Understanding corallite demography to comprehend potential bias in sclerochronology: Analysis of coral modular growth by micro-computed tomography

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Abstract

The discovery of alternating growth bands in the skeletons of massive corals led to the possibility of using them as environmental indicators. However, skeleton formation is the result of the growth of thousands of polyps depositing millimeter-sized CaCO3 structures, called corallites. Nevertheless, the orientation of the corallite trajectories and their position with respect to the colony could be altering the information obtained from the skeleton. In this sense, to obtain reliable information from coral skeletons, it is necessary to understand how polyp population growth influences coral growth rates. For this reason, we present a study that combines computed tomography image segmentation, optical densitometry, and demographic equations to follow the trajectory of corallites in order to model coral growth from the replication of its corallites and understand the responses in terms of their growth. We observed that both corallite replication and skeletal growth characteristics vary significantly according to the position they occupy within the colony. The central zone of the colony promotes corallite replication, and it is in this zone that we measured the highest values of extension and calcification. These variations in vegetative and skeletal growth are possibly in accordance with the variability of available resources and environmental stimuli in different zones of the skeleton. This approach will allow us to explore future lines of research associated with the size limits of different coral species and to observe how different drivers modulate polyp budding.

There are two structural arrangement types in organisms, unitary and modular (Tuomi and Vuorisalo 1989). In the former, shape, development, growth, and longevity are predictable and genetically defined (Harper 1985), whereas in the latter, organisms result from the sum of iterative units called modules, which are specialized, organized in hierarchical levels, and are genetically identical (Harper 1985). The main difference between unitary and modular organisms lies in the shape and longevity of the organism (Tuomi and Vuorisalo 1989). In the unitary organism, the individual and its age can be clearly perceived, while in the second these elements are elusive (Harper 1985). In general, a modular organism has the same population dynamics as a unitary organism, in addition, each module has their demographic characteristics (i.e., born, growth and dies) (De Kroon et al. 2005). During the development of a modular organism, there is a differential distribution of resources among the modules as well as within the whole colony (Kim and Lasker 1998; De Kroon et al. 2005), therefore the analysis of the resource distribution among modules and their implications for the development...
and growth of the organism is key to understanding its life history. Scleractinian corals are modular organisms that are made up of structural units called polyps (Rosen 1986; Darke and Barnes 1993). The colonial structure is derived from the subsequent division of a founding polyp resulting from asexual reproduction (budding) (Darke and Barnes 1993; Li et al. 2020). Each polyp deposits millimeter thin structures of calcium carbonate (CaCO₃) as part of its growth, which together make up the coral skeleton (Dávalos-Dehulú et al. 2008). In corals, two processes have the potential to increase the size of the colony: the increase of the skeleton, as well as the radial growth of living tissue (Anthony et al. 2002). The first is due to the continuous increases in the calcareous structure, known as calcification (Carricart-Ganivet and Merino 2001), while the second is related to increased tissue due to polyp budding (Darke and Barnes 1993; Anthony et al. 2002). The two types of growth are promoted by the replication rate of the polyps and their ability to deposit CaCO₃ (Darke and Barnes 1993; Merks et al. 2004; Li et al. 2020).

Coral life history includes the birth, growth, replication, and death of its polyps (Benedetti et al. 2020; Li et al. 2020). The increase in polyp numbers is related to the availability of resources, which results in age and size growth of the coral (Kim and Lasker 1998; Anthony et al. 2002; Goffredo and Lasker 2006), while polyp deaths may result from disease, competition, and environmental changes (Jackson and Hughes 1985; Preston and Ackerly 2004; Estrada-Saldívar et al. 2020). In addition, as the coral grows, high-density (HD) and low-density (LD) bands are formed as part of the skeleton (Knutson et al. 1972). This banding pattern makes it possible to retrospectively analyze coral skeleton growth using three variables that contain complementary information (i.e., sclerochronological characteristics): (1) skeletal extension rate (cm yr⁻¹), (2) skeletal density (g CaCO₃ cm⁻³), and (3) calcification rate (g CaCO₃ cm² yr⁻¹) (Dodge and Brass 1984; Carricart-Ganivet et al. 2000). Despite the lack of conclusive evidence to explain the relationship between increased tissue by addition of new polyps and the accretion of the colony by CaCO₃ deposition, it is known that both processes are strongly regulated by environmental factors (Anthony et al. 2002; Kaandorp et al. 2005; Galli et al. 2016). Physical and biological drivers modify the polyp replication rate, altering tissue growth and, ultimately, the shape and CaCO₃ contribution of the replication units (Anthony et al. 2005; Kaandorp et al. 2005; Jokiel 2011). Therefore, through the modeling of the replication and death of coral modules, we can gain an understanding of how corals respond to different disturbances (Merks et al. 2004; Kaandorp et al. 2005; Cresswell et al. 2020).

Growth and polyp development in corals have been studied using different approaches. Barnes (1973) observed that the final shape of massive and branching coral colonies is determined by the rate and pattern of polyp replication. The apical polyps of Acropora palmata have a calcification rate 4–8 times higher than the rest of the colony (Fang et al. 1989). Whereas, the sexual and asexual reproductive activity of polyps varies according to their location in the colony (Sakai 1998; Kai and Sakai 2008) and is poorly related with colony size (Gateño and Rinkevich 2003). Recently, Kim and Lasker (1998), Galli et al. (2016) and Benedetti et al. (2020) addressed how polyps compete for resources within the same colony as the polyp population increases using modular population dynamics of octocorals. Their results revealed that the module replication rate and density are related to the number of polyps, number of branches, and age of the colony.

Despite its relevance and implications, modular demography studies have been rarely conducted in stony corals, mainly due to the inability to track the replication of polyps and their association with the age of the colony, since both processes occur within the skeleton (Lartaud et al. 2016). Darke and Barnes (1993) used X-rays to track corallite paths in massive Porites spp. slabs and determined that the average age of a polyp is between 3 and 5 yr, reaching a maximum of 8 yr and that new polyps are born at the top of the Porites mounds. Although these observations provide useful information, the two-dimensional (2D) representation of a three-dimensional (3D) process has the potential to alter the interpretations derived from the replication process due to the potential overlap in the trajectories of the polyps and because only a small portion of the colony is analyzed.

Recently, computed tomography (CT) has been used as a tool to analyze coral skeletons under different approaches, from analyzing coral growth and budding patterns (Li et al. 2020, 2021), to measuring changes in skeletal extension and density (Logan and Anderson 1991; Bosscher 1993), quantifying bioerosion rates (DeCarlo et al. 2015; Fordyce et al. 2020), addressing coral morphology (Kruszynski et al. 2006, 2007; Naumann et al. 2009) and evaluating the relationship between density bands and climate change (Cantin et al. 2010; Manzello et al. 2015a,b). Due to the potential of this technique to understand how corals incorporate environmental and climatic information into their calcareous skeleton (Knutson et al. 1972), the aim of the present contribution is to determine the main demographic patterns of polyps and their potential effect on skeletal formation. Specifically, using CT, the trajectories of all polyps were followed individually to record their life history (budding rate, age, trajectory length, and mortality rate). Then, using modular demographic equations, coral growth models were constructed to understand the responses to different perturbations in terms of their growth, shape, and CaCO₃ contribution. We use this approach on two colonies of the reef-building coral Orbicella annularis. From this information, a series of interrelated questions were posed: Are the demographic patterns of polyps related to the spatial position they occupy in the colony? Are differences in demographic patterns a result of environmental information perceived by the polyps? What effect
do the differential demographic patterns of polyps have on the sclerochronological characteristics of coral colonies? We hypothesized that the sclerochronological characteristics and the demographic fate of the in O. annularis colonies vary depending on the availability and type of resources that each polyp can capture and according to the spatial position they occupy within the colony, as well as the density of polyps present in the colony over time.

**Materials and methods**

**Fieldwork**

We selected O. annularis as a study model because it is a species with a Caribbean-wide distribution (Weil and Knowton 1994). The colonies of O. annularis present a massive growth form, constituted by multiple individual ramets of lobate-columnar shape, with living tissue in the superficial part and senescent zones in the lower sections. Ramets sampling allows, on the one hand, to obtain a representative fragment of an adult colony. On the other hand, it does not interfere with the corallite’s trajectory because they are separate columns. Two ramets were collected: one from an O. annularis colony (12Y) at Anthony’s Key Reef, Roatán, Honduras (16°19’36”N, 86°34’19”W), and the other (6Y) from La Bocana Reef, Puerto Morelos, Quintana Roo, Mexico (20°87’97”N, 86°84’97”W). The colonies at both sites were located at a depth of ~5 m and the ramets were obtained from the apical zone of the colony to minimize the possible influences associated with availability of light and shading from other ramets (Supporting Information Fig. S1). In Roatán, the colony measured 12 cm (diameter) by 13 cm (height), whereas in Puerto Morelos, the colony measured 6 cm (diameter) by 8 cm (height). Organic matter was removed from the colony using a 10% sodium hypochlorite solution, and the skeletons were rinsed with running water, and dried in an oven at 60°C for 12 h. Since each ramet represents the colony’s growth, from this section on, the ramets collected in Roatán and Puerto Morelos will be named colony 12Y and colony 6Y, respectively.

**X-ray CT**

To trace polyp trajectories and analyze the coral skeletal growth bands, both colonies were scanned by X-ray CT, using a GE Medical Systems Optima 540. During the exposure, each image was 0.5 mm thick and was reconstructed in 1.0 mm increments using the “Bone” algorithm.

To explore variation associated with image resolution, the colonies were scanned using a Nikon Metrology XTH H 225ST industrial scanner (Supporting Information Fig. S2). The images were obtained at 200 kV and 350 uA. Each image was 0.049 mm thick and reconstructed in Volume Graphics Studio software (VG StudioMax V.3.2). The images were exported in DICOM format.

**Modular growth parameters**

Corallite trajectories from the beginning (emergence) to end (death/apex of the skeleton) of both colonies, were identified, delimited, and followed using Dristhi paint software (V. 2.6.5) (Fig. 1). To avoid errors in the estimation of the growth parameters resulting from segmentation, verifications were carried out in the coronal, sagittal, and transverse planes (Supporting Information Fig. S3), to ensure that the segmentation coincided with the path of each corallite (Fig. 1B). A 3D model of the trajectory of each corallite was obtained to follow the growth routes of each polyp (Fig. 1C1), the number of times each corallite replicated (i.e., gave rise to a new polyp) (Fig. 1C2), and the length of its trajectory (Fig. 1C3).

3D models of the corallite trajectories were superimposed on the 3D reconstructions of the skeletons that contained alternating HD and LD bands (Fig. 1C4,C5). From the above, the time at which each corallite emerged, replicated, and stopped its trajectory was obtained. The number of bands that were crossed by each corallite path was utilized to estimate mean polyp longevity.

Finally, the number of budding polyps and polyp mortality were compared between the central (from the colony center to 50% of the radius) and lateral zones (50% of the radius to the edge) of the colony (Fig. 1A), to determine if there were areas that promoted or marginalized the replication and death of the polyps (Darke and Barnes 1993). The difference between the central and lateral zones of the colony was evaluated using a Student’s t-test, when the data showed normality and using a Mann–Whitney test when data failed to meet the assumption of normality or homoscedasticity.

**Population dynamics**

Polyp budding and mortality recorded during the monitoring of all corallite trajectories were used to model the growth of a coral colony (Merks et al. 2004; Benedetti et al. 2020) according to the equation proposed by Harper and White (1974). The equation considers each polyp (module), as an individual that is part of a population and the coral colony as a population of polyps (Noble et al. 1979; Kim and Lasker 1998; De Kroon et al. 2005).

\[ P_n^t = P_v + P_s - P_m, \]  

where \( P_n^t \) is the number of polyps that make up the population, \( P_v \) is the number of living polyps, \( P_s \) is the number of new polyps (budding), and \( P_m \) is the number of dead polyps.

The equation generates a model based on intracolonial demographic processes (budding and death of polyps), which allows calculation of the number of polyps that make up the
colony at any time (Noble et al. 1979). Based on the above, logistic models (Pearl and Reed 1920) were performed to obtain the size of the polyp population as a function of the number of polyps at time \( t \) and the age of the colony (Harper and White 1974; Noble et al. 1979). The logistic model was employed since it explained the highest percentage of variation.

\[
\frac{dN}{dt} = r_{\text{max}} \left( K - N/K \right) N, \tag{2}
\]

where \( N \) is the size of the polyp population, \( t \) is the time, \( r_{\text{max}} \) is the polyp replication rate, and \( K \) is the carrying capacity of the colony.

**Sclerochronological characteristics**

Extension rate, density, and calcification values were obtained at different angles (90°, 65°, 45°, 25°) and positions (sagittal, coronal, and axial) of the 12Y colony (Supporting Information Figs. S4, S5). To improve resolution of the density bands, each 2D image was compiled with its adjacent images to create a composite image (Cantin et al. 2010; DeCarlo et al. 2015). Subsequently, the average density of each block of the standard was measured in HU units, to draw a calibration curve, from which the density of the coral (g cm\(^{-3}\)) was derived. The extension rate (cm yr\(^{-1}\)) was estimated as the linear distance between two consecutive LD bands. The mean annual density (g CaCO\(_3\) cm\(^{-3}\)) is defined as the average of X-ray attenuation data between the LD and the HD bands. Finally, the annual calcification rate (g CaCO\(_3\) cm\(^{-2}\) yr\(^{-1}\)) was calculated as the product of the mean annual density and the annual extension rate of each pair of bands (Lough and Barnes 2000; Carricart-Ganivet and Barnes 2007).

To evaluate differences in the extension rates between HD and LD bands and their relationship with polyp replication, season growth rates were obtained (Medellín-Maldonado et al. 2016). The seasonal extension was calculated as the linear distance occupied by each HD or LD band separately. Finally, linear models were generated from the sclerochronological characteristics and the intracolonial growth angles to determine if there is a relationship between these two parameters.

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**Fig. 1.** Segmentation process of polyp routes. (A, Left) Slice (2D image of 0.049 mm thickness of the axial plane) showing the space occupied by individual corallites within the skeleton. The purple zone corresponds to the central zone of the colony, and the white zone to the lateral zone. (A, Right) 3D reconstruction of the segmented trajectories of three founder polyps. (B) 3D visualization of the 12Y colony with some trajectories overlaying the founder polyps (blue fibers). It can be seen how the trajectories coincide with the spaces occupied by the corallites in the axial and coronal planes. (C) Workflow to obtain the length and individual age of polyps: (C1) 3D visualization of the trajectory of a polyp (yellow fiber) and the number of times it replicated (blue fibers); (C2) the distance between the different buds was marked with different colors (green, pink, blue, and yellow points); (C3, C4) the trajectories of the new polyps were traced and measured (the change of color from blue to pink fiber indicates the trajectory being measured); (C5) sprouting marks are superimposed on a virtual slab to determine the year of sprouting, the years of birth of new sprouts, and the year and area where the polyp stopped its trajectory. (D) Sequence of adjacent slices of the axial plane shows a budding process. (E) 3D visualization of all segmented trajectories overlaying in reconstructing the 6Y colony. Each color indicates the order of appearance during colony growth (blue fibers are the first trajectory to appear, orange fibers last trajectories to appear).
Subsequently, by means of a one-way fixed-effects ANOVA, differences in sclerochronological characteristics between the angles and positions of the ramet were identified.

**Results**

**Modular growth parameters**

According to the image analysis, the 12Y colony initiate by 36 founder polyps (i.e., polyps responsible for forming the ramet should not be confused with the primary polyp accountable for settling and creating the colony). The founder polyps, as a result of budding during 12 yr of growth, gave rise to 2006 new polyps for a total of 2042 trajectories (Supporting Information Tables S1, S2). In the 6Y colony, 85 founder polyps were identified, which added 573 new polyps during the 6 yr of growth, giving rise to a total of 658 trajectories (Supporting Information Tables S3, S4). Trajectory tracking is possible using both conventional CT and micro-CT. Micro-CT offers higher resolution, but was only possible for analyzing the 6Y colony, as the 12Y colony size and volume were too large for a micro-CT scan. The accuracy of trajectory tracking is the same for both conventional and micro-CT scans.

Colonies showed significant differences in polyp budding between the HD and LD bands (12Y: Student’s t = 5.19, p < 0.001; 6Y: Student’s t = 4.34, p = 0.007) (Table 1). The HD bands recorded higher polyp replication (12Y = 147.5 ± 25.7; 6Y = 69.33 ± 8.23), compared to the LD bands (12Y = 21.45 ± 4.8; 6Y = 26.33 ± 4.60). Concurrently, the LD bands registered a higher number of polyp deaths (12Y = 31.18 ± 17.68; 6Y = 9.83 ± 5.77), compared to the polyp deaths registered in the HD bands (12Y = 23.16 ± 19.2; 6Y = 5.33 ± 3.52); however, this difference was only significant in colony 12Y (12Y: W = 55; p = 0.005; 6Y: W = 4.5, p = 0.41).

Regarding growth differences, budding predominantly occurs in the central zone of the colonies (12Y = 1537; 6Y = 350 replications) compared to the lateral zones (12Y = 469; 6Y = 223 replications; Supporting Information Tables S5, S6). However, differences were only significant for colony 12Y (12Y: Student’s t = 3.47, p = 0.002; 6Y: Student’s t = 1.65, p = 0.12) (Fig. 2A). On the other hand, the lateral zones registered higher polyp mortality (12Y = 536; 6Y = 82 deaths) compared to the central zone (12Y = 85 deaths, 6Y = 9 deaths); this difference was only observed in the 12Y

| Logistic growth | K   | tm  | r_{max} | df  | AIC  | r^2  | p         |
|-----------------|-----|-----|---------|-----|------|------|-----------|
| Colony 12Y      | 1648| 2007| 0.58    | 13  | 160  | 0.941| <0.001    |
| Colony 6Y       | 1127| 2016| 0.33    | 7   | 55   | 0.976| <0.001    |

K, carrying capacity; tm, time to the inflection point (change from exponential growth to logistic growth); r_{max}, per capita growth rate; N, initial polyps in each colony; df, degree freedom, AIC, Akaike information criterion; r^2, coefficient of determination; p, significance level.

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**Fig. 2.** Modular growth in central and lateral zones of the colony. (A) Number of budding polyps between zones. (B) Number of dead polyps between zones. In all boxplots the lines inside the boxes represent the median and the black dots indicate the outliers.
colony (12Y: \( U = 36, p = 0.03; 6Y: U = 12, p = 0.32 \)) (Fig. 2B). Differences in polyp budding and deaths between the central and lateral zones of the 12Y colony were observable up to eight and 7 yr, respectively.

According to image analysis, the average age of the polyps in colony 12Y was 5.31 ± 0.13 yr; the maximum age was 12 yr (same age as the colony); only one polyp spent most of its life occupying the central zone of the colony. Meanwhile, the average age of the polyps in colony 6Y was 2.02 ± 0.04; the maximum age recorded was 5 yr.

**Corallite population size**

An exponential increase in polyp number was observed in the 12Y colony (\( r = 63.13e^{0.286x}, n = 13, r^2 = 0.908 \)) (Fig. 3B), yet the trend only lasted during the 1st 6–7 yr of growth (2000–2007); during the later yr (2008–2010), exponential growth stopped, and the number of polyps present in the colony actually decreased (2011). The 6Y colony showed exponential modular population growth (\( r = 80.05e^{0.29x}, n = 7, r^2 = 0.95 \)) and maintained exponential growth throughout its entire development, unlike the 12Y colony.

Under the assumption that no population can grow exponentially indefinitely, in addition to the decrease in population growth observed in the 12Y colony, the data were adjusted using logistic growth models and projections of the population increase were made for the next 5 yr of growth in each colony (Fig. 3A; Table 1). The models had higher and significant coefficients of determination for both colonies (12Y: \( K = 1647.72, N = 30.39, r_{max} = 0.58, r^2 = 0.94, \text{AICc} = 160, p < 0.001; 6Y: K = 1647.78, N = 108.95, r_{max} = 0.33, r^2 = 0.98, \text{AICc} = 55, p < 0.001 \)). The 12Y colony registered a higher modular growth rate (\( r_{max} = 0.585 \)) than that registered for the 6Y colony (\( r_{max} = 0.334 \)). Coincidentally, the projections of the logistic models showed that the maximum modular population is 1648 polyps for both colonies.

**Sclerochronological characteristics**

The extension rate (cm yr\(^{-1}\)), mean annual density (g CaCO\(_3\) cm\(^{-3}\)), and annual calcification rate (g CaCO\(_3\) cm\(^{-2}\) yr\(^{-1}\)), which were obtained at each level of inclination of the 12Y ramet, are shown in Fig. 4. Skeleton density showed an opposite trend with higher densities (1.54 ± 0.01 g/cm\(^{3}\)) in the central zone and lower densities (1.31 ± 0.02 g/cm\(^{3}\)) in the lateral zone.
CaCO₃ cm⁻³) at higher levels of inclination (i.e., 25°) than at lower levels of inclination (90°: 1.43 ± 0.01 g CaCO₃ cm⁻³) (Fig. 4A,B). The extension rate decreased as inclination increased (Fig. 4C,D). At a 90° angle, the maximum extension rate reached was 0.87 ± 0.08 cm yr⁻¹, while the minimum extension rate (0.39 ± 0.01 cm yr⁻¹) was recorded at an angle of 25°. The maximum calcification rate was recorded at 90° (1.25 ± 0.11 g CaCO₃ cm⁻² yr⁻¹), and the minimum at 25° (0.60 ± 0.08 g CaCO₃ cm⁻² yr⁻¹), mimicking the trend displayed by the extension rate (Fig. 4E,F).

The ANOVAs showed that there were significant differences in extension rate depending on the angle (F₁₅,₂₆= 10.64, df = 21.84, p < 0.001). In general, there were differences in extension rates between 90° and 45° (p < 0.001), as well as between 25°, 65° (p < 0.001), and 90° (p < 0.001). Density also varied as a function of the angle of inclination (F₁₁,₈₇ = 17.59, df = 3, p = 0.0001). The a posteriori test revealed differences in density between 90° with respect to 45° (p = 0.001) and 25° (p < 0.001), as well as between 65°, 45° (p = 0.03), and 25° (p = 0.004) angles. Calcification rates showed the same trend (F₁₆,₉₃ = 13.47, df = 3, p < 0.001), with differences between 90° with respect to 45° (p < 0.001) and 25° (p < 0.001), as well as between 65°, 45° (p = 0.03), and 25° (p < 0.001).

The extension rates of the HD and the LD bands showed significant differences in both ramets (12Y: Student’s t-test, p < 0.001). The extension rates of the HD and the LD bands showed significant differences in both ramets (12Y: Student’s t-test, p < 0.001).

Fig. 4. Coral growth parameters as a function of the angle of inclination. Mean annual (A) density, (C) extension, and (E) calcification, measured at different growth angles (25°, 45°, 65°, and 90°). The profiles for each growth parameter for the different angles are the mean of five transects measured in different sections of the colony in the sagittal and coronal planes (see Supporting Information Figs. 54, 55). The bold lines within the profiles show the average of the five transects for each angle, while the shaded areas are the SE. Linear trends of (B) density (y = −0.0017x + 1.5842, n = 7, r² = 0.99), (D) extension (y = −0.0077x + 0.1818, n = 7, r² = 0.97) and (F) calcification (y = −0.0105x + 0.3209, n = 7, r² = 0.97), according to each growth angle. (25°, 45°, 65°, and 90°). The “+” signs on the colonies denote the increase or decrease of the sclerochronological characteristics in each area; the larger the symbol, the greater the density, extension, or calcification rates.

Fig. 5. Extension rate between bands of alternating density (HD in red; LD in blue). Values obtained in the maximal growth axis of each colony (90°). In all boxplots the lines inside the boxes represent the median and the black dots indicate the outlayers.
Taken together our results indicate that coral growth results from the extension and division of the polyps, which implies that modification of the skeleton must take place for new polyps to form. This then indicates that the addition of new polyps, and therefore coral tissue, is conditioned by the speed at which the skeleton is deposited (Barnes 1973; Darke and Barnes 1993; Lartaud et al. 2016). According to our analysis, during LD band formation in *O. annularis* available energy is used to extend and modify the skeleton to create enough space between the pre-existing corallites. During the summer season when HD bands are created, new corallites are inserted into the new space resulting in an increased polyp population.

Our results also indicate that polyp budding and death in the central zone are proportionately different when compared to the lateral zones. However, these differences were only significant in the 12Y colony. The absence of significant differences in the 6Y colony may be related to the fact that the diameter and size of the colony at the time of collection was too small to detect differences in budding rates between the central and lateral zones of the colony. This expectation is verifiable since the differences between polyp budings and deaths between the central and lateral zone of the 12Y colony were observable up to 8 and 7 yr, respectively. Growth of modular organisms, such as corals, relies on localized active budding patterns in zones where there is adequate resource availability. Differential access to resources such as light, food, and currents between coral modules determines differences in intracolonial growth patterns (Kim and Lasker 1998; Benedetti et al. 2020; Li et al. 2021). For larger diameter colonies, where access to resources is more variable between modules located in the central and lateral part of the colony, greater significant differences in the budding of modules will be detected. The results of the budding and differential mortality of the polyps in *O. annularis* suggest that these processes are regulated by the position of the polyps and the size of the colony, since these two factors increase the differences in terms of resources availability and environmental stimuli (Kim and Lasker 1998).

The idea that the location where the polyp develops, rather than age, determine survival and its fitness, is complemented by the results that suggest that sclerochronological variables measured in different positions of the colony are related to the angle of inclination and, therefore, to its location in the central/lateral position of the colony. In general, sclerochronological variables tend to decrease progressively towards the lateral part of the ramet, and as the angle of inclination decreases, while the skeletal density is greater in the lateral parts of the colony, attenuating in the upper parts of the colony (Muko et al. 2000; Jokiel 2011). This variation in the sclerochronological characteristics, as well as the differences in budding and mortality, could be related to the quantity and quality of resources that each module perceives, which is progressively modified as the colony grows. For example, variations in the light field, sedimentation, and food availability at colonial level may modify the mortality and replication of corallites, as well as the growth parameters between colony sections (i.e., central vs. lateral) (Kaandorp et al. 2011; Li et al. 2021). Concurrently, logistic growth models also suggest the effect of the position of the polyp and its ability to acquire resources at different growth stages. The models indicate an exponential growth in the 1st years of growth in the two colonies, suggesting that during the early stages of growth resource supply suffices to maintain elevate budding rates (r) so that each polyp has no resource restriction and access to numerous resources. However, the later years of the 12Y colony model indicate that the replication rate of the modules (r) diminish due to a reduction in the budding rate and/or an increase in the mortality of polyps, suggesting that the population parameters fluctuate depending on their population size (i.e., colony size, polyp density) and the environmental factors where the colony develops (Kim and Lasker 1998; Galli et al. 2016; Lartaud et al. 2016). The optimal resource zone (Fig. 4, nest zone) allows colonies to experience exponential growth (*dN/dt* > 0), since each polyp/module present in the colony has almost the same opportunity to access resources. When the population size of the polyps increases and with it, the size of the colony, the amount of resources received by a portion of the population of polyps is no longer optimal (i.e., a turning point of the model), after which the available resources (Fig. 3, red line) intersect with those captured by polyps (Fig. 3, blue line), it is at this point where the growth rate and the mortality rate are equal (i.e., they reach *K*); from this moment, the population size remains constant (*dN/dt* = 0). Another explanation for the cessation in the exponential growth of the polyp population of polyps in a colony may relate to the trade-off theory proposed by Chornesky and Peters (1987), and Hall and Hughes (1996). These authors suggest that small colonies invest resources in budding, as a result of which the colony increases in size, and once a certain size is reached, the energy is used in gamete formation and sexual reproduction, so the generation of new polyps slows down. Numerous studies suggest that the continued growth of colonial marine invertebrates is limited by unfavorable changes associated with the surface-to-volume ratio (Kim and Lasker 1998; Galli et al. 2016; Benedetti et al. 2020), although a synergy between the limitation of resources due to the population increase of the modules and trade-offs should not be ruled out, or that the former leads to the latter.

As observed, coral growth is conditioned by the growth of living tissue and modification of the skeleton (Barnes 1973; Darke and Barnes 1993). These two factors are limited when the polyp population increases; the first, because a higher energy cost is needed to modify the skeleton and generate
sufficient spaces for the insertion of new polyps (Darke and Barnes 1993), while the second implies that, as the population of polyps increases, they will have accessibility to resources such as light, space, and differential heterotrophic feeding (Kaandorp et al. 2011). Because of this, the modular growth observed in logistic models by *O. annularis* can be seen as a strategy to escape the two growth restrictions. On one hand, constantly eliminating modules avoids major modifications of the skeleton and, on the other hand, it adds polyps in areas where there is greater accessibility of resources, such as light, space, and food, therefore, resulting in colonies with columnar growth (Fig. 6). These strategies allow it to maintain a constant vertical extension, managing to continue depositing CaCO₃ at a higher rate, which is why it is considered one of the main reef-building species (Roff et al. 2020).

The results of the demographic model as a consequence of the differential distribution of resources may have important sclerochronological implications. The creation of new skeleton in scleractinian corals is the product of the collective contribution of all the polyps that make up the colony, which deposit “micro-skeletons” on the older skeleton (Dávalos-Dehullu et al. 2008). During this process, each polyp spreads vertically, depositing scatter marking bands of alternating density (Lough and Barnes 1992; Knutson et al. 1972); in turn, each

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**Fig. 6.** Reproduction of polyps in different areas of the *O. annularis* skeleton, reproduced from Sheppard et al. (2017). Elimination of polyps in less favored areas and replication in areas with greater availability of resources. In this way, the deposition of CaCO₃ is constant and greater than other coral species with different growth strategies.
polyp takes the necessary resources and reproduces asexually, giving rise to new polyps, and then dies (Rosen 1986; Darke and Barnes 1993). This constant growth of the skeleton and the turnover in the polyp population captures information from the environment into the coral skeleton depending on the position that each polyp occupies (i.e., central vs. lateral) during the growth of the colony. Therefore, special attention should be paid when obtaining corals cores from big colonies, from which records of hundreds of years of coral growth are obtained. Especially in cores where the banding follows different directions due to the trajectories of corallites in different positions and growth angles, and which, throughout their lifetime were exposed to different environmental conditions (Reed et al. 2021). Consequently, polyps that at one time were located in the lateral zones of the colony, by modifying the coral’s growth angle due to sedimentation, collapse, shading, and so on, can become part of the growth axis (or vice versa) by changing the extension rate, density, and calcification rates in that area, as well as the paleo-environmental signals that are recovered from the core (Rico-Esenaro et al. 2019; Reed et al. 2021). Therefore, more work that addresses the intracolonial variations in polyp replication as a product of differential access to resources, and its relationship with the potential variation in paleo-environmental signals in coral skeletons is needed.

The monitoring of the trajectories of individual coral polyps by CT images and subsequent demographic analysis will allow the exploration of size limits in different coral species as well as the drivers of shape and budding rate. Consequently, case-specific adjustments may be needed when making inferences from coral skeletons to make more precise inferences from past environments.

Data availability statement
All data and computer code are available in the main text or in Supporting Information.

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Conflict of Interest
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