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## CLONAL GROWTH PATTERNS IN COLONIAL ANTHOZOAN CORALS

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**Abstract** Corals are modular organisms that use asexual reproduction (i.e., budding) to increase the size of the colony by adding new polyps. Clonal modularity offers several advantages, such as the ability to sustain partial mortality, redistribute resources internally, replace or repair single modules, and delay senescence, potentially supporting millenary growth. Despite the global importance of coral reefs, little is known about clonal growth rules in anthozoan corals. Coral clonal growth was reviewed to synthesise current understandings and identify gaps driving future research efforts. Despite corals present high plasticity, their growth is dictated by strong intrinsic regularities at different life stages and modularity levels. For example, a six-polyps crown with fixed distances among polyps is typically formed in the early development stages of *Stylophora pistillata* larvae. Similarly, specific developmental regularities are observed in the budding of azooxanthellate Dendrophylliidae polyps, which are consistently maintained across generations and species. In Octocorallia, colony shape is preserved by maintaining a constant ratio between the total number of branches and mother branches. Concurrently, environmental factors (i.e., light and hydrodynamics) play a fundamental role in shaping the final morphology of the colony, driving the architectural design at different levels of modularity. Some species revealed higher plasticity at the branching level in contrast with the predetermined shape assumed by the colony. Several models have been proposed to describe the environmental modulation of coral growth, mostly in branching forms. However, a holistic, universal model applicable to a broader range of coral taxa is still lacking. Understanding the fundamental rules underpinning coral clonal growth is essential to improving predictions of coral reef recovery, inferring stress on coral colonies and guiding restoration efforts.

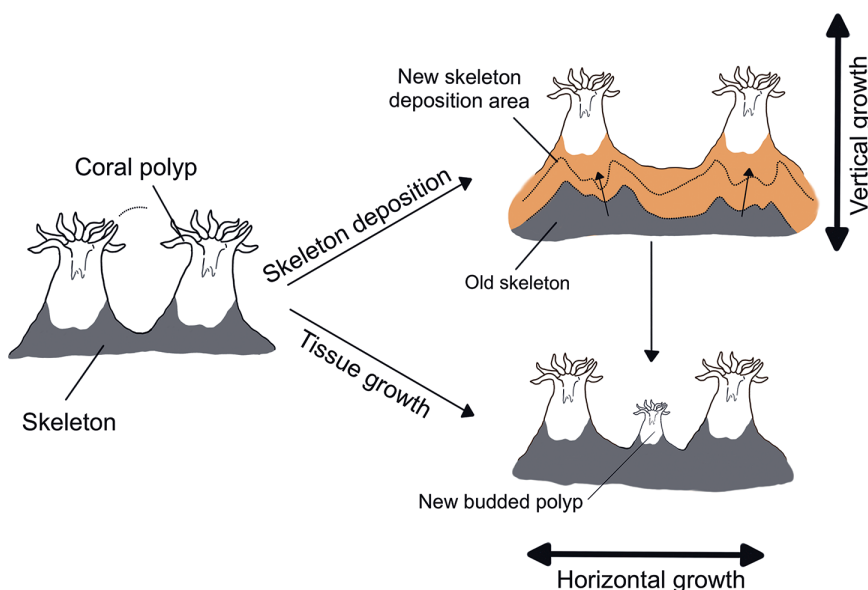
**Keywords:** Clonal Growth; Budding; Modularity; Asexual Reproduction; Growth Model; Coral Morphology; Growth Pattern

## Introduction

Coral reefs are the largest structures of biological origin in the biosphere, engineered by tiny clonal organisms. Coral reef frameworks develop by the growth of coral colonies, supplemented by contributions from other calcifiers. In addition, coral clonal growth is fundamental in responding to disturbances. For instance, the remarkably rapid recovery of coral cover from recent bleaching events in the Great Barrier Reef (AIMS 2022) has been supported largely by clonal growth. Yet, coral clonal growth, as well as other aspects of coral development (i.e., developmental biology, Ball et al. 2004) has received limited attention, particularly compared to the attention received by coral spawning and sexual reproduction, which has been studied on more than 400 coral species (Harrison 2011). A comprehension of coral clonal growth processes is required to understand coral reef formation and recovery from disturbance and to design effective restoration projects. This is particularly important considering that the global coverage of living corals is estimated to have declined by 50% since the 1950s (Eddy et al. 2021).

In contrast to the paucity of studies on coral clonal growth (Supplementary Figure 1), research on clonal growth rules in terrestrial and marine plants has delivered important insights into their growth rules and their application to predict space occupation by clonal plants (Routledge 1990, Marbà & Duarte 1998, Sintes et al. 2005, 2006), the extent and density of plant populations (Bell & Tomlinson 1980, Duarte et al. 1994, Sintes et al. 2005), resource acquisition (Cain et al. 1996), shoot dynamics (Bell & Tomlinson 1980, Marbà & Duarte 1998, 2003) and interactions between neighbouring ramets (Kenkel 1993, Marbà & Duarte 1998, 2003) and species within the community (Llabrés et al. 2022, 2023).

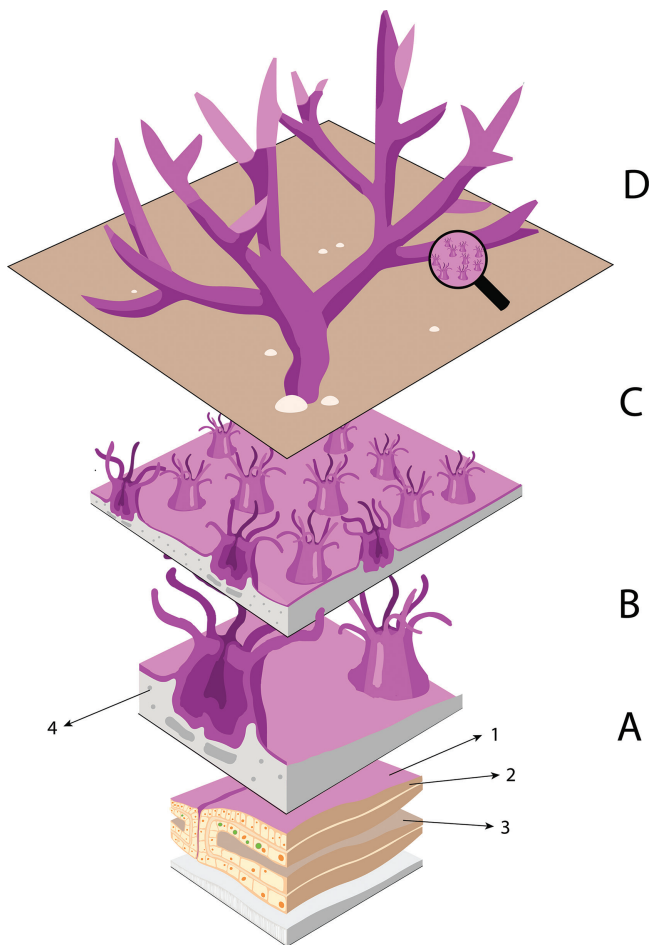
Corals can develop in a solitary growth form, a discrete and physiologically independent organism, or in a colonial form, where a prolonged tissue continuity is maintained across the individual modules, allowing for colony integration. The growth of coral colonies involves two processes, tissue growth (horizontal) and skeleton deposition (vertical), tightly linked to each other (Figure 1).



**Figure 1** A schematic view of skeletal deposition and budding processes in colonial corals. Skeletal deposition is facilitated by the polyps' calcium carbonate deposition, which is responsible for both the vertical growth of the colony and the peripheral expansion that enables the formation of new polyps and horizontal tissue growth (Medellín-Maldonado et al. 2022).

Clonal growth is initiated by the iterative replication and addition of modules (Figure 2) from an initial founder polyp (Boardman et al. 1973). The term ‘module’, initially coined to define plant growth (Harper 1977), describes the basic unit that is replicated to support clonal growth. Modularity brings several advantages, such as the ability to sustain partial mortality and increase fitness by enhancing the total reproductive output of the colonial genotype. Resources are distributed internally from areas of abundance to sites where they are scarce (Hester et al. 1994, Kemball & Marshall 1995, Hutchings & Wijesinghe 1997, Oren et al. 2001). Moreover, modularity implies the capacity to replace or repair single modules, delaying senescence and leading, potentially, to indefinite growth (Harrington & Hughes 1990, Winston 2010). The basic module supporting coral clonal growth is the polyp, defined as the conical organism composed of a tentacle crown, and the exoskeleton hosting the polyp (Figure 2).

Coral colonies extend vertically by accumulating new skeleton. Modification, i.e., growth of the skeleton, is fundamental to create available space for new polyps to arise (Medellín-Maldonado et al. 2022). Despite being closely coupled, tissue growth and skeleton deposition are limited by



**Figure 2** Modularity in coral colonies and coral reefs. Colonial corals are modular organisms, which consist of up to three levels of organisation, individual polyps (B), individual branches (in branching growth forms) made up by the repetition of single polyps (C) and the whole colony (D). In (A), the outer layer of the coral colony, also known as ectoderm (1), covers the mesoglea (2) and the gastrovascular cavity (3). The skeletal corallite underneath the polyp is visible in section (4).

different factors (Barnes & Lough 1992, Darke & Barnes 1993). Light availability, saturation state of calcium carbonate (Marubini et al. 2001) and dissolved inorganic nutrients concentration (Lesser et al. 1994) have been shown to play a role in skeletal growth, whereas organic nutrients availability appears to determine tissue growth rate (Barnes 1973, Graus & Macintyre 1982, Darke & Barnes 1993). Corals have evolved a repertoire of colony morphologies to maximise space occupation and resource acquisition.

Coral polyps multiply clonally through a process known as budding, defined as a gemmation process, where the daughter polyp, or bud, develops its own set of organs, borrowing nothing but an undifferentiated body wall from the parent, which otherwise remains complete (Hill 1935). Coral clonal growth is governed by a combination of a genetically mediated developmental programme and the plastic response to the surrounding environment. In each species, polyps stop growing when they reach a determined size; however, the colony may potentially grow indeterminately, achieving enormous sizes (Hughes et al. 1992), with the largest coral clones reported to reach 13 m across at 500 years of age.

In cnidarians, research has focussed on understanding the variation of colony forms in response to environmental factors (i.e., phenotypic plasticity; Graus & Macintyre 1976, 1982, Bruno & Edmunds 1997, Muko et al. 2000, Kaandorp & Kübler 2001, Todd et al. 2004, Rodolfo-Metalpa et al. 2008, Todd 2008, Filatov et al. 2010, Chindapol et al. 2013). In contrast, little attention has been paid to the more challenging task of defining and elucidating the set of rules that control clonal growth and, therefore, colony shape (Rinkevich 2002, Gateno & Rinkevich 2003, Lasker et al. 2003, Ohno et al. 2015, Guerrini et al. 2021). Different aspects of coral clonal growth have been reviewed in the past by Matthai (1926), Buddemeier and Kinzie (1976), Rosen (1986), Hughes et al. (1992), Lasker and Sánchez (2002), Sánchez (2004), Hughes (2005) and Todd (2008).

Growth models applied to describe coral growth were often borrowed from plant-based models (e.g., “tree architectural model”, Dauget 1991, 1994), given their similar ecology and analogous shape (Connell 1978). In addition, branching colonial organisations have been analysed by mimicking the rules of colony formation through mathematical models based on the accretive growth of the skeleton subjected to the diffusion of resources (e.g., Kaandorp & Sloom 2001). Despite the apparent relative simplicity of each modular unit, corals and colonial marine invertebrates can generate complex architectures (Kaandorp & Kübler 2001, Sánchez & Lasker 2003, Shaish et al. 2007), involving a highly coordinated growth leading to emerging, non-linear properties, as reported for clonal seagrass (Sintes et al. 2005).

Here we review the current understanding of anthozoan coral clonal growth, as a basis to understand and predict patterns of space occupation, resource acquisition, and the competitive and recovery potential of different coral species. Our review also focuses on synthesising past research efforts in describing coral colony growth through mathematical models. Finally, we identify knowledge gaps and key future research directions that need to be addressed to expand our capacity to model and predict coral clonal growth.

## Growth patterns in Hexacorallia

### *Massive Faviidae corals*

Gateño and Rinkevich (2003) analysed the rules governing budding in the massive coral *Favia favaus*, to report that polyp budding was initiated once the polyp reached a threshold of two morphometric fields, consisting of the perimeter of the polyp and its area. They report that a ratio of the two radii ( $r_p$  and  $r_a$ ) greater or equal to the average value of 1.14 can trigger intra-tentacular budding in the species, thereby proposing the first allometric threshold ratio for bud formation described in cnidarians (Gateño & Rinkevich 2003).

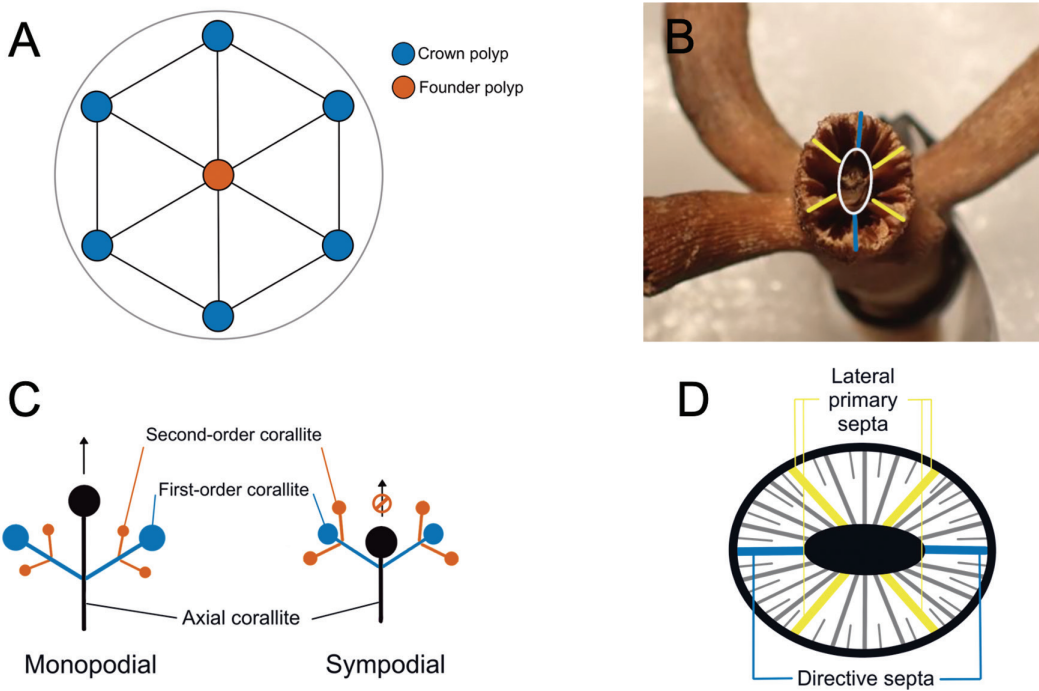
Kai and Sakai (2008) found that budding in single polyp and small (5–8 polyps) colonies of two massive faviids species (i.e., *Goniastrea aspera* and *Favites chinensis*) was initiated when space was available around the polyps, showing that the availability of open area around the polyp can affect budding rate and mode. Budding mode (intra- versus extra-tentacular budding) varied depending on the position of the polyp in the colony. Polyps in the colony margins usually show extra-tentacular budding, whereas polyps surrounded by other polyps usually exhibit intra-tentacular budding. The budding rate was found to be inversely proportional to colony size, as the perimeter-to-area ratio decreases with colony size, resulting in less marginal polyps and space available to expand in larger colonies. The budding response to open space was proposed to be a mechanism to increase colony fitness (Kai & Sakai 2008), as the mortality rate is higher when colonies are young and smaller (Connell 1973, Hughes & Jackson 1980). As a consequence, small colonies, with a low number of polyps and high perimeter-to-area ratios, tend to grow faster, allowing restoration practitioners to use this strategy in a technique known as micro-fragmentation (Page & Vaughan 2014, Page et al. 2018).

### *Branching Pocilloporidae family*

The clonal growth process of several Pocilloporidae coral species has been extensively studied and modelled over time (Supplementary Table 1) and is believed to be genetically controlled for *Stylophora pistillata* (Rinkevich 2002, Shaish et al. 2006). Fifty-three to 121 days after *S. pistillata* larval metamorphosis, a ‘six-polyp crown’ or ‘six-polyp circlet’ is established by budding around the primary founder polyp (FP), maintaining fixed distances ( $1.59 \pm 0.29$  mm) between polyps (Figure 3A). This basic morphometric landscape had already been observed in another Pocilloporidae species, *Pocillopora damicornis (bulbosa)* by Stephenson (1931), and reflects a strong genetic clonal growth programme (Guerrini et al. 2021). The authors hypothesised that the sites of budding are governed by a morphogen (‘isomone’ *sensu* Rinkevich & Loya 1985a) frontier region, with high and low concentration areas, establishing fixed and regular distances among polyps. However, the nature of the hypothetical hormone-regulating spacing has not been elucidated yet, giving rise to questions about the plausibility of a hormone being released in a highly hydrodynamic environment.

An early observation of the branching process in *P. damicornis* came from Stephenson (1931), who described, through longitudinal growth (i.e., branching process), the lateral expansion of the polyps, until reaching a branching stage. After almost a century, Guerrini et al. (2021) described the branching process of another Pocilloporidae species, *S. pistillata*. The authors found that when the distances between neighbouring polyps of the six-polyp crown are shorter (in the range of  $1.08 \pm 0.28$  mm) than the average fixed distance, there is no possibility of expanding the space by lateral retreat growth. Therefore, branching is the solution to resume growth while conforming with the allometric rules (Guerrini et al. 2021).

Different *S. pistillata* genotypes exhibited variable and different architectural designs during growth, each characterised by specific morphometric parameters (Shaish et al. 2006). However, a more comprehensive analysis revealed that clonal growth is characterised by a continuum of architectural patterns of several distinct stages. In particular, three phases can be distinguished. In the beginning, colonies display fast vertical growth and the initiation of some side branches; vertical growth then declines to favour lateral extension, leading to an increase in the ecological volume and bifurcation of branches. Finally, in the last phase, lateral extension is reduced, ecological volume is increased and older branches start to bifurcate. Moreover, Shaish et al. (2007) investigated plasticity at the branch and colony levels. The branching process is also characterised by more plastic morphometries, with individual branch modules exhibiting diverse architectures and developmental trajectories, whereas clonal growth traits are more conserved at the colony level. Conserved colony



**Figure 3** (A) A schematic view of the six-polyp circling in *Stylophora pistillata* early stages after metamorphosis. Around the founder polyp (in red), a crown of 6 polyps (in blue) arises at a fixed distance of  $1.59 \pm 0.29$  mm (six equilateral triangles). Modified from Guerrini et al. (2021). (B) Corallite of a dendrophylliids species from the Eastern Red Sea. In blue are the directive septa; in yellow are the four lateral primary septa. (C) Monopodial growth: The axial corallite (in black) continues to grow upwards giving rise to lateral corallites. Sympodial growth: the axial corallite stops growing; instead, it produces lateral corallites. Modified from Sentoku et al. (2013). (D) A schematic view of the dendrophylliids corallite Portuales plan. Two opposite directive septa are in blue, and four lateral primary septa are in yellow. Modified from Sentoku and Ezaki (2012b).

traits, with plasticity at the branching level, result in variability within species-specific fixed colonial shapes (Loya 1976).

*Pocillopora* species has a widespread distribution across the Red Sea, Indian Ocean and Pacific Ocean to the Eastern Tropical Pacific (Veron 2000) and shows remarkable variation in colony morphology, making identification a challenging task. Several authors focused on modelling the effects of environmental factors in shaping the whole coral colony architecture (Kaandorp 1999, Chindapol et al. 2013). Paz-García et al. (2015) found that under high-flow rates, the morphology of different branching *Pocillopora* species (*P. damicornis*, *Pocillopora verrucosa* and *Pocillopora meandrina*) was more similar among morphospecies compared to low-flow conditions. In particular, branch thickness was significantly higher under high-flow rates, seemingly a coping mechanism of the colony (Paz-García et al. 2015). Branch modularity (i.e., the likelihood of different sets of branch traits to vary in a coordinated way) varied under different flow rates, with branch density, branch diameter and distance among branches showing a stronger connection at the high-flow rate site (Paz-García et al. 2015). Similarly, *S. pistillata* shows morphological plasticity under different light and water flow regimes. Colonies subjected to high water flow and light resulted in more densely branching colonies, whereas thinner and more open branches arose under low light intensity and low flow (Shwartzberg et al. 2012). Under mesophotic conditions, *S. pistillata* has been shown to develop a more plate-like morphology in order to capture more light (Mass et al. 2010).

*Pocillopora damicornis* is one of the most extensively studied coral species, yet its growth and budding pattern remain poorly unknown. Li et al. (2020) used high-resolution computed tomography (HRCT) to investigate the 3D skeletal structure of *P. damicornis* to understand budding, growth and polyp distribution during the growth process. Results revealed that the average diameter of the oral and aboral surface of *P. damicornis* is generally between 0.5 mm and 1 mm, and the average polyps height is between 0.1 mm and 0.6 mm, allowing to reconstruct the average polyp volume, 3600 cm<sup>2</sup>. In *P. damicornis*, although corallites are not related to each other at the micro level, coral growth is a holistic and synchronised process, where the living polyps extend to the surface of the coral from their initial growth point, with no dead polyp present in the internal part of the coral (Li et al. 2020). Whereas the latter could be considered as a species-specific feature, it may not apply to other species (i.e., *Porites*, Darke & Barnes 1993). When a polyp secretes a new calix, it enters the newly created chamber, horizontally closing the previous one in a process known as dissepiment. Each polyp grows along an axis, which points in the direction of the branch. Polyps deviating from the axis commonly stop after four or five inter-septa spaces, thickening the side branches of the colony, which follows a dichotomous branching rule during the colony growth (Li et al. 2020).

Plasticity of growth processes to environmental conditions found for the genus *Pocillopora* was also reported for *P. damicornis*, where light can affect the final colony shape (Li et al. 2020). In particular, calix volume and inter-septal space exhibit larger average volume and inter-septal space when exposed to higher light levels, with growth slowing gradually towards shaded areas. Transplant experiments with the extensively studied and modelled Pocilloporidae species *Madracis mirabilis* revealed that both genotype and environment affect the morphometric traits, in particular, corallite architecture and density, branch diameter and spacing (Bruno & Edmunds 1997).

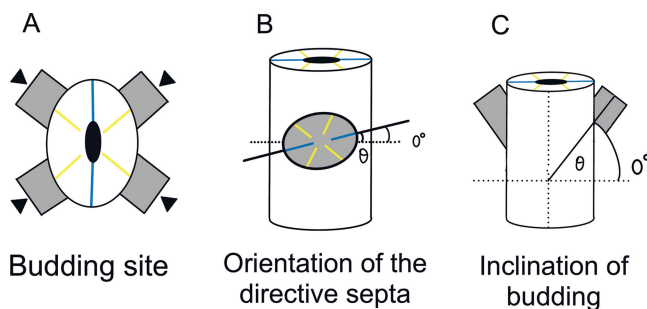
### *Growth regularities in the Dendrophylliidae family*

Intrinsic regularities in the budding of azooxanthellate corals Dendrophylliidae have been extensively studied (Sentoku & Ezaki 2012a–d, 2013, Ohno et al. 2015, Sentoku et al. 2015a,b). Colonial growth of corals lacking symbiotic algae is less influenced by light compared to the zooxanthellate counterpart (Ohno et al. 2015). However, competition for space is severe among corallites, especially in massive and encrusting forms compared to branching forms. In Dendrophylliidae corals, the axial corallite is produced sexually, whereas the first-order and subsequent lateral corallites arise by budding from the preceding corallite. Moreover, a single polyp is present at the individual corallite tip. Corallites are oval with a large calicular diameter (*sensu* Cairns 1994) located in the region containing two directive septa. Four primary septa, also known as lateral primary septa, arise around the mouth (Figure 3B and D).

Colonial azooxanthellate dendrophylliid bud according to specific developmental regularities despite the diversity of growth forms (Sentoku & Ezaki 2012a). Results from a diverse array of species highlighted the fact that different growth forms (bushy, massive, dendroid) can be explained with subtle differences in one or more of the clonal growth parameters, such as budding sites, orientation of directive septa, inclination of budding and the interval of budding (Supplementary Table 2, Figure 4).

Regularities in growth patterns are maintained across all generations, suggesting the presence of strict developmental constraints on asexual reproduction. Lateral corallites bud in various directions to maximise the use of available space and avoid direct contact between polyps. In branching forms (e.g., *Dendrophyllia arbuscula*, *Tubastrea coccinea*, *Dendrophyllia ehrenbergiana*), the resulting colonies can be classified as monopodial, when the axial corallite prolongs continuously upwards, giving rise to several lateral buds, and sympodial, when the axial corallite ceases to grow upwards and through growing and budding, colony extension occurs in one or two lateral corallites (Figure 3C). In monopodial forms, budding sites are located at four lateral primary septa (Sentoku & Ezaki 2012a,c) or on one side of the two primary septa (Sentoku & Ezaki 2012c).





**Figure 4** Schematic diagram of the morphometric measurements conducted. (A) Budding sites. The two directive septa are indicated in blue, and the four lateral primary septa are indicated in yellow. Lateral primary corallites are in light grey. (B) Orientation of the directive septa, which is defined as the angle ( $\theta$ ) between a line connecting the two directive septa (solid line) and a horizontal line (dotted). (C) Inclination of budding, which is defined as the angle between the direction of the lateral corallites (solid line) and a horizontal line (dotted line) oriented perpendicular to the growth direction of the parental corallite (vertical dotted line). Modified from Sentoku and Ezaki (2012c).

Conversely, in sympodial forms, budding sites are restricted to a single primary septum (Sentoku & Ezaki 2012b, 2013). In both sympodial and monopodial species (*D. ehrenbergiana*, *Dendrophyllia boschmai*, *Dendrophyllia cribrosa*, and *Turbinaria peltata*), a distinct polarity at individual corallites has been found to affect the budding site and, eventually, the coral morphology (Sentoku & Ezaki 2012d, 2013). This striking characteristic implies the presence of radio-bilateral symmetrical constraints on the asexual reproduction of a Scleractinia group (Sentoku & Ezaki 2012d). Finally, the same regularities in budding have been found for the zooxanthellate species *T. peltata*, suggesting a strong influence of those underlying regularities on the final growth form in both species whether they contain or lack zooxanthellae (Sentoku et al. 2015a).

#### *Azooxanthellate cold-water corals*

Morphological diversity in cold-water corals is still poorly understood due to the limited accessibility of the deep ocean they inhabit. Sanna and Freiwald (2021) investigated the intraspecific morphological variation in the azooxanthellate caryophyllid *Lophelia pertusa* (recently synonymised with *Desmophyllum pertusum*; Addamo et al. 2016), showing remarkable morphological diversities in both corallites and colonies. However, corallite morphology was mostly decoupled from colony morphology. Three major branching patterns were identified, asymmetrical (uniplanar growth along numerous branches), bushy (simultaneous multidirectional growth) and columnar (longitudinal growth along few branches, often in a zig-zag mode). The number of buds per corallite varied in response to the growth pattern, with higher values in bushy forms. These variations may reflect plastic strategies in response to environmental factors, such as water movement, which implies mechanical stress and food supply. Asymmetric and bushy forms minimise the hydraulic stress in high-energy settings, orientating the branches or reducing the branch length towards the current flow. Conversely, columnar forms are more suitable for low-energy settings, associated with scarcer food availability.

#### **Growth patterns in Octocorallia**

Gorgonian octocorals present a highly complex colonial organisation, spanning from the distribution of single polyps to the branching pattern. At the branching level, Sánchez et al. (2004)

showed that the common assumption of branching as a bifurcation process does not apply to modular marine organisms, which conform to a sub-apical process, where mother branches give rise to daughter branches at a fixed internode length. The highly organised gorgonian tree-like shape is preserved by maintaining a constant ratio between mother and daughter branches (Sanchez 2004).

Branching process in gorgonian has been extensively studied in different species (Sánchez & Lasker 2003, Sánchez et al. 2004, Cadena et al. 2010). Cadena et al. (2010) analysed the association between the branching process and stem canals present at the base and at the terminal segment of the branches of the colony. In fact, an internal tree-like structure is present in gorgonian octocorals, equally diametric-sized hollow vessels, running all along the colony, connected with gastrovascular canal (solenia; Bayer 1973) to exchange nutrients (Gateño et al. 1998). Results revealed that a species-specific constant ratio ( $c$ ) of total and mother branches was maintained in *Eunicea mammosa*, as previously found in Sánchez et al. (2004) (in Caribbean corals,  $c$  ranges between 2 and 13). Moreover, a linear relationship between branches and stem canals was found, suggesting an important role in colony growth. In particular, the number of stems in the holdfast was correlated with the total length of the colony, independently from the number of mother and daughter branches (Cadena et al. 2010).

## Growth models

Morphogenesis is a complex biological phenomenon, whose fundamental principles are still not completely understood. Hence, mathematical modelling is considered an important tool to test hypotheses and help to answer specific questions about developmental processes (Tomlin & Axelrod 2007).

Coral growth models have been mostly focused on the role of environmental factors (i.e., light intensity and water flow) in shaping coral morphology (Kaandorp & Sloot 2001, Chindapol et al. 2013). The ultimate goal was to resolve the interplay between environmental and genetic constraints in defining growth forms and coral shapes. Results supported the hypothesis of very plastic species or levels of modularity (e.g., branching versus whole colony level, see Loya 1976, Shaish et al. 2007, as *Pocillopora damicornis* and Pocilloporidae in general, Kaandorp et al. 2005), and less plastic groups or modules, where tight genetic constraints preclude morphological plasticity (Dauget 1991, Shaish et al. 2007) (Table 1).

**Table 1** Summary of the Principal Models Applied to Simulate Coral Morphogenesis

Model	References
Theoretical model for coral growth	Mistr and Bercovici (2003)
Model for Dendrophyllidae corals modified from Niklas and Kercher (1984)	Ohno et al. (2015)
Tree Architectural model	Dauget (1991)
Hydrodynamically influenced radiate accretive model (HIRAG)	Kaandorp et al. (2001)
Hydrodynamically influenced radiate accretive model (HIRAG) modified from Kaandorp and Sloot (2001)	Merks et al. (2003)
Polyp-oriented radiate accretive growth model (PORAG)	Merks et al. (2004)
PORAG model coupled with diffusion model in <i>Madracis mirabilis</i>	Kaandorp et al. (2005)
PORAG model in <i>Madracis mirabilis</i>	Filatov et al. (2010)
Flow-driven accretive growth model from PORAG Merks et al. (2004) in <i>Pocillopora verrucosa</i>	Chindapol et al. (2013)
Branching and self-organisation model in gorgonians	Sánchez et al. (2004)
Stochastic model for <i>Corallium rubrum</i> growth	Kahramanoğulları et al. (2019)

### *Theoretical model of coral growth*

Among the earliest models developed to describe coral growth, Mistr and Bercovici (2003) adopted a simplified mathematical model to describe growth in a coral subjected to unidirectional flow. Linear stability analysis of the system of equations predicts that the growth of solid (coral) structures will be aligned perpendicular to flow, propagating against flow direction (Mistr & Bercovici 2003).

### *Plant-based models*

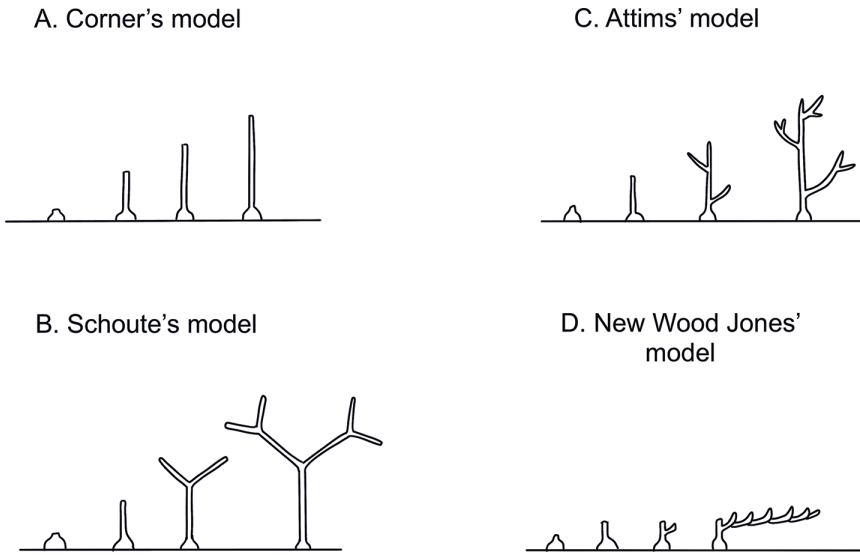
The analogy between plants and corals has been extensively reviewed by Connell (1978), based on a long tradition of ecologists making direct comparisons between plants and corals (Crossland 1913, Squires 1964). Ohno et al. (2015) proposed a voxel-based programme used in addition to a vector model based on the plant modular model of Niklas and Kerchner (1984) to explain colonial dendrophylliids morphogenesis. The model was originally developed for terrestrial plants to predict architectural solutions to maximise plant photosynthetic efficiency, reduce mechanical stress attending vertical growth and optimise the translocation of metabolites. The model aims at predicting architectural solutions that are more efficient than others in plants (Niklas & Kerchner 1984). In this study, the Niklas and Kerchner (1984) model has been further developed by adding a local reference system, similar to the growing tube model of Okamoto (1988). Three parameters were adopted to simulate a range of colonial growth forms, budding orientation, branching angle and interval of budding (Figure 4, Ohno et al. 2015). The regulation of two of the parameters produced two distinct morphologies, branching and massive, represented in nature by two distinct species with different ecological and physical traits, *Tubastrea coccinea* and *Dendrophyllia arbuscula*. However, the model could not generate all coral growth forms available in nature. Thus, Ohno et al. (2015) suggested that other controlling factors (e.g., density of nutrients, water flow and sedimentary conditions), not included in the model, might also affect the growth and morphogenesis of corallites.

Another application of the plant model in coral morphogenesis is Dauget (1991), where architectural methods used for tropical trees were applied to explain constant traits in coral colony forms. Each coral growth form was described using four simple architectural models (Corners's, Schoute's, Attims' and a newly named Wood-Jones' model) and their iteration over time. In particular, the author identified species-specific architecture based on graphic methods (Figure 5). The fundamental element is the axis, which could develop in at least three different ways, by a unique apical polyp (e.g., *Lobophyllia corymbosa*), by multiple apical polyps (e.g., *Acropora palifera*) or by the apical zone of the coenosarc (e.g., *Montipora ramosa*). Moreover, the ramification type affects the general architecture of the colony. The Corners's model (Figure 5A) represents solitary-polyp non-ramified colonies (e.g., *Fungia fungites*), with a single mouth. The Schoute's model (Figure 5B) describes the orthotropic growth with apical ramification, typical of *Acropora* or *L. corymbosa* colonies. Orthotropic growth with lateral and diffuse branching is represented by the Attims' model (Figure 5C), displayed by colonies of *Acropora formosa*. Lastly, the modified Wood Jones' model (Figure 5D) depicts the growth of tabular or plate-like colonies, where growth is plagiotropic in the basal portion and orthotropic in the apical with lateral ramification, resulting in the table forms of *Acropora hyacinthus* colonies.

Despite being able to describe some of the typical growth forms available in nature, those models represent just a visual description of the general coral architecture.

### *Hydrodynamically influenced radiate accretive growth model (HIRAG)*

The hydrodynamically influenced radiate accretive growth model (Kaandorp & Sloom 2001) represents an important milestone, aiming at understanding which aspects of coral growth can be



**Figure 5** Graphic visualisation of the four main architectural models adapted for corals. Modified from Dauget (1991).

explained from environmental and biological constraints, such as genetic regulation and differential tissue and skeletal growth. In their model, growth proceeds by the iterative accretion of layers whose thickness depends on the resource fluxes over the coral transported by advection and diffusion, where the coral surface is represented by a triangular mesh and where vertices and inter-vertex links define the curved coral surface (Kaandorp & Sloot 2001).

However, in this preliminary HIRAG model, two unresolved issues remained. Firstly, branch splitting didn't occur unless a curvature rule was enforced in the model, allowing to move from lobated shapes to branching objects (Kaandorp & Sloot 2001). Further progresses in the model allowed to resolve the branch splitting mechanism and address the reason for morphological variety under the model (Merks et al. 2003).

Secondly, in the early work by Kaandorp and Sloot (2001), a compactification mechanism emerged under high water flow conditions (HIRAG model, Kaandorp & Sloot 2001; Diffusion Limited Aggregation model, Kaandorp et al. 1996). Despite being in line with previous findings in sponges, scleractinian corals and hydrozoans (Kaandorp 1999), the mechanisms behind this phenomenon were not understood. The positive correlation between the object's compactness and Péclet number was not supported by subsequent simulations, suggesting a lack of computational evidence that hydrodynamics influences the compactness of corals (Merks et al. 2003).

### *Polyp-oriented radiate accretive growth model (PORAG) and its applications*

Merks et al. (2004) developed a polyp-oriented model, PORAG, in which coral growth is described as the “collective results of a growth process taking place in the polyps”, as an extension of the HIRAG model proposed by Kaandorp and Sloot (2001). Polyps are modelled individually, as separate entities, which exploit resources, deposit skeleton, bud off new polyps and die. In the PORAG model, the coral surface is represented as a mesh, containing vertices (representing the centre of the coral polyp) and inter-vertex links (representing the coenosarc of the coral), compared to the HIRAG model, where vertices and inter-vertex links do not represent any biological entity. The

model assumes that new polyps arise as space becomes available, to maintain a fixed “inter-polyp” distance, which has a dominant effect on the growth form, especially on the thickness of the branches and the compactness of the colony. Morphogenesis is, hence, a natural consequence of the way in which individual polyps are deployed at the surface of the coral colony. In summary, this model concludes that genetics sets the properties of the individual polyps, whereas environment influences the morphology of the individual polyp and colony (Merks et al. 2004).

Subsequent applications of the PORAG model implemented the effects of environmental factors, such as water flow and inorganic nutrients diffusion, to determine the degree of phenotypic plasticity among colonies of the same species. Computer simulations were supported by 3D images of actual colonies to compare the results. Quantitative comparison of complex real colonies with model outputs is a fundamental prerequisite to verify the models. Complex branching organisms need 3D accurate reconstruction that could include internal structures of the colony. The use of 3D scanning techniques allowed to simplify the objects into a network of lines (skeletonization algorithm; Kruszyński et al. 2007), or using a voxel thinning algorithm (Ramírez-Portilla et al. 2022), where a set of morphometric variables can be extracted.

The PORAG model has been coupled with the diffusion model and applied to simulate morphology processes in *Madracis mirabilis*, assuming a crucial role of dissolved inorganic carbon (DIC) as a limiting factor (Kaandorp et al. 2005). Polyp height and distance were the only species-specific information included in the model. Results revealed that gradients of DIC around coral colonies are responsible for branching colony morphology, highlighting the importance of including advection-diffusion model (Kaandorp et al. 2003) in combination with a morphogenetic model of coral, as done by Chindapol et al. (2013). Light intensity, nutrient availability and the degree of diffusion of the nutrients across the object surface were further implemented in the PORAG model by Filatov et al. (2010) to show how those factors affect growth forms of species belonging to the genus *Madracis*. Under high light intensity and surface diffusion, a transition from thin-branched morphologies to more compact growth forms was observed (Filatov et al. 2010). However, the computational model was not able to generate more irregular shapes (e.g., *Madracis formosa*) (Filatov et al. 2010).

Chindapol et al. (2013) applied the radial accretive growth model (PORAG) coupled with an advection-diffusion equation to study the impact of hydrodynamics on the growth of the scleractinian coral *P. verrucosa*. Simulated morphologies and computed tomography (CT) scans on real colonies exposed to various flow rates confirmed a strong influence of flow conditions on coral morphologies. In particular, results showed an asymmetrical growth of colonies subjected to uni-directional flow conditions, with branching developing towards the incoming currents (Chindapol et al. 2013). However, the model could not resolve finer details (i.e., small-scale roughness of the bumps typical of the species) nor the process of anastomosis – the fusion of branches – which might play an important role in coral morphogenesis.

Moreover, Kücken et al. (2011) argued that the Kaandorp-Merks’ models were not able to describe the morphogenesis of *Stylophora pistillata*, as significant skeletal growth takes place mostly at the branch tips, even though all the parts of the branch have equal access to resources. This contrasts with the Kaandorp-Merks model, where local growth is related to the amount of available resources. A more detailed representation of *S. pistillata* morphogenesis has been developed (Kücken et al. 2011). The mathematical model includes resources and photosynthate transport across the colony, which provides positional information for coral morphogenesis; growth is uniform and takes place only at the tips; and branch splitting is a stochastic event regulated by the presence of resources (Kücken et al. 2011).

### *Branching and self-organisation model in Gorgonians*

Sánchez et al. (2004) presented a model of the dynamical behaviour of branching through colony development based on empirical observations from the octocorals *Pseudopterogorgia bipinnata*

and *Plexaura flexuosa*, where colonies branch subapically, generating hierarchical mother-daughter relationships among branches, rather than a simple bifurcation with two “sister” branches. The model included both the intrinsic subapical branching and an ecological-physiological limit to growth, a maximum number of mother branches.

### *Stochastic model to describe Corallium rubrum growth*

The red coral *Corallium rubrum* is a Mediterranean octocoral, an overexploited, slow-growing species with a calcium carbonate skeleton deposited by the polyps, which can be found between 10 m and 800 m depth. The model developed by Kahramanoğulları et al. (2019) consisted of three rules parameterised with stochastic rates, describing the growth and branching dynamics of *C. rubrum* to capture the phenotypic variability of coral structures in the field. The influence of the environment on individual colonies was well represented, and the model suggested that the morphology of a *C. rubrum* colony can result from two competing processes, branching and growth, the priority of which is regulated by environmental factors (Kahramanoğulları et al. 2019).

## Knowledge gaps

Colony morphology is the result of a single developmental plan, characterised by a continuum of architectural rules, each characterised by specific morphometric parameters. Yet, the body of research that has been focused on elucidating growth form and defining growth rules in colonial anthozoans is rather limited, comprising only 0.05% of the research efforts on coral reefs, despite the importance of clonal growth in the recovery of coral reefs from disturbance (AIMS 2022). This is in contrast to the attention on clonal growth for other habitat-forming marine clonal species, specifically seagrasses (Hemminga & Duarte 2000). As discussed in Marbà and Duarte (2003), different seagrass species display a diverse repertoire of growth programmes, which can be modelled, across species, considering rhizome extension rates, branching rates and angles, shoot mortality rates and the per capita space required by the shoots (Sintes et al. 2005).

Several studies across taxa showed that the body plans of modular organisms are constrained by developmental programmes and environments. In corals, the interest in defining a set of rules describing clonal growth has focused on a limited set of species (Supplementary Table 1) compared to the high species richness of corals (>1000 species of Hexacorallia and >3000 species of Octocorallia). The polyp-oriented model (Merks et al. 2004) emphasised the importance of understanding how single modules bud with respect to the mother polyps, and if a distinct morphogenetic landscape, as described in *S. pistillata* by Guerrini et al. (2021), takes place in different coral species. Models developed to explain coral growth have been mostly focussed on the effect of environmental factors (i.e., light and water flow), often limited to single species and growth forms. Hence, a parsimonious, universal model, able to reproduce coral growth across coral species with a simple set of parameters, as available for seagrasses (Sintes et al. 2005), is yet missing; however, the complexity of coral forms, their high plasticity (Todd 2008) and the gaps in our understanding of the mechanisms that underlie coral development and gene regulation pose a significant challenge.

Another important gap in coral clonal growth research is colony integration. The existence and transmission of cues, molecules and energy resources between remote parts of a colonial structure are prerequisites for colonial holism, fundamental to distinguish “true” colonies from mere aggregates (Jackson 1979, Silén 1981, Rinkevich 2000). However, previous models (i.e., HIRAG and PORAG models) assumed the independence of single polyps, as it seemed a fundamental precondition for the hypothesised coral growth mechanism (Merks 2003). Noteworthy, from a model point of view, in the coral morphogenesis process such as the branches avoidance mechanism, the occurrence of an extracellular hormone (i.e., isomone) would be indistinguishable from a nutrient depletion situation (Merks 2003), both resulting in branches avoidance behaviour. In seagrass,

as in clonal plants in general, resources are transported along rhizomes, and apical dominance, exerted through hormonal control, regulates branching processes (Schwarzschild & Ziemann 2008, Terrados et al. 1997). However, the existence and drivers of mechanisms for clonal integration within coral colonies remain, surprisingly, to be explored, despite clues that clonal integration is likely present in some species. Within the same colony, polyps have integrated physiology, and the shape of the colony is coordinated. For instance, Loya (1976) discovered a tendency of *S. pistillata* colonies to regain the initial symmetry of a sphere when damaged, which requires some degree of clonal integration (Loya 1976). Also, changes in growth directionality were detected in *S. pistillata* branches when confronting isogenic branches (Rinkevich & Loya 1985b) and in *Dendrophyllia cribrosa* branches (Sentoku et al. 2015a,b). These findings reveal the existence of feedback mechanisms able to ‘consider’ the current shape and future growth under a pre-planned coral pattern or the presence of conserved ‘morphogenetic codes’ (Hogan 1999), species-specific rules repeatedly expressed to develop the colony. Sentoku et al. (2015b) proposed the role of individual corallites in sensing and maintaining the distance between branches through sensory recognition of tentacles. Rinkevich and Loya (1985a) proposed the presence of a hypothetical coral ‘isomone’, yet to be identified, with a role as a chemical cue for signalling. Although this hypothesis has never been questioned before, the energetic requirements for releasing a pheromone in a highly hydrodynamic environment raise some doubts about the existence of a chemical compound released into the flow involved in colony integration. Indeed, the underline mechanism to explain existing evidence of communication and coordination remains unknown. A recent experiment by Boudier et al. (2022) used particle tracking and mathematical modelling to reveal polyps’ connection and integration, either on the surface or inside the colony. Results showed a strong species-specific integration among polyps via complex liquid dynamics highly dependent on the cilia orientation typical of every species, suggesting a potential mechanism of colony coordination (Boudier et al. 2022).

## Conclusions

The quest to develop a more holistic approach towards coral growth patterns, aiming to be informative and meaningful at the same time, requires an effort to extract a parsimonious and yet universal set of clonal growth rules that can be used to understand and model clonal growth across colonial anthozoans. These models can be used for heuristic purposes, to better understand coral clonal growth and the resulting growth forms and are also essential to guide restoration and conservation efforts attending to light availability and the response to hydrodynamic disturbances (Cresswell et al. 2020), which are accelerating with increasing global coral loss.

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## Contribution

This work was conceptualised by C.M.D. E.R. performed the data analysis and produced the first draft with inputs from C.M.D., S.S.R., E.L. and T.S. All authors contributed critically to the drafts.

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