

# Branching and Self-Organization in Marine Modular Colonial Organisms: A Model

Juan Armando Sánchez,<sup>1,\*</sup> Howard R. Lasker,<sup>1,†</sup> Erivelton G. Nepomuceno,<sup>2,‡</sup> J. Dario Sánchez,<sup>3</sup> and Michael J. Woldenberg<sup>4,§</sup>

1. Department of Biological Sciences, University at Buffalo (State University of New York), Buffalo, New York 14260;
2. Departamento de Engenharia Elétrica, Universidade Federal de São João del Rei, Pça. Frei Orlando, 170, 36307352, São João del Rei, Minas Gerais, Brazil;
3. Departamento de Matemáticas, Universidad Nacional de Colombia, Bogotá, Colombia;
4. Department of Geography, University at Buffalo (State University of New York), Buffalo, New York 14260

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**ABSTRACT:** Despite the universality of branching patterns in marine modular colonial organisms, there is neither a clear explanation about the growth of their branching forms nor an understanding of how these organisms conserve their shape during development. This study develops a model of branching and colony growth using parameters and variables related to actual modular structures (e.g., branches) in Caribbean gorgonian corals (Cnidaria). Gorgonians exhibiting tree-like networks branch subapically, creating hierarchical mother-daughter relationships among branches. We modeled both the intrinsic subapical branching along with an ecological-physiological limit to growth or maximum number of mother branches ( $k$ ). Shape is preserved by maintaining a constant ratio ( $c$ ) between the total number of branches and the mother branches. The size frequency distribution of mother branches follows a scaling power law suggesting self-organized criticality. Differences in branching among species with the same  $k$  values are determined by  $r$  (branching rate) and  $c$ . Species with  $r \ll c$  had a sigmoid logistic-like growth with a long asymptotic period before reaching  $k$ . Gorgonians exhibit  $c$  and  $r$  values in the range of the conditions for a stable equilibrium ( $c > r/2$  or  $c > r > 0$ ). Ecological/physiological constraints limit growth

without altering colony form or the interaction between  $r$  and  $c$ . The model described the branching dynamics giving the form to colonies and how colony growth declines over time without altering the branching pattern. This model provides a theoretical basis to study branching as a simple function of the number of branches independently of ordering- and bifurcation-based schemes.

**Keywords:** branching growth, treelike networks, modular organisms, self-organization, gorgonian coral, octocoral, colony development.

Branching networks are present in structures ranging from the tiniest vessels in an insect wing through the continental scales of the Amazon or Mississippi rivers systems. Furthermore, organisms such as modular marine colonies (e.g., sponges, corals, bryozoans, and hydroids) are themselves branching structures (Waller and Steingraeber 1985). Growth, resource acquisition, life-history traits, and fitness are all functions of colony growth, shape, and size among modular organisms (Hughes 1983; Hughes et al. 1992). Despite the relevance and universality of branching in modular colonial organisms, there have not been attempts to develop a generalized description of the dynamics of branching, nor is there an understanding of how these organisms maintain their form as they grow (see reviews in Buss 2001; Kaandorp and Kübler 2001; Lasker and Sánchez 2002; Rinkevich 2002). While the models that have been used to date successfully describe form, they do not necessarily lend themselves to characterizations of the development of that form, that is, growth. Similar forms exist among a wide array of other taxa, most notably plants, and again a wide variety of models exist that can generate observed differences in form but do not mimic the growth process (Waller and Steingraeber 1985; Room et al. 1994; Collado-Vives 1997; and Prusinkiewicz 1998). This study develops a model of branching and colony growth using parameters and variables related to modular structures (e.g., branches) in Caribbean gorgonian corals (Cnidaria). The model is based on empirical observations and describes growth as a self-organized process that can be characterized using a few simple parameters. The model uses the simple mode of branching to give form to colonies

\* Present address: National Institute of Water and Atmospheric Research, P.O. Box 14-901, Kilbirnie, Wellington, New Zealand; e-mail: j.sanchez@niwa.co.nz.

† Corresponding author; e-mail: hlasker@buffalo.edu.

‡ E-mail: nepomuceno@ufsj.edu.br.

§ E-mail: geomike@acsu.buffalo.edu.

of gorgonian octocorals and the process attenuating their colony growth through time without altering the branching pattern.

Fundamental to the dynamics of branching is the process of branching itself. Many models and descriptions of branching implicitly characterize the process as one of bifurcation, where a single branch divides into two “sister” branches. Although there are some suggested cases of branching by bifurcation in cheilostome bryozoans (Cheetham 1986) and primitive planktonic graptoloids (C. E. Mitchell, personal communication), examination of colony form and sequential observations on the branching of modular colonial organisms such as gorgonian corals (*Pseudopterogorgia bipinnata*) show that the colonies branched subapically, generating hierarchical mother-daughter relationships among branches (fig. 1D; fig. 2A, 2B; see also Lasker and Sánchez 2002; Sánchez 2002). This pattern occurs among most branching cnidarians as well as most plants (see review in Prusinkiewicz 1998) and fungi (Watters et al. 2000). This observable pattern suggests a different mechanism of branching as opposed to bifurcation.

Branching by bifurcation in noncolonial biotic systems as well as in river systems has received considerable theoretical attention. Ordering systems, which date back to Keill (1708), have been used to describe the topology of branching systems (see Woldenberg 1997). In all of these systems, branches are assigned an order on the basis of their relationship with the branches to which they connect. A variety of different systems have been used to describe biotic systems, including those of Horton (1945), Strahler (1952), Tokunaga (1978), and Horsfield (1981; e.g., fig. 1). These differing systems have a variety of strengths and weaknesses (Horsfield and Woldenberg 1986; Woldenberg et al. 1993). An attraction of these ordering systems is that they often generate relationships between number of branches and order, thus unifying size and colony form (Brazeau and Lasker 1988; Mitchell et al. 1993). However, excessive side branching precludes the use of Horton-Strahler ordering in pinnate corals (Sánchez et al. 2003a). While general patterns in branch number and length can be related to order among some systems (Turcotte and Newman 1996; Pelletier and Turcotte 2000), these patterns are not present in the branching and growth of modular marine organisms such as Caribbean gorgonian corals (Sánchez 2002; Sánchez et al. 2003a), in part because branching patterns do not follow the bifurcation-based process assumed in most ordering systems. The model we present here is based on subapical branching, and although patterns of branch order may be generated as the colony develops, the model does not rely on any schema of branch ordering to predict growth.

An equally important aspect of branching is what con-

trols and limits colony growth, which ultimately will set maximum sizes and branching events. A common pattern of colony growth and development, observed in several marine modular organisms, is that the rate of module and branch production (or growth) decreases with size and age. Some modular organisms have plastic attenuating growth (Sebens 1987). Complete observations on the colony growth kinetics of the branching hydroid *Campanularia flexuosa* have shown that there is a decline in module production as size increases (Stebbing 1981). After growth ceased, those hydroid colonies kept replacing hydranths without becoming senescent. Interestingly the module production rate of *C. flexuosa* through time exhibited cyclic nonlinear behavior, always decreasing after a high peak (Stebbing 1981, figs. 11, 12). Kaufmann (1981) developed a method to fit growth curves to the growth of modular organisms and fit growth data from the encrusting bryozoan *Schizoporella biaperta* to Gompertz growth curves (e.g., sigmoid or logistic like). Although previous observations and modeling approaches suggested the presence of logistic-like behaviors in the development of modular organisms, they do not provide a mechanism of branching or explain how the development is related to form, which are two of the goals for the model presented here.

Colony development in gorgonian corals has also been documented to stop or decrease in a determinate fashion as the colonies reach a certain size. Branch production and elongation of the Pacific gorgonian coral *Muricea californica* decreases as a function of height (Grigg 1974), and sea whip gorgonians (*Leptogorgia* spp.) from the Gulf of Mexico also exhibit reduction of branch growth with height (Mitchell et al. 1993). Colonies of the Mediterranean gorgonian coral *Paramuricea clavata* exhibit size-specific decelerating branching (Coma et al. 1998). Similarly, Lasker et al. (submitted), in a survey of the Caribbean gorgonian *Pseudopterogorgia elisabethae*, showed how individual branches stop growing after 1–2 yr and branching decreases as colony height increases. Growth of the Mediterranean sea fan *Eunicella clavolinii* fits sigmoid growth models (Velimirov 1975), and growth of the deep-sea soft octocoral *Anthomastus ritteri* follows a sigmoid Gompertz growth trajectory (Cordes et al. 2001). Consequently, it is reasonable to think that if colonies decrease branching once they reach a certain size, there could be a fixed maximum number of branches in a colony. These observations also suggest a sigmoid- or logistic-like growth trajectory, which must be met by the predictions of a realistic model of branching.

In this article, we present a model depicting the dynamical behavior of branching throughout colony development. The model incorporates both branching based on self-organization and ecological/physiological constraints. Although the physiological processes that proximally con-

Control branching are still unknown, we wish to show how simple parameters that characterize the branching process can interact dynamically with the environment and preserve colony form throughout development. The goals of the study are to examine the branching process in modular organisms using gorgonian corals as model systems, to identify critical parameters for branching dynamics, and to propose a model characterizing that dynamic. The model is not meant to explain the mechanistic or external controls on branching but rather to enhance our understanding of the overall dynamics of branching. A clear characterization of those dynamics can then provide the basis for investigating the processes controlling branching and for determining the extent to which the same processes operate across taxa and colony forms.

### Branching in Modular Organisms

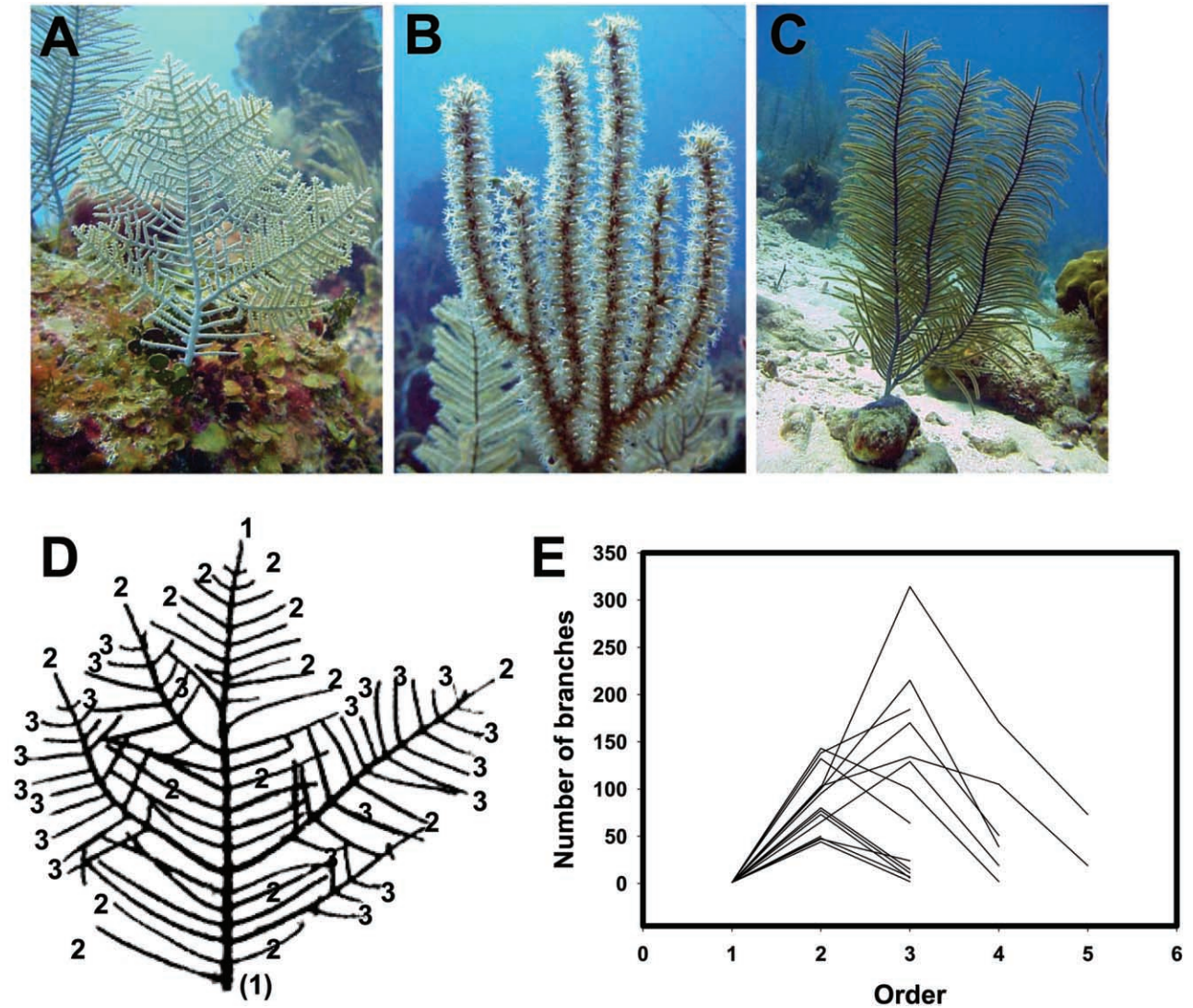
We observed the branching process using gorgonian corals as study systems. Gorgonian corals are present in all of the world's oceans and are the dominant macrofauna on many Caribbean reefs (Sánchez et al. 1998). Gorgonians are octocorals (Cnidaria) containing a semirigid and flexible scleroproteinaceous axis. They produce multibranching treelike networks up to several meters tall and generate branching forms that can be reticulate (sea fans), alternate or pseudodichotomous (candelabra- and sausage-like forms), or pinnate (sea feathers; Bayer 1961, 1973; fig. 1A–1C). We observed gorgonian corals growing and noted that mother branches add daughter branches at approximately fixed distances (or internodes) below the mother branch tip (fig. 2A, 2B). Among pinnate forms, some daughter branches, the pinnules, eventually gave rise to their own daughter branches, but most daughter branches remained simple side branches on a mother branch. Observations of 261 colonies of the gorgonian coral *Pseudopterogorgia elisabethae* over a period of two years (Lasker et al., submitted) indicate that daughter branches throughout the colony can turn into a mother branch.

Characterization of branch order based on “generation” (i.e., daughter, mother, grandmother, etc.) did not exhibit fixed branching ratios. A plot of the number of branches versus order had a parabolic-like behavior, and the cumulative number of branches exhibited sigmoid- or logistic-like behavior (fig. 1D, 1E). This numerical behavior changed shape during colony development, and there does not appear to be a deterministic rule relating order and branch number as occurs in centripetal or centrifugal ordering and bifurcation schemes (Sánchez et al. 2003a). Although the order-branch number patterns reflect a similar species-specific form, the distribution of branches within each colony (i.e., locations of mother branches, number of daughter branches, etc.) is unique.

### A Model of Branching

Colonies from the gorgonians *Pseudopterogorgia bipinnata* (Gorgoniidae) and *Plexaura flexuosa* (Plexauridae) maintained a linear relationship with slope  $c$  between total branches and mother branches (fig. 3). These observations on multiple colony branch networks showed that the ratio between total and mother branches must be dynamically maintained by a balance between production of daughter branches on the existing mother branches and the transformation of old daughter branches to new mother branches when the ratio of total versus mother branches exceeds the value of  $c$ . Each time a mother branch produces a daughter branch, it moves the system (colony) away from a set value of the ratio,  $c$ . The ratio is readjusted back to  $c$  as mother branches are generated. Although we use  $c$  as a constant, when followed during development, this ratio will exhibit very small oscillations around its mean value as a product of these branching dynamics. It is assumed that  $c$  is related to a branching threshold and/or an intrinsic mechanism of branching that is species, colony, or form specific.

Population dynamics of modular organisms should be studied at the level of the intracolony module (Harper and Bell 1979). This will not only accurately describe the process of development but will also portray the form of modular organisms as a consequence of their internal modular population dynamics (Harper and Bell 1979). While gorgonians grow through the iterated replication of individual polyps, the functional module in their growth is the branch (Lasker and Sánchez 2002; Lasker et al., submitted). To describe the branching process dynamically, we model branching as a discrete recurrent process. Instantaneous models such as differential equations cannot realistically explain the process for systems in which variables change discretely (Case 2000). Among slow-growing modular organisms such as gorgonian octocorals, an instantaneous branching rate does not have clear meaning, and colony growth should be calculated over discrete periods of time (Goh and Chou 1995; Coma et al. 1998; Lasker and Sánchez 2002). The discontinuous nature of growth in gorgonian octocorals is illustrated by the growth rings that they produce in their scleroproteinaceous axis (Grigg 1974; Opresko 1974; Mitchell et al. 1993). Those rings indicate the presence of near-zero growth periods, which probably relate to winter or disturbed periods. Discrete models have been used to model colony development where the growing variables are a discrete function of the previous conditions, that is,  $X_{t+1} = f(X_t)$  (Kaandorp 1994). For a branching gorgonian, consider a population of  $S$  mother branches and  $N$  total branches (daughter plus mother branches). The colony develops from a primordial



**Figure 1:** A–C, Photographs of some gorgonian coral colonies in their natural environment, Carrie Bow Cay, Belize (15–20 m). A, *Gorgonia mariae*. B, *Eunicea laxispica*. C, *Pseudopterogorgia acerosa*. D, Colony of *Pseudopterogorgia elisabethae* (San Salvador, Bahamas) in which branches have been numbered based on the order of branching during colony growth. E, Number of branches per order, as depicted in D from 14 colonies of *P. elisabethae* photographed in the San Salvador, Bahamas (Riding Rock Reef, 1998, 17 m).

mother branch such that at  $t = 0$ ,  $S_0 = N_0 = 1$ . Under initial conditions, the number of branches per mother branch increases by  $r$  daughter branches after each iteration from  $t$  to  $t + 1$ , where  $r$  is the branching rate per mother branch. As the number of daughter branches increases with iterations (i.e.,  $t$  to  $t + 1$ ), the ratio of total branches ( $N$ ) to mother branches ( $S$ ) eventually reaches  $c$ . When that condition is reached, the colony generates a new mother branch. Those “mothers” in turn produce “grandchildren branches” with respect to  $S_0$ , and so on

(fig. 2A, 2B). Therefore, the further production of mother branches “avalanches” and has the recurrent form

$$S_{t+1} = S_t + \frac{S_t r}{c}$$

or

$$S_{t+1} = S_t \left( 1 + \frac{r}{c} \right). \quad (1)$$

Iterating equation (1) by discrete periods back in time to get the initial conditions  $S_0$  yields

$$\begin{aligned} S_t &= S_{t-1} \left(1 + \frac{r}{c}\right), \\ S_{t-1} &= S_{t-2} \left(1 + \frac{r}{c}\right), \\ &\vdots \\ S_2 &= S_1 \left(1 + \frac{r}{c}\right), \\ S_1 &= S_0 \left(1 + \frac{r}{c}\right). \end{aligned}$$

Then, multiplying member to member and eliminating common terms at both sides, we obtain

$$S_{t+1} S_t S_{t-1} \dots S_2 S_1 = S_t S_{t-1} S_{t-2} \dots S_1 S_0 \left(1 + \frac{r}{c}\right)^{t+1}.$$

We simplified to

$$S_{t+1} = S_0 \left(1 + \frac{r}{c}\right)^{t+1}$$

or

$$S_t = S_0 \left(1 + \frac{r}{c}\right)^t. \quad (2)$$

Since  $S_0 = 1$ ,

$$S_t = \left(1 + \frac{r}{c}\right)^t.$$

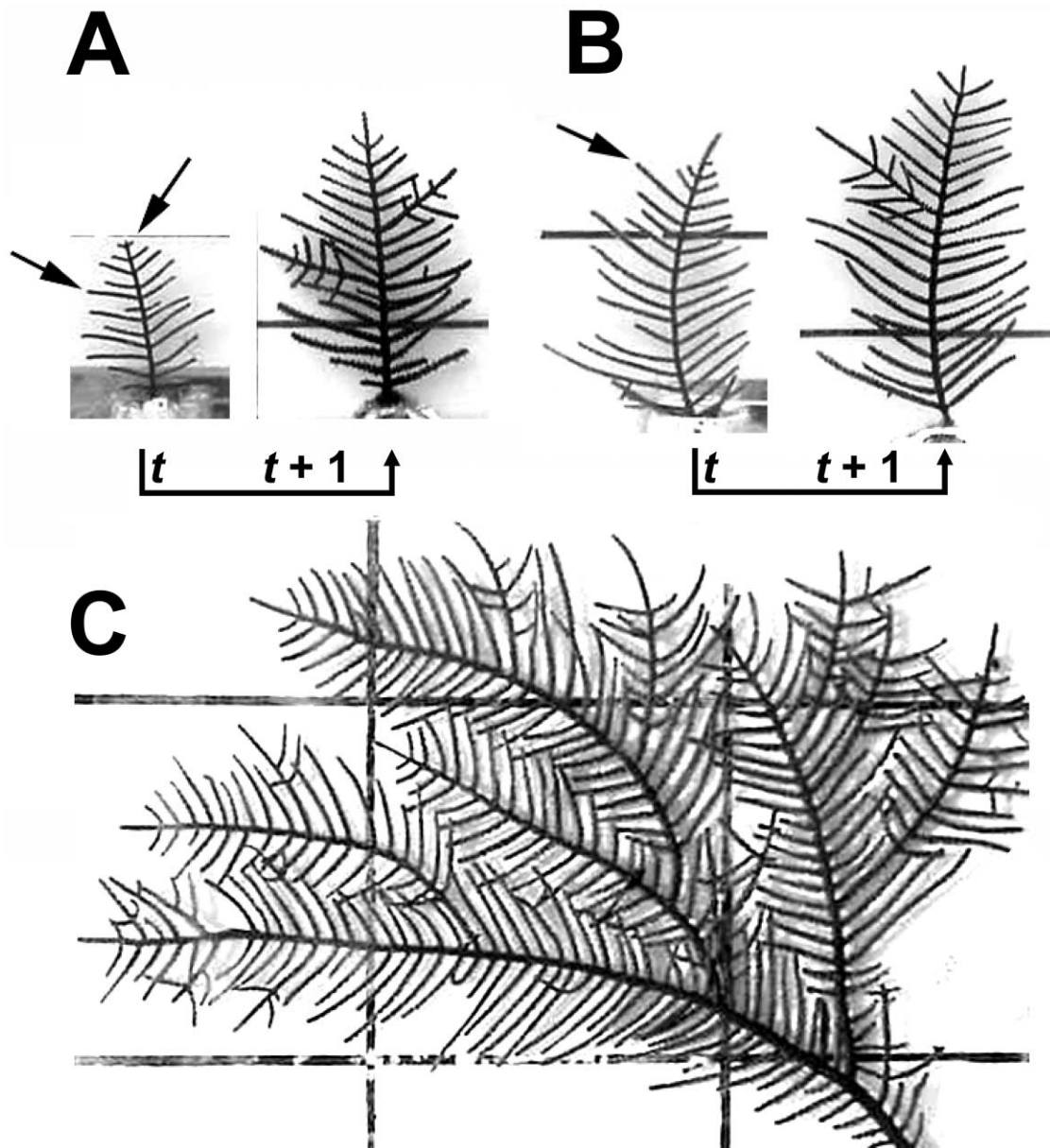
Expressions (1) and (2) describe a process of branching that produces mother branches in a self-organized process. Older mother branches will have more daughter branches and, accordingly, will have more granddaughter branches. The relative number of daughter branches on recently started mother branches will be fewer compared with older mother branches because all of them have the same chance of branching at a given time. Numerically, a hypothetical species with  $r = 12$  and  $c = 20$  produced  $\sim 110$  mother branches after 10 iterations, and the frequency distribution of number of daughter branches per mother branch (assuming an increment of  $r$  daughter branches per mother branch after every iteration) follows a power law depen-

dence (fig. 4A, 4B). If branching is induced by a critical state, the size frequency distribution of daughter branches per mother branch ( $D$ ) will follow a scaling power law of the form  $D(n) \sim n^{-\tau}$ , where  $n$  is the frequency of  $D(n)$  daughter branches per mother branch and  $-\tau$  is a fractal exponent. Consequently, the number of mother branches of a given age increases exponentially as the branch size (i.e., number of daughter branches per branch) decreases. The frequency of mother branches from *P. bipinnata* and *P. flexuosa* had a very similar pattern to iterating expression (1) or (2). These species' growth patterns differ in quantitative ways that reflect their different fractal scaling powers ( $-1.6$  and  $-2.4$ ; fig. 4C, 4D). All the mother branches should increase/decrease branching at the same pace in order to maintain self-organization and form.

#### Limits to Growth

The “intrinsic” branching process described by expression (1) leads to exponential growth that never ends, yet colonies appear to have finite upper size limits. Indeed, most species descriptions include upper size limits (Bayer 1961; Sánchez 2001). The rapid growth that results from the continuing generation of mother branches and daughter branches may generate size-dependent allometric effects, such as branch interference affecting resource capture and growth rates (Kim and Lasker 1998). Consequently, it is reasonable to incorporate an additional parameter into the model that prevents colonies from growing indeterminately. The following model aims to reconcile the intrinsic process of branching as a self-organized criticality with ecological/physiological size-dependent constraints.

This approach shapes the branching process by including an ecological/physiological constraint that is analogous to logistic growth. The expression does not model the proximal mechanisms by which the constraints operate but instead predicts a reduction in branching as the number of mother branches reaches a maximum number,  $k$ . Although there is a centrifugal ordering involved in the process of colony development, the approach will focus on the production of branches only with the information of total–mother branch ratio ( $c$ ) and specific branching rate ( $r$ ), which are independent of ordering. Accounting for branch density-dependent constraints, the maximum number of mother branches,  $k$ , shapes the dynamic branching process into a logistic-like form. The upper size limit is based on the number of mother branches because empirical observations of branching suggest avoidance among the growing tips of mother branches (see similar example in bryozoans: Cheetham and Hayek 1983) and because daughter branches can be treated as appendices that are placed at relatively constant internodes along mother branches. Presumably, the largest naturally oc-



**Figure 2:** Photographs of living colonies of the gorgonian coral *Pseudopterogorgia bipinnata* (San Salvador, Bahamas). *A, B*, Examples of two young colonies in December 1999 ( $t$ ) and July 2000 ( $t + 1$ ); the arrows in  $t$  depict the daughter branches that turned into a new mother branch in  $t + 1$ . *C*, Adult colony showing multiple growing mother branches (grid  $10 \times 10$  cm). Branching observations were carried out at San Salvador, Bahamas, between December 1999 and July 2000 at Riding Rock Reef. Eight young colonies of *P. bipinnata* that still had a single apical (=mother) branch were attached to PVC tubes embedded in a concrete block as in Sánchez and Lasker (2004).

curing colonies of a population, which exhibit low (or asymptotic) branching, are in the neighborhood of  $k$ . The aim of the model presented here is to portray branching as a logistic-like dynamic process that is still dependent on the production of mother branches in the fashion empirically observed in expression (1). Under such circum-

stances we can modify a population discrete logistic equation of the form

$$S_{t+1} = S_t + \frac{S_t r}{c} \left( 1 - \frac{S_t}{k} \right). \quad (3)$$

Since there is an idealized ratio between mother ( $S$ ) and total branches ( $N$ ),

$$c = \frac{N_t}{S_t}, \quad (4)$$

we can calculate the relationship in terms of total branches ( $N$ ):

$$N_{t+1} = N_t \left( 1 + \frac{r}{c} - \frac{r}{kc^2} N_t \right). \quad (5)$$

### Fixed Points and Stability

To determine whether the model will generate a branching colony, including a limit to growth, we can examine the equilibrium points and stability of expressions (3) and (5). Determining the equilibrium points,  $S^*$ , for expression (3),  $S_{t+1} = S_t \Rightarrow$  fixed point; thus

$$S_t = S_t + \frac{S_t r}{c} - \frac{r}{ck} (S_t^2).$$

By algebraic transformations,

$$S_t \left( \frac{r}{c} - \frac{r}{ck} S_t \right) = 0.$$

That is,  $S_1^* = 0$  and  $S_2^* = k$ . To look at the stability of expression (3), we can evaluate the first derivative function, which, for higher dimensions, one takes the well-known Jacobian matrix  $|\mathbf{J}|$ :

$$\frac{\partial S_{t+1}}{\partial S_t} = \left( 1 + \frac{r}{c} \right) - \frac{2r}{ck} S_t.$$

It is clear that the value of the derivative depends on  $S_t$ . A good approach to see the stability is to see how the system behaves close to the fixed points. Thus, substituting the fixed points, we have for the trivial fixed point

$$\frac{\partial S_{t+1}}{\partial S_t} = \left( 1 + \frac{r}{c} \right).$$

For  $r$  and  $c > 0$  the fixed point 0 is unstable, because  $|1 + r/c| > 1$ . In terms of colony development, if the colony has one branch, it will grow until the maximum size ( $k$ ). And for the nontrivial point,  $S_t = k$ ,

$$\frac{\partial S_{t+1}}{\partial S_t} = \left( 1 + \frac{r}{c} \right) - \frac{2r}{c}.$$

For  $|\mathbf{J}| < 1$ , we have  $c > r/2$  and  $r > 0$  as conditions, or just  $c > r/2$ , since by definition  $r > 0$ . Conducting analysis in terms of the total number of branches  $N$  using expression (5), consider the following map:

$$N_{t+1} = F(N_t).$$

The variable  $N^*$  is a fixed point if

$$N^* = F(N^*).$$

The fixed points of a map usually constitute the starting point in the analysis of nonlinear systems (May 1976; Aguirre and Mendes 1996). Two additional procedures were also carried out to analyze branching in terms of total number of branches  $N$  using expression (5).

Let  $N^* = N_{t+1} = N_t$ . Replacing  $N^*$  in expression (5) yields

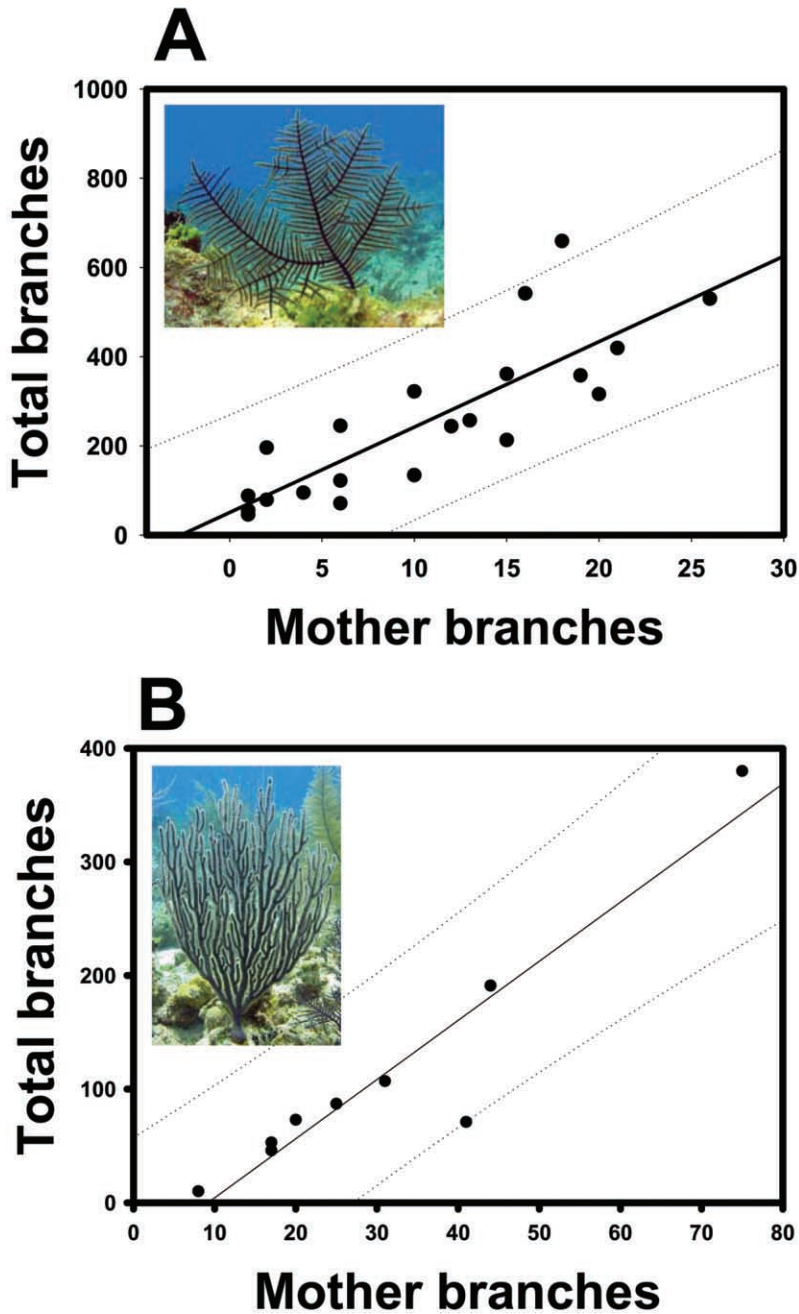
$$N^* = N^* \left( 1 + \frac{r}{c} - \frac{r}{kc^2} N^* \right),$$

which has two solutions:  $N_1^* = 0$  and  $N_2^* = kc$ , the trivial and nontrivial solutions, respectively. The biological meaning of the fixed points is straightforward. The trivial solution is the obvious fact that if a colonial organism has no branches it cannot grow. The nontrivial solution is the maximum size of the colony. While this result seems intuitive, the process leading to this final predictable result is based on relationships between growth and the numbers of mother and daughter branches that have not been considered previously. Using expression (4), it is also possible to determine the maximum number of mother branches, which is  $S^* = k$ .

Analyses of the stability of the fixed points address the question of behavior (i.e., colony growth) when the number of branches is close to one of the fixed points. Generally, a fixed point can be classified as stable, asymptotically stable, or unstable. Let  $N_i$  be a number close to the fixed point and  $\varepsilon_i$  be a small number, such as

$$N_i = N^* + \varepsilon_i.$$

If the sequence of points  $N_t, N_{t+1}, N_{t+2}, N_{t+3}, \dots$  converges to  $N^*$  after a finite number of steps, the fixed point is considered asymptotically stable. In contrast, if the sequence of numbers converges to a number of branches  $N_p$ , such as  $N_p \leq N^* + \varepsilon_p$ , the fixed point is stable. Oth-



**Figure 3:** Plots of the number of total branches versus mother branches per colony with mean and 95% predictive intervals indicated. *A*, From 20 colonies of *Pseudopterogorgia bipinnata* ( $c = 19$ ,  $r^2 = 0.69$ ,  $P < .05$ ). *B*, From nine colonies of *Plexaura flexuosa* ( $c = 5$ ,  $r^2 = 0.88$ ,  $P < .05$ ; San Salvador, Bahamas). The colonies were chosen haphazardly and photographed during 1999 at San Salvador Island (10–17 m depth; Riding Rock Reef), Bahamas. The number of branches was counted as described in figure 1*D*.

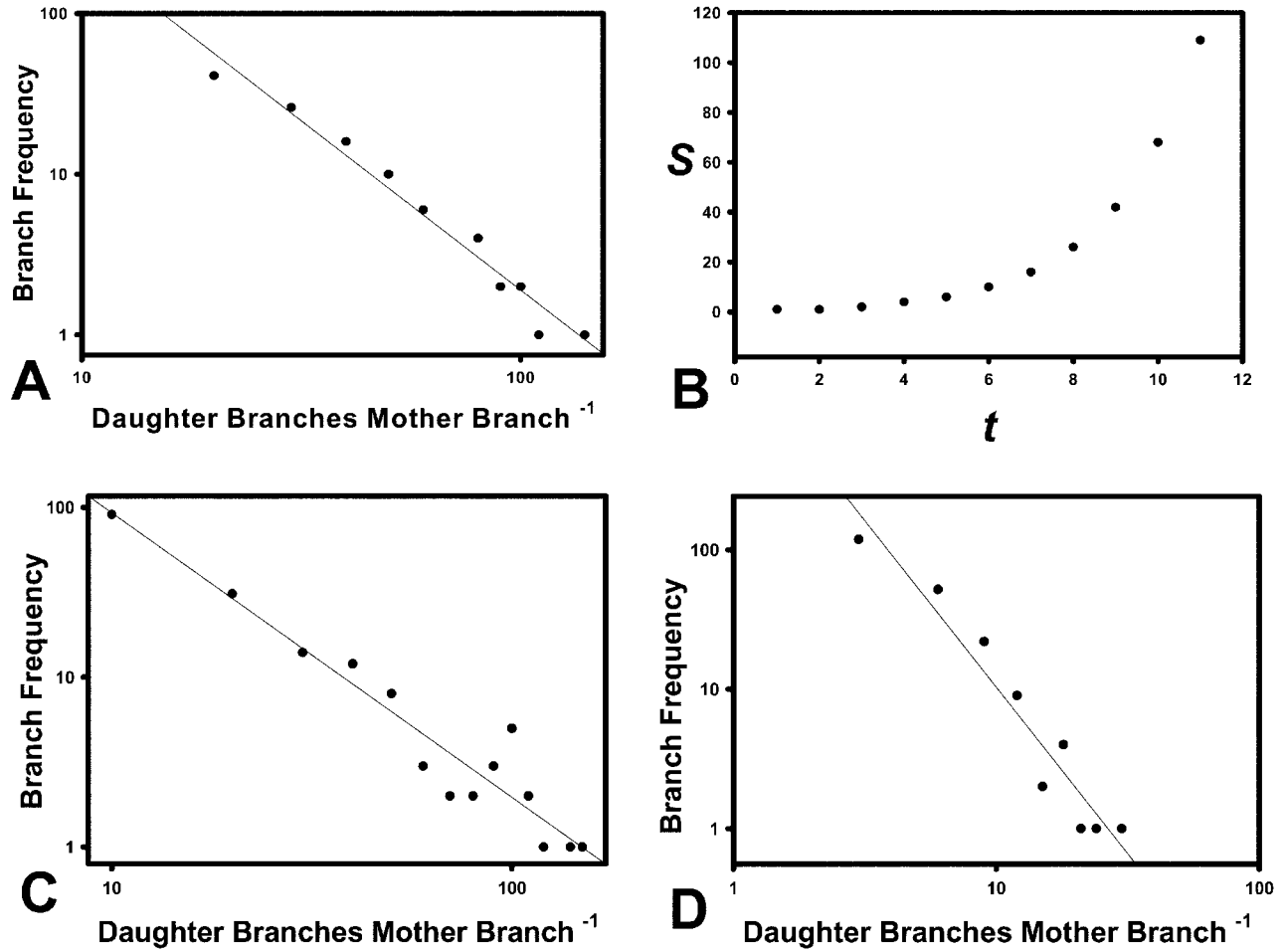
erwise, if the sequence of points diverges, the fixed point is considered unstable.

To analyze the stability of  $N^*$  it is necessary to know whether

$$N_{i+1} = F(N_i) = F(N^* + \varepsilon_i) = F(N^* + \varepsilon_{i+1}) \quad (6)$$

converges to  $N^*$ . Using the Taylor expansion for expression (6) produces





**Figure 4:** A, Size frequency distribution of number of daughter branches per branch in log-log scale from a hypothetical colony generated after 10 iterations of equation (1), with  $r = 12$  (assuming an extension of  $r$  at every mother branch per iteration) and  $c = 20$ , 109 branches mother branches ( $r^2 = 0.96$ ,  $P < .05$ ). B, Cumulative time series of mother branches  $S$ ; data from A. C, Size frequency distribution (daughter branches) from 176 mother branches of 11 photographed colonies of *Pseudopterogorgia bipinnata* ( $r^2 = 0.93$ ,  $P < .05$ ). D, From 211 mother branches of six photographed colonies of *Plexaura flexuosa* ( $r^2 = 0.92$ ;  $P < .05$ ; San Salvador, Bahamas).

$$N^* + \varepsilon_{i+1} = F(N^* + \varepsilon_{i+1}) = F(N^*) + \left. \frac{dF}{dN} \right|_{N=N^*} \varepsilon_i.$$

Because  $N^* = F(N^*)$ , it is possible to write

$$\varepsilon_{i+1} = D\varepsilon_i,$$

where

$$D = \left. \frac{dF}{dN} \right|_{N=N^*} = \frac{dF(N^*)}{dN}.$$

Thus,  $\varepsilon_{i+1} < \varepsilon_i$  if  $-1 < D < 1$ , and the fixed point is asymptotically stable. If  $0 < D < 1$ , the distance between each

iteration decreases monotonically, and if  $-1 < D < 0$ , the approximation exhibits oscillation. Otherwise, if  $|D| > 1$ , each iteration diverges from  $N^*$ , and the fixed point is unstable.

We can now evaluate the stability of the two fixed points of expression (5). For the first fixed point,  $N_1^* = 0$ , we have

$$D_1 = \left. \frac{dF(N_1^*)}{dN} \right|_{N=0} = 1 + \frac{r}{c} - 2N_1^* \frac{r}{kc^2} = 1 + \frac{r}{c},$$

and for the second fixed point,  $N_2^* = kc$ , we have

$$D_2 = \left. \frac{dF(N_2^*)}{dN} \right|_{N=kc} = 1 + \frac{r}{c} - 2N_2^* \frac{r}{kc^2} = 1 - \frac{r}{c}.$$

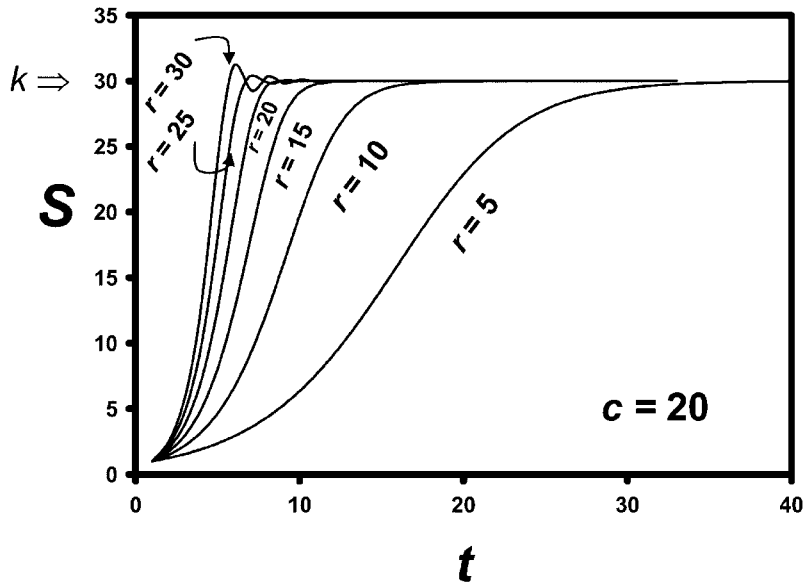
Analyzing  $D_1$  and  $D_2$ , we can draw the following conclusions. First, for  $c > 0$  and  $r > 0$ , the trivial fixed point,  $N_1^*$ , is unstable. Biologically speaking, this means that a colony will increase the number of branches when its number of branches is close to 0 and the constants  $c$  and  $r$  are  $> 0$ . Second, because  $c > r > 0$ , the second fixed point will be monotonically stable. Third, if  $1 < r/c < 2$ , the fixed point will be stable, but it will oscillate. Fourth, if  $r/c > 2$ , the fixed point will be unstable. The last two cases do not make biological sense and are not found in nature as explained below, which could correspond to aberrant forms.

Expression (3) shows that there is initially a steady increment in the number of mother branches  $S_t$  produced until  $S_t$  approaches  $k$ , at which time growth becomes asymptotic (fig. 5). The time series of  $S$ , which is also an indicator of total colony size, had a sigmoid trajectory with a short lag period followed by the interval of rapid exponential increment and, depending on the ratio  $r : c$ , ending after a variable-length asymptotic period or short oscillations close to  $k$  (fig. 5). A survey of 24 species of Caribbean gorgonian corals indicated that there are two main colony architecture outcomes (Sánchez 2004). Those two groups are species with  $c \sim 3$  (all candelabra-like forms and sea fans; alternate and reticulate branching) and low branching rates (Coma et al. 1998) and species with wide  $c$  variances, values of  $c > 13$  (all sea feathers; pinnate branching), and higher branching rates (fig. 2; see also

Lasker et al., submitted). Simulations using parameters similar to those observed empirically exhibited the same qualitative branching behavior (fig. 5), despite notable differences in their colony architectures. Differences in the branching behaviors are determined by the ratio  $r : c$  among hypothetical species with the same  $k$  values. Species with  $r \ll c$  had a sigmoid logistic-like growth with a long asymptotic period before reaching  $k$  (fig. 5). Species with  $r \geq c$  also had rapid branching ending in small oscillations around the value of  $k$ , which stabilizes after an asymptotic trend toward  $k$  (fig. 5). However, most cases of gorgonian corals exhibit values of  $c$  and  $r$  in the range of the conditions for a stable equilibrium at the fixed point (e.g.,  $c > r > 0$  and  $c > r/2$ ). Colonies exhibiting other conditions might generate aberrant branching patterns, and unless grazing or some other disturbance occurs, no natural decrease in size can occur.

### Discussion

Branching in modular colonial organisms can be understood as a self-organized process that preserves a constant ratio of mother-daughter branches. This process is shaped by the changing environment of the growing colony, which is portrayed here as a maximum number of mother branches. As in many ecological systems, branching may have size- and density-dependent constraints that explain the reduction in growth (Kim and Lasker 1998). Colonial



**Figure 5:** Results from the iteration of model (3) using different values of  $r$  (branching rate per mother branch) with a fixed value of  $c$  (ratio of mother to total branches). The arrows show the two cases when  $r < c$ , exhibiting unstable and unrealistic behavior as predicted by the stability analysis.

growth converges stably to the expected maximum number of branches. Assuming no or low branch mortality, branching of modular colonial organisms under the scheme proposed above has a predictable outcome. The model predictions conform well to features observed in several studies on growth of marine modular invertebrates, which also exhibit logistic- or sigmoid-like growth trajectories. These results suggested that branching occurs in a more autonomous and individualistic way that is limited by whole-colony constraints.

#### *Branching and Self-Organized Criticality*

The pattern found among these gorgonians is similar to that of systems whose dynamics can be described by a process of self-organized criticality (SOC; Bak 1996). Self-organized criticality consists of a dynamic behavior around a parameter due to the critical effect of that value in the system such as the case of the slope in the sand pile-avalanche model (Carlson and Swindle 1995). As the pile grows, the slope is maintained by avalanches. The number of critical events (e.g., avalanches) is always increasing because of the dynamics of the system. However, the size of the individual avalanches decays exponentially. In our growth model, the number of mother branches increased exponentially while their size decreased as the colony grows. This type of behavior has been identified in numerous physical systems (sandpiles, avalanches, forest fires, etc.), and there is increasing evidence of similar applications to biological systems. Self-organized criticality has been found in the “avalanches” of alveoli activation during lung inflammation, which is a self-similar branching structure (see review in Csahók 2001). Branched polymer growth has been explained by an SOC state of a regulating rule for the aggregation of monomers (Andrade et al. 1997). Even the punctuated equilibrium evolution model, leading to evolutionary branching, has been described as an SOC phenomenon (see review in Bak and Paczuski 1995).

Among gorgonians, SOC processes allow both branching and the preservation of colony shape through colony development. Branching and colony development can be portrayed as overlapping branching events at multiple mother branches (i.e., growth fronts). Branching acts as a self-organized criticality phenomenon, changing the behavior of the system between branching (i.e., the addition of new branches as the mother branches extend) or the generation of new mother branches from existing branches in order to maintain a constant total branch to mother branch ratio, that is,  $c$ . In a gorgonian coral, production of daughter branches triggers or proceeds synchronously with formation of new mother branches, which in turn triggers formation of additional daughter branches and so

on. The colony keeps branching and producing new mother branches within many mother-daughter systems simultaneously (e.g., fig. 4C).

Although previous examinations of colony organization have focused on branch order (e.g., Brazeau and Lasker 1988), our model demonstrates for the first time that the form and development of branching modular organisms can be partially explained by SOC independent of order. The model shows how the scaling of branch size (both empirical and theoretical) followed power law frequency dependence. The model identifies a critical parameter ( $c$ ) that keeps the system in spontaneous dynamics while preserving form. Should mother branches produce more daughter branches or generate a mother branch? This is the critical state that keeps the colony actively growing. What biological mechanism could provide such a self-organized state? Buss's (2001) model of hydroid colony growth by “intussusceptions,” where colonies keep adding modules responding to a certain threshold of internal fluid tension, is conceptually an SOC. The environmental input from the internal tensions triggers the expression of developmental genes (e.g., *Cnox*) at certain colony regions. A similar approach has been proposed using redox control in hydroids (Blackstone 1999), which also suggests the presence of thresholds triggering colonial expansion. Although we do not know the interplay between resource supply and developmental gene expression in gorgonian corals, the critical state  $c$  in a colony could indicate a differential between resource availability and surplus that could trigger new branching events. Resource supply, strain from current and wave action, and internal transport gradients all could provide cues for branching and are each testable through comparisons of both the dynamics (i.e., timing) of branching and comparisons of  $c$  across environmental gradients and taxa.

In brief, branching in marine modular colonial organisms is both a developmental and ecological process. Although they are among the most basal of metazoans, organisms such as cnidarians contain complex developmental machinery such as homeotic genes (Finnerty and Martindale 1997). The expansion of gene families, such as Hox/ParaHox genes, is believed to have taken place during or before the Cambrian explosion, which has concluded to the associated diversification of body plans in metazoans (see reviews in Morris 1998 and Lundin 1999). Homeobox genes have identified specific functions on development and morphogenesis in derived metazoans. Genes such as transcription factor *Cnox-2* seem to be iteratively expressed throughout development of hydroid colonies (Cartwright and Buss 1999; Cartwright et al. 1999). However, controls on the production of new branches or the extension of existing branches have not been identified in cnidarians (P. Cartwright, personal com-

munication). In addition, colony growth is partially controlled and shaped by environmental stimuli (Buss 2001; Lasker and Sánchez 2002), and computer models demonstrate that with a few rules and environmental inputs it is possible to mimic colonial growth and form with remarkable realism (see review in Kaandorp and Kübler 2001). It is therefore reasonable to think that branching in a modular colonial organism is a combination of both internal and external factors that shape the system dynamically just as in ecological processes such as logistic population growth, predator-prey interactions, and so forth, which was the approach presented here.

#### *Crowdedness and Branch Interference*

Size increment brings along a series of constraints that affect the colony design and module interference (see review in Lasker and Sánchez 2002). Space is the primary limiting constraint for clonal sessile taxa (Jackson 1977). For instance, the design of branching colonies of modular organisms such as cheilostome bryozoans has been shaped both to reduce drag and breakage and to minimize crowdedness and module interference (Cheetham and Thomsen 1981; Cheetham 1986). During the growth of bryozoans, branches initially diverge, and then they progressively converge through further branching and begin to interfere with each other. This interference seems to limit the maximum colony size (Cheetham and Hayek 1983). Stebbing (1981) suggested that the bryozoan *Campanularia flexuosa* stops growing when the spaces for asexual production of zooids are completely filled or in close proximity to other zooids. In gorgonian corals, experimental evidence shows that crowding among branches impedes growth, possibly through the capture of resources at the shaded branches (self-shading; Kim and Lasker 1997). Assuming that low growth is a product of resource depletion, there are allometric constraints for resource capture during modular growth because internal modules begin to be resource depleted by the expansion of new exterior modules (Kim and Lasker 1998). In the particular case of gorgonian corals, the basic colony architecture is maintained (e.g., internode distance and angles), and branching will become crowded and internal shading inevitable. If resources are being depleted as the colony “exploits” its periphery, there should be a maximum extension point (e.g.,  $k$ ) when no surplus is then provided to the base, and growth and branching would stop. The inclusion of a new parameter controlling branching in modular organisms such as  $k$ , or maximum branch capacity, has support from size and interference constraints, which are evident phenomena during colony growth. The complex nature of branching is still modulated critically by the interaction between  $r$  and  $c$ , but global ecological constraints prevail throughout col-

ony development. Direct empirical observations to fulfill a complete ecological theory of branching are needed. Other biological aspects of modular colonial organisms such as reproduction and regeneration were not covered in this model and could have important effects on branching.

#### *Colony Form = Intrinsic Control of Growth?*

Colony growth and form in our model can be predicted by  $r$ ,  $c$ ,  $k$ , and the ratio between  $r$  and  $c$ . While some environmental variation in these parameters may likely exist, these parameters should be considered as intrinsic characterizations of the processes that control branching, in much the same manner that a population's intrinsic rate of increase represents a basic capability. This intrinsic aspect of branching can be considered genetic in nature (see review in Rinkevich 2002). This could be explored similarly with other branching organisms as different as plants. The form of ferns, for instance, resembles the iterative nature of fractals (Campbell 1996), which leaves little room for extrinsic intervention related to form. We suggested here that extrinsic aspects of colony growth are related to their maximum size, crowdedness effects, and allometry, which are included in this model as the parameter  $k$ . Nonetheless, extrinsic effects also have an important effect on colony form, but they should be constant. This can be noticed with the phenotypic plasticity of corals along environmental gradients (Bruno and Edmunds 1997), where they have extraordinary differences in branch lengths, widths, and angles, but it cannot be considered that the environment molded the specific set points of branching at each environment. In any case, the theoretical study of extrinsic controls on branching can be decomposed in more specific parameters than  $k$  itself, which would help us to understand the limits of colony growth.

Straightforward parameters have been identified in this study, and a number of applications and model organisms seem appropriate for future work. The complete development of gorgonian corals may span several years for even the smallest colonies, which makes it difficult to follow the complete branching process. Nonetheless, an equivalence between growth and the cross-sectional area of the axis seems to be present in gorgonian corals (Risk et al. 2002). The model can then be modified to calculate colonial growth in terms of the axial area with the advantage of having the growth signature embodied in the axial rings. Fast-growing hydroids and bryozoans could provide important empirical clues for this model of branching. Using the studied parameters it is also possible to get new answers in the evolution of modular colonial organisms. For instance, changes in colony architecture have been experimentally induced by accelerating and de-

celerating growth rates of colonies from the same species (Blackstone and Buss 1993; Blackstone 1999, 2000), demonstrating that uniform change in the rate of colony development generates different colony forms through heterochrony. Since heterochrony requires that the developmental trajectories of the species follow the same growth function (Rice 1997), this model offered a common way to understand developmental trajectories of modular organisms. For instance, different branching species that had similar values of  $c$  would, therefore, vary in colony form only as a function of their growth rates ( $r$ ) or maximum sizes ( $k$ ), which might be an example of heterochrony. Phylogenetic hypotheses of octocorals are available now (e.g., Sánchez and Lasker 2003; Sánchez et al. 2003b, 2003c), which would help to recognize heterochronic change with respect to hypothetical ancestors. In addition, maximum size and the size of first reproduction in gorgonian corals seem to be very predictable and species specific (Kapela and Lasker 1999), which supports the view that heterochrony can be studied using the model proposed here (e.g., progenesis). Some Caribbean gorgonian octocorals, such as *Pseudopterogorgia elisabethae*, have been harvested for the extraction of anti-inflammatory metabolites by the cosmetic industry (Mayer et al. 1998). The theoretical analysis presented here provides a basis for the development of an individual-based model to study a sustainable harvesting of gorgonian corals. Future observations on colony growth could greatly increase the knowledge in this field by including branching parameters instead of height/width or other indirect measurements of modularity.

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