(GF)</b>	<b>P(TG)</b>
1986, 2004	0.247	0.423
1986, 2009	<b>0.001</b>	<b>0.001</b>
1986, 2013	0.066	<b>0.001</b>
2004, 2009	0.065	<b>0.002</b>
2004, 2013	0.878	<b>0.001</b>
2009, 2013	<b>0.018</b>	0.510

881

882

883 Table 3.

		Growth Forms						Abiotic Components					Trophic Guilds				
		R	DS	IS	FM	HM	DM	V	T	BS	TS	A	PF	AC	ACL	APS	APA
1986	C1	6.9±0.8	1.9±0.7	58.6±2.4	9.5±0.8	1.4±0.6	0	8.0±1.0	0	9.5±1.0	0	0	1.8±0.7	27.3±1.0	40.9±1.3	16.0±0.8	4.6±1.0
	C2	21.3±1.6	3.4±0.8	35.3±2.2	0.5±0.5	0.5±0.4	0	22.7±2.4	0	16.4±1.8	0	0	0.4±0.4	38.4±1.2	12.6±1.4	29.2±2.4	0
	G1	5.2±0.9	1.9±0.7	54.1±3.2	0.2±0.3	0.2±0.3	0	1.7±0.7	0	36.7±3.2	0	0.6±0.5	1.3±0.7	4.5±0.9	4.3±1.2	52.0±1.3	0.6±0.6
	G2	6.7±0.8	4.5±0.6	56.8±2.3	0	0.6±0.5	0	23.1±2.2	0	8.3±1.2	0	0	0	44.3±1.5	24.8±1.5	22.6±1.4	0
	H1	7.7±0.7	2.6±0.7	26.0±2.0	4.2±1.2	1.0±0.6	19.4±2.1	18.4±2.3	0	20.5±1.6	0	0	1.3±0.5	19.8±0.8	8.6±0.8	49.7±1.1	0
	H2	8.6±0.7	1.5±0.6	62.0±1.2	5.9±1.2	1.9±0.9	0.2±0.3	10.5±1.5	1.6±0.7	7.8±1.4	0	0	5.2±1.0	16.8±0.7	11.2±1.4	58.7±1.0	0.2±0.3
	L1	6.8±0.6	0.5±0.4	7.1±0.9	0	0	0	1.7±0.5	0	79.5±1.0	4.4±1.1	0	0	9.8±0.5	6.3±0.8	0	0
	L2	6.1±0.9	0	2.2±0.5	0	0.1±0.2	0	0	0	65.6±1.5	26.0±1.6	0	0	5.0±0.7	2.8±0.6	0.6±0.4	0
2004	C1	19.7±2.0	3.4±0.7	62.4±2.1	6.0±2.0	1.8±0.9	0	6.8±0.8	0	6.0±1.0	0	0	1.8±0.9	20.7±1.5	14.7±1.2	54.4±2.4	2.4±0.9
	C2	13.5±1.2	3.5±0.8	23.9±1.9	0	0	0	41.8±1.8	0	17.3±1.6	0	0	0	50.7±2.1	9.5±1.5	22.5±2.0	0
	G1	5.4±0.9	5.1±0.9	69.9±2.5	0	1.0±0.7	5.3±1.7	5.0±0.8	0	8.2±1.1	0	0	2.1±0.8	18.8±1.3	11.8±1.1	59.2±2.0	0
	G2	9.4±0.8	1.4±0.7	58.0±2.0	0	0.2±0.3	4.5±1.1	13.4±1.3	0	13.1±1.4	0	0	0	20.9±1.1	22.9±1.6	41.7±1.7	1.4±0.7
	H1	8.8±1.3	4.2±0.9	55.6±2.6	18.8±2.3	1.7±0.8	2.0±0.9	3.3±1.0	0	5.4±1.1	0.3±0.3	0	0.9±0.6	12.3±1.2	19.6±1.2	52.3±2.4	9.5±1.6
	H2	4.7±0.9	3.4±0.8	74.5±1.4	0	1.6±0.8	0	0.8±0.6	0	15.0±1.3	0	0	0.3±0.3	9.3±1.1	50.3±1.9	25.1±2.0	0
	L1	1.3±0.5	3.1±0.7	57.2±2.5	0	0	0	0.4±0.5	0	31.9±2.7	6.1±1.3	0	0	5.7±0.8	40.3±1.9	16.1±1.5	0
	L2	5.6±0.8	0.2±0.3	1.6±0.9	1.6±1.0	1.2±0.7	0	0	0	70.1±2.3	19.6±2.1	0	0	6.3±0.8	3.3±0.7	0.7±0.5	0
2009	C1	7.6±1.3	9.8±1.1	77.8±1.6	0	2.6±0.6	0	1.2±0.8	0	1.0±0.6	0	0	2.6±0.6	17.8±1.6	27.6±2.1	48.6±2.7	2.4±0.8
	C2	19.6±1.2	5.8±1.0	48.2±1.7	0.6±0.4	1.2±0.5	0	2.2±0.8	0	22.4±2.1	0	0	3.0±0.6	25.2±1.4	30.2±1.5	15.0±1.8	4.2±0.6
	G1	6.4±0.9	7.2±1.1	79.6±1.3	0	0.6±0.5	0	1.2±0.3	0	5.0±1.3	0	0	0.6±0.5	15.8±1.3	26.4±1.9	51.4±2.1	0.8±0.5
	G2	7.2±1.0	9.0±0.7	69.6±1.2	1.4±0.6	1.0±0.6	0.2±0.3	4.8±1.2	0	6.8±1.1	0	0	1.2±0.5	21.6±1.2	25.4±1.1	43.2±1.4	1.8±0.5
	H1	6.6±0.5	6.6±0.5	73.4±1.0	3.8±1.2	0.6±0.4	0	0.2±0.3	0	7.6±0.8	1.2±0.6	0	1.6±0.6	13.2±0.7	50.0±1.5	26.0±1.6	0.4±0.4
	H2	7.8±0.8	6.2±0.9	70.8±1.4	3.8±1.1	3.4±1.1	0.2±0.3	1.0±0.6	0	1.2±0.6	5.6±1.1	0	3.8±1.0	16.6±1.3	46.6±1.3	26.2±1.3	1.2±0.5
	L1	10.0±0.8	8.8±0.9	68.2±1.1	0	0	0	0.2±0.3	0	9.6±1.2	3.2±1.0	0	0.8±0.5	18.0±0.9	50.0±1.0	16.2±1.4	2.2±0.7
	L2	6.2±0.7	3.4±0.9	5.2±0.5	1.2±0.7	1.4±0.5	0.2±0.3	0	0	59.4±2.3	23.0±2.2	0	0	10.6±0.9	3.4±0.4	3.6±0.5	0
2013	C1	6.7±0.8	8.3±0.8	49.6±1.8	0.3±0.4	1.0±0.4	0.2±0.4	0.1±0.2	0	2.3±0.6	31.6±1.7	0	0	17.3±1.2	1.0±0.4	50.1±1.8	0
	C2	22.2±1.5	19.9±1.0	52.2±1.3	0.7±0.5	0.9±0.5	2.0±0.7	0.1±0.3	0.2±0.3	0.3±0.4	1.4±0.6	9.4±2.2	0	41.7±1.4	0.9±0.5	46.6±2.5	0
	G1	11.8±1.1	13.8±1.1	66.3±1.7	1.8±0.9	2.2±0.7	0.1±0.3	2.3±0.7	0.2±0.4	1.4±0.5	0	0.4±0.4	0	27.1±1.5	2.0±0.7	69.1±1.6	0
	G2	14.6±1.1	13.7±1.2	56.1±1.6	4.4±1.2	0.9±0.5	2.2±0.8	0.2±0.3	7.2±1.1	0.7±0.6	0	8.2±1.2	0	28.6±1.1	0.9±0.5	61.6±1.4	0
	H1	11.6±1.1	8.9±1.0	48.0±1.7	6.3±1.0	0.2±0.3	0.7±0.4	0.1±0.3	7.2±1.6	4.0±0.9	12.8±2.3	7.2±1.6	0	21.4±1.3	0.3±0.3	51±1.2	0
	H2	6.3±0.9	6.4±1.0	32.5±1.1	1.6±0.6	0.7±0.4	4.2±1.1	0	1.0±0.8	5.3±1.0	41.9±1.8	1.0±0.8	0	12.4±1.2	0.5±0.4	38.9±1.5	0
	L1	1.5±0.6	9.2±1.0	27.4±1.5	0.8±0.6	0.7±0.5	0.4±0.5	0.8±0.6	0	21.7±1.6	37.5±2.3	0	0	11.5±1.1	0.7±0.5	28.5±1.6	0
	L2	8.1±1.0	4.9±0.8	3.4±0.6	0.5±0.5	0.8±0.6	0.6±0.5	0.1±0.2	0	58.0±2.1	23.6±2.3	0	0	13.7±1.1	0	4.7±0.4	0



885 Table 4.

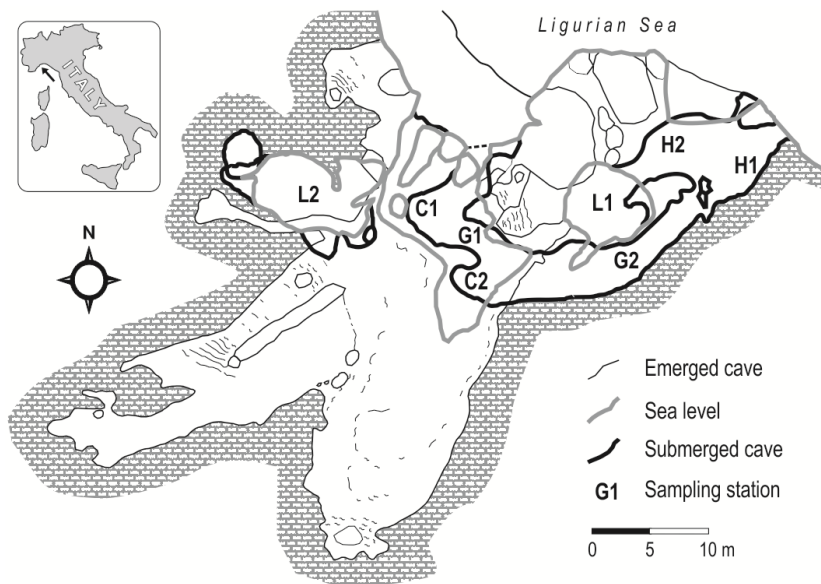
Descriptor	Year			
	1986	2004	2009	2013
<i>Growth forms</i>				
Indeterminate sheets	34.63	44.17	51.38	38.55
Bare substrate	27.13	23.07	11.43	7.50
Runners	19.35	15.73	16.19	16.37
Vines	11.12	7.18	1.64	0.49
Determinate sheets	4.73	7.49	14.56	18.60
Turf and sediment	1.06	1.05	1.93	11.05
<i>Trophic guilds</i>				
Active ciliates	39.02	31.77	27.08	37.93
Active pumping sponges	29.56	37.00	30.82	58.54
Active ciliates with lophophore	29.47	30.35	35.26	2.59

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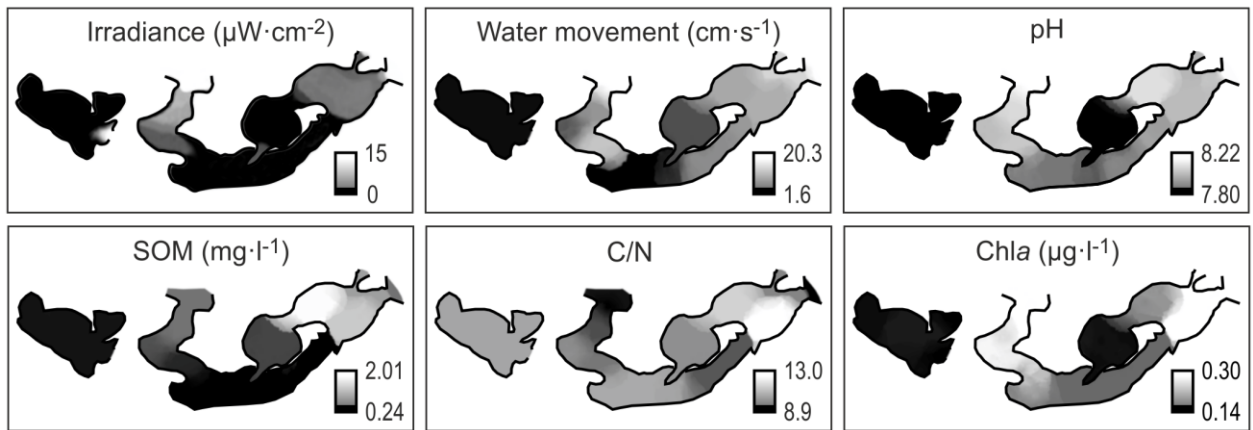
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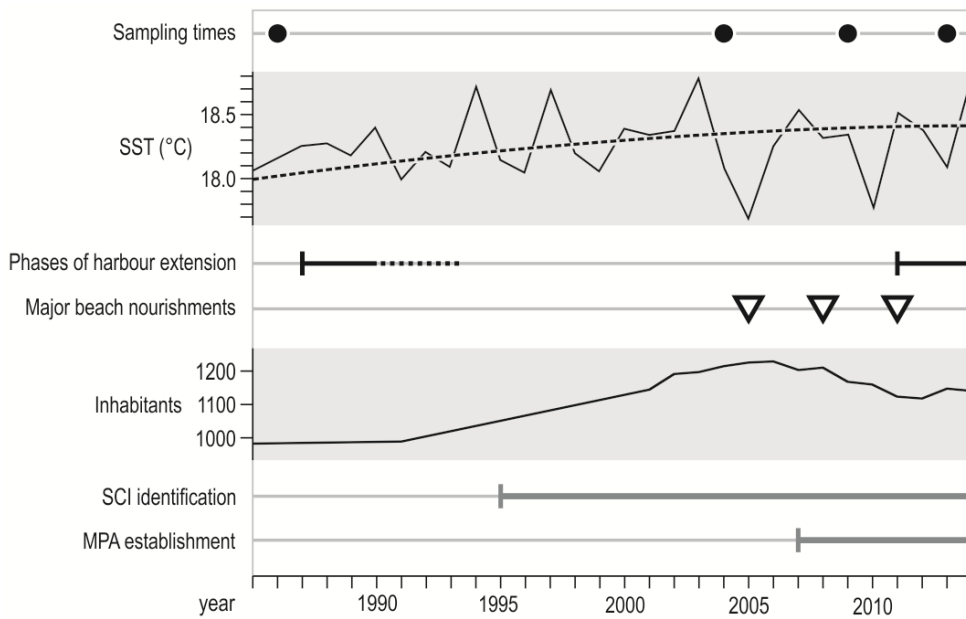
890

891 Figure 1

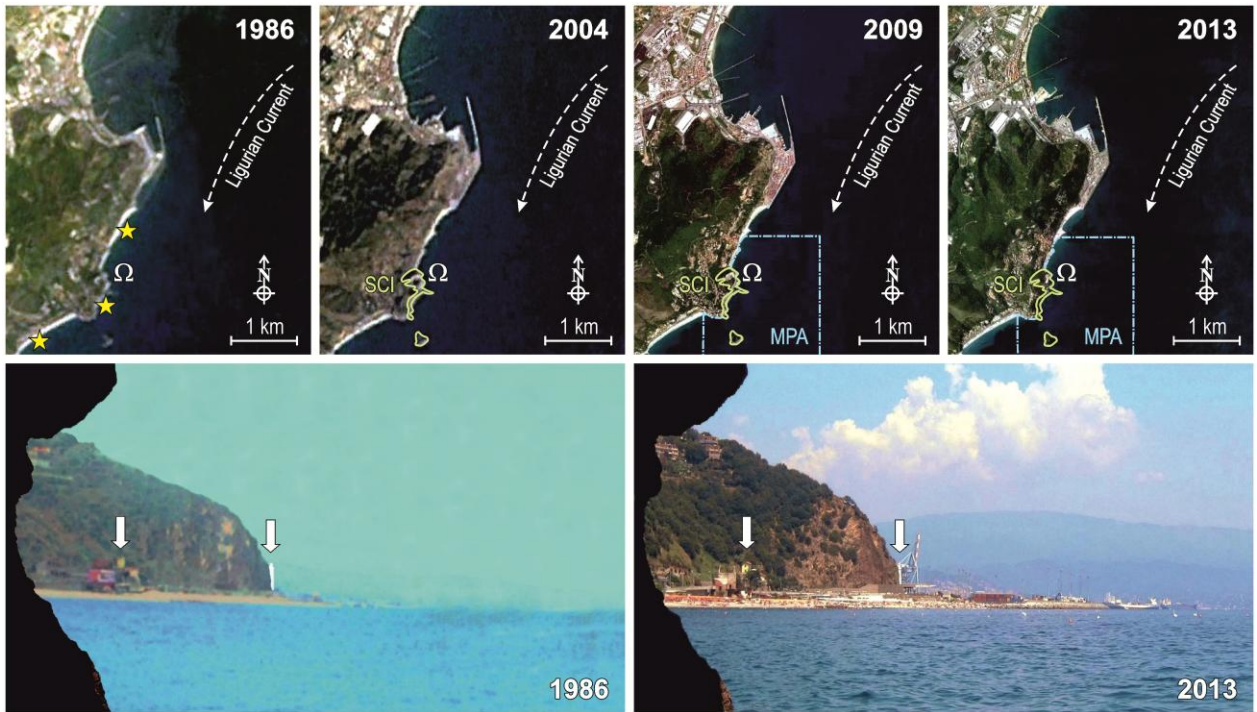
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893  
894 Figure 2  
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896  
897 Figure 3  
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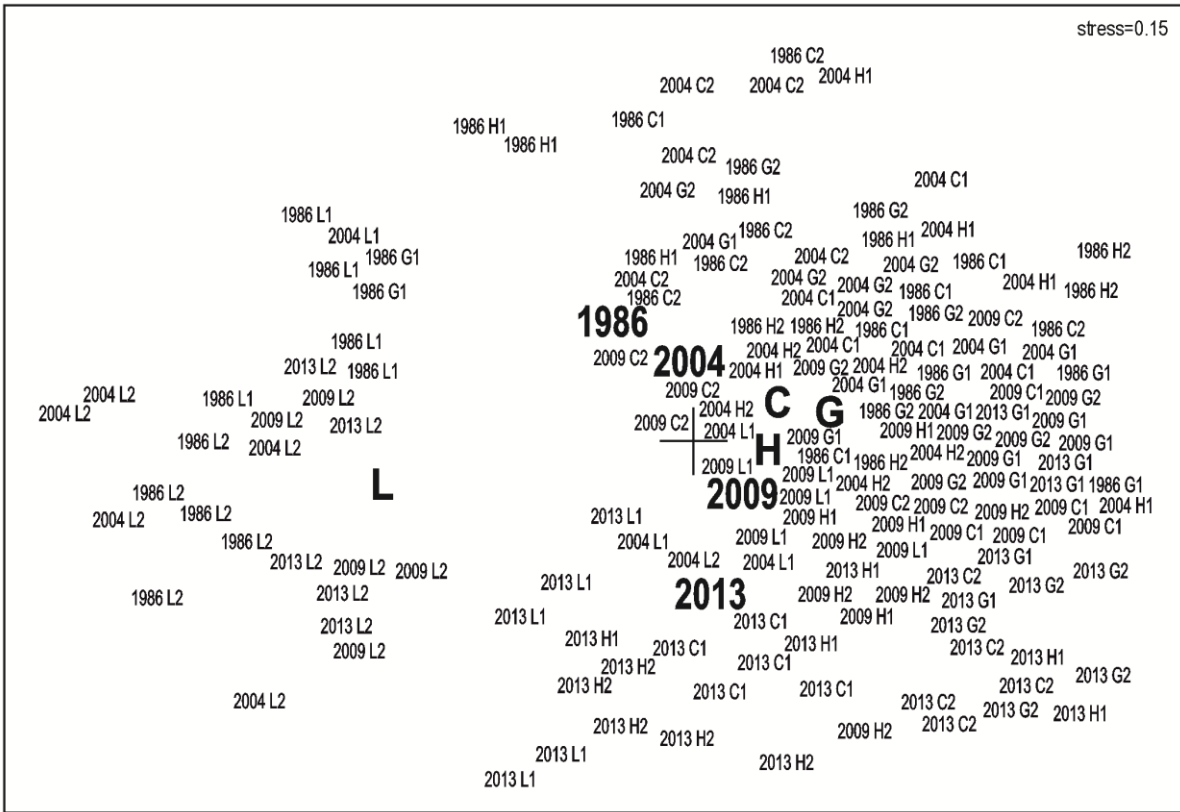


899  
 900 Figure 4  
 901





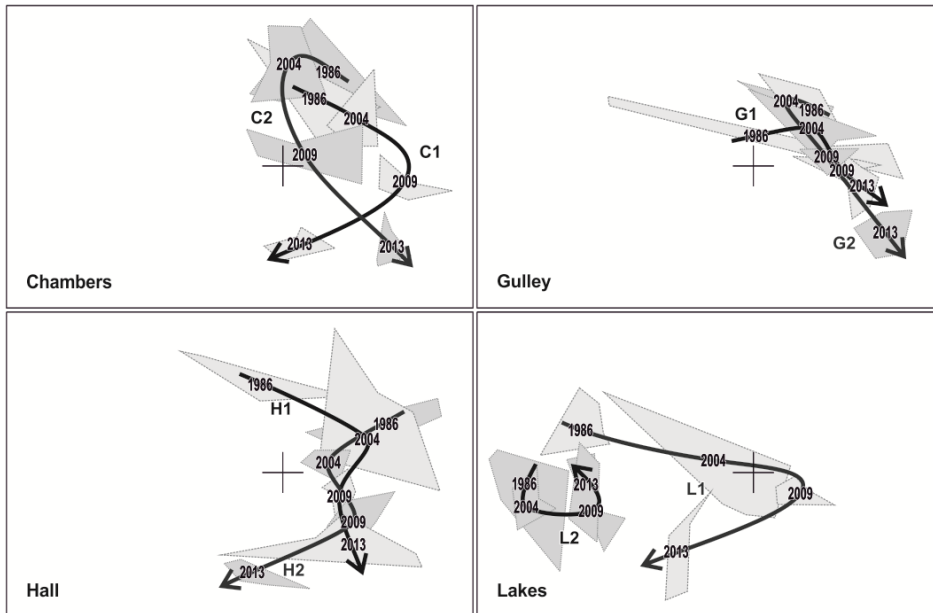
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903 Figure 5



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905 Figure 6

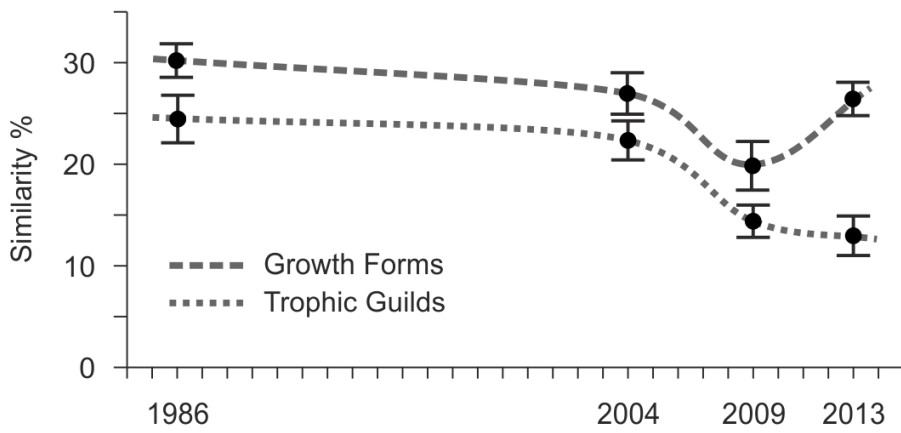
906



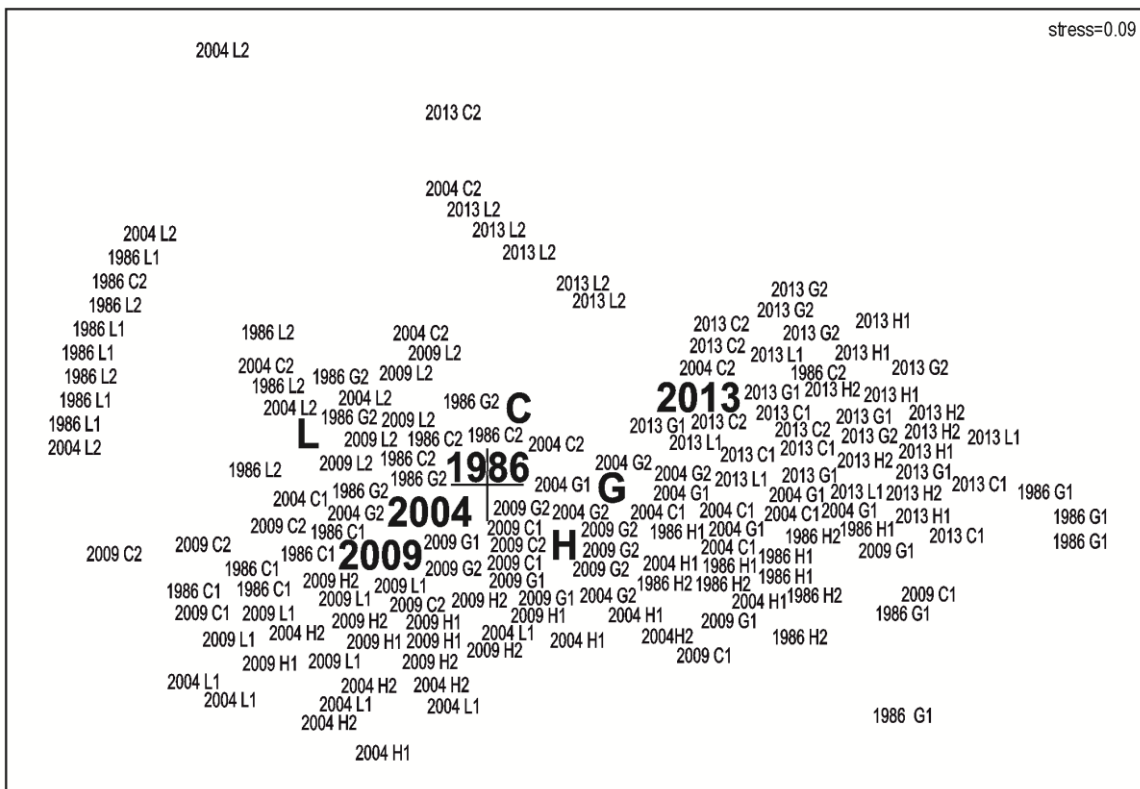
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908 Figure 7

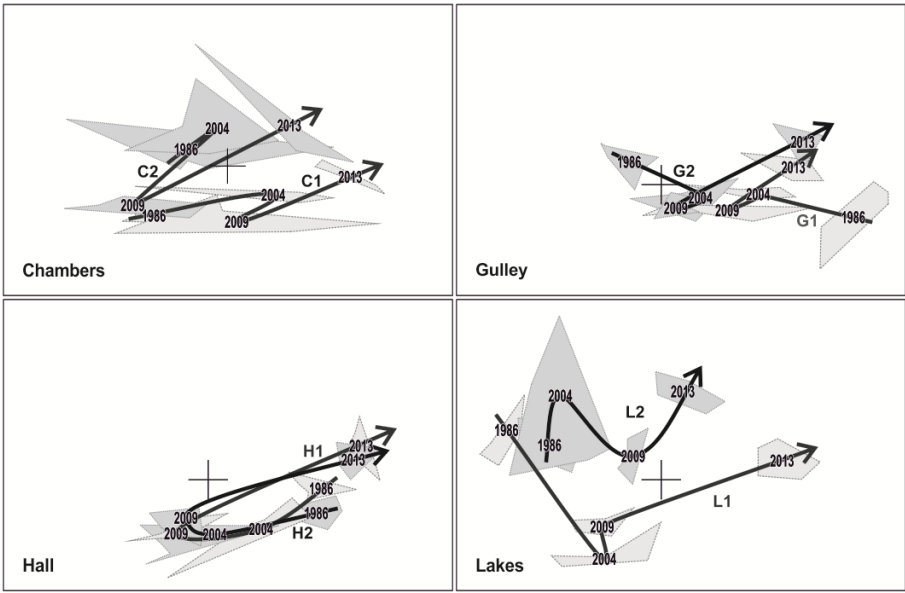
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910  
 911 Figure 8  
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913  
 914 Figure 9



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916 Figure 10