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Coral Reefs
https://doi.org/10.1007/s00338-020-01942-6

REPORT

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

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Received: 12 December 2018 / Accepted: 24 April 2020

Abstract In this paper, we investigated the age distribution and dynamics of polyps in the slow-growing and long-lived gorgonian *Corallium rubrum* (the Mediterranean red coral), applying an a posteriori demographic approach by considering each colony as a population of polyps. In the Mediterranean red coral, new polyps emerge from the coenenchyme in different regions of the colony and their budding rate depends on the age of branches. The age of polyps, branches and colonies were estimated using the organic-matter-staining dating method on thin sections of the colony skeleton. The median age and maximum life span of polyps were 4 and 12 years suggesting the presence of senescence processes: thus a colony renews several times its polyps during life cycle. Polyps were divided into annual age classes, and their mortality rates calculated. The polyp age distribution was then used to construct a mortality table and an algebraic transition matrix based on the age at death of 234 polyps. Finally, the polyp budding rate of a young, unbranched colony was calculated, and polyp temporal dynamics simulated. These findings represent the first steps for developing demographic models able to describe polyp dynamics of old and highly branched colonies.

Keywords Octocoral · Polyp age · Mortality table · Budding rate

Topic Editor Andrew Hoey

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00338-020-01942-6) contains supplementary material, which is available to authorized users.

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Introduction

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

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

Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | LE | TYPESET
MS Code : CORE-D-18-00305R3 | CP | DISK

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

Merks et al. (2004) described coral growth as the "collective result of a growth process taking place in the polyps." In their "polyp-oriented model," polyps are considered as separate units, which during their life cycle deposit skeleton, bud new polyps and eventually die. Each colony can then be considered as a population of polyps and branches (belonging to the same genet; Harper 1977; Galli et al. 2016); thus, its growth over time can be projected by dynamic models based on polyp growth and mortality rates, as well as increase in branch number. Under these circumstances, integrating data from individual and modular growth studies may enhance the understanding of growth in highly plastic corals. Precious corals belonging to the Family Corallidae are generally slow-growing and long-lived, thus, following their growth over the entire life span is a nearly impossible task (Santangelo et al. 2003) and indirect methods to assess colony development in these species are needed (Marschal et al. 2004; Vielzeuf et al. 2008; Benedetti et al. 2016; Kahramanoğullari et al. 2019).

We investigated polyp formation, age and spatial distribution in the highly valuable octocoral *Corallium rubrum* (L 1758; Fig. 1), considering the iteration of the primary modules (polyps) as the lowest level of colony organization. *C. rubrum* is a long-lived Mediterranean gorgonian, whose life span can exceed a century (Marschal et al. 2004; Priori et al. 2013). This species is endemic to the Mediterranean Sea and neighboring Atlantic rocky bottoms, where it dwells between 10 and 1000 m depth. Within this wide bathymetric distribution, shallow (< 50 m), deep (50–200 m), and deeper populations (> 200 m) have been conventionally distinguished by an operative point of view (Santangelo and Abbiati 2001; Costantini et al. 2011; Knittweis et al. 2016). *C. rubrum* has long been subjected to commercial fishing, as its red calcareous skeleton is widely used in jewelry and traded worldwide (*e.g.,* Cicogna and Cattaneo-Vietti 1993; Tsounis et al. 2010). Due to its slow growth rates (~ 0.24 mm y^{-1} in basal diameter; Marschal et al. 2004; Priori et al. 2013; Bramanti et al. 2014; Benedetti et al. 2016), the overharvesting of larger/older colonies has caused an alarming shift in the structure of existing populations toward smaller sizes (Santangelo and Abbiati 2001; Tsounis et al. 2006a; Bramanti et al. 2009; Cau et al. 2016; Garrabou et al. 2017). *C. rubrum* has therefore been included in three different international conventions (EU Directive Habitat, Bern Convention, and Convention on Biological Diversity) and its harvesting is regulated by Mediterranean, national and local/regional rules (GFCM-FAO 2011). For species with long life span and complex life cycle such as *C. rubrum* demographic studies are required to advise policy makers on the most appropriate conservation and management strategies (Santangelo et al. 2007; Bramanti et al. 2009).

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

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

Materials and methods

C. rubrum basic features

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

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

Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | LE | TYPESET
MS Code : CORE-D-18-00305R3 | CP | DISK

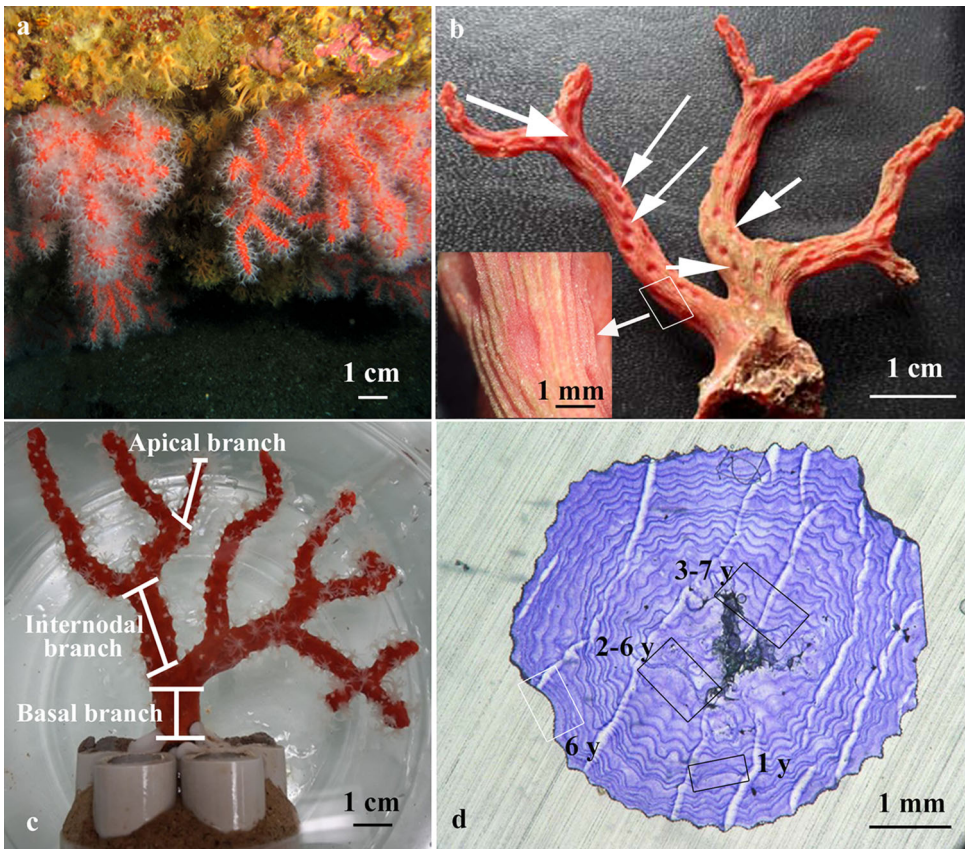

Fig. 1 **a** *Corallium rubrum* colonies in the Marine Protected Area of Cerbere/Banyuls sur Mer (L Bramanti photocredits); **b** A colony depleted of coenechyme (arrows indicate polyp cavity marks) and a detail of crenulated colony axis with a polyp cavity mark without crenulations. **c** Three types 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

superficial channels are small and located within the coenenchyme layer, while the deep channels are larger and located in crenulations (wavelets) along the skeleton surface. When the coenenchyme and polyps are removed, a cavity mark can be distinguished, imprinted on the skeleton just below the polyp (Fig. 1b; Lacaze Duthiers 1864; Grillo et al. 1993; Vielzeuf et al. 2008). The deep channels are absent on the surface of these cavity marks, hence no crenulations are found below the polyps (Fig. 1b; Perrin et al. 2015).

Skeleton formation and dynamics of polyp number

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

The relationship between total number of polyps and branches was tested on 518 intact colonies of different size (out of 695 collected across the Northwestern Mediterranean between 2009 and 2016; Priori et al. 2013; Bramanti et al. 2014; Benedetti et al. 2016; unfortunately no environmental data on sampling sites was at our disposal (sampling details in Supplemental Materials). All the colonies were photographed, numbered and fixed in 4% formalin for laboratory analysis. The total number of polyps and the sex of each colony were determined under a binocular dissecting microscope (Santangelo et al. 2003).

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

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

Polyp age and distribution

The age of polyps was estimated by applying the procedure developed by Vielzeuf et al. (2008) based on the Organic Matrix Staining (OMS) method for colony dating (Marschal et al. 2004), which highlights annual growth rings on decalcified and stained thin sections (50 µm), transversal to colony axis. Only 135 colonies (out of 695) were suitable for this analysis (i.e., without signs of damage by boring sponges). Overall, 197 transverse thin sections cut

Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | LE | TYPESET
MS Code : CORE-D-18-00305R3 | CP | DISK

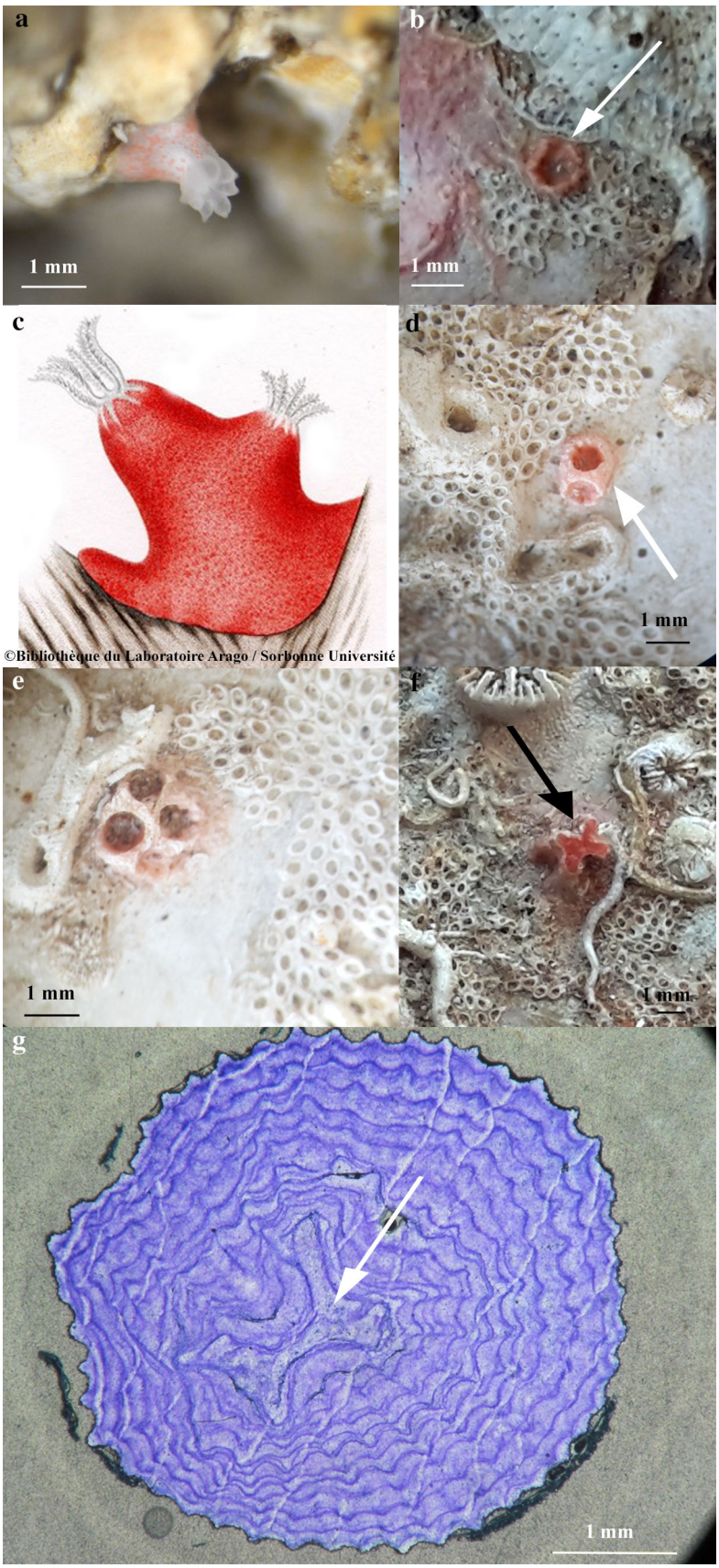

Fig. 2 Formation of *C. rubrum* skeleton starting from the walls of cavity marks: **a** Young colony at 1 polyp-stage (L Bramanti photocredits). **b** Skeleton of the colony at this stage. **c** Young colony at 2 polyp-stage. (after Lacaze Duthiers 1864). **d** Skeleton of the colony at this stage. **e** 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

Journal : Large 338 Dispatch : 18-5-2020 Pages : 12
Article No. : 1942 ☐ LE ☐ TYPESET
MS Code : CORE-D-18-00305R3 ✔ CP ✔ DISK

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

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

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

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

The density of polyps was measured on 10 living colonies maintained alive in aquaria at 17 ± 1 °C (sampling details in Supplemental Materials). The number of polyps on the three branch types (basal n = 10, internodal n = 10 and apical n = 10) was counted under a dissecting microscope. For accuracy, polyp counts were performed twice, and the average value was used for the analysis. The length (distance, in mm, between the branch base and tip) and mean diameter (in mm, at the branch base and tip) of each branch on the colony skeletons were measured with calipers and the branch surface (cm^2) was calculated by approximating their shape to a truncated cone. Polyp density (number × cm^{-2}) was calculated by dividing the polyp number by the area of each branch. In order to account for autocorrelation of data within a colony, polyp density in different branches of colonies was analyzed using a linear mixed model, including the branch types as a fixed effect and the colony as a random effect (model < - lmer(Density ~ Branchtypes +(1|Colony)), using the function 'lmer' in the R package 'lme4′ (Bates et al. 2015). In order to assess the fit of the model, we calculated the marginal and conditional R^2, using the function r.squared GLMM in the package MuMIn (Barton 2019). The marginal R^2 provides an estimate of the proportion of total variance explained by the fixed factor alone, while the conditional R^2 an estimate of that explained by both the fixed and random factors (Nakagawa and Schielzeth 2013). We tested the effects of Branch Type in the linear mixed model with a Type-III ANOVA (Table 1), using Satterthwaite's method (lmerTest package; Kuznetsova et al. 2017). The function 'lsmeans' in the R package 'lsmeans' (Lenth 2016) was used for post hoc comparisons among Branch Type levels. Assumptions of linearity and homogeneity of variance were checked by means of Q–Q plots and by plotting residuals versus fitted values.

Mortality table and budding rate

Based on the age of past polyps, a mortality table was constructed (i.e., a life table based on the age of polyps at 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	F value	Pr (> F)
Branch Type	325.91	162.96	2	18	10.344	0.001022

(b)

Contrast	Estimate	SE	DF	t ratio	p 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

Journal : Large 338 Dispatch : 18-5-2020 Pages : 12
Article No. : 1942 LE TYPESET
MS Code : CORE-D-18-00305R3 CP DISK

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

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

Results

Skeleton formation and dynamics of polyp number

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

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

Polyp age and distribution

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

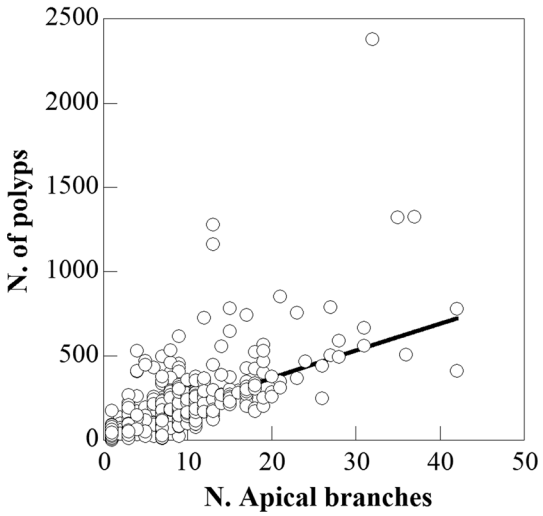

Fig. 3 Relationship between apical branch and polyp number: $y = 23.87x^{0.91}$, $R^2 = 0.62$, $p < 0.01$, ES = 138

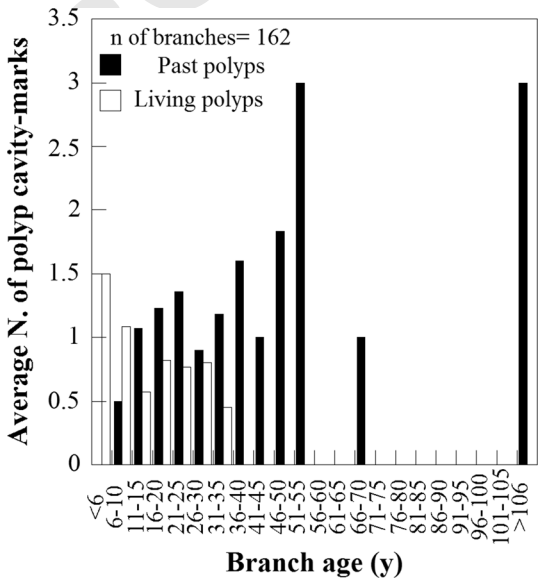

Fig. 4 Mean number of polyp cavity marks per colony branches of different age classes

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

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

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

Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | LE | TYPESET
MS Code : CORE-D-18-00305R3 | CP | DISK

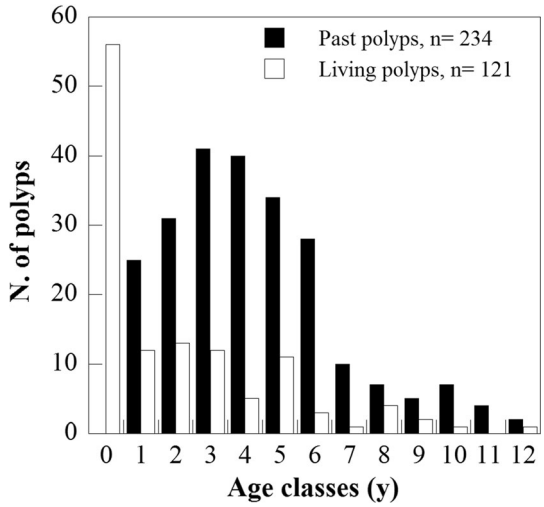

Fig. 5 Age distribution of living and past polyps

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

Polyp age classes (*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)

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

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

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

The density of polyps varied significantly among different branches (Table 1a and Fig. 6a). Post hoc tests indicated that polyp density at the apical branches (16.1 ± 1.7 polyps cm^{-2}, Mean ± ES) was higher than at the basal branch (8.0 ± 1.2 polyps cm^{-2}). Likewise, there was a trend for polyp density on internodal branches to be higher than at the base of colonies, but differences were only marginally significant. There were no differences in polyp density between internodal and apical branches (Table 1b). The linear mixed model explained about 44% of the variation in the data (conditional R^2= 0.436), of which around 40% was explained by the fixed factor (i.e., Branch type; marginal R^2= 0.402).

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

Mortality and Budding rate

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

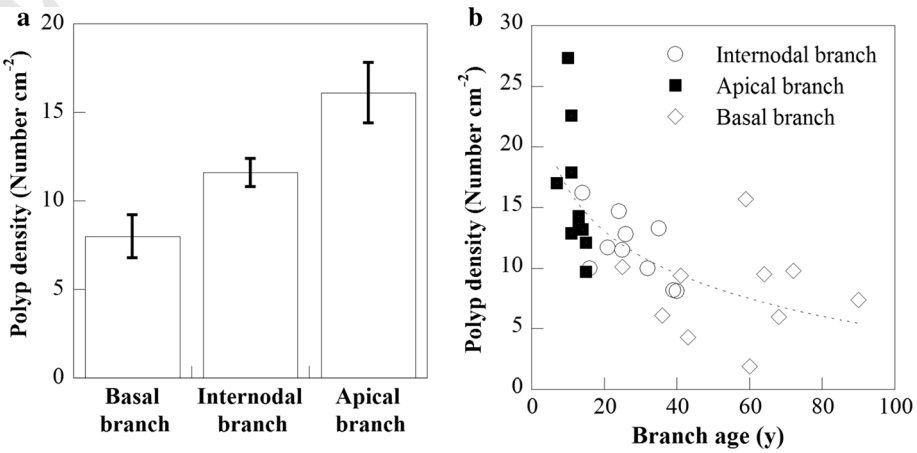

Fig. 6 **a** Polyp density in different branches of the colony. Bars = SE. **b** Polyp density versus age of basal, internodal and apical branches ($y = 28.3\text{-}11.7\log(x)$, $R^2 = 0.47$, $p < 0.05$)

Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | LE | TYPESET
MS Code : CORE-D-18-00305R3 | CP | DISK

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

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

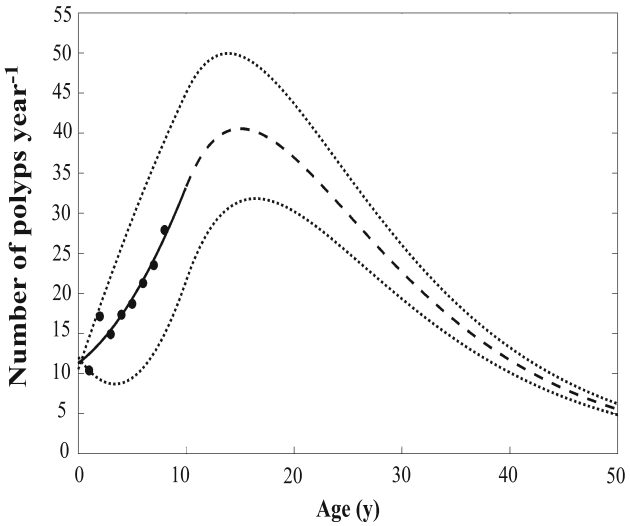

Fig. 7 Branch budding rate over time. Continuous line: values of β_n (branch budding rate) for a young and unbranched colony of age ranging from 1 to 9 years (data from Bramanti et al. 2005 and Santangelo et al. 2007). Dashed line: estimated β_n from 10 to 50 years. The two dotted curves represent the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

Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | LE | TYPESET
MS Code : CORE-D-18-00305R3 | CP | DISK

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

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

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

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

Little is known about the life cycle of coral polyps. The literature data are highly variable, spanning between the observation made by Beklemishev (1969) who described the polyps of colonial anthozoans as "short-lived," and the reports of Wood-Jones (1907) who believed that coral polyps were theoretically immortal. In a more recent study on scleractinian polyps, Darke and Barnes (1993) estimated a mean polyp life expectancy of 5 years and a maximum life span of 8 years. Moreover, they found a significant difference in polyp longevity between colonies collected on reefs characterized by different "bumpiness" (*i.e.,* lenticular growth surface; Darke and Barnes 1993). To date, measures of polyp life span in gorgonian corals are rare. In the Mediterranean red coral, Vielzeuf et al. (2008) report that "…a polyp appears, fulfills its functions, and then disappears after 6–8 years of activity." Using the method described in the foregoing, we determined the age distribution of polyps in *C. rubrum* colonies collected from different geographic areas and depths. According to our results, *C. rubrum* polyps reach their maximum size in the first two years of life and have an average life span of 4 years, with no difference between females and males, suggesting that the different time needed for female and male gonad maturation (two and one year respectively; Vighi 1972) does not influence polyp life span. Fifty-nine percent of new polyps died before 5 years and their maximum life span was 12 years. A 100-year-old colony should then pass through approximately 8 generations of polyps: such polyp renewal could be a key factor in the longevity of this species. In all colonies collected in the different sampling areas, no polyp lived more than 12 years, polyp density decreased with branch age and mortality increased with polyp age: these findings clearly suggest the relevance of polyp senescence in determining colony growth and longevity. However, this does not exclude local, partial mortality due to predation (Priori et al. 2015).

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

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

Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | LE | TYPESET
MS Code : CORE-D-18-00305R3 | CP | DISK

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

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

Acknowledgements We would like to thank A. Malasoma and A. Bernardeschi (TS Lab & Geoservices snc of Pisa) for their help in preparing the red coral thin sections. We also wish to thank G. Galli (Plymouth Marine Laboratory and Istituto Nazionale di Oceanografia e Geofisica Sperimentale, Trieste) for his intriguing questions on polyp life cycle, D. Vielzeuf (CINaM - Centre Interdisciplinaire de Nanoscience de Marseille) for his useful suggestions on the manuscript, and A. Cafazzo for his revision of the English text. This work is part of the PhD Thesis of M.C. Benedetti, which has been funded by Enzo Liverino s.r.l., Chii Lih Coral Co Ltd of Taiwan and the University of Pisa.

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Article No. : 1942 | ☐ LE | ☐ TYPESET
MS Code : CORE-D-18-00305R3 | ☑ CP | ☑ DISK

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Journal : Large 338 | Dispatch : 18-5-2020 | Pages : 12
Article No. : 1942 | ☐ LE | ☐ TYPESET
MS Code : CORE-D-18-00305R3 | ☑ CP | ☑ DISK

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Journal : **Large 338** | Dispatch : **18-5-2020** | Pages : **12**
Article No. : **1942** | ☐ LE | ☐ TYPESET
MS Code : **CORE-D-18-00305R3** | ☑ CP | ☑ DISK