A Formal Description of Radiate Accretive Growth

JAAP A. KAANDORP†

*Department of Computer Science, The University of Calgary, 2500 University Drive N.W.,
Calgary, Alberta T2N 1N4, Canada*

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In this paper a formal description is given of a 2D iterative geometric construction, which simulates a radiate accretive growth process. This type of growth process is found among species of various taxonomic classes of marine sessile organisms. With iterative geometric constructions it is possible to introduce the influence of the physical environment on the growth process, as well as geometric constraints. The iterative geometric construction which simulates the growth process of an organism with radiate accretive growth and the formation of branches, is formalized using an edge replacement system.

1. Introduction

Radiate accretive growth can be defined as a growth process in which layers of material are deposited on top of the preceding growth stages, which remain unchanged. In Fig. 1 this type of growth process is described in a diagram. The thickness of the layers is the highest when the angle between a tangential element and an axis of growth is minimal and decreases for larger angles. The longitudinal elements are set perpendicular on the preceding tangential elements. The tangential elements are situated on the growth lines, formed in succeeding growth stages. This type of growth process can be found among marine sessile organisms from various taxonomic classes: for example, stony corals (Graus & Macintyre, 1982), sponges (Wiedenmayer, 1977; Kaandorp, 1991), coralline algae (Bosence, 1976).

Two typical examples of the structure which emerges in the radiate accretive growth process are displayed in Fig. 2. In order to reveal the layered structure, longitudinal sections, parallel to the axis of growth, were made through branches of different organisms. In (a) a section through a colony of

Montastrea annularis is shown. A slab was taken from such a section, X-rayed and a positive print is made of the negative. The annual growth is visible as dark and light density bands in X-radiographs (see Graus & Macintyre, 1982) and it is possible to distinguish growth lines, which correspond to the tangential lines in Fig. 1. In (b) the skeleton architecture of a branch of the sponge *Haliclona oculata* is shown. The skeleton can be made visible by drying and sectioning the sponge. The effect of drying is that all material, except the skeleton elements (the spicula), virtually disappears by shrinking. The same skeleton is depicted in a line-drawing in (c). In this drawing some of the growth lines of (b) are visualized.

In Fig. 3(a) a tangential view is shown of *M. annularis*. In the diagram of the tangential view (b) it can be seen that the tangential edges of the corallites can be thought to be arranged in a tessellation of predominantly pentagons and hexagons. The same type of arrangement can be observed in a tangential view of *H. oculata* skeleton (Kaandorp, 1991). In both organisms the tangential elements are about equal-sized, there is only a small variation in the basic length of the tangential element. The organisms are built from discrete units with a certain basic size. In both organisms it can be observed that the longitudinal elements vary between a minimum value and a maxi-

†Present address: University of Amsterdam, Kruislaan 403, 1098 SJ Amsterdam, The Netherlands.

FIG. 1. A diagram of a radiate accretive growth process.

mum size, the growth process causes a continuous variation in these elements.

Although both structures in Fig. 2(a) and (b) emerged in a different way, in taxonomically very different organisms and also consist of chemically very different materials, there is an essential correspondence. Both organisms show the radiate accretive architecture as is displayed in Fig. 1. The formation of this generic structure, found in very different taxonomical groups, is the principle of the 2D model of radiate accretive growth discussed in this paper. In both organisms new material is deposited on top of the preceding growth stages. In stony corals it is obvious that the preceding growth form remains unchanged: only the surface of the colony is alive and new material is deposited upon a dead core. In the example of the sponge *H. oculata* it can be demonstrated in marking experiments that the preceding stages remain unchanged (Kaandorp & de Kluijver, 1992). Both organisms as well as other examples with radiate accretive growth are characterized by a radiate symmetry: a longitudinal section of a single branch, parallel to the axis of growth, will always show about the same (in some cases the branch is flattened). In organisms with radiate accretive growth where branching growth forms emerge in the growth process, growth takes place at the tips of the organism. These tips grow almost independently, growth is only limited by steric hindrance and is not limited by the development of other structures (e.g. the roots in

a seed plant). The growth at the tips can be described as a parallel process in which an overall control in the final shape of the organism lacks.

Because of the features listed in the preceding paragraph some important simplifications can be made in a morphological model of the radiate accretive growth process. The most obvious simplification is that, because of the radiate symmetry, some aspects of the growth process can be described with a two-dimensional model. It is also possible to construct a morphological model which simulates the growth process on the level of the basic building elements (in *H. oculata* these are the spicula, in *M. annularis* the corallites). This type of model will be much more complex for organisms lacking these simplification features (e.g. seed plants).

A well-known model for simulating the morphology and development of biological objects are the L-systems (Lindenmayer, 1968). L-systems have been applied widely for biomorphological description (Hogeweg & Hesper, 1974; Prusinkiewicz & Lindenmayer, 1990). The actual growth process is a non-deterministic process, partly because it is influenced continuously by the environment (for example, the supply of nutrients and the local light intensities for marine sessile organisms) and growth is limited by geometric restrictions. A very obvious geometric restriction is that growth cannot take place at a site in space which is already occupied by the growing object. This type of limitation and the influence of the

FIG. 2. Longitudinal sections, parallel to the axis of growth, through organisms with radiate accretive growth. In (a) a section through a column-shaped colony of the stony coral *M. annularis* is shown. In (b) a section through the sponge *H. oculata* is displayed. In (c) the section of (b) is depicted in a line-drawing showing all the longitudinal lines of (b) and some of the growth (tangential) lines. The insertion of new longitudinal lines (arrow 1) as well as the deletion of a longitudinal line (arrow 2) are marked.

FIG. 2.—*continued.*

FIG. 3. (a) A tangential view of the surface of a colony of *M. annularis*.

FIG. 4. Example of a growth form of the sponge *H. oculata*.

Fig. 3(b)

FIG. 3. (b) a diagram of the surface displayed in (a).

environment cannot easily be described with a L-system.

In this paper a formal description is given of an iterative geometric model of the radiate accretive growth process and the influence of the physical environment, in two dimensions. The growth process will be modelled in an iteration process (see Fig. 5),

in which the formation of the skeleton, as seen in a longitudinal section (Fig. 2), is simulated. In each iteration step a layer consisting of new longitudinal elements (perpendicular to the preceding layer of tangential elements) and new tangential elements (the new surface of the object) is constructed. The tangential and longitudinal elements represent the basic building units in the actual organisms. In *M. annularis* they represent, respectively, the tangential and longitudinal edges of a corallite [see Fig. 2(a)]. In *H. oculata* they represent, respectively, the tangentially and longitudinally oriented spicula. In the 2D simulation the tangential elements are situated on growth lines of the object, this is a simplification of the actual situation in which these elements are arranged in a tessellation of mainly penta- and hexagons. It will be demonstrated that it is possible to introduce geometric constraints and the influence of the environment in this geometric model.

The model discussed below simulates a branching organism with radiate accretive growth. The model is presented in a general form and consists basically of two components: the first represents the internal properties of the organism and the second the influence of the environment on the growth process. The model will be illustrated by using the two organisms, *M. annularis* and *H. oculata*, mentioned above. Except that both organisms are taxonomically very different, they are ecologically very different. In *M. annularis*, as in many other Scleractinians (see Porter, 1974; Edmunds & Spencer Davies, 1989), photosynthesis is the main energy source. In *H. oculata* the heterotrophic energy source is used exclusively by filtering suspended material from the environment.

FIG. 5. Iteration process in which the radiate accretive growth process is modelled.

(1)

Line	Rule	List of edges and attributes
1	<i>initiator generator</i>	$(edge(V_0, V_1, F, (0, 1))); \dots (edge(V_{n-1}, V_n, F, (0, 1)));$
2		$(edge(V_i, V_{i+1}, F, (prev_DA_x, prev_DA_y))) \rightarrow$
3		$(edge(V_i, V_{i+1}, NF)); (edge(M_{1j}(V_i), M_{2j}(V_i)), NF);$
4		if $(l > inhibition_level)$ then
5		$(edge(M_{3j}(V_i), M_{4j}(V_i)), F, (prev_DA_x, prev_DA_y));$
6		else
7		$(edge(M_{3j}(V_i), M_{4j}(V_i)), SF, (prev_DA_x, prev_DA_y));$
8		$(edge(V_i, V_{i+1}, NF)) \rightarrow (edge(V_i, V_{i+1}, NF));$
9		$(edge(V_i, V_{i+1}, SF, (prev_DA_x, prev_DA_y))) \rightarrow$
10		$(edge(V_i, V_{i+1}, SF, (prev_DA_x, prev_DA_y)));$
11	<i>continuity_rule</i>	$M_{3j}(V_i) \rightarrow b0, M_{4j}(V_i) \rightarrow b1$
12	<i>insertion_rule</i>	if $(\ b1, c0\ > s)$ then
13		$(edge(b0, b1), F, (prev_DA_x, prev_DA_y)) \rightarrow$
14		$(edge(b0, b1), F, (prev_DA_x, prev_DA_y));$
15	<i>deletion_rule</i>	$(edge(n0, n1), F, (prev_DA_x, prev_DA_y));$
16		if $(\ b1, c0\ < s)$ then
17	<i>association_rule</i>	$(edge(b0, b1), F, (prev_DA_x, prev_DA_y)) \rightarrow;$
18		$prev_DA_x \rightarrow new_DA_x, prev_DA_y \rightarrow new_DA_y$
19	<i>avoidance_rule</i>	if $(\ pb, pv\ < s)$ then
20		$(edge(b0, b1), F, (new_DA_x, new_DA_y)) \rightarrow$
21		$(edge(b0, b1), SF, (new_DA_x, new_DA_y))$
22		if $(\ pn, pv\ < s)$ then
23		$(edge(n0, n1), F, (new_DA_x, new_DA_y)) \rightarrow$
24		$(edge(n0, n1), SF, (new_DA_x, new_DA_y)).$

This sponge exhibits branching growth forms as displayed in Fig. 4. It will be demonstrated that growth forms of both organisms can be simulated with a (subset) of the rules applied in the general model of radiate accretive growth. In this paper the biological relevance of the rules which are introduced in the model will be indicated briefly, since this is discussed in more detail in two preceding papers (Kaandorp, 1991; Kaandorp & de Kluijver, 1992). The iterative geometric constructions are formalized using an edge replacement system. In such a system edges are replaced by new edges or rewritten in an iteration process. The complete edge replacement system is given in (1). The details of this system will be discussed in the next section.

2. An Iterative Geometric Construction Simulating Radiate Accretive Growth

2.1. THE INITIAL OBJECT: THE INITIATOR

The iterative construction in Fig. 5 starts with an initial object the *initiator* which consists of n unconnected tangential edges:

$$edge(V_0, V_1); \dots edge(V_{n-1}, V_n); \quad (2)$$

arranged in a semi-circle. The distance between the end points of an edge is equal-sized:

$$\forall 0 \leq i < n: \|V_{2i}, V_{2i+1}\| = s. \quad (3)$$

The size s is the length of a tangential edge and corresponds to the basic length of the tangential skeleton elements in the actual objects (see Fig. 3). All other constants which will be used later on in the model are expressed in this basic unit. The form of the initiator is chosen because the growth process of many marine sessile organisms with radiate accretive growth starts as an encrusting layer, where from small hemi-spherical protrusions the branches develop.

2.2. THE BASIC CONSTRUCTION: THE GENERATOR

The basic geometric construction is shown in Fig. 6. On each tangential edge a new tangential edge with length s is constructed, together with a longitudinal edge with length l . The length l is determined by a product of four functions f , h , L and k [see (4)]. These functions all return values in the range $[0, 1]$ and will be discussed in more detail below.

$$l = s \cdot f(\alpha) \cdot h(rad_curv) \cdot L(\theta) \cdot k(c). \quad (4)$$

The length l may vary between a lower limit (details about the lower limit will follow below) and an upper limit. For simplicity reasons this upper limit is assumed to be equal to s . In reality this upper limit will be a species-specific characteristic and depends on the properties of the skeleton architecture. The angle α in this construction is the angle between a tangential element and the axis of growth, while γ is the angle between the vertical and the axis of growth.

The vertices of the new edges ($P1, P2, P3, P4$ in the geometric construction) can be obtained from the original vertices V_i, V_{i+1} in a series of transformations. The transformations (using homogeneous coordinates) are matrix operators, where $T(x, y)$ indicates a translation over the vector $[x, y]$ and $R_p(\gamma)$ a rotation about an angle γ using the vertex P as rotation point. With the notation $M_j(P)$ the transformed vertex of vertex P using the matrix M_j in iteration step j is indicated. The transformations used to obtain the new vertices are:

$$\begin{aligned} Dx &= 0.5(Vx_{i+1} - Vx_i) \\ Dy &= 0.5(Vy_{i+1} - Vy_i) \\ M_{1j} &= T(Dx, Dy) \\ M_{2j} &= R_{P1}(\gamma) \cdot T(Dx + l \sin(\alpha), \\ &\quad Dy - l \cos(\alpha)) \cdot R_{P1}(-\gamma) \text{ if } (\alpha > \pi/2) \\ M_{2j} &= R_{P1}(\gamma) \cdot T(Dx - l \sin(\alpha), \\ &\quad Dy + l \cos(\alpha)) \cdot R_{P1}(-\gamma) \text{ if } (\alpha \leq \pi/2) \\ M_{3j} &= M_{2j} \cdot T(-Dx, -Dy) \\ M_{4j} &= M_{2j} \cdot T(Dx, Dy). \end{aligned} \quad (5)$$

The construction is described by the edge replacement system in (6) in which unconnected edges are used. The edges in this system have two attributes, the first one can be in two states: F ("fertile") and NF ("non-fertile"), the second attribute [the vector

(DA_x, DA_y)] will be discussed later on. Only the edges in the state F participate in new construction steps. The construction starts with a series of fertile tangential edges of the *initiator* and in the new object only the tangential edges at the boundary are in the state F .

2.3. THE SECRETION FUNCTION $f(\alpha)$

Longitudinal sections of *H. oculata* [Fig. 2(b) and (c)] show that the growth velocity depends upon the angle between the tangent of the surface and the axis of a column-shaped sponge tip. The highest growth velocities occur in parts of the sponge where the surface and the axis of growth make an angle of 90 degrees, while the velocities decrease to zero at an angle of about 180 degrees. This phenomenon can be explained by the presence of the spicule-secreting cells, which exhibit the highest activity close to the tip, where they are situated in an area with the highest supply of material suspended in the water. Indeed, in sections of growing sponge tips, where the spicula-secreting cells are stained (see Brien *et al.*, 1973), it can be seen that the spicula-secreting activity is the highest at the tips of the sponge and decreasing towards the sides. Towards the sides the access to suspended material as well as the secretion decreases. In the example of the sponge, with internal secretion of elements, growth of the longitudinal elements is related to the angle α between a tangential element and an axis of growth. This dependence is modelled by the function $f(\alpha)$ [(7)].

FIG. 6. Construction of a new tangential and a new longitudinal element.

(6)

Line	Rule	List of edges and attributes
1	initiator generator	$(edge(V_0, V_1), F, (0, 1)); \dots (edge(V_{n-1}, V_n), F, (0, 1));$
2		$(edge(V_i, V_{i+1}), F, (prev\ DA_x, prev\ DA_y)); \rightarrow$
3		$(edge(V_i, V_{i+1}), NF); (edge(M_1(V_i), M_2(V_i)), NF);$
4		$(edge(M_3(V_i), M_4(V_i)), F, (prev\ DA_x, prev\ DA_y));$
5		$(edge(V_i, V_{i+1}), NF); \rightarrow (edge(V_i, V_{i+1}), NF);$

In Fig. 7 measurements of longitudinal fibres, done in the sample from Fig. 2(a), are plotted in a graph. The length l of the longitudinal fibres, between two successive growth lines, and their angle α with the axis of growth were measured. In this figure the measurements were normalized using the length of the longitudinal fibre parallel to the axis of growth. The mean values are indicated with "■" marks, the minimal and maximal value for a given α is displayed as a vertical line. This graph is based on 141 measurements in eight different growth rings. In the same graph the function $f(\alpha)$ is plotted (visualized with "*" marks); it can be seen that this function can be used to approximate the rate of secretion of longitudinal elements as a function of the angle α .

This function $f(\alpha)$ is only relevant for organisms with radiate accretive growth with internal secretion of the elements. It is not relevant for Scleractinia as *M. annularis*, since in these organisms the material is deposited externally on a dead core. For organisms with internal secretion this function $f(\alpha)$ is the basic

cause of the radiate accretive structure. In the autrophic class with external secretion the radiate accretive structure has a different cause; this subject will be discussed in more detail in the section on the modelling of the influence of light intensity on the growth process.

$$f(\alpha) = \begin{cases} 1.0 & \text{for } \pi/2 - \pi/n \leq \alpha \leq (\pi/2 + \pi/n) \\ \sin((\pi/2)/(\pi/2 - \pi/n) \cdot (\pi - \alpha)) & \text{for } 0 \leq \alpha < (\pi/2 - \pi/n), (\pi/2 + \pi/n) < \alpha \leq \pi. \end{cases} \quad (7)$$

The constant n represents a widening factor in function f ; in the growth process of a branching organism with radiate accretive growth the tip widens before it splits into new branches. Without widening the sponge would remain a non-branching column, as will be explained in the section on the formation of branches. The widening represents a region in the tip where the secreting activity is not influenced by a lower access to the suspended material in the environment. This will cause a small area of equal maximal

FIG. 7. Plot of measurements of the (normalized) length of l longitudinal fibres between two successive growth lines [the sample from Fig. 2(a) was used] and the angle α between the longitudinal fibre and the axis of growth. The measurements are indicated with "■" marks. In the same graph $f(\alpha)$ is shown, indicated with the "*" marks.

FIG. 8. Construction of the new vertices b_0 and b_1 , satisfying the continuity rule [see (1) and (9)].

growth velocities at the tip of an organism with radiate accretive growth. The widening factor is a species-specific parameter in the model. The function $f(\alpha)$ is an approximation of the secretion of longitudinal elements as a function of α .

2.4. LIMITATIONS OF THE TRANSPORT SYSTEM, THE FUNCTION $H(RAD_CURV)$

A function in which the longitudinal length l also depends on the radius of curvature (rad_curv) measured in the contours of the object is shown in (8). The rad_curv can be measured as the radius of the circle through three points on the circumference of the growing object, situated on neighbouring tangential elements. The minimum distance between these points is the length of a tangential edge s . The rad_curv becomes infinitely large when the three points are situated on a line. In the case where the points are situated on a hollow site of the contour of the object rad_curv is negative. The length of the longitudinal

FIG. 9. Construction of a new tangential element with vertices n_0 and n_1 in the insertion rule [see (1) and (10)].

FIG. 10. Development of new growth axes in the model. An old axis of growth $prev_DA$ is replaced by two new ones (new_DA_0 and new_DA_1).

edge becomes zero as soon as the radius of curvature is larger than a certain (fixed) maximum (max_curv). The length l attains the maximum value when the radius of curvature is less than a fixed minimum (min_curv).

$$h(rad_curv) = 1.0 -$$

$$(rad_curv - min_curv) /$$

$$(max_curv - min_curv) \text{ for}$$

$$min_curv \leq rad_curv \leq max_curv$$

$$h(rad_curv) = 1.0 \text{ for } rad_curv < min_curv$$

$$h(rad_curv) = 0.0 \text{ for } rad_curv > max_curv. \quad (8)$$

With the parameter rad_curv the amount of contact of the elements with the environment is expressed. In Fig. 11 the relation between rad_curv and the amount of contact with the environment is depicted. The amount of contact with the environment can be described as a quotient of the surface ΔS through

FIG. 11. Relation between rad_curv and the amount of contact with the environment. With ΔS the surface is indicated through which nutrient can pass to an area with distance d from the surface.

which nutrient can pass and the area (with distance d from the surface) being supplied with nutrient:

$$\frac{\text{surface}}{\text{supplied area}} = \frac{\Delta S}{\Delta S \cdot d \left(1 - \frac{d}{2 \cdot \text{rad_curv}}\right)} = \frac{2 \cdot \text{rad_curv}}{d(2 \cdot \text{rad_curv} - d)} \quad (9)$$

In formula (9) it can be seen that the amount of contact decreases for an increasing value of rad_curv , for $\text{rad_curv} \gg d$ this can be approximated with $h(\text{rad_curv})$ (1.0 is maximal contact and 0.0 minimal). The parameter min_curv defines the lower limit, values for rad_curv below this limit do not affect the growth process. Both parameters are expressed in units s , the length of the tangential elements. In this function the amount of contact with the environment is taken to be proportional to the radius of curvature. As soon as the top is widening too much, the amount of contact with the environment becomes suboptimal and the growth velocity at the top decreases, resulting in a branching object.

In general the tip-splitting for an organism with radiate accretive growth can be modelled with the function $h(\text{rad_curv})$ [(8)], which expresses the limitations of a certain transport mechanism of nutrients through the tissue. The parameter max_curv is a species-specific parameter which describes the capacity of the transport system, it depends on external water movements as well: in an environment with a higher rate of water movement, the transport system is supported by these external movements (Vogel, 1974) and a relatively higher value is applied for max_curv .

2.5. THE LOWER LIMIT OF THE LENGTH OF A LONGITUDINAL ELEMENT: *INHIBITION_LEVEL*

When growth of a fertile edge is inhibited, the *fertilization* state of this edge is changed into "non-active". The growing object is limited by active and non-active fertile edges; only active edges will participate normally in generating new edges during subsequent growth stages. In this object growth only takes place at the tip. It is useful to make a distinction in active and non-active fertile edges. With this distinction it is possible that non-active tangential elements, under certain circumstances, can participate again in the growth process. Their state is then changed into active and growth (which will be indicated as secondary growth) can take place. In the replacement system the edges which are in the state "non-active" are indicated with the attribute *SF* [lines 1-10 in (1)].

The biological interpretation of the threshold value *inhibition_level* is the minimal possible length of the longitudinal elements. The longitudinal element in *H. oculata* can vary in length because of the construction of the longitudinal bundles, which consists of a row of about two spicula thick. The length l can vary between a certain upper limit, which is species-specific and depends on s , the size of a tangential element, and a certain lower limit *inhibition_level*. The interpretation of the lower limit *inhibition_level* is that the skeleton is built of discrete elements and the longitudinal bundles cannot become arbitrarily short. Under certain circumstances, for example when the tissue of the sponge is damaged locally, secondary growth can take place at these non-active sites. In the model this can be simulated by changing the status of non-active fertile edges again into active.

The lower limit for the longitudinal elements is only relevant for the organisms with radiate accretive growth with internal secretion. In the Scleractinia where the material is secreted superficially the length of the longitudinal elements can vary between almost zero and the upper limit. A growth velocity of zero in the Scleractinia indicates local dying of polyps.

2.6. MODELLING THE COHERENCE OF THE SKELETON

In order to obtain continuous growth lines in the model it is necessary to introduce a rule ensuring that neighbouring tangential elements are situated on a continuous curve (the *continuity rule*). Without this rule the tangential elements are growing independently, without a connection with the neighbouring tangential elements. This rule can be introduced in the replacement system in (1) (lines 1-11) as a rule, which ensures that three neighbouring tangential edges $[(a0, a1); (M_{3j}(V_i), M_{4j}(V_i)); (c0, c1)]$; (see Fig. 8) are situated on a continuous curve. The new vertices $b0$ and $b1$ are determined in the following way:

$$\begin{aligned} pb &= M_{2j}(V_i) \\ pa &= 0.5(a0 + a1) \\ pc &= 0.5(c0 + c1) \\ d &= \|pa, pc\| \\ b0 &= pb - 0.5 \cdot s/d(pa - pc) \\ b1 &= pb + 0.5 \cdot s/d(pa - pc). \end{aligned} \quad (10)$$

A second growth rule, which is necessary to obtain a continuous growth line, is the addition of new tangential elements, when there is enough space between two neighbouring elements (*insertion rule*). Without this rule gaps would appear in the growing object, increasing in size after each iteration step; the

tangential and longitudinal elements would not form a coherent skeleton any longer and the skeleton would disintegrate. This rule is introduced in the replacement system of (1) (lines 1–15), where a new tangential edge ($n0, n1$) is inserted between two neighbouring tangential edges ($b0, b1$) and ($c0, c1$) (see Fig. 9). The vertices $n0$ and $n1$ of the newly inserted tangential edge (see also Fig. 9) are determined in (11).

$$\begin{aligned} pb &= M_{2j}(V_i) \\ pc &= 0.5(c0 + c1) \\ d &= \|b1, c0\| \\ n0 &= b1 + 0.5 \cdot (d - s) / d \cdot (c0 - b1) \\ n1 &= b1 + (s + 0.5 \cdot (d - s)) / d \cdot (c0 - b1). \end{aligned} \quad (11)$$

In reality tangential and longitudinal elements are arranged in continuous lines, caused by the fact that the spicule bundles form one connected mesh [see Fig. 2(a) and (b)] in the example of the sponge *H. oculata*. In the case of *M. annularis* and other Scleractinia, the theca of the polyps cannot grow independently from their neighbours: they are imbedded in the same structure. In general this phenomenon, that units in a growing organism cannot grow independently from the neighbouring units because they are embedded in a common structure, is represented in the model by the *continuity rule*.

The second rule applied in the iteration process is also related to the conservation of the coherence of the skeleton. During the growth process the circumference of the model as well as the real organism with radiate accretive growth is increasing continuously.

The consequence is that the size of the polygons, tessellating the surface of the organism (see Fig. 3), would increase in subsequent growth steps, when no new tangential elements are inserted. In reality the tangential elements in *H. oculata*, with the size of one spiculum, cannot remain connected and the skeleton would collapse. In the case of stony coral, gaps would occur between the theca of neighbouring polyps. In order to conserve the coherence new polyps have to be inserted. The insertion of new tangential elements, with which the coherence of the skeleton is conserved, is simulated by the *insertion rule*. The insertion of new tangential elements causes the emergence of new longitudinal lines; this can also be observed in both longitudinal sections (see arrows in Fig. 2). Both coherence conserving rules, the *continuity* and the *insertion rule*, are relevant for all types of organisms with radiate accretive growth.

2.7. FORMATION OF NEW GROWTH AXES

New growth axes emerge on the surface of the growing object on sites where a (local) maximum in growth velocities occurs. In Fig. 10 a growing object is shown, in which two local maxima develop. The first seven layers in the object are fertile tangential elements, associated with a single growth axis (*prev_DA*). In the eighth layer two local maxima and one minimum develop. In the eighth and next layers, fertile elements are associated with new growth axes *new_DA₀* (the fertile elements to the left of the local minimum) and *new_DA₁* (the elements to the right of the local minimum). The association of fertile elements with a specific growth axis is determined in a new rule (the *association rule*). In the edge replace-

FIG. 12. Two simulated forms of the radiate accretive growth process, by applying the iteration process shown in Fig. 5. The length of the longitudinal element l is determined by the functions $f(\alpha)$ and $h(rad_curv)$, while $L(\theta)$ and $k(c)$ remained constant and are set to the value 1.0. In form (a) the parameter *max_curv* [eqn (8)] was set to 0.1, in form (b) this value was set to 0.3.

ment system (1) the direction of the growth axis is defined by the attribute (DA_x, DA_y) . In the replacement system (DA_x, DA_y) is initially set to $(0, 1)$. The direction of new growth axes corresponds with the direction of longitudinal elements, where local maxima develop. The fertile tangential elements are associated with the nearest growth axis in a procedure as described in Fig. 10. In the *association rule* the previous growth axis ($prev_DA_x, prev_DA_y$) is replaced by the direction of the new formed growth axis (new_DA_x, new_DA_y).

The biological meaning of *association rule* is that the protruding parts of the real organism with radiate accretive growth are situated in areas with the highest supply in nutrients and will develop the highest growth velocities. As a consequence, the protrusion increases in size and new branches (axes of growth) are formed.

2.8. ADDITIONAL RULES FOR THE FORMATION OF BRANCHES

Two new rules are necessary when new growth axes are to be generated during the formation branches. During this process some active fertile edges will be enclosed by surrounding active fertile edges and a situation occurs where there is not enough space for the new tangential elements. In order to prevent intersections between neighbouring tangential elements, edges of this type are removed from the object. After this longitudinal lines so far always ending in a tangential edge will now end somewhere in the object. This rule (*deletion rule*) is the reverse of the *insertion rule*. Without the removal of non-fitting elements from the skeleton a dense accumulation of elements would appear. In the replacement system in

FIG. 13. The light intensity I on the surface is determined by the cosine θ , the angle of incidence of the light beam and the surface normal and the intensity I_s of the light source.

FIG. 14. Simulated form of an autotrophic organism with radiate accretive growth. The length of the longitudinal element l is only determined by the function $L(\theta)$ in eqn (4), all other functions remained constant and were set to the value 1.0.

(1) non-fitting elements are removed in the lines 16–17.

Another colliding situation arises when branches intersect. A rule preventing intersections [*avoidance rule* in (1)] changes the status of active fertile elements, that approach too much, into non-active. Without applying collision detection a physical impossible situation would emerge where branches of the object would grow through each other. In the replacement system the vertex pv is a midpoint on a tangential edge, which is not one of the neighbouring tangential edges $[(a0, a1) \text{ and } (c0, c1)]$ from Fig. 8.

The deletion of new tangential elements causes the disappearance of longitudinal fibres in the growth process. This can also be observed in the longitudinal section [see arrow 2 in Fig. 2(c)]. Without the removal of non-fitting elements from the skeleton a dense accumulation of elements would appear and the coherence of skeleton would be disturbed.

In the model growth ceases as soon as branches are at the point of intersection. The *avoidance rule*, applied in the 2D model, is a simplification of the reality. In actual branching objects (see Fig. 4) branches that are at the point of intersection can avoid each other in the third dimension. In many marine sessile organisms branches which intersect also fuse with each other (anastomosis).

Under natural conditions, especially on a sheltered growth site, water movement and food supply as well as the growth velocity will be slowed down or stopped when branches collide. In many stony corals it can be observed that when branches approach each other too closely growth is suppressed (this is well described for the stony coral *Acropora formosa* in Oliver, 1984). This aspect of the growth process, where branches are not allowed to approach each other too closely, can be modelled with the *avoidance rule*. The effect that the growth velocity decreases because approaching branches locally deplete the same nutrient source can be modelled in a more natural way by including the influence of local nutrient concentrations on the growth process. This last point will be discussed in

more detail in the section on the nutrient distribution function $k(c)$.

2.9. A COMBINATION OF THE PREVIOUS MODELS

When in the iteration process of Fig. 5 the length of the longitudinal element l is determined by the function $f(\alpha)$ and $h(rad_curv)$, while $L(\theta)$ and $k(c)$ remain constant and are set to the value 1.0, a model of a branching organism with radiate accretive growth is obtained. In the growing object small areas with equal-sized longitudinal edges arise at the top. The radius of curvature increases and the value returned by h decreases. The result is that l decreases and the object starts branching. A more evolved object generated with this construction is shown in Fig. 12(a). This object is constructed with the value

$n = 18$ in $f(\alpha)$ in (7) and obtained after 220 iterations. In this figure only the tangential lines, the growth lines, are shown. A relative large value of max_curv [see Fig. 12(b)] leads to more flattened branches.

In this model the radiate accretive growth of a branching organism with the highest growth velocities at the protrusions is united with the restrictions of the transport system of nutrients through the tissue.

2.10. THE LIGHT INTENSITY FUNCTION $L(\theta)$

A simple light model (Foley *et al.*, 1990) is presented in (12). In this model the light intensity I (Watt m^{-2}) on a surface is determined by the cosine θ , the angle of incidence of the light beam and the surface normal and the intensity I_s of the light source (see Fig. 13). The light beam corresponds to the vertical, for

FIG. 15. Simulated form of an organism with radiate accretive growth, in which the growth process is influenced by the nutrient distribution. The length of the longitudinal element l is determined by the functions $f(\alpha)$, $h(rad_curv)$ and $k(c)$, while $L(\theta)$ remained constant and was set to the value of 1.0 in eqn (4). The parameter max_curv [eqn (8)] was set to 0.1 while the parameter η in (14) was set to the value 1.0.

this tropical species (*M. annularis*) the light source is assumed to be positioned in the zenith.

$$I = I_s \cos(\theta) \quad (12)$$

$$L(\theta) = \cos(\theta).$$

In Fig. 14 an object is simulated in which the length of the longitudinal elements l is determined by the relative decrease in light intensity [$L(\theta) = I/I_s$]. In this object the two coherence conserving rules, *insertion* and *continuity rule*, are applied to ensure that the tangential elements remain connected.

In the autotrophic example *M. annularis* [see Fig. 2(a)] growth velocities are highest at the tip of the column-shaped colony, the corallites are secreted superficially. Growth of the corallites is related to the angle θ of the corallite with respect to the light source and the vertical is the axis of growth.

2.11. THE NUTRIENT DISTRIBUTION FUNCTION $k(c)$

With the Laplace equation the nutrient concentration c in a diffusion process, which is in a steady state, can be described:

$$\nabla^2 c = 0. \quad (13)$$

It is possible to determine the local concentration c in a field where an object grows and is consuming the nutrient. The DLA model, based on this equation has been applied to model forms of bacteria colonies (see Meakin, 1986; Fujikawa & Matsushita, 1989, 1991). With the DLA model the growth process of an organism, which can be considered as an aggregate of loose particles (e.g. a bacteria colony), can be simulated.

In the method described briefly below, the iterative geometric construction with which the growth process of an organism can be simulated and where the composing elements are consolidated in a coherent structure (e.g. the corallites in a coral colony) is combined with the Laplace equation. The combination is done by mapping the geometric model on a lattice and by approximating the local nutrient concentrations around the object. After each iteration step (Fig. 5) the boundary of the object was mapped on a lattice of 1000×1000 sites. The boundary was mapped onto the lattice by drawing the edges with a modified version of the Bresenham algorithm (Foley *et al.*, 1990). This algorithm is usually applied for drawing line segments, visualized in pixels, on a pixel screen. The contour within the boundary, consisting of occupied sites in the lattice, was filled by using a scan-line algorithm (Foley *et al.*, 1990). After the mapping, the growing object represented by occupied sites in the lattice, was set to the concentration zero.

A linear source of nutrient (Meakin, 1986) was simulated by setting the top of the lattice to the value 1.0 (the maximum concentration) and the bottom row to zero. The local concentrations surrounding the object were estimated for all sites in the lattice by approximating a solution of the Laplace equation (see Ames, 1977; Niemeyer *et al.*, 1984). After the calculation of the concentrations, for each tangential element in the geometric model an estimation was made of the local concentration gradient. In this estimation an exponent η [eqn (14)] was assumed to describe the relation between the local field and the concentration (Niemeyer *et al.*, 1984; Meakin, 1986).

$$k(c) = c^\eta. \quad (14)$$

This estimation was used in the calculation of the length l of new longitudinal elements in the iteration process (Fig. 5) by multiplying the product $f(\alpha).h(\text{rad_curv})$ [eqn (4)] with the function $k(c)$ [eqn (14)] [$L(\theta)$ remained constant and was set to the value 1.0].

A more evolved object generated with this model is shown in Fig. 15. In this picture the basins of equal ranges of nutrient concentration are visualized in alternating black and white (Mandelbrot & Evertsz, 1990). The nutrient concentration decreases when the black or white basin is situated closer to the object. In the object the value of max_curv [eqn (8)] was set to 0.1 while η [eqn (14)] was set to 1.0.

Next to the secretion of new layers of growth proportional to the angle of the axis of growth and tip-splitting the growth process of a heterotrophic organism which is filtering suspended material from its environment (e.g. *H. oculata*), is determined by the local nutrient concentrations. This influence can be observed from two more aspects in the growth process of *H. oculata*. The sample from Fig. 4 shows negative substrate-tropism and suppression of growth of shielded branches. There is a clear tendency in the sponges to grow from the substrate. This effect can also be observed in the case when the sponge grows on the ceiling of a cave. The suspended material is supplied from the area above or under the sponge, which can be modelled as a linear nutrient source. When branches approach each other too closely they deplete the same nutrient source which suppresses the growth velocity. In Fig. 15 it can be seen that the nutrient is locally depleted at sites, enclosed by branches, this effect suppressed growth of shielded branches. The *avoidance rule* in the iteration process can be partially captured, in this way.

3. Conclusions

With the edge replacement system from (1) and eqn (4) for determining the length l of new longitudinal elements, a general model of radiate accretive growth is obtained. Many of the organisms with radiate accretive growth can be modelled with a subset of the rules discussed in this paper. Growth of *M. annularis* and many other Scleractinia where light is the main energy source, can be modelled by applying the coherence conserving rules (*continuity* and *insertion rule*) in the edge replacement system, while in the determination of l only the light model $L(\theta)$ is relevant. In a simulation model of a branching organism, as *H. oculata*, with radiate accretive growth the coherence conserving rules (*continuity*, *insertion* and *deletion rule*) and a rule which represents the formation of branches (*association rule*) are necessary. The tip-splitting is modelled by a function $h(\text{rad_curv})$ which describes the limitations of the transport system of nutrients through the tissue. The secretion function $f(\alpha)$ is necessary for taxa as sponges where new material is internally secreted and where the preceding growth stages consist of living tissue. In the case of a heterotrophic organism the influence of the nutrient distribution can be modelled with the function $k(c)$. Since branches which are approaching too closely are competing about the same nutrient source, the *avoidance rule* can be partly modelled. In many Scleractinians, where a well-defined distance exists between neighbouring branches, a rule (*avoidance rule*) is necessary to mimic this feature. It is useful to create a model of radiate accretive growth in which both the influence of the light intensity $[L(\theta)]$ and the nutrient distribution $[k(c)]$ is included. With such a model the growth processes of organisms which use both the autotrophic and the heterotrophic energy source (e.g. the scleractinian *Acropora palmata*, see Bythell, 1988) can be captured.

A crucial simplification is that the growth process is modelled in 2D. In reality the situation that the nutrient is depleted between the branches (see Fig. 15) will occur less frequently because nutrient will be supplied from more directions. The diffusion model can describe the situation under sheltered conditions. Under exposed conditions laminar and turbulent flows will disturb this pattern. In a model in which both $L(\theta)$ and $k(c)$ influence the length l of newly added longitudinal elements, the simple light model of eqn (12) will be not sufficient: in a branching organism in which the light intensity influences the growth process also, cast shadows of the branches should be included.

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