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Morphological variability in azooxanthellate scleractinian dendrophylliids governed by regular modes of asexual reproduction: A computer simulation approach

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Abstract. Morphogenetic mechanisms in modern Scleractinia provide insights into the habitats and growth forms of corals living in different environmental conditions. Scleractinian morphogenesis has been studied primarily in relation to extrinsic (e.g. environmental) factors, irrespective of specific regularities in budding and their impacts on growth forms. Morphogenesis in colonial dendrophylliids can be modelled by taking these developmental traits into account, so as to understand how intrinsic developmental factors affect morphologies resulting from colonial growth. We used a simple, voxel-based program to simulate the morphogenesis of dendrophylliid corals. Three parameters (budding orientation, inclination of budding, and interval of budding) were adopted to simulate a range of colonial growth forms, regardless of whether the forms exist in nature or not. The regularity of budding was fully taken into account, and various colonial morphologies were gained, even under strict regularity. The regulation of two of the parameters (inclination of budding and budding interval) gives rise to two distinct types of morphologies (branching and massive forms) that are represented by the extant taxa *Dendrophyllia arbuscula* and *Tubastraea coccinea*, respectively. This suggests that the growth forms of individual dendrophylliid colonies vary according to habitat conditions, and that they can be simulated by modifying only a few parameters, even given rigid developmental constraints on budding.

Key words: Azooxanthellate Scleractinia, branching, budding, computer modelling, voxel model

Introduction

Modern zooxanthellate and azooxanthellate scleractinians exhibit a wide variety of growth forms and exploit a wide range of marine habitats. Morphogenetic analyses of extant corals provide environmental insights into how and why specific corals live in particular niches.

A number of studies have been conducted on the colony forms of corallites (Graus and Macintyre, 1976; Geister, 1977; Chappell, 1980; Merks *et al.*, 2004; Chindapol *et al.*, 2013; Filatov *et al.*, 2010). Most, if not all, of these studies focus on colonial growth and morphological variations as related to extrinsic environmental factors, such as light levels, wave power, and nutrient flows and levels, whereas the effects of intrinsic factors have been largely ignored. However, in modular organisms, intrinsic factors, such as the size of zooids, the angle between two branches, and the frequency of branching, can affect the growth forms and the modes of life (Niklas and Kerchner, 1984; Ryland and Warner, 1986). These affect the ways in which the organisms obtain nutrients efficiently or resist the flow of water.

Recently, it was noted that colonial azooxanthellate dendrophylliid Scleractinia bud according to specific developmental regularities, although a variety of different growth forms are observed in nature (Sentoku and Ezaki, 2012). The morphologies of azooxanthellate scleractinians, i.e., those without symbiotic zooxanthellate, are less dependent on light conditions, and thus fewer factors need to be considered in the formation of colonies. Specific developmental regularities that govern budding in Scleractinia include the following: (1) offset corallites always occur around the sites of one, two, or four primary septa, other than the two directive septa; (2)

the directive septa of offset corallites tend to be oriented nearly perpendicular to the growth direction of parental corallites; (3) offset corallites grow diagonally upwards; and (4) these regularities are valid in axial and subsequent corallites throughout all generations of the colony.

Several previous works have simulated the morphogenesis of modular animals (Honda, 1971; Cheetham and Hayek, 1983; Niklas and Kerchner, 1984). These studies used simple, vector-based models with few parameters. Computer simulation analyses offer a variety of advantages to the study of colonial scleractinian morphology, including the ability to (1) explore morphological variations in slow-growing organisms; (2) generate a wide range of theoretically possible morphologies, regardless of their actual existence in nature; and (3) easily quantify properties such as volume, number of corallites, and other measurable factors, and so on. In this study, a voxel model was used in addition to a vector model. The vector model is used to trace the growth of a corallite, and the voxel model is used to judge the possibility of growth for each corallite and to visualise the generated model. Voxel data have a simple data structure and are thus easily manipulated. They can be processed by various software programs, easily divided or combined, and handle continuous variables that are difficult to express in numerical formulae. Moreover, voxel models are suitable for visualizations. In a voxel-based model, dividing or slicing is far easier than with a vector-based model. One advantage of using voxels is that it is possible to assign color information to each cell. However, voxel data files are large, and the accuracy of a voxel-based model is largely determined by the number of cells used in the data set. This can be solved by using both voxel and vector models in a high-performance environment with sufficient memory and CPU performance.

In this study, morphogenesis in colonial dendrophylliids was modelled by taking developmental regularities into account so as to understand how intrinsic growth factors affect the morphologies of the colonial growth forms. First, we simulated a wide variety of dendrophylliid colonial forms that include two morphologically distinct patterns (the branching form of *Dendrophyllia arbuscula* and the massive form of *Tubastraea coccinea*). Next, we explored the causes of the different growth forms, under the same regularities. Finally, the relationship between the regular modes of budding and the various modes of growth was carefully evaluated in terms of the adaptive strategies of corals in different habitats.

Materials and methods

Family Dendrophylliidae

The family Dendrophylliidae comprises 29 genera and 364 species, of which 20 genera and 166 species are extant. Modern dendrophylliids are distributed worldwide (except Antarctica) and in a wide range of water depths (0–2165 m); their wide distribution is related to adaptive variations in their growth forms. The dendrophylliids are characterized by irregularly porous theca, through which extratentacular mesenterial extensions protrude, as a result of a synapticulothecated wall. The upper and axial margins of the lower cycles of septa are smooth. Septa are generally arranged according to the Pourtalès plan (Cairns, 1994, 2001).

The specimens used in this study are registered in the Department of Geosciences, Graduate School of Science, Osaka City University, Japan (OCU 6637, 6639, 6660). They were collected at water depths of 0–60 m in the sea off Minabe (Wakayama Prefecture) and off Minamiise (Mie Prefecture) in southwestern Japan.

Reproduction of azooxanthellate scleractinians

Azooxanthellate scleractinians, in which symbiotic zooxanthellate are absent, acquire nutrients by capturing food particles (such as plankton) or by absorbing dissolved nutrients. Azooxanthellate growth forms are, therefore, less influenced by light levels. Of course, their colonial forms can still be influenced by extrinsic environmental factors, such as wave power, nutrient flows, and neighbouring organisms. Colonial scleractinians exhibit both sexual and asexual reproductive processes. Asexual reproduction is generally considered to occur either by budding or division. Dendrophylliids mainly reproduce by means of budding.

During budding, a "parent" corallite gives rise to a set of four "daughter" corallites, which, in turn, produce "granddaughter" corallites, and so on. In dendrophylliids, septa are arranged hexametrically in four cycles. The six primary septa develop first, followed in succession by secondary, tertiary, and quaternary cycles of septa (Figure 1D). The two septa parallel to the greater calicular diameter (GCD) are called directive septa.

Details of the growth model

The model proposed here is based on that of Niklas and Kerchner (1984), and it was further developed by adding a local reference system, such as was used in the growing tube model of Okamoto (1988). The present model is defined by three parameters: the branching angle (θ), the orientation of the branching plane (φ), and the budding interval (i), as shown in Figure 2. θ (in degrees) is the angle between the growth vectors of the

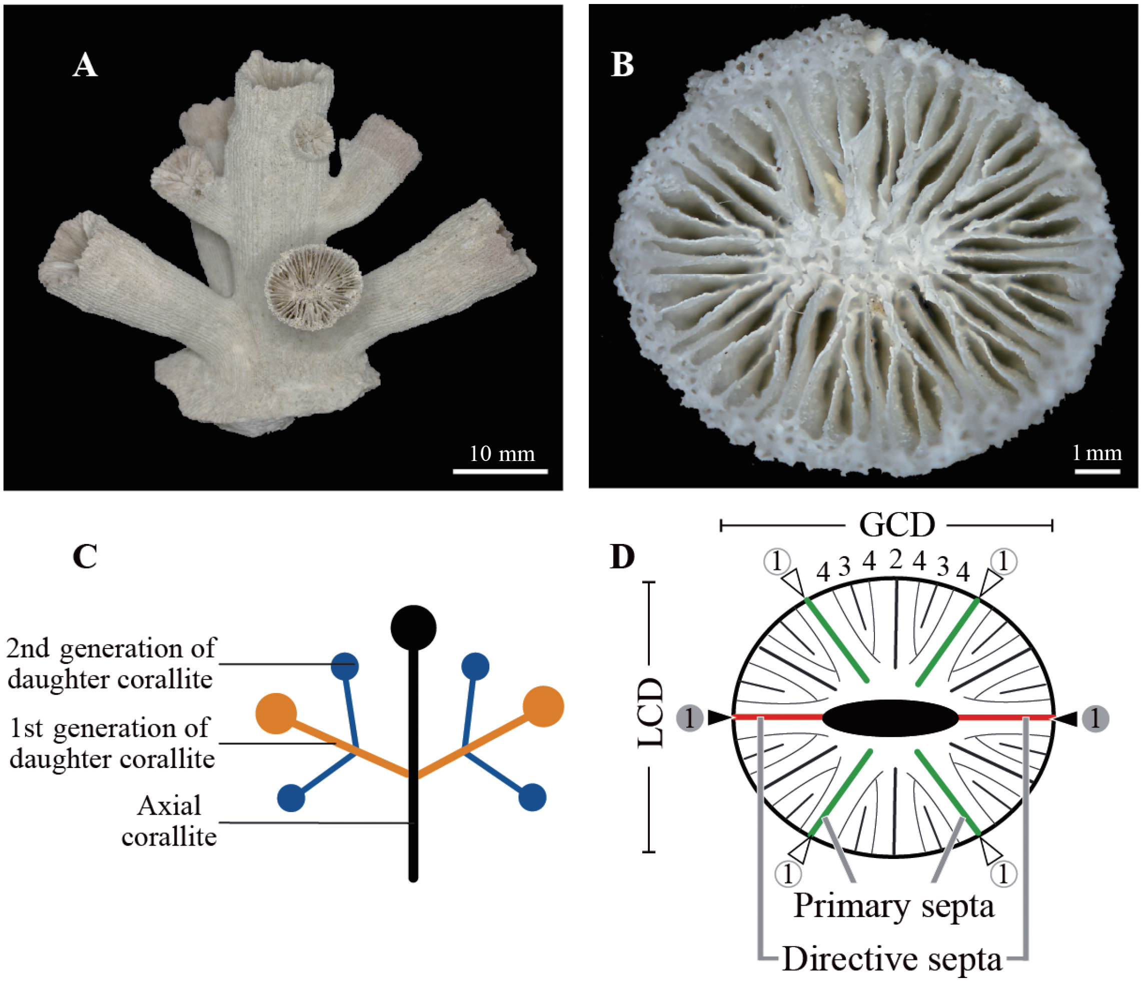


Figure 1. A corallum of *Dendrophyllia arbuscula* and the names of each part. **A,** a corallum of *Dendrophyllia arbuscula* (OCU6639); **B,** a single calyx of OCU6639; **C, D,** schematic diagrams of a monopodial branching pattern and the structure of a calyx (after Sentoku and Ezaki, 2012).

parent and daughter corallites; based on the developmental regularities of colonial azooxanthellate dendrophylliid Scleractinia noted in Sentoku and Ezaki (2012), θ was limited to the range 0°–90°. φ (in degrees) is defined as the angle between the branching plane and the plane of the directive septa of the parent corallite; the range of φ was limited to 0°–90° because of the symmetry of the nondirective primary septa. i is the distance between the current and the most recent budding points along the parent corallite (or the distance between the budding point and the basal point in the case of an initial budding). i was normalized with respect to the radius of the founder axial corallite and is thus expressed as a relative value. The initial radius of a set of budding corallites is smaller than the radius of their parent corallite. The radius of each corallite was set to increase at each step by 0.02 times the radius of the axial corallite, until it reaches the same radius as the axial corallite. The ranges of φ and i were limited by the ratio of the initial radius of the daughter corallites to the radius of their parent corallite because of the thickness of the base of the daughter corallites. In the present study, the initial radius of the budding corallites was fixed to be 0.7 times the radius of the axial corallite; thus, the range of φ was 34.99° to 55.01°, and i was greater than 1.4. A theoretical morphospace of dendrophylliids was constructed with various values of θ, φ, and i.

In the computer simulation, a coordinate system of three vectors was installed at the growing edges of each corallite. This system served as an independent and locally defined reference system, and it was based on the model of Okamoto (1988). The origin of each coordinate

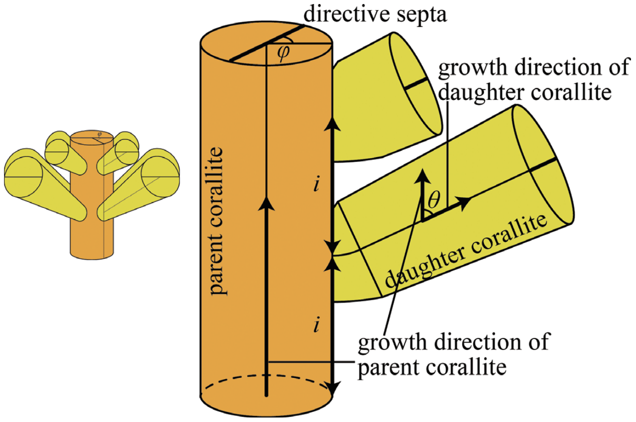
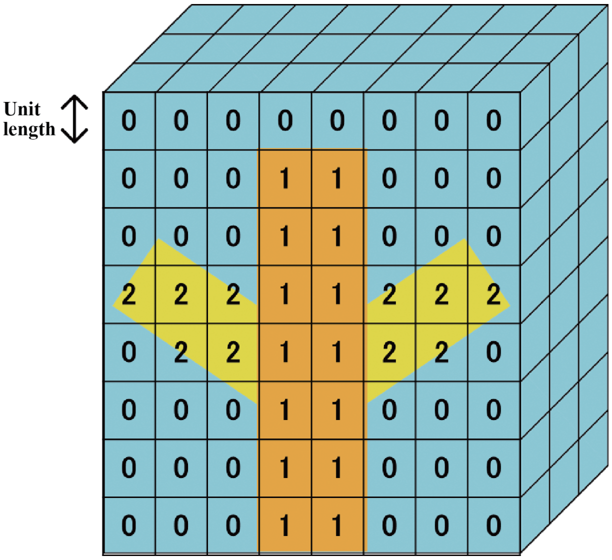


Figure 2. Schematic diagram showing the rationale for the theoretical model of formation of a monopodial coral colony. The growth of each cylindrical corallite and the budding of daughter corallites produce a hypothetical colony. The geometric pattern is determined by the branching angle (θ), the orientation of the branching plane (φ), and the budding interval (i).



0	0	0	0	0	0	0	0
0	0	0	1	1	0	0	0
0	0	0	1	1	0	0	0
2	2	2	1	1	2	2	2
0	2	2	1	1	2	2	0
0	0	0	1	1	0	0	0
0	0	0	1	1	0	0	0
0	0	0	1	1	0	0	0

Figure 3. Schematic diagram illustrating a voxel model. The values assigned to each voxel represent the generation of the corallite. The unit length and unit volume are defined in terms of the side length and volume of the voxel.

was placed at the center of the circular growing margin of the corallite (“growing point”). The **Z** vector (“growth vector”) points toward the direction of growth of the corallite, the **X** vector is perpendicular to **Z** and is parallel to the directive septa, and the vector **Y** is perpendicular to both **X** and **Z**. Morphogenesis and the colonial forms of dendrophylliids were simulated in a 400 × 400 × 400 three-dimensional voxel space (Figure 3). The side length of one voxel is equal to the unit length of the vector space, and thus the volume of one voxel is equal to the unit volume of the vector space.

The axial corallite starts to grow at the central voxels on the bottom plane of the defined space. In this model, the ground surface is represented by the bottom of the voxel space. Each corallite continues to grow until its growing edge comes in contact with either another corallite or the bottom of the voxel space. Growth of each corallite is accompanied by occasional buddings that occur at intervals of i. At each step of the simulation, the following steps are taken for each corallite to determine whether growth and/or budding occur. The growth of the corallite is terminated if the voxels adjacent to the growing face are already occupied by another corallite (i.e., a preexisting individual interferes with the growing corallite) or the growing face of the corallite in question already occupies the bottom voxel in the voxel space. When the distance between the growing point and the basal point reaches i, the daughter corallites bud for the first time, and subsequent buddings occur each time the distance between the growing point and the most recent previous budding point reaches i. A new coordinate system is then installed for each of the new daughter corallites, and the origins are placed at the growing point of the parent corallite. The above procedure is repeated until a preset number of steps have been completed. During this process, it is possible to visualize the voxel data by using the Virtual Reality Modelling Language (VRML: http://www.web3d.org).

In the simulations, the values of θ and ϕ were varied in the ranges of $0° \leq \theta \leq 90°$ and $35° \leq \varphi \leq 55°$, respectively, with increments of 5°; i was varied between 1.5 and 3.5 with increments of 0.5. The radius of the axial corallite was set to 10, and for each one, the amount of growth per step was set to unity. A total of 475 theoretical forms were generated, including variants that are not found in nature. The morphological properties of a colony were calculated for each hypothetical model as follows: (1) the volume of the colony, (2) the total number of terminated corallites, (3) the total number of unterminated corallites, and (4) the total number of branched corallites. The volume of a colony was defined as the total number of voxels occupied by several corallites. Secular changes in the three properties were monitored during the first 200 steps of each simulation.

Results

Several monopodial patterns observed in actual dendrophylliid colonies can be generated by using various

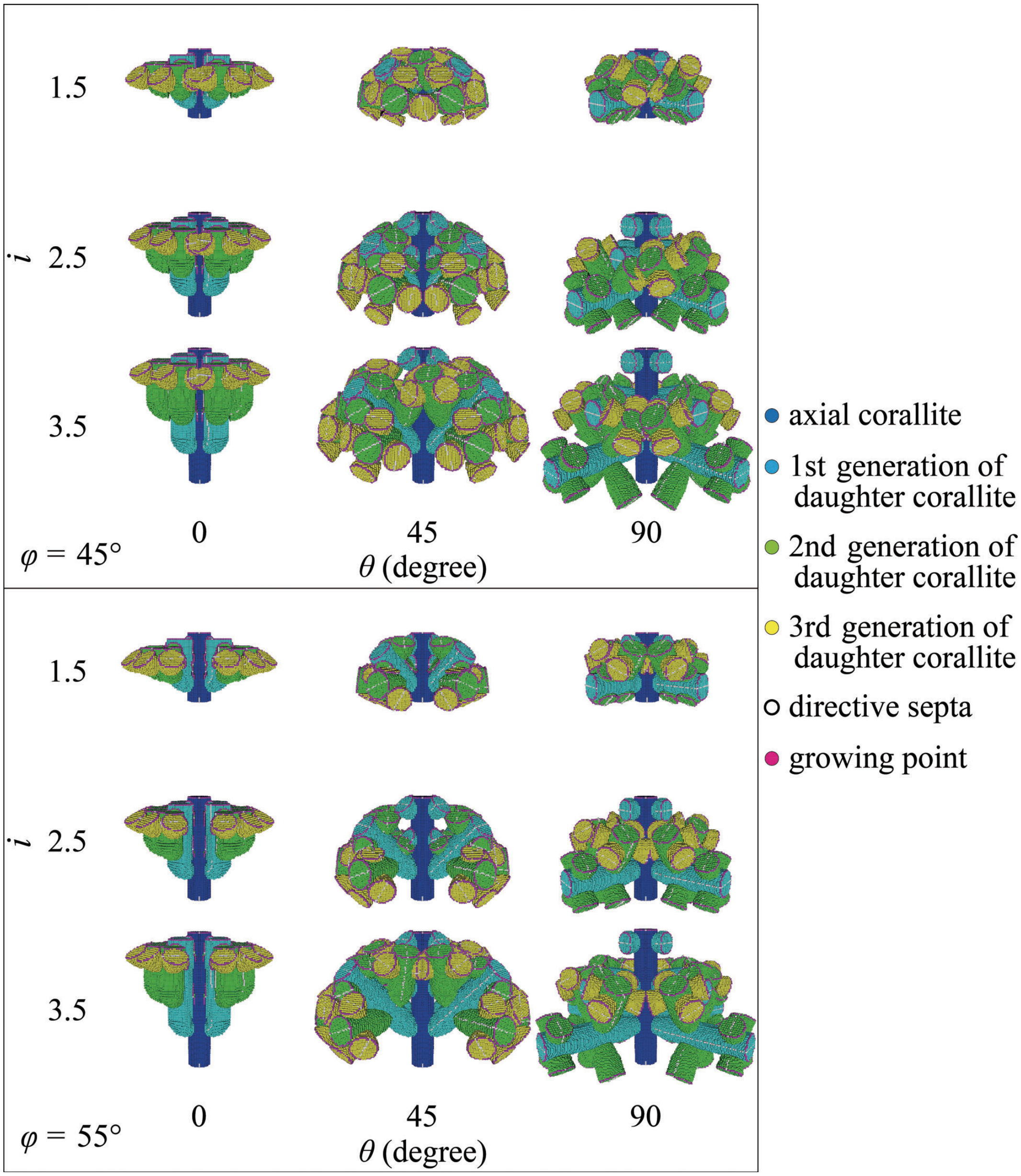


Figure 4. Theoretical morphospace composed of θ and i at φ values of 45° and 55°, showing selected examples of computer-generated colonies. Each model was obtained 10 steps after the budding of the daughter corallites of the third generation; the parameters were fixed throughout the simulation.

combinations of θ, φ, and i (Figure 4). The maximum number of generations was 14 when $i = 1.5$, and the minimum was 6 when $i = 3.5$. The lower the value of i, the more generations the generated colonies have. A cupulate form is produced when θ is close to 0, whereas the model produces a dome-shaped appearance when θ is large (Figure 4). Models with smaller values of i tend to have larger colonies. Within the allowed range of φ, it has only a small effect on the form of the colony. This suggests that the orientation of the branching plane is not an important factor in the morphological variation of dendrophylliids.

Figures 5 and 6 show secular changes in the morphological properties of a colony for θ equal to 10° or 65°, i equal to 1.5 or 2.5, and $\varphi = 45°$. The total number of corallites and the number of terminated corallites both

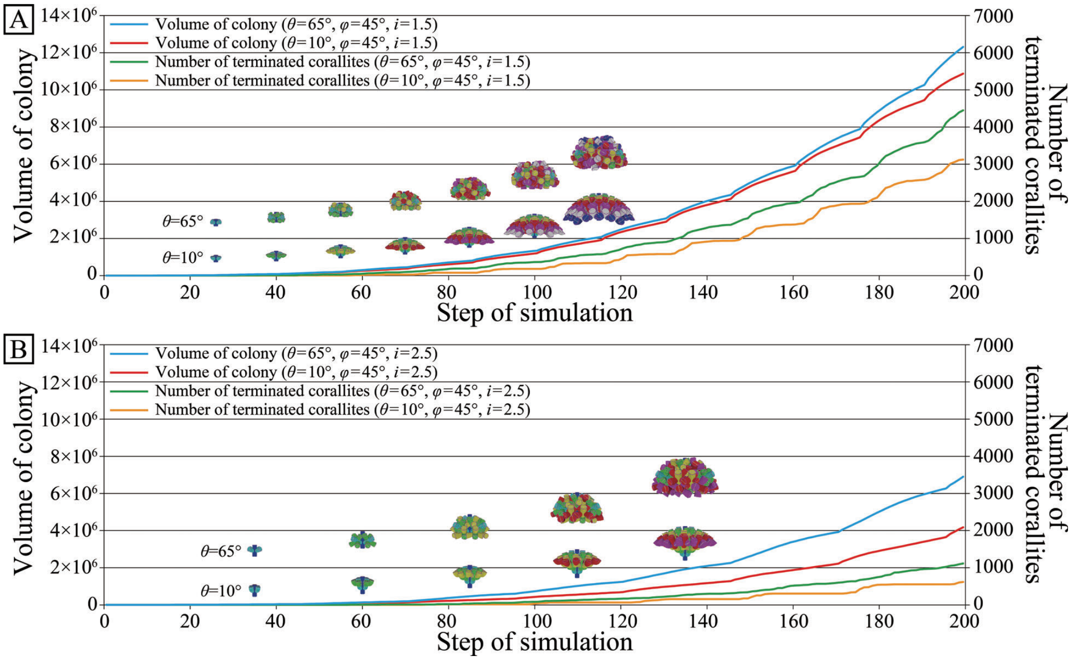


Figure 5. Secular changes in the volume of the colony and the number of terminated corallites during the first 200 steps of each simulation run, with examples of the colonial forms. θ =10° or 65°; φ = 45°; **A,** i = 1.5; **B,** i = 2.5.

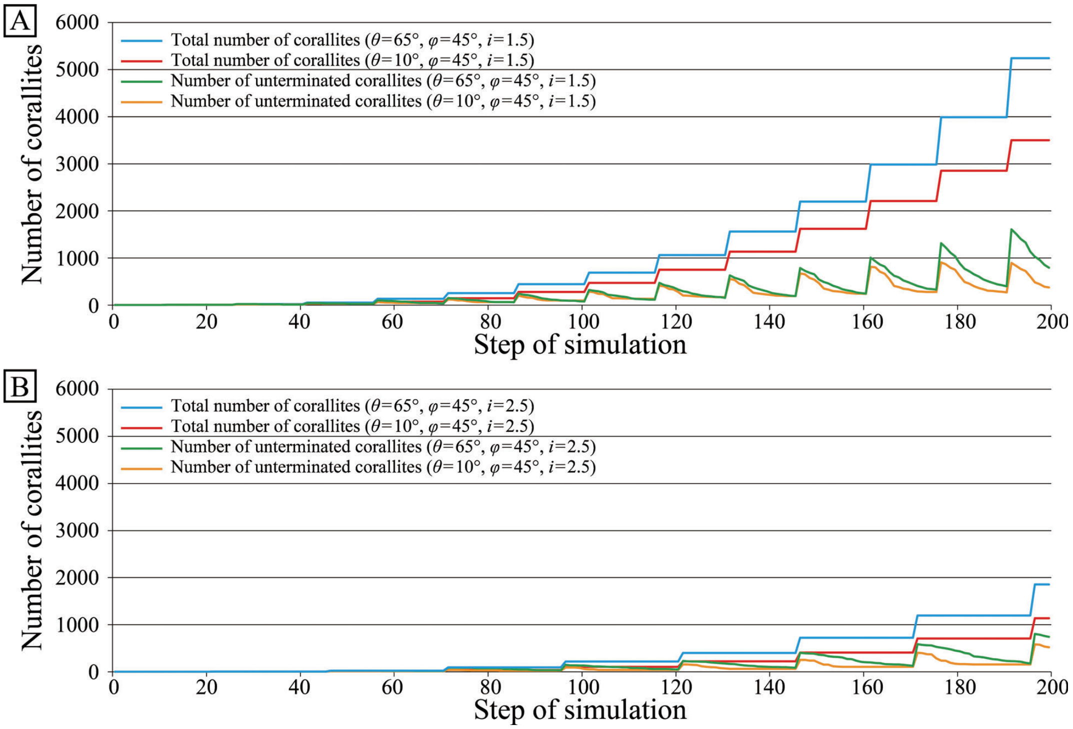


Figure 6. Secular changes in the total number of branched corallites and the number of unterminated corallites during the first 200 steps of each simulation run. θ = 10° or 65°; φ = 45°; **A,** i = 1.5; **B,** i = 2.5.

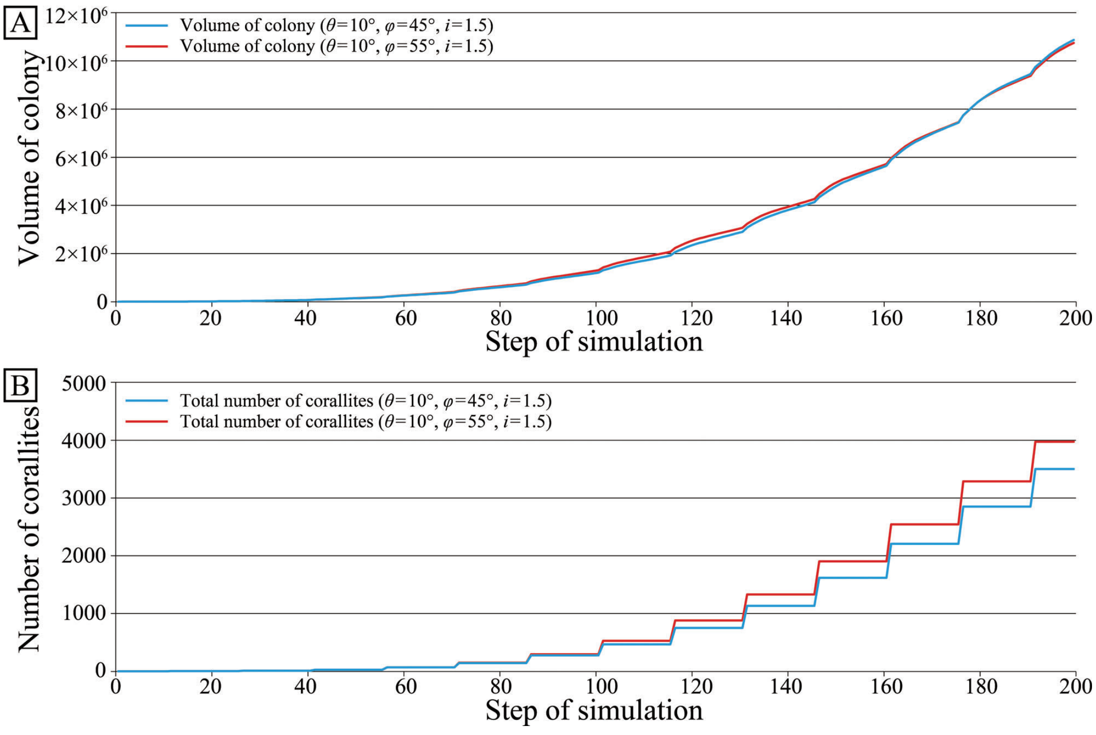


Figure 7. Secular changes in the volume of the colony (**A**) and the total number of branched corallites (**B**) during the first 200 steps of each simulation run. $\theta = 10°$; $\varphi = 45°$ or $55°$; $i = 1.5$.

increase with time. The number of still growing corallites gradually rises with their repeated increasing and decreasing according to time proceeding. For fixed values of φ and i, the volume of a colony with $\theta = 65°$ is larger than that of one with $\theta = 10°$, and this is independent of the stage of growth (Figure 5). This difference is more conspicuous when $i = 2.5$ (Figure 5B) than it is when $i = 1.5$ (Figure 5A). A comparison between the results with $i = 1.5$ and $i = 2.5$ indicates that the growth rate of the volume is lower for a larger value of i. These results suggest that a shorter budding interval results in a larger colony, particularly when the branching angle is large. Reducing θ or increasing i reduces the total number of branched corallites, as well as the numbers of terminated and unterminated corallites (Figures 5 and 6).

Figures 7 and 8 indicate the secular changes in the morphological properties of a colony for various values of the parameters ($\varphi = 45°, 55°$; Figure 7: $\theta = 10°$, $i = 1.5$; Figure 8: $\theta = 65°$, $i = 2.5$). The different values of φ result in only slight differences in the volume of a colony and its growth rate (Figures 7A and 8A), particularly when $\theta = 10°$ and $i = 1.5$. The total number of branched corallites was consistently larger when $\varphi = 55°$ than when $\varphi = 45°$ (Figures 7B and 8B).

In sum, both the volume of the colony and the number of corallites increase with increases in the branching angle or decreases in the budding interval. A large number of corallites can be readily produced when the branching plane rotates far from the directive septa of the parent.

Discussion

In such a massive growth form as *Tubastraea coccinea*, corallites are densely packed so as to form a robust colony. Chappel (1980) mentioned that globose or encrusting coral colonies are assembled under high hydrodynamic stress or relatively high subaerial exposure. *T. coccinea* inhabits shallower waters than does *Dendrophyllia arbuscula* (0–100 m and 40–240 m, respectively), where wave energy may be higher. The most effective way to form a massive colony is to adopt a small branching angle and a short budding interval (Figure 9A, B). This condition keeps the parent and its daughter corallites close to each other, resulting in the formation of a densely packed colony. However, this condition tends to cause space conflicts between the parent and daughter corallites and to obstruct further bud-

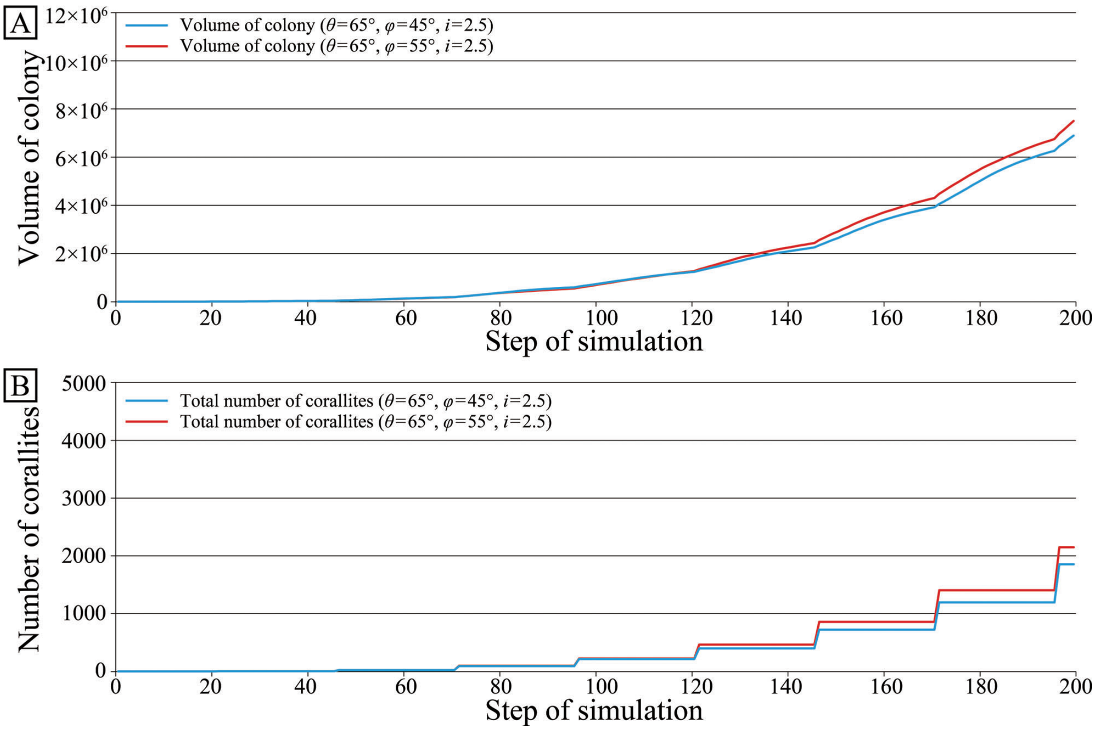


Figure 8. Secular changes in the volume of the colony (**A**) and the total number of branched corallites (**B**) during the first 200 steps of each simulation run. $\theta = 65°$; $\varphi = 45°$ or $55°$; $i = 2.5$.

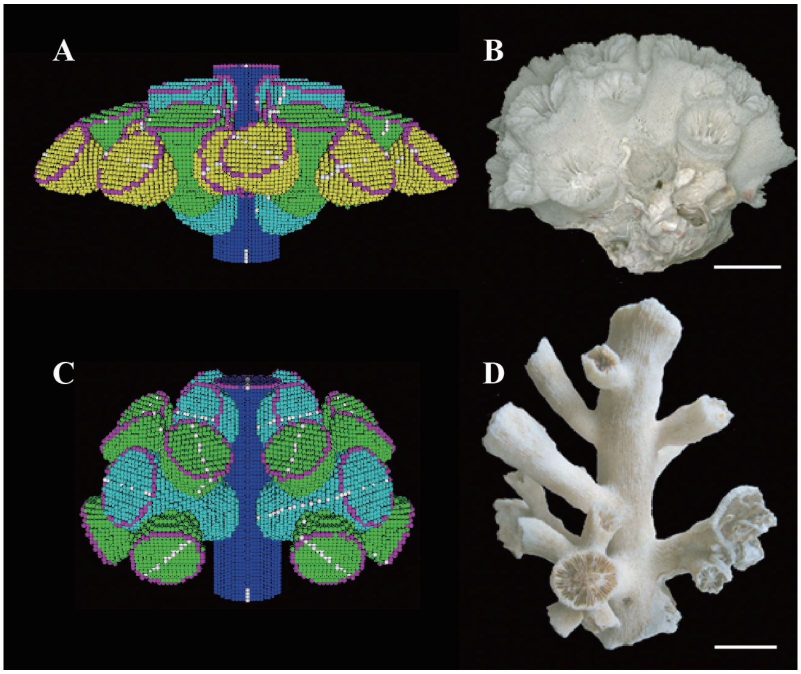


Figure 9. Selected examples of computer-produced colonies at the 50th step of a simulation (**A, C**) that mimic extant dendrophylliid scleractinians (**B, D**). **A,** $\theta = 10$, $\varphi = 45$, $i = 1.5$; **B,** *Tubastraea coccinea* (OCU6660), an example of a massive colony; **C,** $\theta = 65$, $\varphi = 45$, $i = 2.5$; **D,** *Dendrophyllia arbuscula* (OCU6637), an example of a branching colony. Scale bar = 10 mm.

ding from the parent and its daughters. In addition, a colony with a small branching angle tends to have a smaller volume and fewer corallites (Figures 5 and 6).

In contrast, a large branching angle with long budding intervals tends to produce a loosely packed branching form with a small number of corallites, such as is typically observed in *Dendrophyllia arbuscula* (Figure 9C, D). This branching form appears to be less robust than the massive form. However, the larger branching angle reduces the risk of conflicts among the parent and its descendants, allowing continuous growth throughout the colony. Indeed, a terminated corallite is rarely observed in *D. arbuscula*, at least in a relatively small colony. In addition, a long interval between buddings permits a parent corallite to utilize more resources for its own growth. This explains one of the reasons that *D. arbuscula* has corallites that are relatively large compared to those of the other colonial dendrophylliid corals.

The possible range of orientations of the branching plane is constrained by the initial thickness of the corallites. However, the effect of the orientation on the basic geometry of the colony is limited, even if the corallites are thin enough. Since a set of four daughter corallites buds simultaneously, the theoretical range of the rotation angle φ is restricted by the symmetry with respect to $\varphi = 45°$ (ignoring the orientation of the directive septa and considering only the branching pattern).

By regulating the values of only two parameters, we obtain both branching and massive growth forms for dendrophylliids; these have notably different physical and ecological traits, even when we place rigid constraints on the development of budding. This diversity in the character of the colonies allows them to adapt to a variety of habitat conditions. However, in nature, we see many more variations in colonial dendrophylliid corals (such as dichotomous and sympodial branching) that cannot be fully generated by the theoretical model proposed in this study. Other controlling factors (e.g. density of nutrients, water flow, and sedimentary conditions), which were omitted for simplicity in the present model, might affect the growth and morphogenesis of corallites. Further study is required to decipher other possible parameters that might affect the morphologies and morphogenesis of a whole group of dendrophylliid corals.

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