Verification of fractal growth models of the sponge *Haliclona oculata* (Porifera) with transplantation experiments

J. A. Kaandorp[1] **and M. J. de Kluijver**[2]

[1] Department of Computer Science, Institute of Taxonomic Zoology, University of Amsterdam, Kruislaan 403, 1098 SJ Amsterdam, The Netherlands
[2] Institute of Taxonomic Zoology, University of Amsterdam, Mauritskade 57, 1009 AT Amsterdam, The Netherlands

Abstract. The growth form of the sponge *Haliclona oculata* is to a significant extent determined by the environmental conditions in which the form emerges. One of the main environmental parameters affecting the growth form is exposure to water movement. In this study, a morphological growth model is used to simulate the effect on the growth process of a change in exposure to water movement. Predictions based on the model are verified by experiments in which sponges from a sheltered growth site are transplanted to an exposed site, and vice versa. The effect of the transplantation on growth forms is determined by morphological comparisons. By combining the morphological simulation model with interpretation of growth forms, it becomes possible to use the growth form of *H. oculata* for bio-monitoring purposes. This form reflects the environmental conditions governing the growth process.

Introduction

In two previous studies (Kaandorp 1991 a, b) a two-dimensional model was presented which simulated the radiate-accretive (terminology after Wiedenmayer 1977) growth process of the sponge *Haliclona oculata*. This growth process can be retraced by examining the skeleton of the sponge. The skeletal structure can be made visible by drying and sectioning the sponge. The skeleton of *H. oculata* consists of elements (spicules) which are linked to form fibres and are consolidated in a three-dimensional network. In longitudinal sections through branches of the sponge, two types of fibres can be distinguished: ascending fibres (referred to here as longitudinal fibres) and transverse connections (tangential fibres). This architecture develops via a growth process in which new layers of material are added to the tips of the branches. The tangential fibres may correspond to the outer surfaces of earlier growth stages. The three-dimensional network of spicules exhibits a radial symmetry, so that any longitudi-

nal section (parallel to the axis of the tip) will always display about the same structure (Kaandorp 1991 b).

The growth of *Haliclona oculata* can be modelled as an iterative process (see Fig. 1). In this two-dimensional model the skeletal architecture, as seen in longitudinal section parallel to the axis of a branch of the sponge, is simulated. An important aim of constructing models that simulate growth forms is to obtain a better understanding of the way in which certain growth forms emerge. In constructing such models it is necessary to describe the various aspects of the growth process with formal rules, leading to a better understanding of growth forms, so that those parameters in the models which are responsible for certain aspects of the growth forms can be identified. The identification of these parameters can be used as a basis for experiments: when the assumptions which are made in the models are correct, it should be possible to verify them experimentally. An important objective of growth models is that they enable simulation experiments to be carried out. For this purpose it is necessary that the models not only generate an object that resembles the actual growth form, but that all rules applied in the growth model have a biological basis. Different stages in the growth process can be simulated and an important feature of these models is that they allow the effect of environmental changes on the growth forms to be predicted.

The present case-study species, *Haliclona oculata*, generally exhibits thin-branching growth forms under sheltered (from water movement) conditions and plate-like forms under more exposed conditions. The overall body shape of this sponge tends to be more or less flattened. A more detailed description of the forms found in the range of sheltered to exposed conditions, together with the corresponding two-dimensional model, is given by Kaandorp (1991 b). The large plasticity in sponge growth forms, due to differences in exposure to water movement, is a well-known phenomenon (e.g. Bidder 1923, Warburton 1960, Barthel 1991).

Haliclona oculata is very suitable as a case-study subject, for several reasons. Growth lines are formed in the

skeleton, which makes it possible to retrace the growth process. The species branches more or less in one plane and the skeleton displays radial symmetry; both aspects allow the growth of this sponge to be simulated with a two-dimensional model. Although its growth process is relatively simple, this species exhibits a wide range of growth forms in which the influence of the environment is clearly visible. In addition, a practical reason for selecting this species was the fact that it is a common species in The Netherlands, which made it a suitable experimental subject.

The aim of the present study was to verify predictions made by a two-dimensional model which simulated the radiate-accretive growth process of the sponge under different environmental conditions. This was done with transplantation experiments, whereby the effect on growth of transplanting a sponge from a sheltered situation to an environment more exposed to water movement, and vice versa, was tested by comparing the sponge shape before and after the experiment.

Transplantation experiments provide an important method for testing the validity of simulation models. When sponges are transplanted, the normal growth process is interrupted and some of the environmental parameters are modified; a simulation model which takes these parameters into account should be able to predict changes in the growth form and the final resulting growth form. The growth forms of a sponge reflect environmental conditions to a significant extent and can be used to monitor those conditions. An important application of simulation models with a well-tested biological relevance is bio-monitoring. By using the actual growth forms and a simulation model, periods of environmental stress which may lead to interruptions in the growth process can be retraced. Besides the influence of exposure to water movement, such interruptions may be caused by the occurrence of pollutants, silt or other changes in the environment.

One study in which transplantation experiments were used to gain insight into the range of growth forms in two closely related hydrocoral species of the genus *Millepora* was carried out by de Weerdt (1981). Other studies in which computer models and transplantation experiments have been used for causal explanation of different growth forms of marine organisms under varying environmental conditions are Graus (1977), and Graus and Macintyre (1982) [both on the coral species *Montastrea annularis* (Scleractinia)].

One mathematical model for bio-morphological descriptions which is often applied in botany is the L(indenmayer)-systems (Lindenmayer 1968, Prusinkiewicz and Lindenmayer 1990). In L-systems objects are represented by strings of symbols in a formal language. The strings themselves do not contain geometric information; additional drawing rules are necessary in order to translate the strings into a morphological description. In L-systems it is less convenient to introduce geometric restrictions, as occurs for example in the growth of branching organisms, in which growth stops as soon as branches intersect. L-systems seem to be less applicable to growth models when the influence of the physical environment

on the growth process must be taken into account, because the physical environment cannot be modelled with L-systems.

Many growth patterns in physics and biology can be modelled with "Laplacian" models, also known as diffusion-limited aggregation (DLA) models (e.g. Witten and Sander 1981, Stanley and Ostrowsky 1987). In these models growth of objects is simulated in a cellular automaton; in such an automaton the growth pattern is represented by positions in a lattice. Many simulations using the DLA model have been carried out in a two-dimensional lattice. Growth is simulated by adding sites to the growth pattern in an iteration process. DLA models can be generalized to describe many growth phenomena known from physics (Sander 1986) and can be applied in biology for modelling growth forms of organisms which can be considered aggregates of small particles. During the growth process the particles do not exhibit interactions, e.g. the formation of a structure different from an aggregate. This model has been applied in biology to model forms of bacteria colonies (Fujikawa and Matsushita 1989, Matsuyama et al. 1989) and growth forms of dendritic hermatypic corals (Nakamori 1988). An advantage of this method is that it enables the physical environment of growing objects to be modelled. A crucial disadvantage, however, is that it is quite difficult and artificial to use a cellular automaton for describing the morphological aspects of many growing biological objects.

Methods

Simulation experiments

As stated above, the growth of *Haliclona oculata* can be modelled as an iterative process (Fig. 1). In this paper only a short description of the (two-dimensional) model is given; a detailed description can be found in Kaandorp (1991 a), and details concerning the biological significance of the model can be found in Kaandorp (1991 b). The length l of a new longitudinal element is determined by a product of three functions, $f(\alpha)$, $h(rad\_curv)$ and $g(lowest\_value)$. All functions return values in the range 0.0 to 1.0.

$$f(\alpha) = \begin{cases} 1.0 & \text{for } \pi/2 \le \alpha \le (\pi/2 + \pi/n) \\ \sin[(\pi/2)/(\pi/2 - \pi/n) \times (\pi - \alpha)] & \text{for } (\pi/2 + \pi/n) < \alpha \le \pi. \end{cases} \quad (1)$$

$$h(rad\_curv) = 1.0 - (rad\_curv - min\_curv)/(max\_curv - min\_curv)$$
$$\text{for } min\_curv \le rad\_curv \le max\_curv \quad (2)$$

$$h(rad\_curv) = 1.0 \text{ for } rad\_curv < min\_curv$$

$$h(rad\_curv) = 0.0 \text{ for } rad\_curv > max\_curv.$$

$$g(lowest\_value) \quad (3)$$
$$= \text{random value from the interval } [lowest\_value - 1.0].$$

$$l = \begin{cases} s \times f(\alpha) \times h(rad\_curv) \times g(lowest\_value) \\ \text{for } f(\alpha) \times h(rad\_curv) \times g(lowest\_value) > inhibition\_level \\ 0.0 \text{ for } f(\alpha) \times h(rad\_curv) \times g(lowest\_value) \le inhibition\_level. \end{cases}$$
$$(4)$$

The argument α in function f represents the angle between an axis of growth (see dashed lines in Fig. 1) and a tangential element. The function f attains a maximum value when $\alpha = \pi/2$ and a minimum for $\alpha = \pi$. Its biological significance lies in the fact that water movement is strongest at the tip of the sponge, where the sponge has
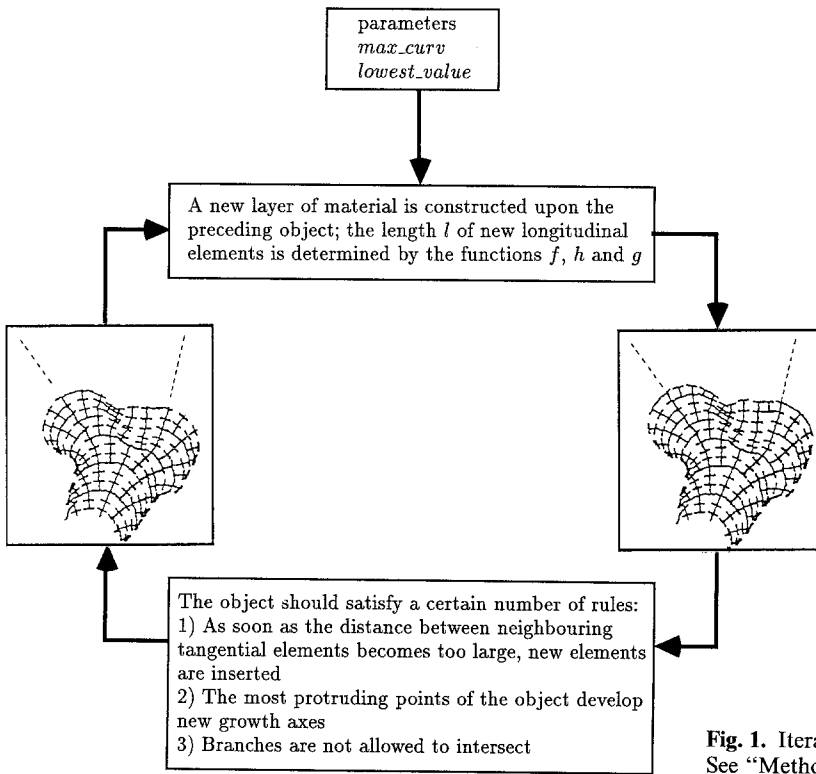
Fig. 1. Iterative process for modelling growth of *Haliclona oculata*. See "Methods" for description of functions

the greatest, access to suspended material in the water and can develop the highest growth velocities.

Function *h* returns a normalized version of the local curvature, computed from the radius of curvature *rad_curv*, which in turn is estimated from a set of points situated on neighbouring tangential elements. The quantity *rad_curv* is allowed to vary within a pre-set range. Its biological significance is that, especially under conditions with little water movement, the sponge is not able to pump water with suspended material to sites in the tissue which are not in short-distance contact with the environment; thus growth decreases, the sponge starts branching, and an old axis of growth is replaced by new axes. The aquiferous system in *Haliclona oculata* is poorly developed compared to that of related species such as *Haliclona simulans*. There is an extensive aquiferous system in *H. simulans*, and erect growth forms emerge in the same type of growth process (radiate-accretive). A consequence is that in *H. oculata* only thin-branching and plate-like forms emerge during growth, while in *H. simulans* more voluminous and globular forms develop (Kaandorp 1991 b).

The function *g* (Eq. 3) models the extent to which the growth process is disturbed by the environment on the growth process. This function returns uniformly distributed random values in the range [*lowest_valve* −1.0]. The effect of selecting a value slightly below 1.0 for *lowest_value* is an increase in the amount of plate formation at the extremities of the objects. Thin-branching forms are generated by selecting the value 1.0 (no disturbance of the growth process).

In the iteration process three rules are applied. The first rule is that the tangential elements should be connected with each others; as soon as the distance between neighbouring tangential elements becomes too large, new elements are inserted. Secondly, the most protrusive (local extreme) points of the object develop new growth axes; biologically, this means that these parts of a real sponge develop the highest growth velocities. Thirdly, branches are not permitted to intersect.

In the simulation experiments only two parameters were varied: *max_curv* and *lowest_value* (see Fig. 1). Sheltered conditions were simulated by selecting a low value for *max_curv* and a value of 1.0

for *lowest_value*. Exposed conditions were simulated by selecting a higher value for *max_curv* and 0.8 for *lowest_value*. The other parameters in the model (*inhibition_level*, *s* and *min_curv*) remained constant in these experiments; they should be regarded as parameters which reflect the specific properties of the skeletal architecture, such as the size of the spicules and the consolidation of these elements in the skeleton.

Transplantation experiments

Transplantation experiments were carried out from 11 March to 30 April 1989 (Expt 1) and from 30 November 1989 to 17 March 1990 (Expt 2). An important reason for selecting periods in early spring and winter was that growth of *Haliclona oculata* is often stunted by the occurrence, in late spring and especially in summer, of algae and diatoms on the sponge surface, often resulting in partial death of the sponges. This species is found in The Netherlands at depths between 2 and 22 m, where it grows on various types of hard substrate.

During both periods sponges were collected from a sheltered location (Site 1, Lake Grevelingen; depth 8 m) and two exposed locations (Sites 2 and 3, both in the Eastern Scheldt; depth 5 m) in The Netherlands (Fig. 2). Sites 1 and 2 have abundant *Haliclona oculata* populations. Site 3, although containing a sparse *H. oculata* population, was chosen because sponges there are highly exposed to water movement. For the experiments only small specimens were collected, in order to avoid complicated growth forms which make it more difficult to interpret the effect of transplantation.

At all sites additional sponges were collected before and after the experiments, to be used for comparing the effects of the experiments on the growth forms, as explained below.

In the second experiment (30 November 1989 to 17 March 1990), an improvement was introduced whereby the sponges were photographed before transplantation. For exact measurements, some branches were marked with minute stainless-steel needles. The needles were stuck into the surface of the sponges so that the heads

of the needles were flush with the surface of the sponge. After being marked the sponges were affixed to long nails with insulated electric wire (Fig. 3). The sponges were supported by a small notch in the head of the nail in order to ensure, that they remained erect. The nails with the sponges were inserted into the substrate at the test sites. After a period of about 3 mo the sponges were recollected and photographed anew. In the second experiment the photographs were taken using the contours of the transplants before the experiment: the sponges were positioned exactly within the original contours, so that the growth process could be followed by comparing the original and the new contour of the sponge. The position of the needles was detected by x-ray photography.

In the experiments for each site some sponges were returned to the original growth site (the control experiment) and some were transplanted to a site with a different degree of exposure to water movement. The experiment is summarized in Fig. 4, in which the number of transplants and the degrees of exposure to water movement are indicated. The erosion values shown in Fig. 4 are taken from the literature (see de Kluijver 1989) and are used to indicate the degree of exposure to water movement at the test sites. The erosion value is expressed as the weight loss of gypsum blocks (g h^{-1}) during a lunar day (24 h 45 min); this value is an indication of overall water movement – no distinction is drawn between turbulence and currents. The erosion values were measured, during the transplantation experiments at the three test sites. Besides exposure measurements, the sedimentation load at the three test sites was determined. Sedimentation is a limiting environmental parameter for the growth process of sponges; excessive sedimentation (especially of fine sediment) may lead to occlusion of the inhalant pores of the aquiferous system (see Brien et al. 1973). For this reason, measurements of the daily sedimentation load at the three test sites were also made during the experiments, by using sediment traps and by taking samples of the upper 1 cm layer of the bottom sediment. In the bottom samples a distinction was made among different size fractions (measured in mm) by using seven graded sieves (from 2.8 to 0.05 mm). Details about sedimentation measurements can be found in de Kluijver and Leewis (in preparation).

Comparison of growth forms

In a previous paper (Kaandorp 1991 b) growth forms from sites ranging from exposed to sheltered were compared. This comparison was done by measuring the diameters of circles fitting just within the branches (Fig. 5). The experimental results were summarized in diagrams of sponge contours after the experiments (see for example Fig. 9). In the second experiment, the contours of the sponge before the experiment were also added. In the diagrams the positions of the needles (determined by x-ray photographs) were indicated. These contours were used for fitting circles within the branches.

Diameters of three types of circles were measured: diameter da of the largest circle (a) which fits in the branch just before ramification; diameter db of the largest circle (b) just after ramification; and diameter dc of the largest circle fitting within the top of a branch (see Fig. 5). The value for this last circle should vary between da and db. This assumption was verified by comparing the dc data sets with the da and db data sets. The reason for using this measure instead of da or db was that only in long-term growth experiments are sufficient ramifications formed to allow for enough measurements of da and db, but long-term experiments are more difficult to interpret because of the heightened chance of damage to the transplanted sponges over time.

In order to determine the effect of transplantations on the degree of plate formation at the extremities of branches, the measured dc values were compared to a set of dc values measured in material collected from the three test sites. In the first experiment this data set was obtained from the additional material collected for this purpose. In the second experiment this set was obtained using the contour photographs of the transplants before the experiment. Ad-
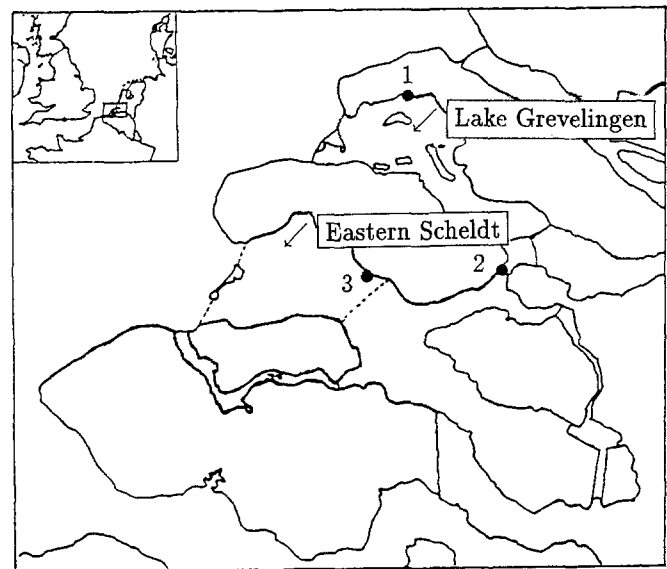

Fig. 2. Study area in The Netherlands showing the sampled localities. (1) Sheltered location in Lake Grevelingen; (2), (3) two exposed sites in the Eastern Scheldt
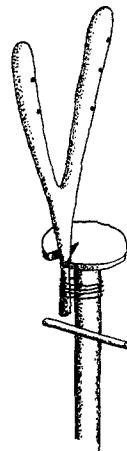

Fig. 3. Diagram of *Haliclona oculata* affixed to a nail for the transplantation experiment

ditionally, in the second experiment, the amount of material added to the top of the sponge (dg) during the test period was measured as the distance from the point of intersection between the growth axis and the surface before the experiment to that after the experiment (dotted line in Fig. 5).

Results

Simulation experiments

The sponge forms generated in the simulation experiment are shown in Fig. 6 A and B. In Form A the parameters *max_curv* and *lowest_value* (see Fig. 1) were initially set to a low value (0.10) and 1.0 (no disturbance), respectively. Without interrupting the iteration process, these values would result in the thin-branching from shown in Fig. 6 C. In Form A, however, this process was interrupt-
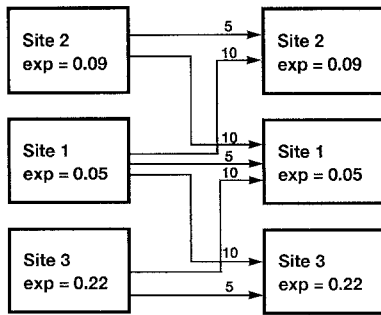
Fig. 4. Summary of transplantation experiment. Degree of exposure to water movement is indicated for each site (see Fig. 2) by the corresponding erosion values (exp). Numbers above arrows = no. of experimental individuals
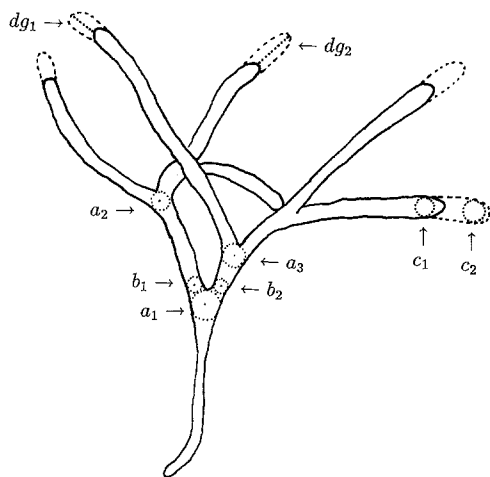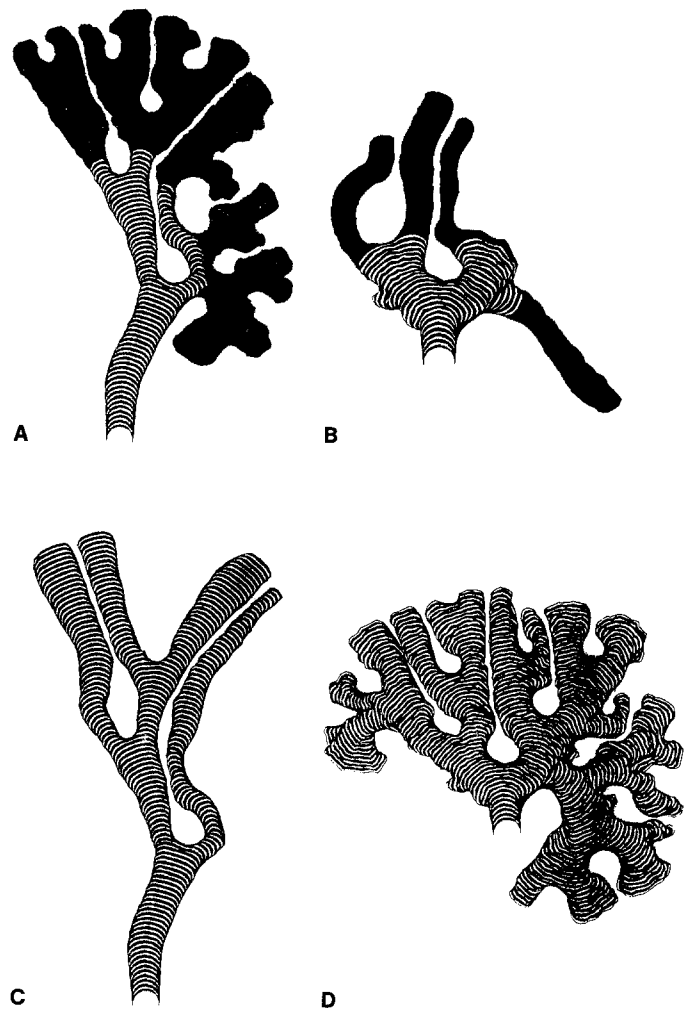

Fig. 5. Diagram of contours, showing locations of the measured circles. Circle a is the largest circle which fits in the branch just before ramification, b is the largest circle just after ramification, and c is the largest one which fits inside the top of a branch; da, db and dc are the corresponding diameters. dg is a measure of the amount of material added during the test period to the sponge tip

Fig. 6. Simulated forms of *Haliclona oculata*, using the iterative process shown in Fig. 1. In Form A the parameters *max_curv* and *lowest_value* were initially set to a relatively low value 1.0 and the iterative process was then interrupted and the parameters were set to a high value and 0.8. In Form B the reverse procedure was applied. Forms C and D resulted from the iterative process without interruption (parameter settings were the initial ones for A and B, respectively)

ed and disturbed by setting the parameter *lowest_value* to 0.8; simultaneously, *max-curv* was increased (from 0.10 to 0.30). In Form B the reverse experiment was carried out: *lowest_value* was initially set to 0.8 and a high value for *max_curv* was used; during the generation these parameters were set to 1.0 (disturbance is stopped) and to a lower value, respectively. Without this latter interruption, Form D would emerge.

Transplantation experiments

The assumption that the distribution of dc was situated between the distributions of da and db (see also Fig. 5) was tested by applying a two-sample rank test to values obtained from the additional material collected at all

Table 1. *Haliclona oculata*. Results of two-sample rank test carried out to test the assumption that the distribution of diameter dc was situated between those of diameters db and da (see Fig. 5). For the first experiment this test was performed for data sets obtained from the additional material collected at the three test sites; for the second experiment measurements were made using contours of the transplants before the experiment

Site	Diameter	Result (first experiment)	Result (second experiment)
1	da	dc left of da	dc left of da
	db	dc right of db	dc equals db
2	da	dc left of da	dc left of da
	db	dc right of db	dc right of db
3	da	dc left of da	dc left of da
	db	dc right of db	dc right of db

Table 2. *Haliclona oculata.* Mean values for the three types of diameter (see Fig. 5) measured at the three test sites in the first and second experiments. n_x: no. of observations; s_x: standard deviation

	$\overline{db}$	n_{db}	s_{db}	$\overline{dc}$	n_{dc}	s_{dc}	$\overline{da}$	n_{da}	s_{da}
(A) Expt 1									
Site 1	0.15	102	0.04	0.16	51	0.03	0.26	102	0.05
Site 2	0.20	131	0.06	0.24	50	0.07	0.36	131	0.08
Site 3	0.19	46	0.04	0.21	28	0.04	0.32	24	0.05
(B) Expt 2									
Site 1	0.15	52	0.05	0.15	47	0.03	0.24	44	0.07
Site 2	0.20	52	0.05	0.24	50	0.08	0.33	52	0.06
Site 3	0.18	43	0.04	0.18	51	0.04	0.29	41	0.08

Table 3. *Haliclona oculata.* Survival of transplants

Source site	Target site	No. of transplants	No. of survivors
(A) Expt 1			
1	1	5	1
1	2	10	8
1	3	10	7
2	2	5	4
2	1	10	9
3	3	4	4
3	1	10	5
(B) Expt 2			
1	1	5	5
1	2	10	9
1	3	10	7
2	2	5	4
2	1	10	10
3	3	5	3
3	1	10	10

Fig. 7. *Haliclona oculata.* Longitudinal section of a sponge tip in which the surface of a previous growth stage is marked with needles (1.5 mo experiment). The surface can be reconstructed by interconnecting the ends of the needles

three test sites. In all three cases the hypothesis that the distribution of *dc* was the same as those of *da* and *db* was tested against the alternative that they differed by a translation, and in all cases a significance level of 5% was applied. The results of this test are shown in Table 1. In only one case was this hypothesis accepted. In Table 2 the mean values of the three types of diameters are listed for the three test sites; values in Table 2 A were measured in the additional material collected at the sites, and those in Table 2 B were determined from sponge contours before the experiment.

The survival rate of the transplants is shown in Table 3 (see also Fig. 4). The low survival rate of transplants at Site 1 in Table 3 A was probably due to human activity. A relatively low transplant survival rate could be observed at Site 3 in Table 3 A and B.

Fig. 7 shows a longitudinal section through a marked sponge tip. The original sponge surface before the experiment can be retraced using the ends of the needles.

Three examples of transplanted sponges are presented in Fig. 8. Sponge A was transplanted from a sheltered site (Site 1) to an exposed site (Site 2), and for Sponge B the reverse was done. Sponge C was accidentally positioned horizontally on the nail (see Fig. 3), and in Fig. 8 it can be observed from the attachment wire (the circle next to the holdfast of the sponge) that this sponge grew horizontally.

Fig. 9 shows the resulting diagrams for the transplanted sponges presented in Fig. 8 A and B. The circumference of each sponge at the beginning of the experiment is indicated with a dotted line (for non-marked branches this was only possible in the second experiment), and at the end of the experiment as a continuous line. The position of the needles, detected using x-ray photographs, is also shown.

Changes in the form of transplants were determined by comparing the *dc* data sets from the additional material collected at the test sites to the *dc* data sets measured in the transplanted sponges. Both data sets were com-

Table 4. *Haliclona oculata*. Comparison of the dc (indicated as dc_o) data set obtained from the additional material collected at the source site with the dc (indicated as dc_r) data set measured in the transplants at the target site (Expt 1); and comparison of the dc (indicated as dc_o) data set obtained from contours of transplants before the experiment with the dc (indicated as dc_r) data set measured in the transplants at end of the experiment (Expt 2). n_x: no. of observations; s_x: standard deviation; index o: measurements at beginning of experiment; index r: measurements at end of experiment; $-$: no observations

Source site	Target site	n_r	$\overline{dc_r}$	s_{dc_r}	Result	n_o	$\overline{dc_o}$	s_{dc_o}
(A) Expt 1								
1	1	3	0.18	0.03	r equals o	51	0.16	0.03
1	2	28	0.19	0.04	r right of o	51	0.16	0.03
1	3	26	0.21	0.06	r right of o	51	0.16	0.03
2	2	23	0.27	0.08	r equals o	50	0.24	0.07
2	1	36	0.20	0.07	r left of o	50	0.24	0.07
3	3	26	0.29	0.06	r right of o	28	0.21	0.04
3	1	17	0.21	0.06	r equals o	28	0.21	0.04
(B) Expt 2								
1	1	19	0.25	0.06	r right of o	47	0.15	0.03
1	2	37	0.29	0.09	r right of o	47	0.15	0.03
1	3	13	0.21	0.08	r right of o	47	0.15	0.03
2	2	26	0.24	0.06	r equals o	50	0.24	0.08
2	1	57	0.28	0.08	r right of o	50	0.24	0.08
3	3	$-$	$-$	$-$	$-$	51	0.18	0.04
3	1	43	0.25	0.09	r right of o	51	0.18	0.04

Table 5. *Haliclona oculata*. Values of dg for the transplantation experiments done from 30 November 1989 to 17 March 1990. n: no. of observations; s_{dg}: standard deviation; $-$: no observations

Source site	Target site	n	$\overline{dg}$	s_{dg}
1	1	16	1.07	0.40
1	2	28	1.82	0.93
1	3	13	0.95	0.47
2	2	18	1.22	0.48
2	1	47	1.53	0.46
3	3	$-$	$-$	$-$
3	1	31	1.26	0.44

Table 6. Erosion values measured with gypsum blocks ($g\,h^{-1}$) at the three test sites in 1989 and 1990. n: no. of observations

Site	Minimum	Mean	Maximum	n
1	0.05	0.07	0.08	4
2	0.06	0.09	0.14	20
3	0.06	0.13	0.16	8

Table 7. Sedimentation loads and dominant sediment fractions at the three test sites in 1989 and 1990

Site	Sedimentation ($g\,m^{-2}\,d^{-1}$)	Dominant fractions (mm)
1	10–1 160	0.09–0.30
2	30–1 150	0.15–0.30
3	270–1 450	<0.09

pared by applying the two-sample rank test. Results of the comparison are summarized for both experiments in Table 4.

Table 5 presents values of dg (i.e., the amount of material added to the sponge tip) measured in the transplants in the second experiment. Erosion values measured in 1989 and 1990 are given in Table 6. The corresponding sedimentation loads and dominant sediment fractions are shown in Table 7.

Discussion

The diagrams in Fig. 9 indicate that growth only took place on certain parts of the sponges, i.e., at the tips. This is most evident in the longitudinal section shown in Fig. 7, where the sponge surface at the beginning of the transplantation can be retraced by interpolating the ends of the needles. This is consistent with the simulation models, in which growth only occurs at the apices. Only at the trunk of the sponge, close to the nail, could secondary growth be observed. In photographs (see Fig. 8) it appeared that the head of the nail was partly covered with sponge tissue; the attachment wire was also incorporated into the sponge tissue. This secondary growth was probably induced by local damage inflicted on the sponge when it was removed from the substrate.

Fig. 7 reveals that growth in the right branch stopped as soon as the (marked) left branch overgrew the right branch. In a previous paper (Kaandorp 1991 b) it was assumed that, especially at sheltered sites (the sectioned sponge shown here is from Site 1; see Fig. 2), water movement and food supply, as well as growth velocity, decrease when branches collide. Fig. 7 provides experimental evidence of this effect. Under exposed conditions this effect is less critical, since due to the relatively high degree of water movement the food supply will be higher at the parts of the sponge which are shielded from the environment by the canopy of branches. Under exposed conditions collision of branches may more often lead to anastomosis or avoidance. This process, in which branches avoid each other by escaping in the third dimension, can only be adequately modelled with a three-dimensional model. In a sheltered situation the collision of branches can be modelled only partly using the third rule of the iteration process (see Fig. 1), because under sheltered conditions growth in shielded branches will be slowed down, so that anastomosis and avoidance of branches are less often observed.

In the transplantation experiments a clear tendency of sponges to grow from the substrate was observed. This appeared in transplants which were positioned horizontally (see Fig. 8 C). This negative substrate-tropism could especially be observed under sheltered conditions; the same effect can be seen in sponges growing on cave ceilings. In general the minimal angle between the axis of growth (Fig. 10) and the vertical axis will be smaller under sheltered conditions than under exposed conditions. This negative substrate-tropism can be explained hydrodynamically: assuming laminar flow, the water move-
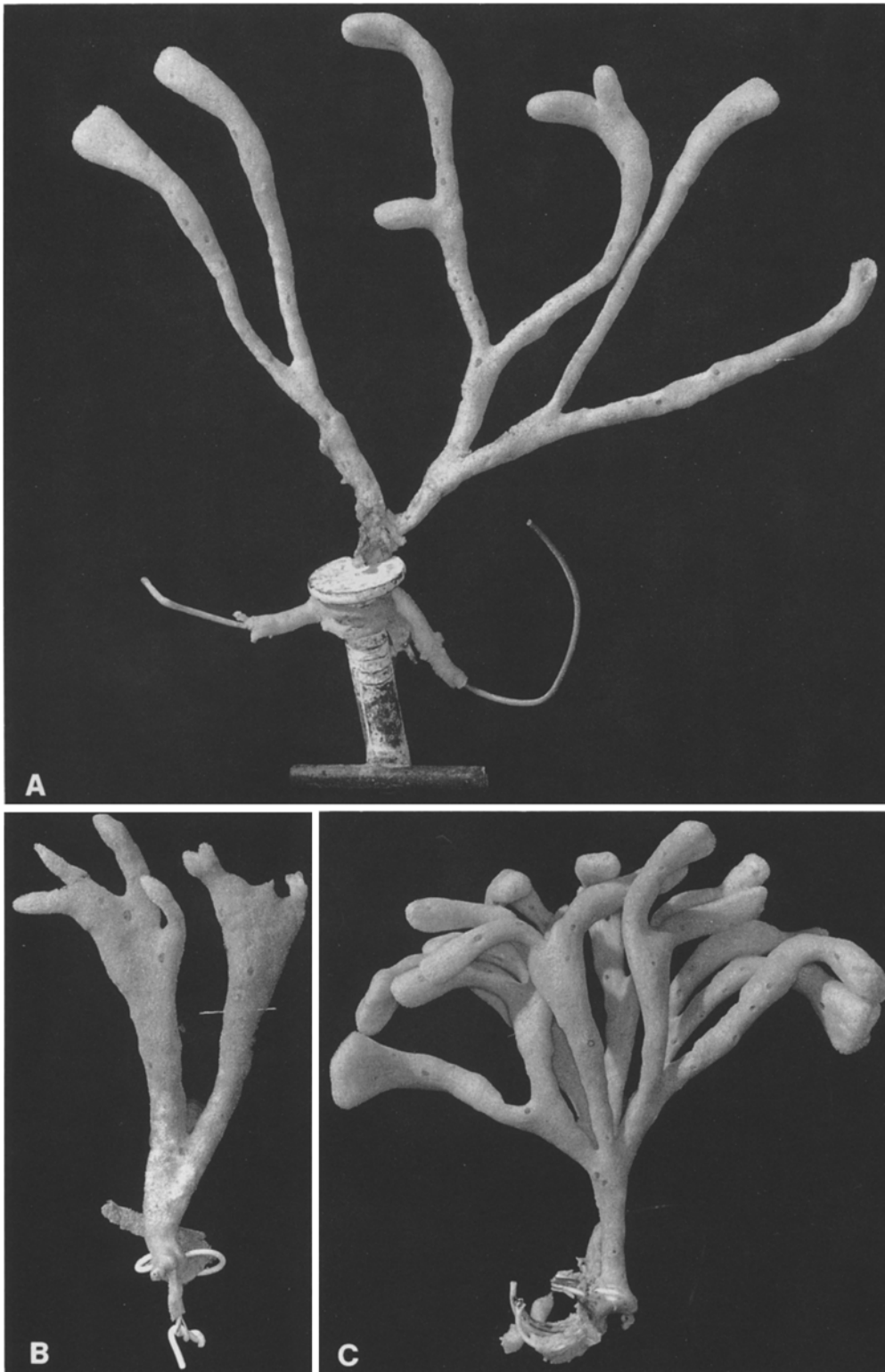
Fig. 8. *Haliclona oculata.* Examples of transplanted sponges. Sponge A was transplanted from the sheltered Site 1 to the exposed Site 2; for Sponge B the reverse was done. Sponge C is a transplant which was positioned horizontally on the nail (see Fig. 3). (A), (C) 3.5 mo experiment; (B) 1.5 mo experiment

ment is zero just at the (fixed) substratum and increases quadratically with distance from the substratum until the velocity of the laminar flow is reached (e.g. Vogel and Bretz 1971, Vogel 1983); this causes the sponge to grow from the substrate towards the area with the highest flow velocities and the greatest supply of suspended material.

Under sheltered conditions the vertical gradient in water velocity (together with the food supply and resulting growth velocity) will be more pronounced than under exposed conditions, resulting in a smaller minimal angle between a given axis of growth and the vertical axis. In the model in Fig. 1 this negative substrate-tropism is not
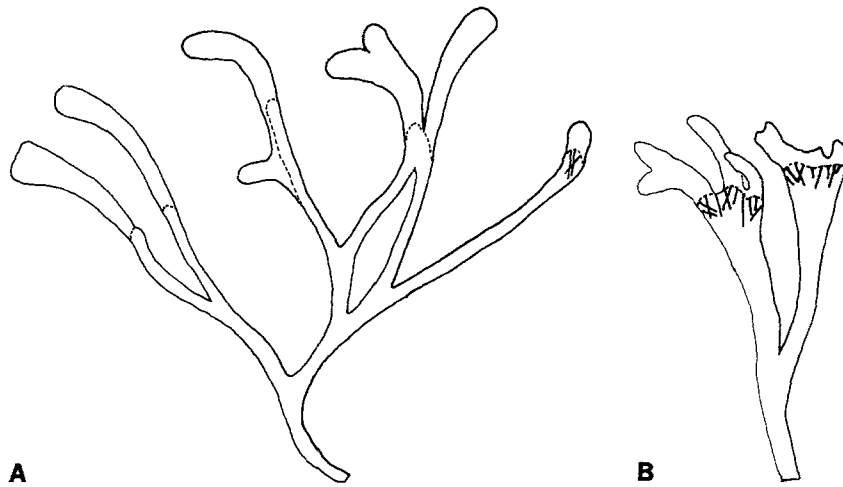
Fig. 9. Contours of *Haliclona oculata* used in transplantation experiments. Sample A was transplanted from a sheltered to an exposed site; for Sample B the reverse was done (A) 3.5 mo and (B) 1.5 mo experiment
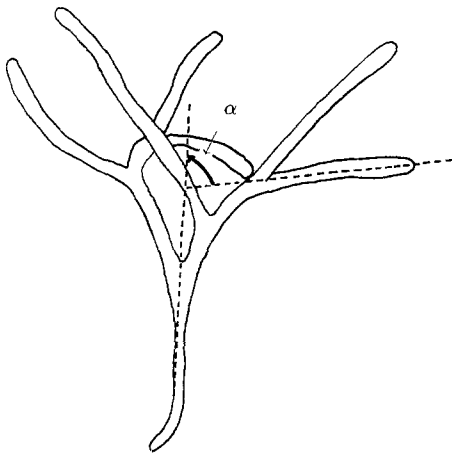
Fig. 10. Determination of the minimal angle between an axis of growth of a sponge (or simulated object) and the vertical axis

(yet) included; this would require the incorporation of a hydrodynamic model.

The model predicts that a sponge transplanted from a sheltered site to an exposed site will yield thin-branching sponges with plate-like ends (Fig. 6 A). The reverse experiment should yield palmate sponges with thin distal branches (Fig. 6 B). The predicted forms were indeed found in the transplantation experiments. In Figs. 8 A and 9 A a thin-branching sponge is shown which was transplanted from the more sheltered Site 1 (mean erosion value 0.07 g h^{-1}; see Table 6) to the more exposed Site 2 (mean erosion value 0.09 g h^{-1}) and which exhibits plate-like extremities. In Figs. 8 B and 9 B a sponge with which the reverse experiment was carried out displays a palmate form with thin distal ends.

In general the shift from thin-branching to plate-like forms and the occurrence of palmate forms could be demonstrated by comparing values of *dc* (diameter of the largest circle fitting in the top of a branch; see Fig. 5) in sponges at the end of the transplantation experiment with the values at the beginning of the experiment. As ex-

plained in the "Methods", the diameter *dc* was used for practical reasons (instead of *da* and *db*; see Fig. 5), and it was assumed that the distribution of *dc* was situated between the distributions of *da* and *db*. Tables 1 and 2 show that this assumption was correct. In Table 4 A it can be seen that the value of *dc* increased when sponges were transplanted from the sheltered site to the exposed Site 2, which indicates increased plate formation comparable to that depicted in Fig. 8 A. For the reverse experiment a decrease in *dc* and in plate formation could be observed, resulting in palmate objects. In the control experiments, in which sponges were returned to the source site, it appears that the transplantation experiment itself did not result in a shift in the distribution of *dc* for Sites 1 and 2.

In the second experiment (30 November 1989 to 17 March 1990) a shift from plate-like to thin-branching forms, resulting in palmate sponges, could not be demonstrated. In the experiments carried out at Sites 1 and 2 a general increase in plate formation was found (see Table 4 B). This general increase in *dc* can be explained by the occurrence of two severe storms (25 January and 26 February 1990) which struck the area with forces of 30 and 26 m s^{-1} respectively (average over 1 h), resulting in an overall increase in water movement at the test sites. The difference between the sheltered and the exposed site disappeared. Although in this experiment the emergence of palmate forms could not be demonstrated, the findings could explain why typically palmate sponges are sometimes found in the normally sheltered Lake Grevelingen (see Fig. 2). An example of such a palmate form is shown in Fig. 11. During storms and the period afterwards, when the water movement gradually diminishes, thin-branching sponges at this location form plate-like ends. Subsequently the location becomes sheltered again. The plate-like ends presumably die off because the tissue is not in short-distance contact with the environment, or they are gradually transformed into palmate growth forms. The result also suggests that sponge growth forms are potentially useful for monitoring environmental parameters.

In Table 5 values of *dg* measured in the transplants in Expt 2 are compared for the three test sites. In general it

Fig. 11. *Haliclona oculata.* Example of a palmate sponge, a form which is occasionally found on sheltered locations as Lake Grevelingen (see Fig. 2)

is expected that growth velocity increases when the water movement and food supply increase at a given test site. Because of the stormy weather during the test period it was not possible to make a strong distinction between exposed and sheltered locations; all locations were probably more or less exposed.

Transplants at Site 3 exhibited a remarkably low growth velocity (Table 5) and relatively low survival (Table 3). During the second test period it was difficult to find enough living specimens to carry out the transplantation experiments. The deviant values at Site 3 can be explained by its relatively high sediment load. Table 7 shows that the minimal sediment load was high (270 g m^{-2} d^{-1}) compared to that at the other test sites, with bottom sediments mainly in the <0.09 mm fraction.

The simulation models make possible some predictions about the effect of environmental changes on sponge growth forms. Thus, growth forms may be used

to monitor environmental parameters. By comparing growth forms from various sites and using simulation models, it becomes possible to detect sites with deviant environmental conditions.

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