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# The fractal branching of an arborescent sponge

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**Abstract** The fractal properties of specimens of a planar branching sponge *Raspailia inaequalis* (Porifera, Demospongiae) were determined by analysing digitised photographs. The specimens, collected from a single site in northeastern New Zealand, had a wide range of morphology. Three different fractal methods were used: box counting; a method that gives the scaling of branch length with distance from the base of the fan; and an allometric analysis of the dependence of frontal area on specimen size. All three approaches gave a similar value for the fractal dimension. The conjecture that the specimens have a fractal branching structure is consistent with the results of a Horton analysis of their branching pattern. There is a significant relationship between fractal dimension and number of fingers, which implies that a simple count of the number of fingers is as useful for discriminating between individuals as the more complex fractal analysis. Using this relation, sponges from a site with less water movement are inferred to have a lower fractal dimension. This result is in agreement with the predictions of the Kaandorp model of sponge growth.

## Introduction

The description of the indeterminate growth forms of many sessile marine invertebrates is often only achievable in qualitative terms. The lack of ability to describe growth form accurately has hampered the use of external morphology as a diagnostic character and has made interpretations of the interaction between the growth form and the environment difficult to achieve. Since the popularisation of fractals (Mandelbrot 1982), many authors have used fractal methods to provide some quantification of morphology and to demonstrate the dependence of growth form on environmental parameters. Seaweeds (Corbit and Garbary 1995; Kubler and Dudgeon 1996), corals (Basillais 1997), the sponge *Haliclona oculata* (Kaandorp 1991; Kaandorp and de Kluivjer 1992), and gorgonians (Burlando et al. 1991; Mistri and Ceccherelli 1993) provide examples of marine organisms that have been shown to have fractal properties. Despite the successful application of fractals to the study of biological form, the commonly used methodologies lack any ready biological interpretation. Changes in measured fractal dimension can be caused be different branching patterns, surface elaborations, or simply through a different arrangement of the prepared specimen. Moreover, many objects may have the same fractal dimension, even though they are qualitatively quite different in appearance.

In the study reported here, several different fractal analyses were carried out on specimens of the arborescent sponge *Raspailia inaequalis* [Dendy 1924; also referred to as *Axinella* sp. A by Pritchard et al. (1984) and *Axinella* sp. 1 by Battershill (1987)]. This sponge has a planar habit, typically with a sympodial dichotomous branching pattern, which meant that photographs of the specimens could be used for morphometric analysis. A principal aim was to compare the box-counting method (Feder 1988), which is the most commonly applied technique for determining fractal dimension, with other approaches. The intention was to determine whether fractal methods give useful morphometric information. An additional motivation for studying the fractal properties of arborescent sponges was the model of sponge growth developed by Kaandorp (1991, 1994a, b, 1995). In this model the growth of branches is away from the substrate and other branches, towards increasing flow. If the growth rate is proportional to the flow speed in the vicinity of a branch tip then iteration of this basic growth rule, together with a rule controlling

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branching, leads to a fractal structure. This provides an explanation of why filter-feeding branching marine invertebrates may be expected to be fractal. A prediction of this model is that specimens from a high-flow environment will have a higher fractal dimension than specimens of the same species from a low-flow environment (Kaandorp 1991, 1999; Kaandorp et al. 1996). The analysis presented here provides data that can be used to help determine the applicability of the Kaandorp model.

## Materials and methods

### Sponge specimens and habitat

The sponge *R. inaequalis* is endemic to northern New Zealand, where it is found on sub-tidal rock platforms that have a thin (< 3 cm) sediment covering. In the localised sites where *R. inaequalis* is known to occur it forms an important component of the sponge-characterised community. Some aspects of the ecology and population structure of this species are described in Battershill (1987).

Forty-five specimens were collected at Leigh Reef (36°17′28″S, 174°49′13″E) by SCUBA, on 18 July 1995. The sponges were obtained from within 10 m of the boat anchor, at a depth of 24 m. They were chosen to represent the range of morphological variation, although small sponges (< 5 cm high) were not collected. On return to shore the drip-dry wet weight, $W$ (g); the height, $H$ (cm); and the number of branch-tips or fingers, $F$, of the sponges were measured. Each sponge was photographed laid flat against a black background, with a standard scale bar. The specimens were then preserved by drying at room temperature.

A count was made of the number of fingers of tagged *R. inaequalis* individuals from the Sponge Garden (36°15′58″S, 174°47′35″E), approximately 5 km distant from Leigh Reef and within the Leigh Marine Reserve, and their height was measured. The sponges were in three 10 m × 10 m areas, situated 30 m apart along a line running north to south through the centre of the 20-m deep Sponge Garden reef. All of the fractal analyses were carried out on the Leigh Reef specimens; the inter-comparison with the Sponge Garden site was included to test whether the prediction of the Kaandorp model holds for this species.

Aanderaa current meters were deployed at both the Leigh Reef and Sponge Garden sites. The current meters were set to a sampling interval of 30 min and positioned 4 m above the seabed. The meters were put in place on 13 September 1995 and retrieved 7 weeks later on 1 November. Tidal analyses of the current records were performed by fitting the data with harmonic components at the same frequencies as the major tidal constituents, using the software TIRA (available from the Proudman Oceanographic Laboratory).

### Image processing

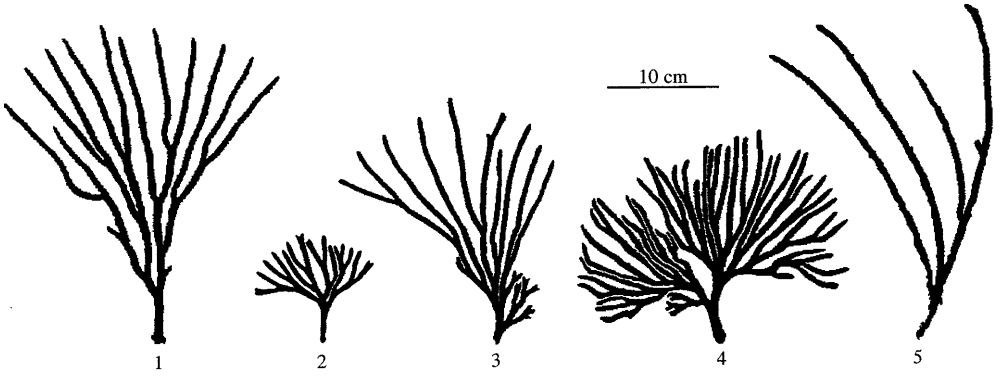
Pre-processing of the digitised photographic slides, using routines written in Matlab, included removing stray light pixels from the dark background, filling in any dark pixels on the image of the sponge, and determining the scale (pixels/cm) from the bar. Background pixels were set to zero and all other pixels were set to one (Fig. 1). From the binary image the frontal area, $A$ (cm$^2$), of each sponge was calculated from a count of the non-zero pixels.

A skeletal branching structure was obtained from the binary images using the following sequence. Firstly, each non-zero pixel was given the value of its distance to the nearest zero pixel. Secondly, an ordered list of the non-zero pixels was made, sorted first by value, then within each group of equal-valued pixels by the average value of their nearest neighbours. Finally, the pixels were progressively set to zero, beginning with those that were closest to the boundary, and so of lowest value, until only a pixel-wide digital skeleton remained. This gave an objective method of determining the branching structure. Once the skeletal pixels had been found, the vertices and branch-tips were identified and their positions held fixed. To remove the step-like pixel structure from the skeletons, the branches were smoothed by 20 passes of a three-point running-mean filter. On all the passes each point was shifted halfway to being directly between its two neighbours. From these smoothed morphological skeletons the branch lengths could be calculated. Because of the well-defined branching structures of the specimens, the resulting morphological skeletons accurately reflected the branching of the sponges, with very few spurious fingers being generated. Figure 2 shows the morphological skeleton of the specimen illustrated in Fig. 1 (number 1) and defines the terminology that will be used throughout the article. The numbers on the branches refer to the Horton analysis (see below).

For the skeletonisation procedure to work correctly the binary images required some pre-processing. Like many sponges, *R. inaequalis* is anastomosing: branches that touch while the sponge is growing eventually fuse together. Because of the axially condensed structure of the branches these anastomoses were easily identified. They were removed from the images by inserting a line of zero-valued pixels between the branches. A few of the sponges had been damaged while growing and had a confused, three-dimensional structure. The images were hand edited so the skeletonisation process would correctly recognise the underlying branching pattern.

Once the morphological skeleton had been identified the length of branch, $l(r)$, within an along-branch distance, $r$, from the primary vertex was calculated. The characteristic size of each sponge fan was then determined from the radius of gyration, $r_g$. This is defined as the distance for which $l(r_g) = l_{total}/2$, where $l_{total}$ is the total branch length of the sponge fan.

**Fig. 1** Digitised images of five of the sponge specimens, showing a range of morphologies



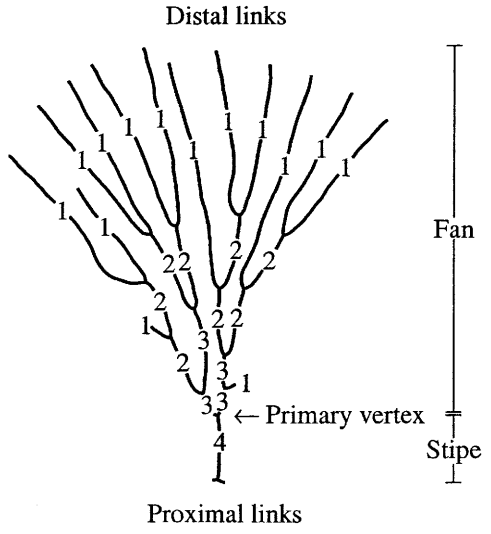



**Fig. 2** The morphological skeleton of sponge 1, from Fig. 1, with terminology used in the description of the branching pattern. The *numbers* are the Strahler order, $\omega$, of the branches. The *small lines* at the base of the stipe are excluded from the analysis. Contiguous links of the same order are counted as a single branch, so this specimen is order $\Omega = 4$, with 2 order-3 branches; 5 order-2 branches; and 14 order-1 branches or fingers

The statistical methods and terminology used throughout this article follow Sokal and Rohlf (1981).

### Box-counting dimension

To calculate the box-counting dimension, a grid of squares of size $r$ is placed over the image and the minimum number of squares, $N$, that contain the image, for any position of the grid, are counted. The procedure is repeated to obtain $N$ as a function of $r$ (Feder 1988). In the implementation used here, the number of non-zero pixels was first counted. The resolution of the image was then halved by summing groups of four pixels together, and the count was repeated. This was continued until the image had only a single non-zero pixel. By performing the whole procedure 12 times, using a random offset of up to a pixel in either direction before each change of scale, an estimate of the minimum count at each resolution was obtained. The fractal dimension and associated uncertainty were then determined by linear regression of $\log(N)$ on $\log(r)$. It was intended that the box-counting dimension reflect properties of the branching structure of the sponges, so the lower limit on the scaling relation was set at the width of the branches, which ranged from 3 mm up to 1 cm. The box-counting dimension is usually calculated from the boundary of planar images. Here it made no difference whether the entire image or only the boundary was used. For simplicity, the dimension was calculated from the whole image. At the upper end the scaling was limited by the size of the specimens. When forming the regression relation, the upper limit for the pixel size was set to be between one-quarter and one-half of the largest dimension of the specimen.

### Allometric relations

The fractal dimension of the sponge fans could also be estimated from the scaling of frontal area, $A$, with their radius, $r_g$, by performing a model II reduced-major-axis (RMA) regression of $\log(A)$ against $\log(r_g)$. The resulting dimension was called the allometric dimension, $d_{\text{Allometric}}$. Allometric analyses of the relations between the other measures of sponge morphology, height $H$, number of fingers $F$, and wet weight $W$, were also carried out.

### Branching structure

There are several methods of characterising ramifying networks that can be applied to biological structures, such as the sponge morphoskeletons (Berntsonn 1997). Horton analysis (Horton 1945; Strahler 1952) was used here to enable comparison of the branching structure of *R. inaequalis* with other ramifying forms and to help establish whether the branching of *R. inaequalis* is self-similar.

The fundamental step of Horton analysis is the assignment of a Strahler order, $\omega$, to each link of the network (Fig. 2). Firstly, the most distal links, the fingers, were labelled $\omega = 1$. Then, proceeding from the fingers towards the stipe, an order was given to each link via the following rule: if the two distal links that joined at a vertex had orders $\omega_1$ and $\omega_2$ then the proximal link was given an order $\omega = \omega_1 + 1$, if $\omega_1 = \omega_2$, or an order $\omega = \max(\omega_1, \omega_2)$, if $\omega_1 \neq \omega_2$. Contiguous links of the same order were regarded as forming a single branch. The order of the entire sponge, $\Omega$, was then defined as the Strahler order of the stipe. For gorgonians this ordering is found to be natural, in the sense that branches of similar order have similar function (Mitchell et al. 1993).

Once the Strahler order of the branches had been defined, the bifurcation ratio $r_B(\omega) = N(\omega)/N(\omega + 1)$, and the length ratio, $r_L(\omega) = L(\omega + 1)/L(\omega)$, were calculated, where $N(\omega)$ was the number of branches of order $\omega$, and $L(\omega)$ was their average length. If a network has a self-similar branching structure then these ratios are independent of $\omega$, so the entire network has well-defined bifurcation and length ratios, $R_B = r_B$ and $R_L = r_L$. In this case, the ratios may be calculated as $R_B = \text{antilog}(-\beta_B)$ and $R_L = \text{antilog}(\beta_L)$, where $\beta_B$ and $\beta_L$ are the respective slopes of the model I regression lines of $\log(N)$ and $\log(L)$ on $\omega$.

### Branch dimension

The branch dimension, $d_{\text{Branch}}$, was defined as the slope of the linear regression of $\log(l)$ on $\log(r)$, for $r_{\min} < r < r_g$. It was assumed that within the radius of gyration the sponge had finished growing, so the branch dimension reflected properties of the final development of the branches. The lower limit, $r_{\min}$, was chosen to provide a sufficient range of scales for the calculation of the dimension, while maintaining a linear relationship between $\log(l)$ and $\log(r)$.

In this analysis $r$ was measured along the branches. This had the advantage that the cumulative length, $l(r)$, did not depend on how the fingers are arranged. With $r$ defined in this way, the branch dimension does not reflect the embedding of the ramifying form in space, but rather intrinsic properties of the branching pattern.

## Results

### Box-counting fractal dimension

Figure 3 shows the dependence of the number of pixels needed to cover the images on the pixel size, for all 45 specimens. Between a pixel size similar to the width of the branches ($> 0.3$ cm) and less than half the size of the specimens, the relationship is approximately linear (the minimum correlation coefficient is $r^2 = 0.996$, which is significant: $n \geq 4$; $P < 0.01$). The box-counting dimension calculated over this range of scales varies between $d_{\text{Box}} = 1.44$ and $d_{\text{Box}} = 1.75$, with a mean value of $d_{\text{Box}} = 1.60 \pm 0.012$. The estimates of the box-counting dimension of single specimens have an rms standard error of 0.028.

To test the linearity of the data, the box-counting dimensions obtained using only the largest two pixel sizes were compared with those derived using only the smallest two sizes. If the underlying relation were linear

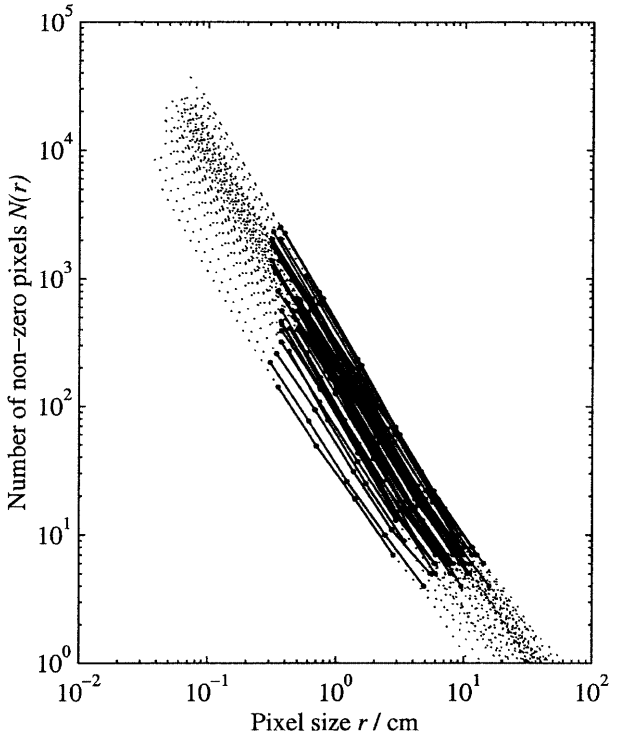



**Fig. 3** Variation of pixel number with pixel size, for all 45 specimens. The *solid lines* show the region used to calculate the box-counting dimension

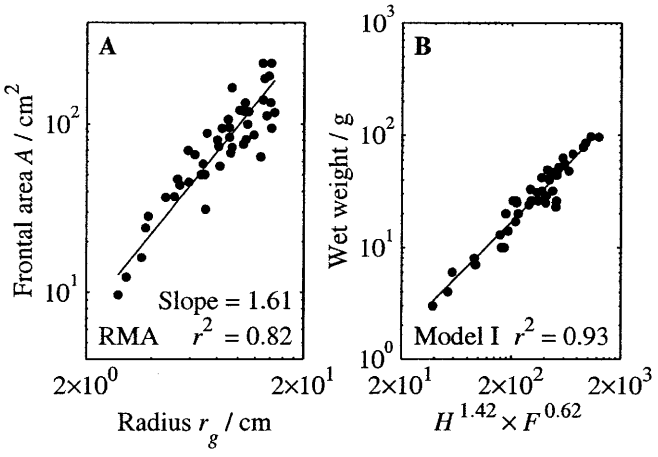



**Fig. 4** **A** Allometric relation between frontal area and radius of gyration. The *line* marks the model II reduced-major-axis (RMA) regression relation. **B** A model I bivariate regression of wet weight on sponge height and number of fingers gives a close fit to the data

then the mean difference between these dimensions should be zero, instead $\overline{\Delta d}_{\mathrm{Box}} = -0.173 \pm 0.0206$ ($H_0$: $\overline{\Delta d}_{\mathrm{Box}} = 0$ was rejected; $t_s = 8.4$; $P < 10^{-10}$). The slope of log[$N(r)$] flattened at the larger sizes. This implies that the box-counting dimension was not strictly well defined, as its value depended on the range over which it was calculated. Although the curvature is significant, the variation this caused in the value of the box-counting dimension was small. It was therefore assumed that a box-counting dimension could be meaningfully ascribed to each specimen.

The box-counting dimension of the specimens was not correlated with the height of the sponges ($r^2 = 2.1 \times 10^{-4}$; n.s.), but there was a significant correlation between the box-counting dimension and the number of fingers ($r^2 = 0.629$; $P < 10^{-10}$), with the consequent model I regression $d_{\mathrm{Box}} = (1.600 \pm 0.0073) + (7.0 \pm 0.65) \times 10^{-3} \times (F - 21.2)$, defined on the range $5 \leq F \leq 50$. Sponges with more branch-tips had a higher box-counting dimension, and so the box-counting dimension reflected branching complexity. For sponges from this population a count of the fingers enables an estimate to be made of the fractal dimension, with a similar standard error to that obtained directly from the box-counting procedure.

## Allometric relations

There was a high correlation between log($A$) and log($r_g$) ($r^2 = 0.82$; $P < 10^{-10}$), with the RMA regression log($A$) = (4.264 ± 0.0200) + (1.61 ± 0.105) × log($r_g$/8.145), defined for $2.80 < r_g < 14.55$(Fig. 4A). The allometric scaling dimension was $d_{\mathrm{Allometric}} = 1.61 \pm 0.105$, which was not significantly different from the mean of the box-counting dimensions. The relation between wet weight and the height of the sponges was $W \sim H^{1.78 \pm 0.139}$ ($r^2 = 0.74$). The difference between this exponent and $d_{\mathrm{Allometric}}$ was reflected in the relations $W \sim A^{1.12 \pm 0.035}$ ($r^2 = 0.96$) and $H \sim r_g^{1.01 \pm 0.035}$ ($r^2 = 0.95$). Wet weight was also correlated with the number of fingers: if two sponges are the same height then it is expected that the sponge with more fingers will be heavier. A model I multiple regression of log($W$) on log($F$) and log($H$) gave the predictive relation $W = (8.5 \pm 0.289) \times 10^{-2} \times H^{1.42 \pm 0.076} \times F^{0.62 \pm 0.061}$. The resulting correlation coefficient was a high $r^2 = 0.925$ (Fig. 4B), indicating the order that underlies the apparent morphological diversity of the specimens.

## Horton analysis

The Leigh Reef specimens displayed a wide variation in morphology: although it might have been expected that taller sponges should have more fingers, there was no correlation between the height of the sponges and the number of fingers (Fig. 5) ($r^2 = 0.0013$; n.s.). The Strahler order of the collected specimens varied between $\Omega = 2$ and $\Omega = 5$, with most (29) of the sponges being order $\Omega = 4$. In general, specimens with more fingers were higher order: there was a significant linear relation between log($F$) and $\Omega$ ($F_s = 73.28$, $df = 1, 2$; $P < 0.05$), with the linear regression giving $F \propto (2.05 \pm 0.18)^{\Omega}$.

The linear regression of log[$N(\omega)$] on $\omega$ was a close fit to the data (Fig. 6A). This suggests that, despite their variable morphology, the sponges had a statistically self-similar branching pattern. The mean bifurcation ratio,

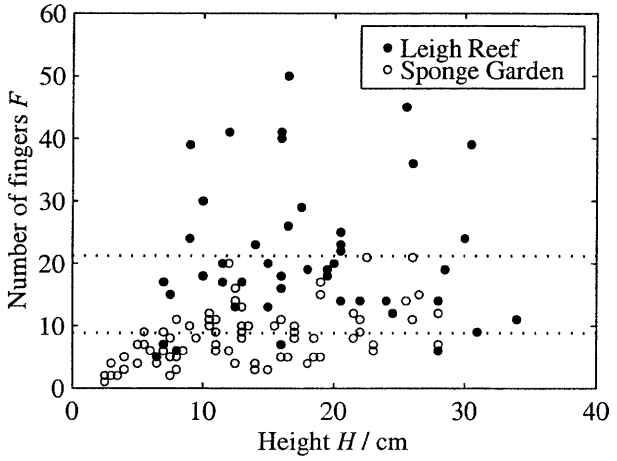



**Fig. 5** The variable morphology of the specimens from both sites is illustrated by the low correlation between height and number of fingers. The *dashed lines* represent the mean number of fingers of specimens from the two populations that are taller than 5 cm

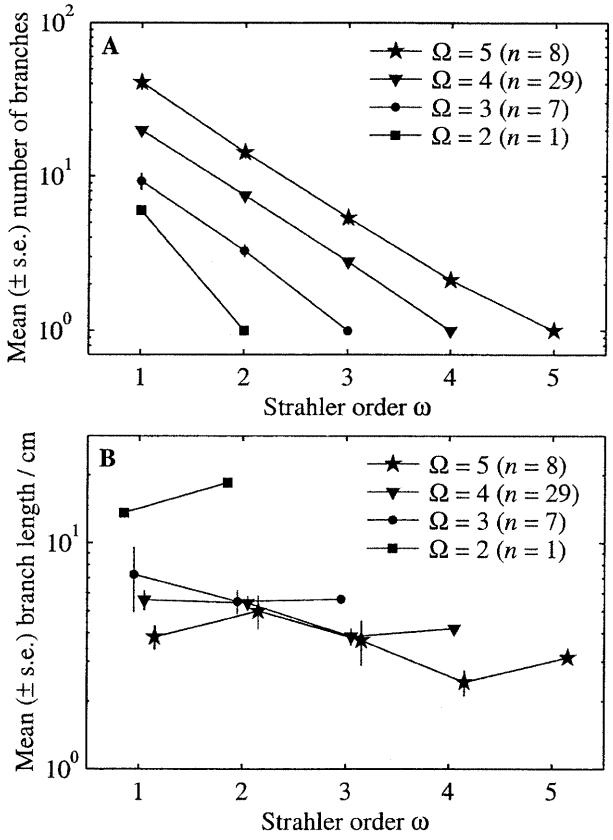



**Fig. 6** Horton analysis of the morphological skeletons. Mean branch number (**A**) and length (**B**) for specimens of each order (the number of specimens is shown in brackets). Where error bars are not visible they are smaller than the size of the plotting symbols, or else there is only one sample so the standard error is not defined. Symbols in **B** are offset in the *x*-direction so that they do not overlap

estimated from the $\Omega > 2$ specimens, was $\bar{R}_B|_{\Omega=3,4,5} = 2.71 \pm 0.046$ ($n = 44$). The single $\Omega = 2$ specimen (Fig. 1, number 5) was an outlier, with a bifurcation ratio, $R_B|_{\Omega=2} = 6.00$, more than 7 seven standard errors from the mean of the other sponges. The variation of branch length with order required a more careful interpretation (Fig. 6B). For the order-5 sponges $r_l(2) \sim r_l(3)$, and the length ratio, $r_l(2)$, of the order-4 sponges had a similar value. From these ratios it was estimated that $R_L = 0.75 \pm 0.043$, so the distal branches were typically longer than the proximal branches. This trend was not followed by the most proximal branches, which included the stipes. These branches were longer than expected and so did not fit into the apparently self-similar branching pattern of the fan. Nor did the fingers have the length that would be expected from self-similarity. This was likely to be because the growth in branch length occurs at the branch tips, so the first-order branches were shorter than they would have been if growth had continued. The first-order branches were also shortened by the skeletonisation process, which eroded the length of the branch tips by an amount similar to their radius of curvature (1–2 mm).

## Branch dimension

The relationship between the radius, $\log(r)$, and the cumulative branch length, $\log(l(r))$, was not linear (Fig. 7). For small values of $r$ there were no branchings and so branch length was proportional to distance from the primary vertex. For $r$ larger than the radius of gyration the length tended to the total branch length of the sponge fan, and the curve flattened. Nevertheless, a branch dimension could be defined by regression of $l(r)$ on $r$, over the range $r_{min} < r < r_g$, where $r_{min}$ was arbitrarily chosen to be the distance to the vertex which was fourth closest to the primary vertex. This choice allowed the branching to have reached sufficient complexity before beginning the regression. To ensure that the relation was calculated over at least some range of scales, the branch dimension was only estimated for the 26 specimens for which $r_g > 2r_{min}$. The range of the branch dimension was $1.04 \leq d_{Branch} \leq 2.06$, with a mean value, $d_{Branch} = 1.63 \pm 0.047$ ($n = 26$), which was not significantly different from the mean of the box dimension. The branch density fell with distance from the primary vertex, and this branching pattern was likely to have been the source of the low box-counting fractal dimension of the sponge specimens.

As a test the branch dimensions were calculated, for the same specimens, on the ranges $r_{min} < r < r_{min} + (r_g - r_{min})/2$ and $r_{min} + (r_g - r_{min})/2 < r < r_g$. The mean difference between these two estimates, $\overline{\Delta d}_{Branch} = -0.07 \pm 0.045$, was not significant ($t_s = 1.73$; $n = 26$; $P > 0.05$). Using this simple test, $d_{Branch}$ appears well defined for the specimens with a sufficient range of scales to enable it to be calculated. The branch dimension was correlated with the box-counting dimension ($r^2 = 0.41$; $n = 26$; $P < 0.001$). If the sponges were fractal both dimensions should have provided independent estimates of the same fundamental quantity;

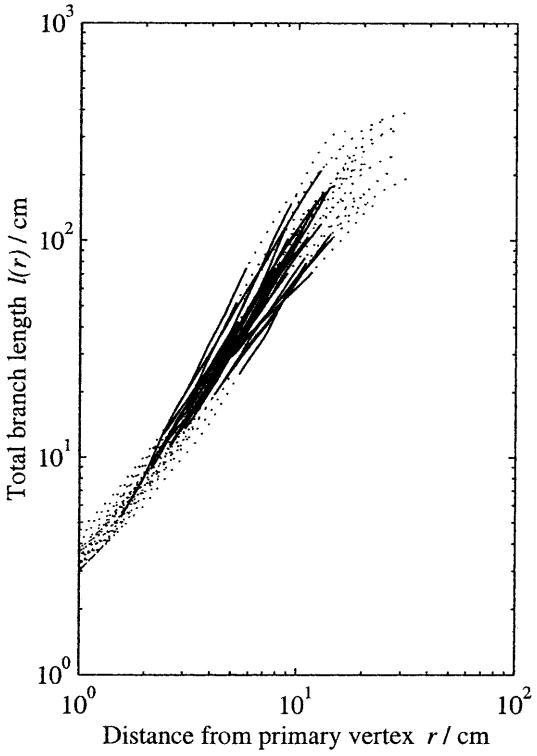



**Fig. 7** Dependence of branch length on distance from the primary vertex. The relation is clearly not linear over the whole range. The *solid lines* mark the portions of the curves used to estimate the branch dimension

however the RMA regression relation between the two dimensions, $d_{\text{Branch}} = (1.63 \pm 0.036) + (3.7 \pm 0.58) \times (d_{\text{Box}} - 1.60)$, had a slope different from 1 ($t_s = 4.7$; $n = 26$; $P < 10^{-4}$). This discrepancy was possibly because the box-counting dimension was calculated from the entire images, whereas the branch dimension was calculated from the morphological skeletons.

### Comparison between sites

The Sponge Garden specimens of *R. inaequalis* that were taller than 5 cm had a mean of 8.8 ± 0.51 ($n = 69$) fingers, compared with a mean of 21.2 ± 1.69 ($n = 45$) fingers for the specimens collected from Leigh Reef (Fig. 5). By using a Kolmogorov–Smirnov test, the cumulative probability distribution of the number of fingers was found to be significantly different between the three Sponge Garden areas and the Leigh Reef site ($P < 0.01$). In contrast, there was no significant difference in the distribution of the number of fingers of sponges from any two of the Sponge Garden areas ($P > 0.05$). This implied that the sponges from the Sponge Garden had a less complex branching pattern. If the same regression relation between number of fingers and box-counting dimension could have been assumed to hold for the Sponge Garden specimens as held for those from Leigh Reef, then they would have had an average fractal dimension of $d_{\text{Box}} = 1.506 \pm 0.0035$ ($n = 83$).

The current meter deployed at the Sponge Garden recorded good data throughout its deployment, but the meter at Leigh Reef only recorded for 15 d, sufficient to resolve the springs-neaps cycle. At Leigh Reef the rms current speed was 22.4 cm/s, the $M_2$ tidal ellipse had a semi-major axis of 27.2 cm/s, at 33° from North, with a semi-minor amplitude of 1.0 cm/s, and the residual current was 10.1 cm/s, in a direction 53° from North. The $M_2$ tide at the Sponge Garden site had a semi-major amplitude of 5.5 cm/s, at 53° from North, with a semi-minor amplitude of 0.51 cm/s. Over the period during which the Leigh Reef current meter obtained data, the rms current speed at the Sponge Garden was 7.4 cm/s and the residual current was 4.9 cm/s, at 53° from North. The currents at the Sponge Garden are substantially weaker than the currents at Leigh Reef. It is important to note, however, that the Aanderraa current meters do not give any information on the high frequency wave and swell-driven currents. These may at times be stronger than the tidal flows and so may be the dominant environmental control on the growth form of the specimens.

## Discussion

All three of the methods used for estimating the fractal dimension of these sponges gave statistically indistinguishable estimates of the mean fractal dimension of the collected specimens. This implies that the apparently fractal structure of these sponges is a result of their branching structure rather than being due to varying branch width, surface elaborations, or an artefact of the way the specimens were prepared.

The simplest and most direct method of determining the mean fractal dimension of these sponges was the allometric method. In general this has great advantages: it can be calculated for specimens with a three-dimensional morphology, and it is relatively independent of the way the specimens are prepared. In addition, allometric scaling relations are known to be important determinants of life-history strategies (e.g. Sebens 1982) and often have biophysical interpretations (Denny 1988). Because of this the allometric dimension is potentially a measure of ecological importance. The only problem is that the allometric dimension cannot be calculated for a single specimen and so has limited morphometric value. The allometric analysis demonstrated other scaling relationships that do not have an obvious fractal interpretation but that revealed that there is order behind the morphological variability of the specimens. In particular, the wet weight could be accurately estimated from height and number of fingers, two quantities that can be quickly determined in the field. It would be interesting to weigh sponges from other sites to explore the variation of this relation between populations growing under different conditions.

A box-counting dimension could be assigned to each specimen. Although there was evidence of consistent departure from a fractal relation it was felt that this departure was relatively minor and so the dimension could be defined. For this population it was found that an estimate of box-counting dimension could be obtained from a simple count of the branch tips, this estimate having the same error as that obtained by following the box-counting procedure itself. For these sponges the harvesting, preparation, and digital analysis of the specimens is not needed to estimate a fractal dimension – the number of branch tips may be quickly counted in the field, without damaging the sponges. A count of the branch tips, together with an allometric analysis, gives all the information provided by the commonly used box-counting dimension, without the same difficulties of definition or interpretation. The count of branch tips demonstrates that the sponges at the higher energy site are more densely branched, in agreement with the predictions of the Kaandorp model. Because the number of fingers can be rapidly counted in the field, it would be possible to extend the study to examine the morphological variability over a wide range of sites.

The close correspondence between tip number and box-counting dimension raises what appears to be a serious objection to the fractal analysis. By definition, the fractal dimension should be independent of the size of the sponge. If fractal dimension is to be a useful property then as a sponge with a particular genotype and environment grows, its fractal dimension should remain unchanged. As these sponges mature they will produce more branch tips, so it seems that their fractal dimension will increase as they develop. This objection is not as serious as it first appears. Specimens with a higher fractal dimension will rapidly produce more branch tips than specimens with a lower dimension. Because their growth is not indefinite and the sponges never get beyond a certain size, this will induce the observed correlation between branch tip number and fractal dimension.

Although it predates the development of fractals, Horton analysis provides a succinct method for analysing the scaling properties of branching structures and gives the most detailed information. Because of the simple interpretation of the bifurcation and length ratios such analyses are very useful for morphometric comparisons. Horton analyses of five different species of gorgonian have found bifurcation ratios larger than 3 (Brazeau and Lasker 1988; Mitchell et al. 1993). The specimens of *R. inaequalis* have a significantly different branching structure, being less pinnate or more fan-like than the gorgonians. The Horton analysis allows the difference to be quantified. It has been suggested that for many biological systems the variation of branch length with order is better described by an arithmetic rather than a logarithmic relation (Park 1985). The data, summarised in Fig. 6B, are unable to distinguish between these possibilities due to the small number of order-5 sponges. This highlights a problem with the application of fractal techniques to the study of biological specimens: there is often an insufficient range of scales to allow fractal properties to be unambiguously determined. Horton analysis, by itself, shows that the branching pattern of these sponges is consistent with self-similarity but does not allow a stronger statement to be made. Importantly, however, the Horton analysis enables exceptions from self-similarity to be identified. In particular, it showed that the stipes were longer than would be expected purely from scaling considerations. This is interesting, as in the Kaandorp growth model the fractal structure is determined by the flow around the sponge and over the substrate. Because the boundary layer above the substrate will be much larger than the boundary layer around the sponges, a longer stipe might be expected. Measurements could be made on other arborescent invertebrates to check whether this was a general result. An advantage of making an analysis of the abstracted branching structure is that it can be carried out on specimens for which the projected image is impossible to work with. For example, an analysis of a three-dimensional branching structure could be performed by measuring branch lengths manually. This has been done for several species of tree (Leopold 1971). Clearly, these methods can only be used when the object to be analysed has a well-defined branching structure. Some finger sponges and corals have a more amorphous lobed morphology, which would be difficult to resolve into uniquely defined branches. For species such as these, only methods such as the calculation of box-counting and allometric dimensions could be used.

The consistency of the data with a fractal morphology raises some questions. The Kaandorp model suggests one way in which an organism such as a sponge, which has an indeterminate growth pattern, can grow in a branching fractal form. The question of the adaptive value of a fractal morphology has not been addressed. In studies of river networks, fractal branching patterns are found to be optimal, in that they minimise some cost function (Rinaldo et al. 1992). It has also been suggested that fractal structures such as networks of blood vessels (West et al. 1997) or the foraging trails of ants (Ganeshaiah and Veena 1991) occur as optimal solutions to transport problems. It would be interesting to explore the question of whether the fractal branching structures found for these sponges, and in other marine invertebrates, are in any sense optimal.

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