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1 REPORT

2 **Polyp longevity in a precious gorgonian coral: hints toward**
3 **a demographic approach to polyp dynamics**

4 **Maria Carla Benedetti**¹ · **Lorenzo Bramanti**² · **Cristina Priori**¹ · **Fabrizio Erra**¹ ·
5 **Mimmo Iannelli**³ · **Fabio Bulleri**¹ · **Giovanni Santangelo**¹

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8 **Abstract** In this paper, we investigated the age distribu-
9 tion and dynamics of polyps in the slow-growing and long-
10 lived gorgonian *Corallium rubrum* (the Mediterranean red
11 coral), applying an a posteriori demographic approach by
12 considering each colony as a population of polyps. In the
13 Mediterranean red coral, new polyps emerge from the
14 coenenchyme in different regions of the colony and their
15 budding rate depends on the age of branches. The age of
16 polyps, branches and colonies were estimated using the
17 organic-matter-staining dating method on thin sections of
18 the colony skeleton. The median age and maximum life
19 span of polyps were 4 and 12 years suggesting the presence
20 of senescence processes: thus a colony renews several
21 times its polyps during life cycle. Polyps were divided into
22 annual age classes, and their mortality rates calculated. The
23 polyp age distribution was then used to construct a mor-
24 tality table and an algebraic transition matrix based on the
25 age at death of 234 polyps. Finally, the polyp budding rate
26 of a young, unbranched colony was calculated, and polyp
27 temporal dynamics simulated. These findings represent the

first steps for developing demographic models able to 28
describe polyp dynamics of old and highly branched 29
colonies. 30

Keywords Octocoral · Polyp age · Mortality table · 32
Budding rate 33

Introduction 34

Modularity is a common feature among plants and inver- 35
tebrates. Nowadays, the term modular is mainly used as 36
synonymous of hierarchical and refers to the repetition of 37
homogenous units at different organization levels (Rosen 38
1986; Kim and Lasker 1998; Hageman 2003). The first 39
definition of corals as modular organisms can be found in 40
Harper (1977). Polyps, embedded in the coenenchyme, are 41
the primary modules of colonial corals. They are the basic 42
units of a colony, likely determining its shape by regulating 43
the growth of branches (second-order modules, called 44
structural units, Hageman et al. 1998; Hageman 2003). 45
Therefore, the fundamental body plan of a colonial coral, 46
often characterized by different growth forms, results from 47
the repetition of units, *i.e.* polyps and branches of several 48
orders and varying lengths (Williams 1975; Harper 1977; 49
Harper and Bell 1979; Burlando et al. 1991; Lasker et al. 50
2003; Sánchez and Lasker 2003; Sánchez et al. 2004; 51
Goffredo and Lasker 2006). 52

Morphological plasticity, typical of modular organisms, 53
is likely the result of genotypic variability or phenotypic 54
response to local environmental conditions (*e.g.*, Shaish 55
et al. 2006, 2007; Sánchez et al. 2007; Rowley et al. 2015; 56
Guizien and Ghisalberti 2017). The optimal shape of a 57
stony-coral colony is the result of the polyp ability to 58
calcify (Matsumoto 2004; Goffredo and Lasker 2006) and 59

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A5 Maria Carla Benedetti
A6 carlottabenedetti88@hotmail.it

A7 ¹ Department of Biology, University of Pisa, CoNISMa, Via
A8 Volta 6, 56126 Pisa, Italy

A9 ² Sorbonne Université, CNRS, Laboratoire d'Ecogéochimie
A10 des Environnements Benthiques, LECOB,
A11 66650 Banyuls-sur-Mer, France

A12 ³ Department of Mathematics, University of Trento, Via
A13 Sommarive 14, 38123 Povo, TN, Italy

60 can thus be affected by polyp distribution and density
61 (Rossi et al. 2019). For example, ramified gorgonians have
62 evolved a prey capture structure by which barbed tentacles
63 of polyps and branches form an efficient fishing net inter-
64 cepting water flow thus feeding on detrital particulate
65 organic matter (POM) and microplankton (Barham and
66 Davies 1968; Grigg 1972; Russo 1985; Coma et al. 2001;
67 Kaandorp and Küler 2001; Tsounis et al. 2006b; Picciano
68 and Ferrier-Pagès 2007; Pedoni et al. 2009; Gori et al.
69 2011).

70 Merks et al. (2004) described coral growth as the
71 “collective result of a growth process taking place in the
72 polyps.” In their “polyp-oriented model,” polyps are
73 considered as separate units, which during their life cycle
74 deposit skeleton, bud new polyps and eventually die. Each
75 colony can then be considered as a population of polyps
76 and branches (belonging to the same genet; Harper 1977;
77 Galli et al. 2016); thus, its growth over time can be pro-
78 jected by dynamic models based on polyp growth and
79 mortality rates, as well as increase in branch number.
80 Under these circumstances, integrating data from individ-
81 ual and modular growth studies may enhance the under-
82 standing of growth in highly plastic corals. Precious corals
83 belonging to the Family Corallidae are generally slow-
84 growing and long-lived, thus, following their growth over
85 the entire life span is a nearly impossible task (Santangelo
86 et al. 2003) and indirect methods to assess colony devel-
87 opment in these species are needed (Marschal et al. 2004;
88 Vielzeuf et al. 2008; Benedetti et al. 2016; Kahra-
89 manoğullari et al. 2019).

90 We investigated polyp formation, age and spatial dis-
91 tribution in the highly valuable octocoral *Corallium*
92 *rubrum* (L 1758; Fig. 1), considering the iteration of the
93 primary modules (polyps) as the lowest level of colony
94 organization. *C. rubrum* is a long-lived Mediterranean
95 gorgonian, whose life span can exceed a century (Marschal
96 et al. 2004; Priori et al. 2013). This species is endemic to
97 the Mediterranean Sea and neighboring Atlantic rocky
98 bottoms, where it dwells between 10 and 1000 m depth.
99 Within this wide bathymetric distribution, shallow
100 (< 50 m), deep (50–200 m), and deeper populations
101 (> 200 m) have been conventionally distinguished by an
102 operative point of view (Santangelo and Abbiati 2001;
103 Costantini et al. 2011; Knittweis et al. 2016). *C. rubrum*
104 has long been subjected to commercial fishing, as its red
105 calcareous skeleton is widely used in jewelry and traded
106 worldwide (e.g., Cicogna and Cattaneo-Vietti 1993;
107 Tsounis et al. 2010). Due to its slow growth rates
108 ($\sim 0.24 \text{ mm y}^{-1}$ in basal diameter; Marschal et al. 2004;
109 Priori et al. 2013; Bramanti et al. 2014; Benedetti et al.
110 2016), the overharvesting of larger/older colonies has
111 caused an alarming shift in the structure of existing pop-
112 ulations toward smaller sizes (Santangelo and Abbiati

2001; Tsounis et al. 2006a; Bramanti et al. 2009; Cau et al. 113
2016; Garrabou et al. 2017). *C. rubrum* has therefore been 114
included in three different international conventions (EU 115
Directive Habitat, Bern Convention, and Convention on 116
Biological Diversity) and its harvesting is regulated by 117
Mediterranean, national and local/regional rules (GFCM- 118
FAO 2011). For species with long life span and complex 119
life cycle such as *C. rubrum* demographic studies are 120
required to advise policy makers on the most appropriate 121
conservation and management strategies (Santangelo et al. 122
2007; Bramanti et al. 2009). 123

124 A first step to assess population demographic dynamics
125 is estimating the age of its components (Bramanti et al. 125
2017). Age distribution data can be used for developing 126
life history tables and for projecting population trends 127
over time by means of algebraic transition matrices 128
(Caswell 2001; Fujiwara and Caswell 2001; Santangelo 129
et al. 2015). 130

131 In this paper, we scale this approach down from the
132 population to the colony level, considering a single col-
133 ony as a population of polyps. While several studies have
134 dealt with aging in octocorals (e.g., Sherwood 2006;
135 Thresher et al. 2009), little is known about the aging and
136 life span of polyps. We applied a novel method for
137 assessing the age of Mediterranean red coral polyps
138 (Vielzeuf et al. 2008) and their turnover to build a life
139 history table (mortality table). In order to estimate the
140 budding rate of polyps in a young colony and to project
141 its structure through time, a transition matrix of polyp
142 survival was constructed by means life history data. Thus,
143 our work focuses on: (1) early skeleton formation and
144 dynamics of polyp number, (2) distribution of polyp age
145 and density across the colony, (3) polyp life span, mor-
146 tality and variations in budding rate through time.

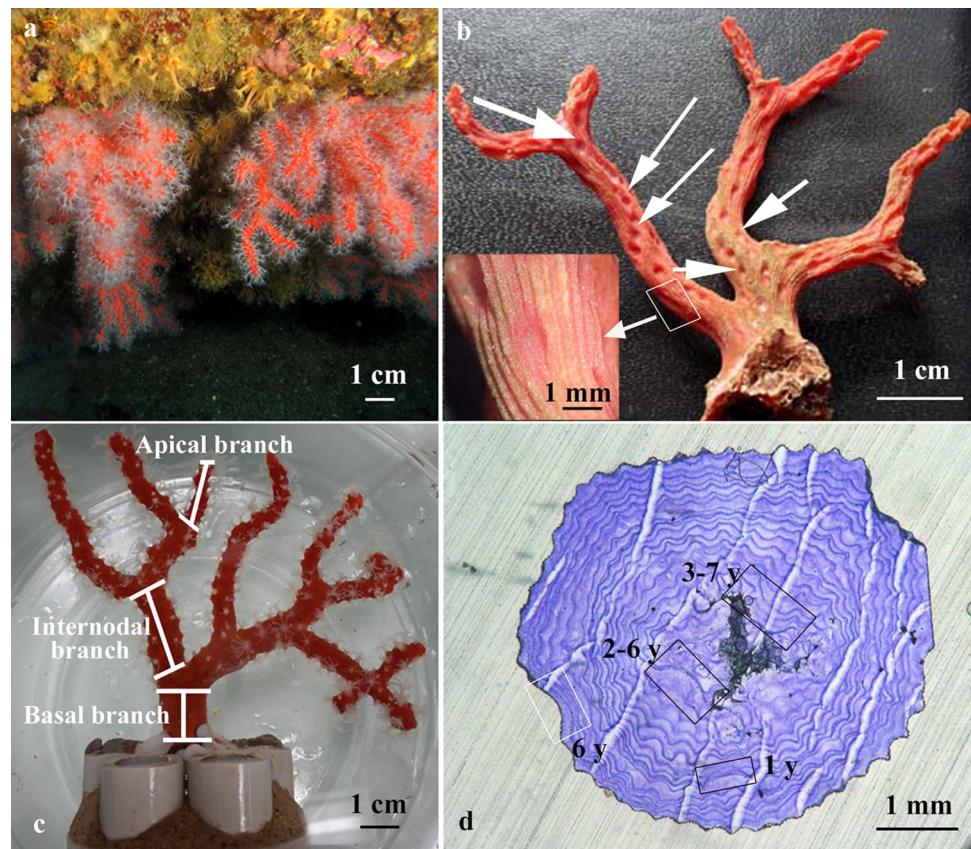
147 Materials and methods

148 *C. rubrum* basic features

149 The Mediterranean red coral is gonochoric at both the
150 polyp and colony levels and is characterized by a long life
151 span and an early age at first reproduction (Santangelo
152 et al. 2003; Gallmetzer et al. 2010). It is an internal brooder
153 whose larvae are released yearly in late summer and settle
154 within 20–25 days (L Bramanti personal observ.). After
155 settlement, metamorphosis occurs in approximately
156 10 days (L Bramanti pers. observ.) and a new colony starts
157 growing (Lacaze Duthiers 1864; Vighi 1972).

158 Similarly to other colonial octocorals, *C. rubrum* has
159 polyps embedded in the coenenchyme, and their gas-
160 trovascular cavities are interconnected by superficial and
161 deep gastrodermal channels (Lacaze Duthiers 1864). The

Fig. 1 **a** *Corallium rubrum* colonies in the Marine Protected Area of Cerbere/Banyuls sur Mer (L Bramanti photorecredits); **b** A colony depleted of coenechyme (arrows indicate polyp cavity marks) and a detail of crenulated colony axis with a polyp cavity mark without crenulations. **c** Three types of branches in a *C. rubrum* colony; **d** Thin OMS section of colony axis where annual growth rings are highlighted. Three dead (black rectangles) and one living polyp cavity mark (white rectangle) are shown



162 superficial channels are small and located within the coe-
 163 nenchyme layer, while the deep channels are larger and
 164 located in crenulations (wavelets) along the skele-
 165 ton surface. When the coenechyme and polyps are removed,
 166 a cavity mark can be distinguished, imprinted on the skele-
 167 ton just below the polyp (Fig. 1b; Lacaze Duthiers 1864; Grillo
 168 et al. 1993; Vielzeuf et al. 2008). The deep channels are
 169 absent on the surface of these cavity marks, hence no
 170 crenulations are found below the polyps (Fig. 1b; Perrin
 171 et al. 2015).

172 Skeleton formation and dynamics of polyp number

173 The early skeleton formation in 1–4-year-old colonies
 174 (settled on artificial substrates; see Bramanti
 175 et al. 2005, 2007) has been examined under a dissection
 176 microscope (40–60 x; Fig. 2).

177 The relationship between total number of polyps and
 178 branches was tested on 518 intact colonies of different size
 179 (out of 695 collected across the Northwestern Mediter-
 180 ranean between 2009 and 2016; Priori et al. 2013; Bra-
 181 manti et al. 2014; Benedetti et al. 2016; unfortunately no
 182 environmental data on sampling sites was at our disposal
 183 (sampling details in Supplemental Materials). All the
 184 colonies were photographed, numbered and fixed in 4%
 185 formalin for laboratory analysis. The total number of

186 polyps and the sex of each colony were determined under a
 187 binocular dissecting microscope (Santangelo et al. 2003).

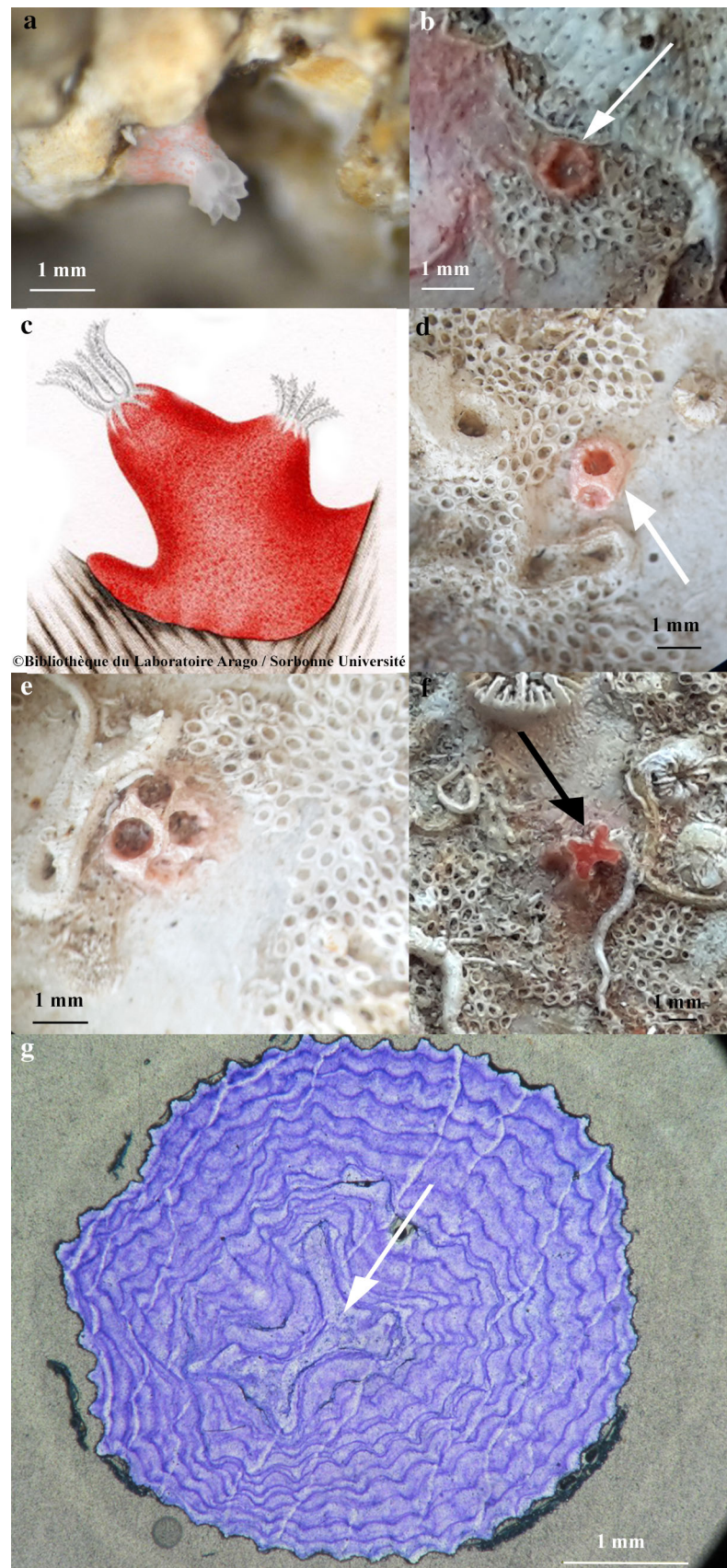
188 Three types of branches were identified in each colony:
 189 basal, internodal and apical. The basal branch corresponds
 190 to the base of the colony, the internodal branch is the first
 191 branch generated by the branching process (i.e., the largest/
 192 oldest branch of the colony; Benedetti et al. 2016) and the
 193 apical branch was chosen randomly among the tips
 194 (Fig. 1c).

195 The relationship between the number of apical branches
 196 and the number of polyps was assessed by means of linear,
 197 power, logarithmic and exponential fits and the one with
 198 the highest R^2 was selected. Significance was tested by
 199 Pearson's correlation coefficient on log/log transformed
 200 data.

201 Polyp age and distribution

202 The age of polyps was estimated by applying the procedure
 203 developed by Vielzeuf et al. (2008) based on the Organic
 204 Matrix Staining (OMS) method for colony dating (Mars-
 205 chal et al. 2004), which highlights annual growth rings on
 206 decalcified and stained thin sections (50 μ m), transversal to
 207 colony axis. Only 135 colonies (out of 695) were suit-
 208 able for this analysis (i.e., without signs of damage by
 209 boring sponges). Overall, 197 transverse thin sections cut

Fig. 2 Formation of *C. rubrum* skeleton starting from the walls of cavity marks: **a** Young colony at 1 polyp-stage (L Bramanti photocredits). **b** Skeleton of the colony at this stage. **c** Young colony at 2 polyp-stage. (after Lacaze Duthiers 1864). **d** Skeleton of the colony at this stage. **e** Skeleton of a young colony at 4 polyp-stage. **f** Skeleton of a 2–3-year-old colony: this “x profile” will form the central core in older colonies. **g** Thin section of an older colony axis: the central core is highlighted by the arrow



210 along the branches (135 basal sections and 62 internodal
211 and apical sections) were stained and examined to identify
212 the locations of polyps (i.e., cavity marks) and to estimate
213 their age. On thin sections, each annual growth ring is
214 made up of two seasonal bands (light and dark), with
215 crenulations in correspondence to the deep gastrodermal
216 channels (Fig. 1b, d). As these channels are absent on the
217 cavity mark surface, the lack of the crenulated layer along
218 growth rings indicates the presence of a polyp, and the
219 number of non-crenulated growth rings gives an estimate
220 of polyp age (Fig. 1d; Vielzeuf et al. 2008). A cavity mark
221 where the non-crenulated layer reaches the most external
222 growth ring (i.e., the most recent) indicates a polyp that
223 was still alive at the time of colony collection. When such a
224 marker was not present in the last growth ring (Fig. 1d), we
225 assumed that the polyp was already dead at the time of
226 collection (hereafter called “past polyp”). Polyps still alive
227 at the time of sampling were excluded from the calculation
228 of longevity and life span.

229 The mean number of living and past polyp marks were
230 divided according to the age of the colony at the level at
231 which the thin section was cut. The age of branches was
232 determined by applying the OMS method ($n = 162$).

233 As data were not normally distributed, a nonparametric
234 analysis (Mann–Whitney) was applied to test if polyp age
235 differs between females ($n = 82$) and males ($n = 93$), and
236 between shallow ($n = 168$) and deep ($n = 63$) populations.

237 The average width of polyp cavity marks (i.e., the linear
238 distance between the two edges of the depression), mea-
239 sured on the most evident cavities ($n = 114$), was used as a
240 proxy for polyp diameter. Polyp growth rates (mm y^{-1})
241 were then calculated as the ratio between cavity mark
242 width and polyp age.

243 The density of polyps was measured on 10 living
244 colonies maintained alive in aquaria at 17 ± 1 °C (sam-
245 pling details in Supplemental Materials). The number of
246 polyps on the three branch types (basal $n = 10$, internodal

247 $n = 10$ and apical $n = 10$) was counted under a dissecting
248 microscope. For accuracy, polyp counts were performed
249 twice, and the average value was used for the analysis.
250 The length (distance, in mm, between the branch base and
251 tip) and mean diameter (in mm, at the branch base and
252 tip) of each branch on the colony skeletons were mea-
253 sured with calipers and the branch surface (cm^2) was
254 calculated by approximating their shape to a truncated
255 cone. Polyp density ($\text{number} \times \text{cm}^{-2}$) was calculated by
256 dividing the polyp number by the area of each branch. In
257 order to account for autocorrelation of data within a
258 colony, polyp density in different branches of colonies
259 was analyzed using a linear mixed model, including the
260 branch types as a fixed effect and the colony as a random
261 effect (model < - lmer(Density ~ Branchtypes +(1|Col-
262 ony)), using the function ‘lmer’ in the R package ‘lme4’
263 (Bates et al. 2015). In order to assess the fit of the model,
264 we calculated the marginal and conditional R^2 , using the
265 function r.squared GLMM in the package MuMIn (Barton
266 2019). The marginal R^2 provides an estimate of the propor-
267 tion of total variance explained by the fixed factor alone,
268 while the conditional R^2 an estimate of that explained by both
269 the fixed and random factors (Nakagawa and Schielzeth
270 2013). We tested the effects of Branch Type in the linear
271 mixed model with a Type-III ANOVA (Table 1), using
272 Satterthwaite’s method (lmerTest package; Kuznetsova et al.
273 2017). The function ‘lsmeans’ in the R package ‘lsmeans’
274 (Lenth 2016) was used for post hoc comparisons among
275 Branch Type levels. Assumptions of linearity and homo-
276 geneity of variance were checked by means of Q–Q plots and
277 by plotting residuals versus fitted values.

278 Mortality table and budding rate

279 Based on the age of past polyps, a mortality table was
280 constructed (i.e., a life table based on the age of polyps at
281 death; Bergher 1990; Arrigoni et al. 2011; Table 2). In this

Table 1 (a) Type-III ANOVA of polyp density. (b) Post hoc comparisons among Branch Type levels

(a)						
	Sum Sq	Mean Sq	Num DF	Den DF	<i>F</i> value	Pr (> <i>F</i>)
Branch Type	325.91	162.96	2	18	10.344	0.001022
(b)						
Contrast	Estimate	SE	DF	<i>t</i> ratio	<i>p</i> value	
Apical-basal branches	8.06	1.78	18	4.541	0.0007	
Apical-internodal branches	4.43	1.78	18	2.494	0.0560	
Basal- internodal branches	− 3.63	1.78	18	− 2.047	0.1298	



282 table, polyps were divided into yearly age classes, and the
283 number of dead (X_i) and survivors (S_i) during each age
284 interval reported.

285 Mortality values were used to construct a survival
286 transition matrix (Table 3), in which the nonzero entries in
287 the lower diagonal are the probabilities (σ_i) of polyp sur-
288 vival from one age class (i) to the next ($i + 1$). The data
289 presented in Tables 2 and 3 were used to develop a model
290 describing the polyp budding rate in a young, unbranched
291 colony; as this rate is most likely similar to that of a new
292 branch, this parameter will hereafter be referred to as
293 “branch budding rate.” Then, the polyp number at the
294 colony base was projected over a period of 50 years. A
295 detailed description of the model and calculations of bud-
296 ding rate variability are reported in the Supplemental
297 Materials.

298 Results

299 Skeleton formation and dynamics of polyp number

300 The early formation of the skeleton was described on the
301 basis of the observation of polyp cavity marks in 1–4-year-
302 old colonies. A few weeks after larval settlement, the new
303 whitish polyp starts to deposit sclerites in the coenosarc,
304 forming the first cavity of the primary polyp (L Bramanti
305 personal observations; Fig. 2a, b). After two months, when
306 the young colony has two polyps (Fig. 2c), two adjacent
307 cavities are visible in the skeleton (Fig. 2d). Four cavities
308 from a quartet of adjacent polyps were evident in 1-year-
309 old colony skeletons (Fig. 2e). During the first 4 years,
310 only the skeleton between adjacent cavities grows and form
311 an “x-shaped profile” (from a vertical point of view,
312 Fig. 2f), which becomes the butterfly-like structure
313 observed in the transversal sections of the central skeletal
314 core of > 4 years old colonies (arrow in Fig. 2g).

315 In branched colonies, older than 10 years, there was no
316 relationship between colony age and polyp number. How-
317 ever, a significant, correlation described by a power func-
318 tion was found between the number of polyps in a colony
319 and the number of its apical branches ($y = 23.87x^{0.91}$,
320 $R^2 = 0.62$, $p < 0.01$, $n = 548$; Fig. 3). This suggests that
321 the total number of polyps is linked to the number of
322 branches rather than to colony age.

323 Polyp age and distribution

324 A total of 197 transversal sections of *C. rubrum* skeletons
325 were examined and 355 polyp cavity marks identified (234
326 of past polyps and 121 of polyps that were still alive at the
327 time of colony collection). Living polyps were more
328 abundant in sections cut from the younger branches of a

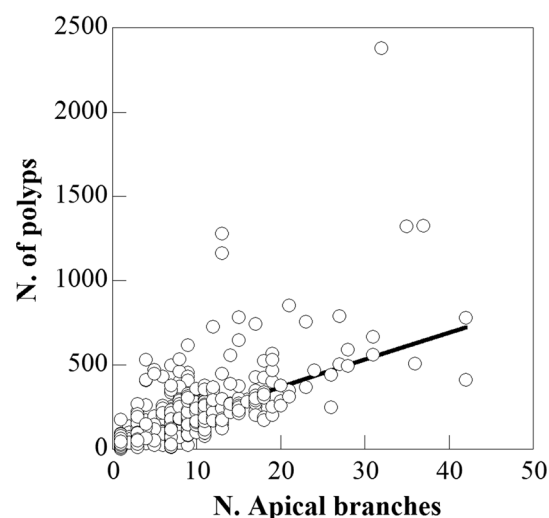


Fig. 3 Relationship between apical branch and polyp number: $y = 23.87x^{0.91}$, $R^2 = 0.62$, $p < 0.01$, $ES = 138$

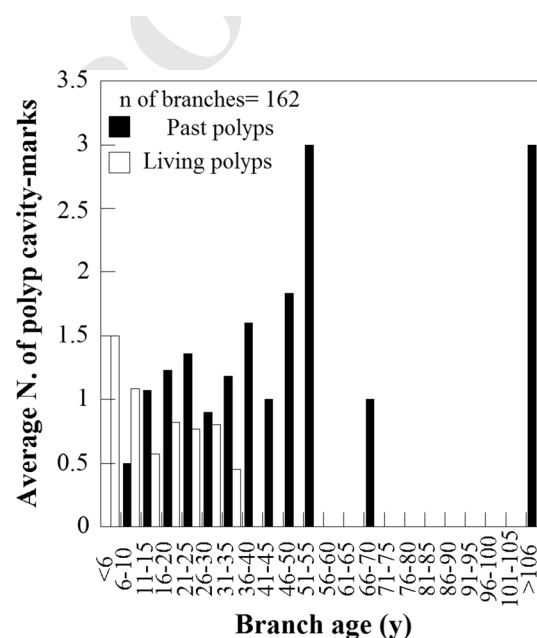


Fig. 4 Mean number of polyp cavity marks per colony branches of different age classes

colony (< 10 years), with their number decreasing with 329
branch age. Only past polyp markers were found on branch 330
sections older than 35 years (Fig. 4). 331

Despite the wide variability in polyp longevity, no polyp 332
(out of the 355 examined) was older than 12 years sug- 333
gesting that senescence is likely an important process in 334
regulating polyp dynamics within colonies. The median 335
age of past polyps and their maximum life span were 4 and 336
12 years, respectively ($n = 234$; Fig. 5). 337

As expected, living polyps were generally younger than 338
past ones, accounting for 45% of the < 1-year-old ones. 339

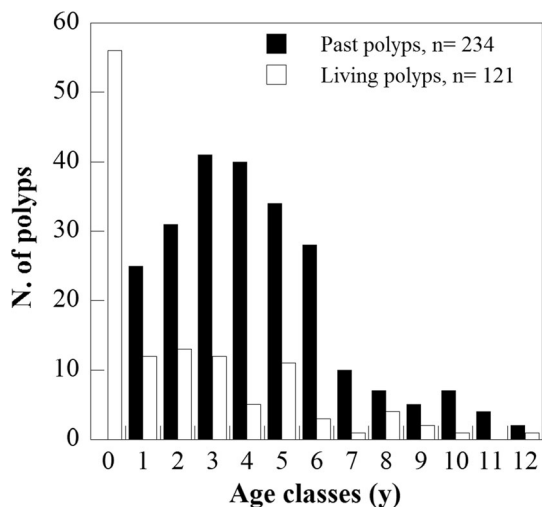


Fig. 5 Age distribution of living and past polyps

340 As < 1-year-old polyps do not form cavity marks in the
 341 growth ring layer, it is not possible to individuate these
 342 polyps on the thin sections, but they can be identified only
 343 if they were alive at the time of collection through the
 344 remains of their tissue.

345 There was no significant difference in longevity between
 346 polyps of female and male colonies (Mann–Whitney Test,
 347 $n = 82, n = 93, p > 0.05$) while polyps of deeper colonies
 348 were significantly older than those of shallow ones (5.5 vs.
 349 4 years, Median, Mann–Whitney Test: $n = 66, n = 168;$
 350 $p < 0.001$).

351 The median diameter of cavity marks was 1.0 mm (C.I.
 352 0.98–1.03 mm, $n = 114$), and it is reached within the first
 353 or the second year of polyp life.

354 The density of polyps varied significantly among dif-
 355 ferent branches (Table 1a and Fig. 6a). Post hoc tests
 356 indicated that polyp density at the apical branches
 357 (16.1 ± 1.7 polyps cm^{-2} , Mean \pm ES) was higher than at
 358 the basal branch (8.0 ± 1.2 polyps cm^{-2}). Likewise, there
 359 was a trend for polyp density on internodal branches to be

Fig. 6 a Polyp density in different branches of the colony. Bars = SE. **b** Polyp density versus age of basal, internodal and apical branches ($y = 28.3 - 11.7 \log(x), R^2 = 0.47, p < 0.05$)

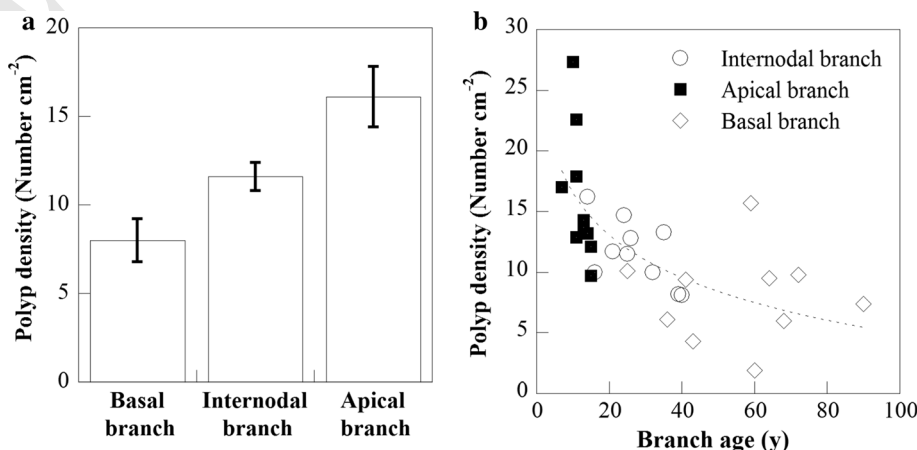


Table 2 Mortality table constructed from the age at death of 234 polyps

Polyp age classes (<i>i</i>)	X_i	S_i	l_i
1–2	25	234	1.00
2–3	31	209	0.89
3–4	41	178	0.76
4–5	40	137	0.59
5–6	34	97	0.41
6–7	28	63	0.27
7–8	10	35	0.15
8–9	7	25	0.11
9–10	5	18	0.08
10–11	7	13	0.06
11–12	4	6	0.03
12–13	2	2	0.01
13–14	0	0	0.00

X_i = number of polyps that died during each age interval; S_i = number of survivors at the beginning of each age interval; l_i = survival probability of class 1 polyps to age class (*i*) (number of survivors as a fraction of newborns)

360 higher than at the base of colonies, but differences were
 361 only marginally significant. There were no differences in
 362 polyp density between internodal and apical branches
 363 (Table 1b). The linear mixed model explained about 44%
 364 of the variation in the data (conditional $R^2 = 0.436$), of
 365 which around 40% was explained by the fixed factor (i.e.,
 366 Branch type; marginal $R^2 = 0.402$).

367 Polyp density decreased with the age of branches and
 368 higher values were found at some tips (Fig. 6b).

Mortality and Budding rate

369
 370 Mortality regularly increased with polyp age and 59% of
 371 polyps died before the age of 5 years (age classes 5–6). All

Table 3 Survival transition matrix of a *Corallium rubrum* polyp population. The diagonal represents the portion (σ_i) of polyps that raised by one class to the following each year

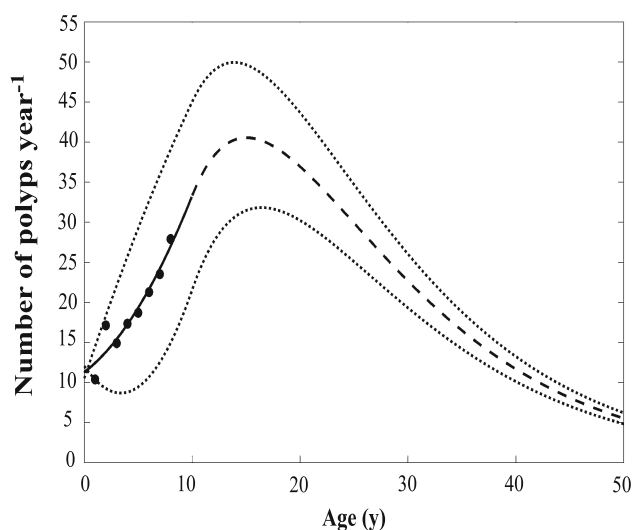
$$\begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0.89 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.85 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.77 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.71 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.65 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.56 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.71 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.72 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.72 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.46 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.33 & 0 \end{pmatrix}$$


Fig. 7 Branch budding rate over time. Continuous line: values of β_n (branch budding rate) for a young and unbranched colony of age ranging from 1 to 9 years (data from Bramanti et al. 2005 and Santangelo et al. 2007). Dashed line: estimated β_n from 10 to 50 years. The two dotted curves represent the variability of β_n

polyps of a new, annual cohort (age class) died within 12 years; thus the complete turnover of a colony could occur several times during its life cycle (e.g., a colony 100 years old could renew its polyps about 8 times).

A mortality table was constructed using the age at death of past polyps (Table 2). In this table, polyps were divided into 13 yearly age classes, and the yearly number of dead (X_i) and survivors (S_i) were reported. The polyp mortality table was, then, used to compile a survival transition matrix which describes the portion of polyps that, for each year, passed from one age class to the following (Table 3). The matrix was then applied to develop a dynamic population model which fits the polyp budding rate of a young, unramified colony (data from the literature in Supplemental

Materials) and projects this rate up to 50 years (during this time the young colony became the basis of an older, larger one; Fig. 7). According to the model, the yearly number of polyps increases (up to 40 polyps year⁻¹) with the age of branches and, after 15–16 years, it decreases reaching the lowest value (< 10 polyps years⁻¹) at 50 years. The model is based on average values and the variability around these values was calculated as reported in Supplemental Materials and represented by dotted lines in Fig. 7.

Discussion

Understanding the mechanisms underpinning the organization of polyps by an a posteriori demographic approach could shed some new light on the growth of long-lived, branched gorgonians. In *Corallium rubrum*, the colony shape may be described by a blend between the bifurcation model, in which “a single branch divides in two sisters branches” (Brazeau and Lasker 1992) and the mother–daughter branching model, in which “colonies branching subapically, generating hierarchical mother–daughter relationships among branches” (Lasker et al. 2003; Sánchez et al. 2004; among others). Simulations of the modular growth of *C. rubrum* colonies have been developed on the basis of simple stochastic rules and results suggested that the morphology can result two conflicting processes, branching and growth, priority of which is regulated by environmental factors (Kahramanoğullari et al. 2019).

In the Mediterranean red coral, the overall number of polyps is correlated with colony age during the first years of life (Bramanti et al. 2005), while in the older colonies, such as those examined here, this correlation is lost. In these larger colonies, the number of polyps is a function of the total number of apical branches that, despite the wide variability in their size, are characterized by higher polyp density. As the first ramification starts around 10 years (Benedetti et al. 2016), the lack of a correlation between polyp number and colony age in > 10 years old colonies is likely the result of a large variation in the branching process.

While the reproductive cycle of *C. rubrum* is well known (Vighi 1972; Santangelo et al. 2003), the mechanisms regulating the production of new polyps are still poorly understood. The highly variable colony morphology recorded in several octocorals, often considered as a consequence of large variability in hydro-mechanical forces (Patterson 1980; Chindapol et al. 2013; among others), could be driven by polyp density and distribution. Perrin et al. (2015) suggested that the direction of growth of new branches in *C. rubrum* could be influenced by the position of the polyp with respect to the tip: “...radially distributed polyps could favor a uni-directional vertical growth, while

436 polyps located at the very tip of the branch could favor the
437 emergence of a ramification.” Occasionally, some polyps
438 can drive the growth of further secondary branches starting
439 from the base or well below the colony tips, probably by
440 increasing the production of sclerites at their bases (Perrin
441 et al. 2015; Benedetti et al. 2016).

442 A first attempt to model the evolution over time of polyp
443 number in a *C. rubrum* colony was recently made by Galli
444 et al. (2016), who assumed that new polyps are produced
445 by the older ones via a budding process that depends on the
446 number of polyps at budding time. However, differently
447 from scleractinians (e.g., Richmond 1997; Gateño and
448 Rinkevich 2003) and some octocorals (Lan da Silveira and
449 Van't Hof 1977), no budding in already existing polyps has
450 ever been documented in *C. rubrum*. The only description
451 of new polyp formation in colonies of this species dates
452 back to about 150 years ago, when the French naturalist,
453 Henry Lacaze Duthiers, described the “blastogenesis of a
454 polyp” as a “small whitish tumor” appearing on a point on
455 the colony surface (Lacaze Duthiers 1864). The lack of
456 polyp budding in the Mediterranean red coral has been
457 further confirmed by other researchers (S Rossi and G
458 Tsounis, pers. comm.). In conclusion the formation of new
459 polyps likely occurs on some points of the gastrodermal
460 channels embedded in the coenenchyma, following
461 modalities that are still unknown.

462 An analysis of the polyp distribution along colony
463 branches of different ages may provide a proxy for the
464 local budding rate of polyps. We found a significantly
465 higher density of polyps at the tips that together with its
466 decrease with increasing age suggests a higher rate of
467 production of new polyps in the younger parts of the col-
468 ony. Such observation is supported by the faster growth
469 rates in young colonies (Bramanti et al. 2005; 2007) and at
470 the tips (Benedetti et al. 2016; Lartaud et al. 2016). The
471 higher polyp density found at some tips, indicating faster
472 growth in some branches, could lead to directional and
473 asymmetrical colony growth.

474 At the base of branched colonies, polyp density and
475 diameter growth rates are lower and vertical growth stops
476 (Bramanti et al. 2014; Benedetti et al. 2016). The small
477 number of polyps found in this portion of the colony could
478 be explained by the limited plankton supply due to the
479 reduced current and the trophic shadow cast by higher rank
480 branches (Kim and Lasker 1997). We should then expect
481 that the sparse polyps found at the colony base may either
482 change their tentacles in response to a lower food supply
483 (Abel 1970; Lopez-Gonzalez et al. 2018) or shift from a
484 trophic to a cleaning/sweeping function.

485 Little is known about the life cycle of coral polyps. The
486 literature data are highly variable, spanning between the
487 observation made by Beklemishev (1969) who described
488 the polyps of colonial anthozoans as “short-lived,” and the

489 reports of Wood-Jones (1907) who believed that coral
490 polyps were theoretically immortal. In a more recent study
491 on scleractinian polyps, Darke and Barnes (1993) estimated
492 a mean polyp life expectancy of 5 years and a maximum
493 life span of 8 years. Moreover, they found a significant
494 difference in polyp longevity between colonies collected
495 on reefs characterized by different “bumpiness” (*i.e.*,
496 lenticular growth surface; Darke and Barnes 1993). To
497 date, measures of polyp life span in gorgonian corals are
498 rare. In the Mediterranean red coral, Vielzeuf et al. (2008)
499 report that “...a polyp appears, fulfills its functions, and
500 then disappears after 6–8 years of activity.” Using the
501 method described in the foregoing, we determined the age
502 distribution of polyps in *C. rubrum* colonies collected from
503 different geographic areas and depths. According to our
504 results, *C. rubrum* polyps reach their maximum size in the
505 first two years of life and have an average life span of
506 4 years, with no difference between females and males,
507 suggesting that the different time needed for female and
508 male gonad maturation (two and one year respectively;
509 Vighi 1972) does not influence polyp life span. Fifty-nine
510 percent of new polyps died before 5 years and their max-
511 imum life span was 12 years. A 100-year-old colony
512 should then pass through approximately 8 generations of
513 polyps: such polyp renewal could be a key factor in the
514 longevity of this species. In all colonies collected in the
515 different sampling areas, no polyp lived more than
516 12 years, polyp density decreased with branch age and
517 mortality increased with polyp age: these findings clearly
518 suggest the relevance of polyp senescence in determining
519 colony growth and longevity. However, this does not
520 exclude local, partial mortality due to predation (Priori
521 et al. 2015).

522 Our data indicate a significantly greater polyp age in
523 colonies collected in deeper (50–130 m depth) than shall-
524 ower areas (30–35 m depth). This difference is likely due
525 to the higher mean colony age found in deeper populations
526 (Tsounis et al. 2006a; Priori et al. 2013; Bramanti et al.
527 2014; Benedetti et al. 2016). As observed in several marine
528 modular organisms (Sánchez et al. 2004 and references
529 herein), the polyp budding rate in *C. rubrum* decreases with
530 branch age. Given that colony growth rate and polyp pro-
531 duction are higher during the first years of colony life
532 (Bramanti et al. 2005, 2014), it was expected that polyp
533 production would be faster in younger and less branched
534 colonies with respect to older ones.

535 Using the mortality table of polyps, a transition matrix
536 and a dynamic population model were set out to represent
537 the branch budding rate of polyps over a life span of
538 50 years. In a young, unbranched colony, the branch bud-
539 ding rate increases up to 15 years of life, to decrease in the
540 following period, when the formerly young colony
541 becomes the basis of an older, branched one. Such bell-

542 shaped trend is consistent with the reduction of polyp
543 density observed in the older parts of a colony, likely due
544 to senescence.

545 The demographic model proposed in this paper
546 describes the modular growth of young, unbranched *C.*
547 *rubrum* colonies. Our findings represent a first step toward
548 the development of advanced polyp dynamic models aimed
549 at representing the complex growth of older, ramified
550 colonies, in which also the second factor of modularity (*i.e.*
551 the branching process) and the variability of the growth
552 process, should be included.

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