

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

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13

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 CO₂ 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 m² (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 cm², 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 ± 1.81 and 30.87 ± 1.39 , respectively; $p = 0.001$), but then recovered in 2013
286 (26.83 ± 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 ± 1.97 to 13.32 ± 1.41 ; $p = 0.001$), and the main differences occurred
308 between 2004 and 2009 (from 22.83 ± 1.72 to 14.72 ± 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 Ω
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.

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

879

880 Table 2.

Years	P(GF)	P(TG)
1986, 2004	0.247	0.423
1986, 2009	0.001	0.001
1986, 2013	0.066	0.001
2004, 2009	0.065	0.002
2004, 2013	0.878	0.001
2009, 2013	0.018	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±11	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.

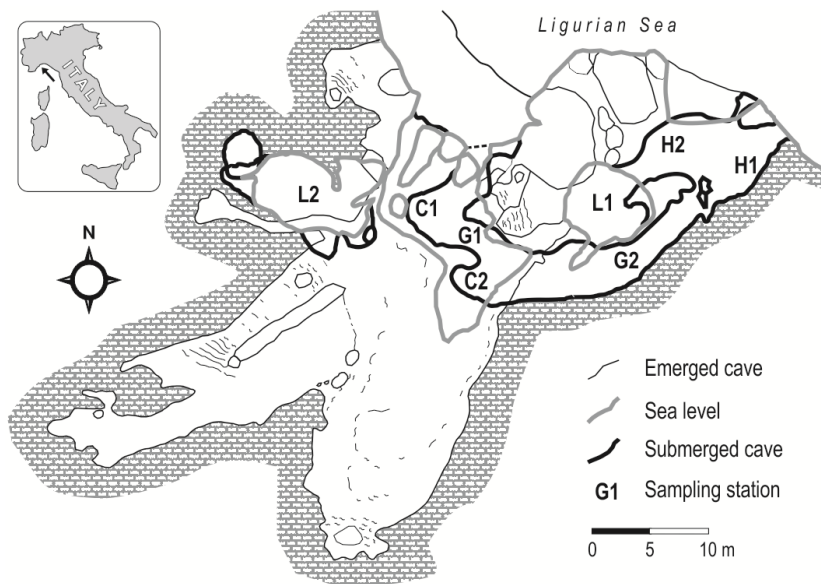
Descriptor	Year			
	1986	2004	2009	2013
<i>Growth forms</i>				
Indeterminate sheets	34.63	44.17	51.38	38.55
Bare substrate	27.13	23.07	11.43	7.50
Runners	19.35	15.73	16.19	16.37
Vines	11.12	7.18	1.64	0.49
Determinate sheets	4.73	7.49	14.56	18.60
Turf and sediment	1.06	1.05	1.93	11.05
<i>Trophic guilds</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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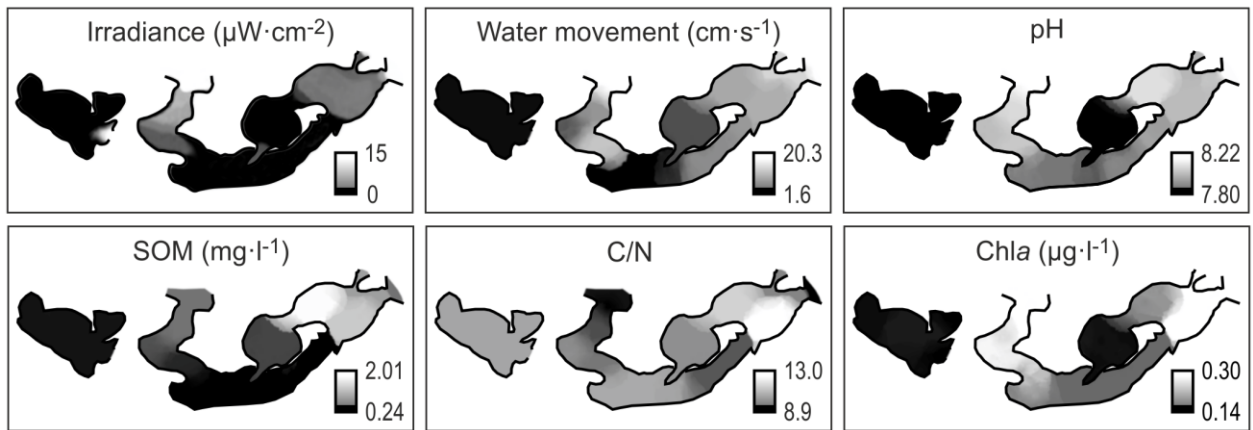
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891 Figure 1

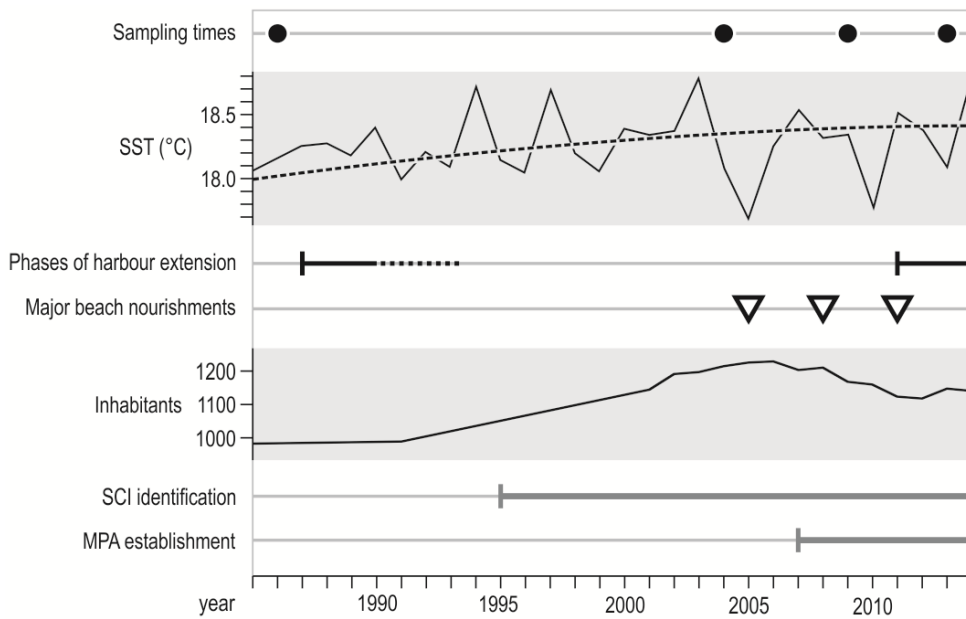
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894 Figure 2

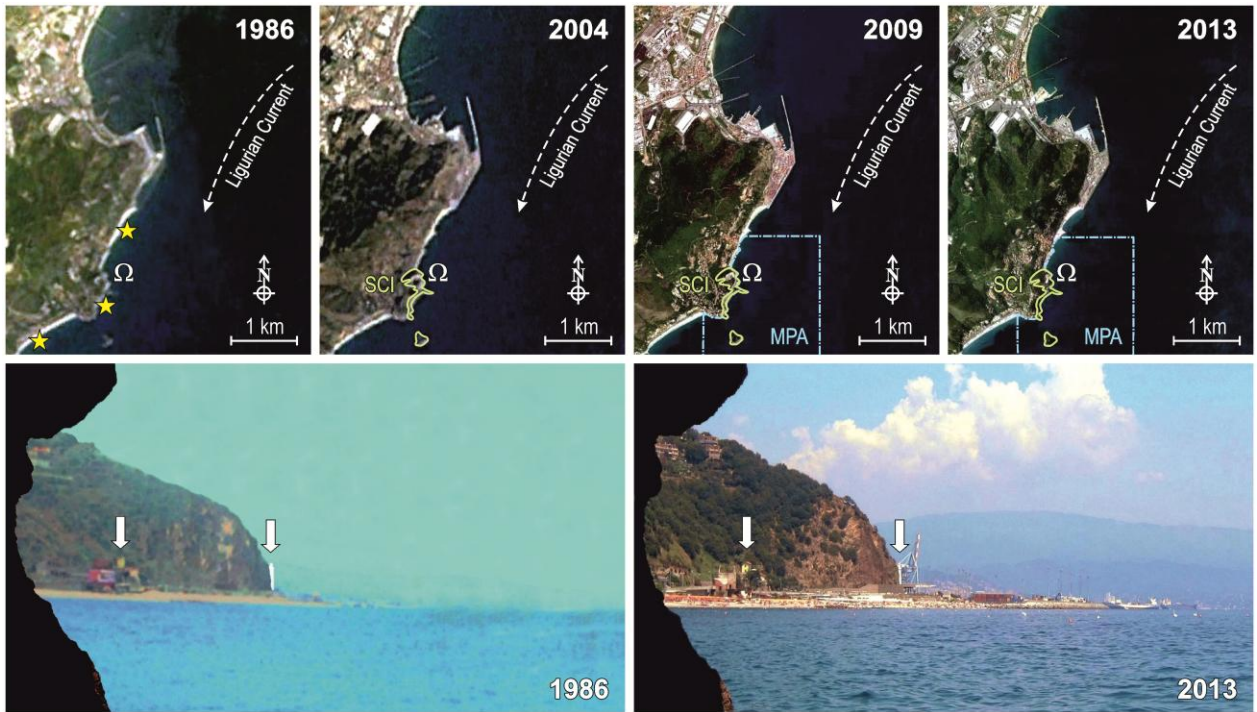
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897 Figure 3

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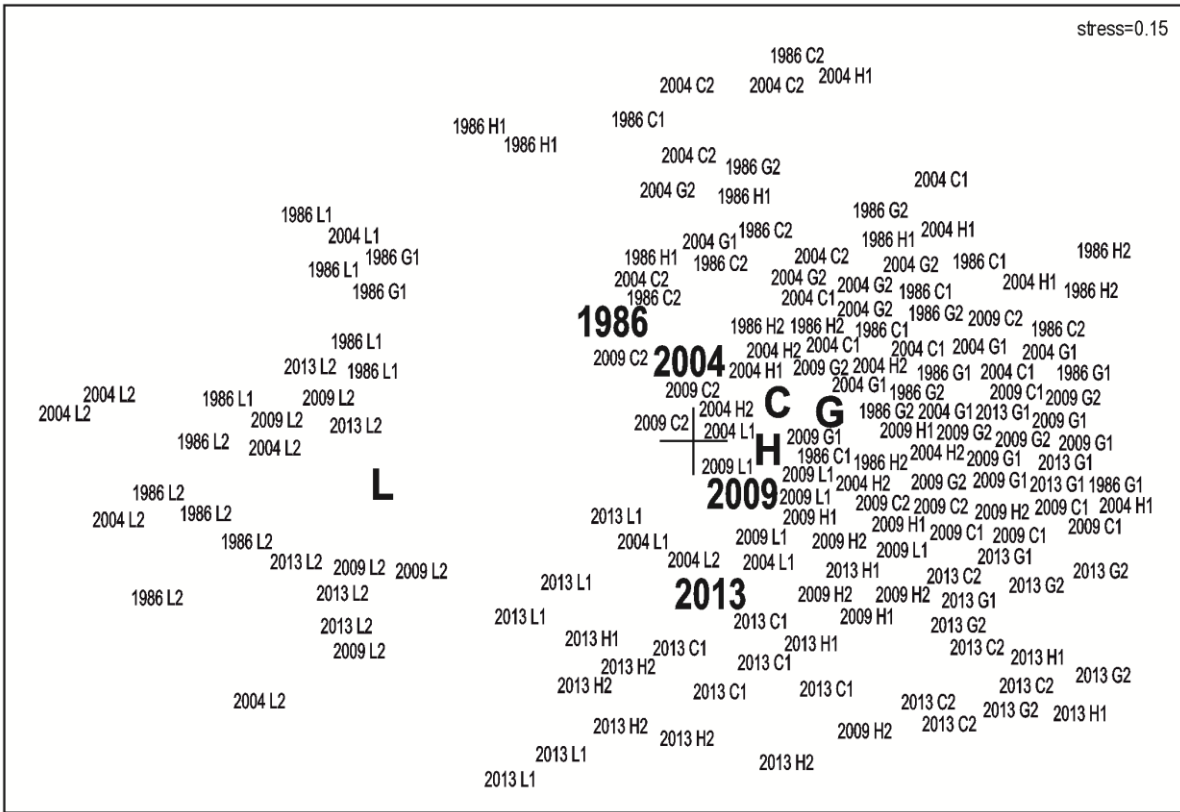


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Figure 4



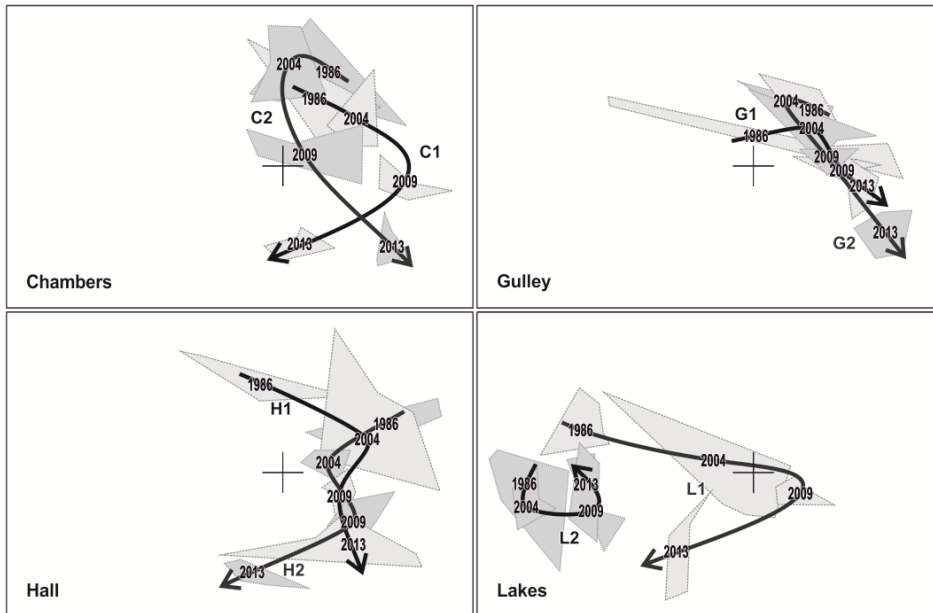
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903 Figure 5



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905 Figure 6

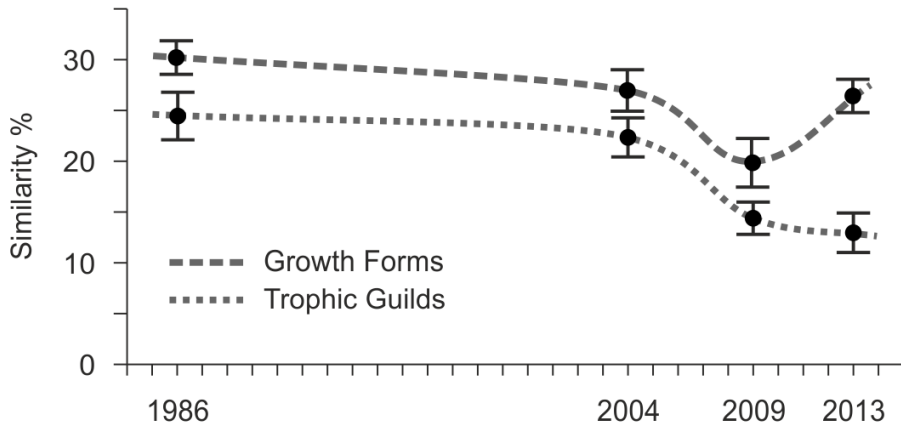
906



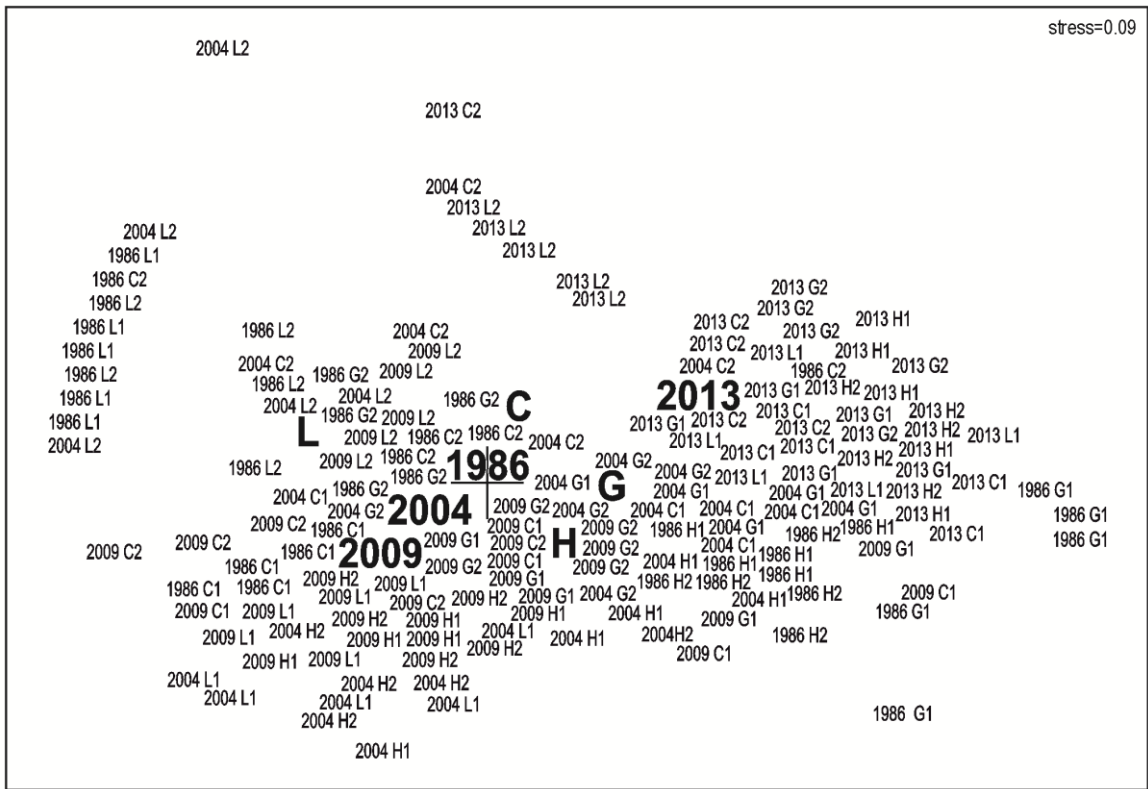
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908 Figure 7

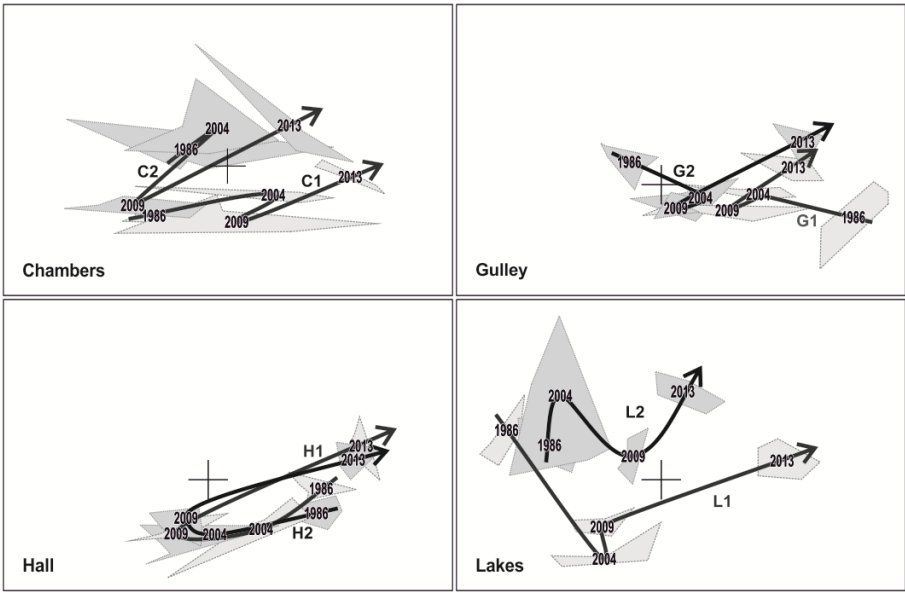
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 911 Figure 8
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 914 Figure 9



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916 Figure 10