Fractal and multi-fractal patterns of seaweed settlement

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May 19, 1995

Abstract

The distribution of algae is examined at several different scales. Juveniles are found to be in clumps which are randomly dispersed throughout the community. Within these clumps there is a great wealth of pattern which may be related to the substrate complexity either during settlement of propagules or indirectly via grazing patterns. Fractal dimension analysis suggests that this changes through time. After the recruits had settled for over three months the substrate complexity was no longer found to be important to the fine pattern of small scale clumping. We look at the spatial distribution of juvenile algae and report on their fractal structure. [27] We speculate on underlying mechanisms.

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1 Introduction

The consideration of macroalgal distribution on different spatial scales has often shown communities to be patchy. Agents responsible for this heterogeneity vary according to the scale under consideration. A major factor controlling algal distribution on a biogeographical scale is sea temperature, while local scale influences are water movement, the topography of the coast, and the local flora and fauna [42]. On a small scale the distribution of algae has rarely been examined and the mechanisms responsible have only recently begun to receive attention [36].

For example, one feature of macro-algal communities is the restriction of algae to hard substrata which provides suitable holdfast attachment. Suitable hard substrata is often intermingled with sand areas resulting in patchiness [36, 5]. Abundance estimates associated with high variances suggest that algae are clumped at small scales [36]. Small scale clumping has been shown for several large dominant macroalgae [10, 17, 34]. A study on *Xiphophora gladiata* showed clumping at scales of 10, 20 and 40cm, only the last of which could be explained by variation in the physical environment [34]. It was suggested that the smaller scales of clumping were due to biological factors, possibly associated with propagule release. However, these distribution analyses were restricted to mature macroalgae and did not consider the patterns of juveniles.

While final communities may be very different to initial ones, this does not trivialise the processes of recruitment or the early life stages of the algae. The consideration of juvenile patterns may be important as the adult distribution may reflect that of the spores [36]. In an attempt to understand the pattern of mature macroalgal stands it must therefore be important to consider the pattern of the recruits that is, before many processes act to arrange them. One needs to address the issue of why algal propagules settle where they do in the first place.

Most analyses employed to assess plant distributions are based on testing for non-random spatial distributions. These are conducted on scales of pre-selected quadrat sizes, rather than exploring the distribution for its own scales of pattern. Thus, only preconceived distributional patterns have been recorded [34]. Fractal dimensions as an index of the distribution may be a useful tool to avoid the problem of forcing predetermined spatial scales on the vegetation [31, 26, 39, 25]. The concept of fractals is based on the idea that an object may have similar detail over a range of scales. Many methods are available to find fractal dimensions, most of which are straight-forward to apply [39], although care is needed in the interpretation. The fractal dimension is a measure of how the plants fill the space they occupy.

The aim of this study was initially to determine the pattern of recruits and secondly to correlate this with the likely processes and/or physical attributes of the system, in particular the substrate topography. The small scale pattern of juveniles was followed for three months after they were first visible to determine whether there was any change in the pattern. Spatial patterns of recruits on natural substrates were also compared to that of flat settlement plates. The comparisons were undertaken to determine whether there was any difference in the patterns which could be attributed to topographical details. Patterns were analysed by both conventional methods (a nearest neighbour analysis) and also by computing the fractal dimension. The distribution of the adults were also examined. The small scale patterns of the recruits on the natural substrate and settlement plates were analysed by calculating the Hausdorff fractal dimension.

It was noted that the settlement patterns were not evenly spread over the areas mapped and that while some recruits were tightly clumped others were more isolated. A multi-fractal analysis of the patterns was also undertaken and is compared to that of homogeneous fractal distributions of similar dimension. The detected multi-fractal nature of the juveniles may be due to any of a variety of mechanisms. However, we argue that one possibility is through the action of predators of a hierarchy of sizes.

Throughout the body of this paper, discussion of mathematical analysis is at a superficial and informal level in order to concentrate upon the application. Mathematical details are relegated to the Appendix.

2 Description of the study site and methods

The field site for this experimental study was at Cape Jervis, South Australia (Figure 1). The study site is approximately 100m from the shore at low tide at a depth of 5m to 6m. The substrate at the site is a mosaic of rocky platforms intermin-



Figure 1: location map of study site which is shown by the small arrow.

gled with sand patches. The community on the rock platforms is fucoid dominated (particularly *Cystophora spp.*), while the sand areas are dominated by the seagrasses *Posidonia* and *Amphibolis*. The recruitment of fucoids were observed to be in clumps throughout the community. These "clumps" varied in shape, size and position. The following surveys were undertaken to determine the distribution of "clumps" of recruits in the community and also the small scale distribution of the recruits within the clumps.

2.1 Clump distributions

A nearest neighbour analysis was utilized to determine the distribution of recruits and adults within the community using the method utilised by Chapin *et al* [8]. Points were chosen on the substrate randomly. The distance from this random point to the nearest clump of recruits was measured and the distance from that clump to its nearest neighbouring clump was also measured. This procedure was also repeated for mature algal plants. The ratio of point-plant : plant-plant distances were determined by repeating this a minimum of thirty times for each site to see if the algae exhibited a clumped (ratio> 0.88), random (ratio= 0.88) or regular (ratio< 0.88) distribution [1].

2.2 Individual plant distributions

Five $1 \times 1m$ clearances were made by removing algal material in late September 1991. These clearances were made during the recruitment season for the dominant species *Cystophora expansa* (Areschoug), Womersley [40]. The clearances were intended to eliminate the variation of competition between recruits at the centre of the clearances and the surrounding community. A concurrent experiment was conducted to determine the effects of competition between recruits and the mature algal community (Emmerson and Cheshire, in prep.). Recruitment appeared to be inhibited on some regions of the substrate (personal observation) and we felt that it would be better knowing that recruitment was actually possible into the area by clearing the algal material and monitoring recruitment into those areas. No visible recruits were present in these areas. At the time of the clearances, a series of settlement plates were also placed into the system.

A "fucoid mapper" was developed to map the spatial pattern of recruit individuals. It consisted of a clear perspex board ($22.5cm \times 28.5cm \times 1.0cm$) with legs in each corner which could be placed directly above the substrate allowing the observer to locate the position of individuals below. A clear acetate sheet was placed on the upper surface of the perspex and held in position with bulldog clips, the position of each juvenile was recorded on this sheet. Spatial patterns of randomly selected areas of juveniles near the centre of the clearances were mapped. Notes were made of biological and topographical features in the areas mapped. The mapped sites were ranked according to their substrate topography. The sites were ranked from simple through to complex, where simple refers to a flat site and complex referrs to those substrates that were highly variable. At each mapping exercise the settlement plates were considered to be the simplest substrates present as they were flat surfaces.

The raw maps from the mapping exercise were then traced onto clean sheets and the nearest neighbour index calculated as before. The average distance between individuals was also calculated. Maps were made from the time the recruits were first visible to the naked eye (78 days after clearances) with three more readings taken at approximately monthly intervals. Maps were made on days 105, 143 and 173 after clearing. Six maps were made on the natural substrate within the clearances and three settlement plates were mapped for each mapping exercise. Only one specific site was mapped continuously throughout the duration of the survey due to the difficulty in relocating such a small area under water.

2.3 Calculation of the fractal dimensions

The fractal dimension of a pattern of points expresses that the structure of the pattern is strongly similar over a wide range of length scales, whether the points represent plants as herein, clouds, ore bodies, rivers or aggregations [27]. In order to discern such a similarity we have to explore the pattern over many scales of length, and in particular to see how the plants are clumped together on the different scales. Choosing a length-scale r, we may find how many discs of radius r,¹ say $\mathcal{N}(r)$, must be used to completely cover the set of points. In essence this determines that there are \mathcal{N} "clumps" of plants on a length-scale r. The basic tenant of fractal geometry is that over a wide range of lengths-scales this count varies with r according to a power law

$$\mathcal{N} \sim r^{-D} \tag{1}$$

where *D* is called the *fractal dimension* or sometimes the *Hausdorff dimension* [27].

This definition of dimensionality agrees with the ordinary Euclidean dimension when it is applied to Euclidean objects. For example, the number of discs of radius r needed to cover a line or curve segment of length L is approximately $\mathcal{N} = L/(2r) \sim r^{-1}$ which gives a fractal dimension of D = 1. Also, a single point only ever needs $\mathcal{N} = 1 \sim r^0$ discs to cover it and so has a fractal dimension of D = 0.

¹Often squares of side r are used instead of discs—it makes no difference at our level of analysis.

Experimental data typically consists of a finite number of plants, say N (see Figure 11 for example); the scaling law (1) can only hold over a finite range of length-scales. On very small length-scales, smaller the the minimum plant separation, $\mathcal{N} = N \sim r^0$, and the set looks like a set of N distinct 0-dimensional points. On large length-scales, larger than the largest separation of the plants, $\mathcal{N} = 1 \sim r^0$, and the set looks like one 0-dimensional "blob." It is only on the intervening length-scales that it is possible to discern a fractal nature; it is typically agreed that a power law (1) needs to hold over at least a decade before claiming that experimental data has a fractal nature.

As explained further in Appendix A.1, we plot $\log(1/\mathcal{N})$ versus $\log r$ and seek to find a straight line fit of slope D over a range of length-scales sandwiched between two horizontal regimes. The horizontal fit for length-scales smaller than the minimum resolvable exhibits the discreteness of the data; the horizontal fit for large length-scales displays the finite size of the experimental recording. When a straight line of slope D can be fitted to the intervening length-scales, then the data is said to have a fractal dimension of D.

3 Results

3.1 Nearest neighbour analysis

The canopy plants were found to have a clumped pattern; however, it was noticed that many of these algae had fused holdfasts. The survey was repeated treating those individuals with fused holdfasts as a "canopy unit." The degree of clumping and the variance associated with it decreased. Of the total 180 canopy plants considered 37.2% formed "canopy units". A large proportion of the canopy plants within the community have holdfasts sharing the same point of attachment. It is unclear whether this sharing of the holdfasts occurs when both algae are settling or whether recruits are able to settle on the holdfasts of algae which are already growing. It was observed that many recruits had the same holdfast attachment position.

The clumps of recruits were found to be randomly distributed throughout the community. At all times the nearest neighbour analysis found the distribution of juveniles to be clumped. The degree of clumping remained constant through time (Table 1) The average distance between individual juvenile plants was similar until the final reading at 173 days. There was no difference between the settlement plates and the natural substrate.

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Table 1: nearest neighbour table.

Figure 2: digitised distribution of 197 juvenile fucoids on one of the perspex plates at time 1. The axes' units are centimetres. As shall be discussed in the section on multi-fractals, in this and the three subsequent figures the different symbols denote different estimated scaling exponents α : \square , $\alpha \leq 1$; \square , $1 < \alpha \leq 1.3$; \circ , $1.3 < \alpha \leq 1.6$; \times , $1.6 < \alpha \leq 1.9$; \diamond , $1.9 < \alpha \leq 2.2$; and \square , $2.2 < \alpha$.

3.2 Fractal nature

During the course of the experiment 35 drawings were made of fucoid sites. The number of fucoids in any one site varied from 267 down to as few as 20. Although all the data was analysed, we concentrate on those sites with over 80 plants as we felt that the results for fewer plants were unreliable. Of these, we present four as being representative of those that show a fractal nature. The discretised data for the selected sites is plotted in Figures 2–5. Each plotted symbol represents one holdfast of a plant or a group of plants sharing the same holdfast. The different symbols used are irrelevant to this section; they are discussed in Section 4.

Observe that although the fucoids appear fairly randomly spread, in some sites, such as shown in Figure 3, there are "bald" patches, while in other sites, such as in Figure 4, many of the fucoids appear to be distributed in roughly "linear" features. One view is that it is the pattern of "bald" patches of many sizes, or the pattern of



Figure 3: digitised distribution of 267 juvenile fucoids on the site rledge at time 1. The axes' units are centimetres.



Figure 4: digitised distribution of 104 juvenile fucoids on the site *photopoint* at time 1. The axes' units are centimetres.



r1flatt2 - scaling exp

Figure 5: digitised distribution of 88 juvenile fucoids on the site rlflat at time 2. The axes' units are centimetres.

linear features over many sizes, that gives the distribution its fractal nature.

One problem with this study was the ranking of the substrate complexity, which was largely subjective, based on observed features. It is recognized that processes acting on a smaller scale than that which can be observed may be important to the settling and survival of individuals. Another difficulty was the relatively small number of plants in any one site, in the range 20–267 plants, with which to attempt to make reliable dimension estimates.

The estimated fractal dimensions associated with the spatial distribution of juveniles ranged from 1.26 to 1.91. Most of the distributions were of a fractal nature. For the first three months, a discernable fractal nature was found in all but one of the maps. At the last reading only 4 of the 9 maps had a fractal nature. This may have been a consequence of the small number of plants typically present at the final reading. The fractal nature typically held over the range 0.6 ± 0.1 cm to 11.5 ± 0.1 cm (values represent mean $\pm 95\%$ confidence interval): the upper limit certainly represents the overall size of each mapped region (due to the size of the mapper) and so this fractal nature may well extend to much larger length-scales; the lower limit may be due to errors in mapping the locations of the plants or to their finite size giving rise to a cut-off. The range over which the fractal nature held did not change through time.

On the perspex plate, Figure 2, the digitised data is a reasonably accurate expression of the fucoid distribution. However, on the rocky sites, the underlying

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Figure 6: plots of $\log_{10}(1/N)$ versus $\log_{10} r$ for the data in Figures 2–5 (the curve for the *plate2t1* data has been displaced by 0.2 to the right for clarity). The slopes of these curves in the region $-0.4 < \log_{10} r < 1$, that is over the length-scales from about 0.5cm to 10cm, indicate a fractal nature with dimensions of $D \approx 1.91$, $D \approx 1.60$, $D \approx 1.41$ and $D \approx 1.26$, respectively.

topography is not smooth and the planar digitised data does not express any of the vertical variability in the plants location. Nonetheless, it is a generic property of fractals [27, p303] that a smooth projection of an object in space onto a surface, as is done by the mapping procedure, results in an object of dimension which is either the same as the original, or dimension 2, whichever is smaller. In our data from rocky substrates, the dimension estimates were consistently less than 2 and so we surmise that the dimension of the originally 3D distribution in space is the same as the dimension of the 2D digitisation.

There was no correlation between the number of plants present and the fractal dimension at any time period ($F_{\text{time}=1}(1,5) = 0.2378$, $F_{\text{time}=2}(1,5) = 0.0776$, $F_{\text{time}=3}(1,6) = 2.069$, $F_{\text{time}=4}(1,2) = 14.893$). The fractal nature was not merely an artifact of the number of recruits present.

To analyse the relationship between the substrate complexity and the fractal dimension of the settlement pattern the Spearman Rank Correlation statistic was calculated. To do this the fractal dimensions were ranked and this rank compared with that of the substrate ranking. The only significant correlation was found for time 1 ($r_s = 0.9429$, $r_{sig.} = 0.886$, $\alpha = 0.05$, d.f. = 4, P = 0.033). There was no significant correlation for the last three readings ($r_s = 0.4296$, d.f. = 5; $r_s = 0.2142$, d.f. = 5; $r_s = 1.00$, d.f. = 2). This may reflect that processes occurring after the main settlement, such as predation or competition, tend to reduce the influence of the substrate complexity.

What about time=2?.

3.3 Other observations

In both the cleared areas and the undisturbed areas there were regions in which there was no visible recruitment of any species. These distinct patches ranged from 10 square centimetres to approximately 40 square centimetres. The presence of other algae also affected the position of juvenile recruitment. In particular a red alga, *Erythroclonium muellerii* (Sonderi), which formed a dense mat had no recruits beneath or amongst it. Various other turfing alga may have actually promoted or inhibited recruitment and survival of juveniles (e.g. *Dictyota sp.* and *Colpomenia sinuosa*). Many juveniles grew from under *C. sinuosa* which may have provided protection for the small juvenile algae.

4 Multi-fractal nature

Previous sections show that settlement sites of young fucoids on 20cm square areas are spread in a clumpy pattern. These clumps have a fractal dimension ranging from 1.2–1.9. Some recruits clearly occur in clumps while others appear to be quite isolated—perhaps most easily appreciated in Figures 4 and 5 where plants

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denoted by \blacksquare typically occur in tight clumps whereas those denoted by \times occur in sparsely populated regions. This does not happen with homogeneous fractals where the distribution in the neighbourhood of each plant is similar. The concept of multi-fractals, an intertwined union of fractal subsets with different scaling exponents, thus appears relevant to the spatial distribution of plants.

One of the better descriptions of multi-fractals is by Feder [13, Chapt. 6]. Another good discussion, specific to an experimental situation, is by Sreenivasan [38, \S 5]. Here we first summarise the concepts of a multi-fractal distribution, then we investigate the multi-fractal nature of the experimental plant distributions.

4.1 The spectrum $f(\alpha)$

In order to quantify the above mentioned differences between plants, we first have to quantify differences between the distribution of plants in any neighbourhood. The Lipschitz-Hölder scaling exponent α is one measure of the pattern of density of plants as seen in any neighbourhood.

For each plant j, let $\nu_j(r)$ be the fraction of plants within a distance r of the jth plant, i.e. $\nu_j = N_j(r)/N$ where $N_j(r)$ is the number of plants within a distance r (counting the plant itself for convenience). If

$$\nu_j(r) \sim r^{\alpha} \tag{2}$$

over a significant range of r between the minimum resolution and the gross size of the set, then the scaling exponent α is associated with the j th plant.

Roughly, for a non-uniform distribution of plants: a high value of the scaling exponent α corresponds to a region of sparse plants within regions of denser clumps of plants; a low value of α corresponds to a dense cluster of plants among a sparser distribution. For this reason, α has been called the "crowding index" [16]. These features are discussed further in Appendix A.2 and can be seen in Figures 2–5 where different symbols have been used to tentatively assign each plant to within some range of α .

We now address how the Lipschitz-Hölder exponent α may be used to quantify aspects more subtle than the overall fractal dimension. Recognising that each plant has an estimated value of α associated with it, one approach is to calculate the fractal dimension f of all those plants associated with a common value of α . For example, in Figures 2–5 we could imagine computing the fractal dimension of: plants drawn as \blacksquare giving f for $\alpha \approx 0.9$; plants drawn as \square giving f for $\alpha \approx 1.2$; etc. In principle the dimension f may be calculated for any value of α , and so forms a curve. This $f(\alpha)$ curve is called the multi-fractal spectrum.

In practise, the spectrum is computed via generalised dimensions and mass exponents as described in the Appendix. However, it is important to note that due to

the relatively few plants at each site, the numerically obtained multi-fractal spectra have only rough quantitative accuracy. The numerical spectra may be judged as follows: the left-hand part of the curve is fairly accurate; while the right-hand part of the curve is likely to be in error by about 10-20%.

The issue of accuracy in the presence of a limited amount of data is an important one and has received much attention [15, 33, 3]. However, we approach this issue by comparing the results from the fucoid data with the same numerical analysis applied to synthetic data which has the same overall characteristics. Thus we can see explicitly the range of results obtainable from a variety of fractal models, and how these compare with the results from the experimental data.

4.2 Fucoid recruit results

Numerically determined multi-fractal spectra for the fucoid distributions of Figures 2–5 are shown in Figure 7. We compare these $f(\alpha)$ curves with numerically determined spectra Figure 8, for artificially generated homogeneous fractals with a similar overall Hausdorf dimension. Ideally, the $f(\alpha)$ curves for the homogeneous data should just be a single point at $f = \alpha = D$. Due to the limitations of the finite amount of data used, the numerically determined curves are broadened to cover a range of $\Delta \alpha < 0.5$. But this is still much narrower than the typical range of α displayed for the fucoid data where $\Delta \alpha$ ranges from about 1.5 and up. Note that the narrowest fucoid spectrum, that for the site *rlflat* and shown as the short-dashed curve in Figure 7, is the most reliable as it is has the highest number of data plants. Hence we are confident that the distribution exhibits a multi-fractal nature.

4.3 Predation

One plausible mechanism for the generation of a multi-fractal distribution involves a random pattern of grazing by predators of many different sizes.

We suppose that there is a very high mortality rate so that there were originally very many infant plants. For the moment assume that initially these are more or less evenly distributed over the settlement site, as seen for example on the settlement plates. These plants are grazed upon by predators. If the predators are of many sizes, and each predator grazes a random patch of the site, the patch being of a size characteristic of the predator so that there are many sizes of grazed patches, and eat predator destroys a fraction f of the plants in their patch, then the resulting distribution of plants may be multi-fractal.

For example, a deterministic construction based on this idea reduces to a method to construct the binary multi-fractal [13, $\S6.2$] as shown schematically in Figure 9. Consider a one-dimensional spread of plants at a site. The one largest predator eats



Figure 7: multi-fractal spectra $f(\alpha)$ for the fucoid data: _____, the *plate* data shown in Figure 2; - - -, the *rledge* data shown in Figure 3; - - -, the *photopoint* data shown in Figure 4; ____, the *rlflat* data shown in Figure 5.



artificial random fractals - f(alpha)

Figure 8: numerically determined multi-fractal spectra $f(\alpha)$ for three homogeneous artificial fractals: —, 64 points on a fractal of dimension D = 1.26; - - -, 125 points on a fractal of dimension D = 1.46; and - - -, 216 points on a fractal of dimension D = 1.63.



Figure 9: an initially uniform distribution of plants (dots), shown at the top, are attacked by a hierarchy of predators (solid lines) destroying half the plants (dots) in their grazed patch to form a binary multi-fractal, shown at the bottom.

Figure 10: pure Cantor set with dimension $D = \log 2 / \log 3$

a fraction f of the in the left-half of the site (f = 1/2 in the figure). There are two of the next largest predator, and they each eat the fraction f of the plants in the two quarter size patches which are in the left-halves of the two halves. There are four of the next largest predator, and they eat the fraction f of the plants in the four eight size patches which are the left-halves of the four quarters. And so on to smaller and smaller sizes. This generates a binary multi-fractal with parameter p = 1/(2 - f).

Note that the same multi-fractal pattern will arise independent of the order in which the predators arrive. Our construction with the large predator first was just a convenience to make the construction more akin to that of other constructions of the binary multi-fractal. Indeed, it is likely that the small scale grazers do their damage first while the plants are still small. We believe that the crucial feature in this one-dimensional construction is that the number of grazers, or at least the number of grazing episodes, is roughly inversely proportional to the grazer size. For a distribution of plants on a surface, the number of grazers should be roughly proportional to the inverse square power of their size.

The above argument of predation leading to multi-fractality has been based upon an underlying distribution of plants which is spread uniformly randomly on the substrate. However, some of the data exhibit such low-dimensions, as low as D = 1.2, that the proposition of an underlying uniform spread is unreasonable. Furthermore, we have presented evidence that Hausdorff dimensions are correlated with substrate complexity. Nonetheless, the predation mechanism for generating a multifractal nature should still be valid when applied to an underlying plant distribution which is itself a fractal distribution.

For example, on a one-dimensional substrate we could distribute plants on a Cantor set of dimension $D = \log 2/\log 3$ as shown in Figure 10. Then a hierarchy of predators eating the clumps of plants unevenly leads to a multi-fractal. Indeed, the clumpiness of such a fractal distribution gives a natural mechanism for bounding the extent of the region that any one predator eats. For example, if this Cantor set distribution was of overall length L, then a predator of a size to graze the left half patch, of size L/3, would detect a barren region of length L/3 before the right half patch and so may choose not to traverse across the wasteland. Similarly on all the smaller scales.

5 Discussion

Pre-settlement factors affecting the distribution of algal propagules include the texture of substratum [18, 7, 22], prevailing water currents [36], spore availability [7], the presence and distribution of other algae: e.g. turfing algae, canopy plants [19, 9, 23], and the method of dispersal from adults [21]. The small scale clumping of juveniles could be due to pre-settlement factors related to dispersal [34]. However, for this particular community it is unlikely because Cystophora species have a life history, often described as direct [40], in which eggs are released from the conceptacles individually and fertilised in the water column. In comparison with other species where eggs may be released in groups. The occurrence of numerous individuals of the same species sharing a single holdfast can not be explained by factors during propagule release. This is further supported by multispecies holdfast attachment as was observed. In contrast, Sargassum sp. have zygotes which remain on the thalli of adult plants until they are large and then individually "drop off" the adult plant onto the substrate [21]. The distribution of these would be expected to be clumped around the adults but not at the fine scale that was observed for many recruits in the community.

Forces impinging on a solitary individual may be very different to those acting on an individual surrounded by similar organisms [37]. This group structure may provide protection from grazers and support from wave motion [17]. The small scale clumping of recruits is reflected in the canopy plants, many sharing the same attachment position. Initially, one might expect that groupings of individuals may result in increased competition for light and nutrients resulting in a negative effect on individuals. There are three important aspects involved when considering this situation. Firstly, the balancing of any competitive effect experienced by an individual must be outweighed by the benefits from the protection which each plant receives by grouping otherwise such grouping would not occur. The "canopy unit" arrangement may serve to lessen the community pressure. Secondly, the influence that this "canopy unit" exerts on the surrounding community may be very different to the influence exerted by solitary individuals. The "canopy unit" may exert greater pressure on the surrounding community than a solitary individual. Thirdly, competition may result in a decreased growth rate rather than influencing mortality which would not have been detected in this study. Nevertheless, the frequency of this small scale clumping indicates that it is not detrimental for individuals to grow in very close proximity.

Fractals provide us with a tool which considers patterns in ecology on many scales. Their value in ecological work has been considered by various authors [29, 6, 26, 25], although few have actually made use of them [4, 31]. The use of fractal dimensions in examining algal settlement distributions has shown that areas with topographic detail have patterns which may initially be related to the topog-

raphy. The juvenile distributions varied in their pattern from highly clumped to uniformly random. Uniformly random distributions have previously been found on settlement plates [22] although this did not involve an analysis of the fractal dimension. Initial patterns of recruits on topographically variable natural substrate had settlement patterns with low fractal dimensions while settlement plates and flatter rock surfaces had settlement patterns with high fractal dimensions. This result means that although the recruits are found in clumps throughout the community, on topographically variable surfaces there tends to be a high degree of clumping within clumping. The degree of clumping within clumping was related to the variability of the rock surface, at least in the initial stages.

Fine scale topographical details may provide microsites for the settling of individuals [18] in a similar way that seeds aggregate in depressions in the soil [30]. Once propagules have settled factors such as the effects of succession and competition between algae [12, 19], grazers [20], natural disturbances in the creation of space e.g. storms, El Nino [41, 11] may become important. The importance of these factors differ for different species in different environments. Algal settlement patterns may be a reflection of the topographical detail and the combined effects of topography and other factors. Although initial patterns of settlement implicate the importance of topography, other factors must be acting on recruits, dissolving any correlation between the fractal dimension and topography within the first three months after settlement. Unless the surface of the natural substrate is examined with equipment such as an underwater microscope [24] to examine initial stages, the pattern observed is really the net result of both settlement and post-settlement processes.

Most natural substrates are not even, resulting in a patchy mosaic of substrate suitability throughout the community. Substrate selection has been shown for larvae of sea urchins [7] and also for algal spores [18]. As an example, survival of the algal species *Pelvetia fastigiata* varies with topography, being higher on rock outcrops or ridges [17]. The other aspect of substrate suitability in this community are regions where the substrate had no recruits of any species. These were considered to be uncolonisable rock with the lack of recruits attributed to several possibilities. This could be due to a feature of the actual substrate preventing recruitment, or it may have been due to allelopathic effects from previously settled algae. Alternatively it may be due to interactions with the surrounding community.

Presence of a red turfing alga has been shown to inhibit recruitment of the dominant algal species in previous studies [9]. A similar inhibition appears to be happening in the community under study. A thorough examination of the areas where the red algae *Erythroclonium muellerii* was growing showed no fucoid recruits. The presence of the red alga inhibited either recruitment or growth through either providing a physical barrier to prevent settlement, or by shading the settled recruits to the extent that no growth was possible. Alternatively inhibition may have oc-

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curred through the actions of chemical allelopathy [23].

Spatial heterogeneity is a well known attribute of many vegetative systems. In this study we have found that the distribution of all stages of algae on a local scale is patchy. The hypothesis being tested here is whether this patchiness is a result of where the algae settle with respect to the substrate or whether it is primarily a product of processes occurring after those initial settlement stages. The conclusions are that many features of the community affect the initial distribution of recruits in particular small scale topographic details. However, as the recruits grow, other processes become more important than the substrate topography (e.g. competition with each other, grazers) which results in the mature algae also having a patchy distribution.

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A Mathematical details

A.1 Estimation of fractal dimensions

To estimate the fractal dimension of a set of settlement sites of plants we have used the following algorithm based on ideas originally proposed by Grassberger & Procaccia [14].

Let $N_j(r)$ be the number of plants (neighbours) within a distance r of the jth plant, noting that $N_j(r) \ge 1$ as we always count the jth plant itself. Then an estimate of the number of discs of radius r needed to cover the plants, $\mathcal{N}(r)$, may be obtained by letting $\nu_j(r) = N_j(r)/N$, which is the fraction of the plants within a distance r of the jth plant, and computing

$$\mathcal{N}(r) = \frac{1}{N} \sum_{j=1}^{N} \frac{1}{\nu_j(r)} \,. \tag{3}$$

A crude argument to support this formula is as follows. The *j*th plant is surrounded by $N_j(r)$ plants within a distance *r* and so they may all be covered by just one disc



artificial random fractal of D =1.26

Figure 11: An artificially generated distribution of N = 64 plants which, if the generation continued indefinitely, would have a fractal dimension of D = 1.2619. Here this fractal nature only really ranges from 0.37cm to 10cm.

of radius r; of this disc, a fraction $1/N_j$ of it is "used" to cover the *j*th plant, and so $1/N_j$ is the *j*th plant's contribution to the count of the number of discs needed to cover the set.

Plotting $\log(1/\mathcal{N})$ versus $\log r$ we seek to find a straight line fit of slope D over a range of length-scales sandwiched between two horizontal regimes. When a straight line of slope D can be fitted to the intervening length-scales, then the data is said to have a fractal dimension of D. See Figure 12 which exhibits a fit of dimension D = 1.25 to the artificial data shown in Figure 11 which purportably has a dimension of D = 1.2619. This close agreement between the theoretical dimension and the experimentally determined dimension is very good in view of



artificial random fractal of D =1.26 - hausdorf

Figure 12: The plot of $\log_{10}(1/N)$ versus $\log_{10} r$ for the artificial fractal of Figure 11; together with a best fit transcendental curve.

the relatively few data points.

As shown above, the fundamental numerical task in all of this work is the fitting of a straight-line to data points on a log-log plot; this has to be done accurately and reliably many thousands of times. This is difficult to do routinely because we have little knowledge beforehand of the range in which this straight-line behaviour will be exhibited.

However, we know that the domain of interest should lie between two horizontal domains. Thus, to the data plotted in the $\xi\eta$ -plane where $\xi = \log_{10} r$ and $\eta = \log_{10}(1/\mathcal{N})$, we fit the transcendental curve

$$\eta = \bar{\xi} + D\frac{1}{2} \left\{ \zeta_1 \log \left[2\cosh((\xi - \xi_1)/\zeta_1) \right] - \zeta_2 \log \left[2\cosh((\xi - \xi_2)/\zeta_2) \right] \right\}$$
(4)

where $\bar{\xi} = \frac{1}{2}(\eta_{+\infty} + \eta_{-\infty})$ and $D = (\eta_{+\infty} - \eta_{-\infty})/(\xi_2 - \xi_1)$. Such a curve consists of three domains: horizontal and asymptotic to $\eta = \eta_{-\infty}$ for $\xi \ll \xi_1$; horizontal and asymptotic to $\eta = \eta_{+\infty}$ for $\xi \gg \xi_2$; and asymptotically a straight-line of slope D for $\xi_1 \ll \xi \ll \xi_2$. The two transitions at ξ_1 and ξ_2 between these domains occurs exponentially and over a width in ξ of ζ_1 and ζ_2 . The computational task was then to vary the four parameters, ξ_1 , ξ_2 , ζ_1 and ζ_2 , in order to minimise the root-meansquare distance between the curve and the data points; this minimisation was done using the NAG routine E04FDF.

With a little modification to avoid degenerate curve fits this procedure worked reliably. For a given set of data, the number D determined by the best fit gives the desired exponent of the power law. Since the middle "straight-line" domain essentially ranges from ξ_1 to ξ_2 , the difference $\xi_2 - \xi_1$ estimates the range of length-scales over which the fit is valid; in this application this domain spanned length-scales varying by at least a factor of ten and often a factor of 30 which is adequate for confidence in the results.

Note that at no stage have we tried to quantify the errors of our estimated dimensions. Firstly, the derived data points of the $\mathcal{N}(r)$ curve for any fractal is *not* a smooth curve plus independent noise, instead the variations in the curve are correlated from one scale r to another. Second, there are systematic errors in the use of $\nu_j(r)$. These two aspects of the above procedure make quantifying errors very difficult.

A.2 Multi-fractal nature

Naively, we expect the Lipschitz-Hölder scaling exponent α , introduced in Section 4.1, to be the dimension (actually the correlation dimension) of the set—consider the following examples.

- 1. An evenly spaced distribution of plants along a line displays a linear variation, $\nu_j \sim r^1$, for r larger than the spacing, and $\alpha = 1$ is indeed the dimension of a line.
- 2. Plants placed on a grid in the plane display a quadratic variation $\nu_j \sim r^2$ to correspond to the two dimensions of the planar distribution.
- 3. On the classic Cantor set, as shown in Figure 10, we find that $\nu_j \sim r^{\alpha}$ where once again α is the fractal dimension $\alpha = \log 2/\log 3$.

But these distributions are very special—they have a very even spread of plants. What if the distribution is non-uniform?

Consider an example where, in one space dimension, plants are located at $x_j = \pm |j|^p$ for some power p. Viewed from the plant $x_0 = 0$, it is readily verified that $N_0(r) \sim r^{1/p}$, i.e. the scaling exponent is $\alpha = 1/p$. For example:

- p = 2 locates plants at $x_j = \pm j^2$ which are increasingly far apart the further the plants are from the origin, and gives $\alpha = 0.5$, a low value;
- p = 1/2 locates plants at $x_j = \pm \sqrt{|j|}$ which are more and more closely spaced away from the origin, and gives the high value of $\alpha = 2$.

This last example shows that the scaling exponent can be much higher than the dimensionality of the space in which the plants are placed—a somewhat perplexing feature until rendered commonplace by familiarity.

The Lipschitz-Hölder scaling exponent α , based from any plant, characterises a combination of the fractal dimension of the set of plants and the relative density of plants in the immediate neighbourhood when compared to the distribution further away.

A.3 Mass exponents and the multi-fractal spectrum

A computational difficulty is to calculate the multi-fractal spectrum.

Adapting the description in Feder [13, §6.7], partition the plane into squares of side δ and disregard empty squares. In a total of N points, let $N_i(\delta)$ be the number of points within the *i*th square. Assigning the *mass* or *probability* of the *i*th square to be $\mu_i = N_i/N$, we calculate for various exponents q

$$\mathcal{N}(q,\delta) = \sum_{i} \mu_{i}^{q} \sim \delta^{-\tau(q)} ; \qquad (5)$$

where we anticipate that the mass exponent $\tau(q)$ can be discerned over a reasonable range of length-scales δ by plotting $\log \mathcal{N}$ versus $\log \delta$. Note that $\tau(1) = 0$ as $\sum_i \mu_i = 1$; and that $\tau(0) = D$, the Hausdorff fractal dimension of the set, as \mathcal{N} is then just a count of the non-empty squares.

By examining how the mass exponent τ varies with q we can recover information about regions of the multi-fractal with different scaling exponents. The basic reason for this is that as q increases, the sum $\sum_i \mu_i^q$ is dominated by the large values of μ_i which correspond to the regions of dense plants; conversely, as q becomes increasingly negative the sum is dominated by the small values of μ_i which correspond to the regions of sparse plants. As outlined by Feder [13, §6.8], arguments then lead to the multi-fractal spectrum being given parametrically as

$$\alpha(q) = -\frac{d\tau}{dq} , \qquad f(q) = q\alpha(q) + \tau , \qquad (6)$$

though numerically it is more reliable to use the property that

$$f(\alpha) = \min_{\alpha} \{ q\alpha + \tau(q) \}$$
(7)

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binary multiplicative fractal - mass exponents

Figure 13: The mass exponent curve $\tau(q)$ for the multi-fractal data displayed in Figure 14.

which is the approach we take. Geometrically, if we consider a mass exponent curve, such as the one shown in Figure 13, then $\alpha(q)$ is the negative of the slope of the curve at any given q, while f(q) is the intercept of the tangent to the curve with the τ -axis. Thus we can easily appreciate that for the typical concave multi-fractal mass exponent curve that is shown in Figure 13: the scaling exponents extend over a finite range, that limited by the two slopes for large and small q; and the fractal dimensions f have a maximum at q = 0 of $f = \tau(0) = D$, the Hausdorff fractal dimension.

Note that for a uniform fractal distribution of plants, such as that shown in Figure 11, the mass exponent curve reduces to a straight line of slope -D. Thus, for all q the negative slope is $\alpha = D$ and, since $\tau(1) = 0$, the vertical intercept is

f = D.

We are inclined towards using a scheme which is different in detail to calculate the mass exponent $\tau(\delta)$, one based on the correlation dimension as also proposed by Pawelzik & Schuster [32], see also [16]. We estimate

$$\mathcal{N}(q,r) = \frac{1}{N} \sum_{j=1}^{N} \nu_j^{q-1} \,. \tag{8}$$

Recall that $N_j(r)$ is the number of plants (neighbours) within a distance r of the jth plant, and that $\nu_j(r) = N_j/N$ is the fraction of plants within a distance r. As argued early, the jth plant is surrounded by $N_j(r)$ plants within a distance r and so they may all be covered by just one disc of radius r, and this disc contains a mass $\mu_j = \nu_j$; of this disc, a fraction $1/N_j$ of it is "used" to cover the jth plant, and so $(1/N_j)\nu_j^q$ is the jth plant's contribution to the sum appearing in (5).

Plotting $\log \left(\mathcal{N}^{1/(q-1)} \right)$ versus $\log r$ we seek to find a straight line fit of slope $D_q = \tau/(1-q)$ over a range of length-scales sandwiched between two horizontal regimes. We estimate the "generalised dimension" or "Renyi dimension" D_q rather than $\tau(q)$ so that the straight line fit is much the same for all values of q. As commented on by Feder [13, §6.9]: D_0 is then the Hausdorff dimension; D_1 is known as the *information dimension*, recognised in the multi-fractal spectrum as the tangential intersection of the $f(\alpha)$ curve with the line $f = \alpha$; and additionally, D_2 is known as the correlation dimension.

For a uniform fractal, such as that in Figure 11, each plant in the fractal is associated with the same value of α and so f is just the fractal dimension D of the whole set. Also, the earlier examples show that in this case the value of α is also the same as the fractal dimension, and so $f = D = \alpha$. Note that in these cases the curve is just a single point, f is not defined for any other values of the scaling exponent.

An example of a non-uniform fractal, the so-called binary multiplicative fractal, and its associated multi-fractal spectrum is discussed in detail by Feder [13, §6.2]. Briefly, this is a one-dimensional fractal formed by unevenly distributing plants on the interval [0, 1). First, a proportion p < 1/2 are assigned to the left-half [0, 1/2) and the remaining greater proportion p' = 1 - p to the right-half [1/2, 1). Second, the plants in each half are unevenly assigned to their own halves according to the same uneven proportions. Third, the plants in each of these quarters are assigned unevenly to their halves according to the same rule. And so on. This generates a multi-fractal whose multi-fractal spectrum is given parametrically by

$$\alpha = -\left[\xi \log_2 p + \xi' \log_2 p'\right] \tag{9}$$

$$f = -[\xi \log_2 \xi + \xi' \log_2 \xi']$$
(10)

for $0 \le \xi \le 1$ and where $\xi' = 1 - \xi$. The $f(\alpha)$ curve looks like an upside down parabola, peaking at f = 1 (the fractal dimension of the set) at $\alpha = -\frac{1}{2}\log_2(pp')$, and stretching from $\alpha_{\min} = \log_2(1/p')$ to $\alpha_{\max} = \log_2(1/p)$. Most of the plants in this multi-fractal contribute to the peak of this curve as this is the set of the highest fractal dimension; at the peak the scaling exponent $\alpha > 1$ (for $p \ne 1/2$) and so most plants are surrounded by denser clusters! The relatively few plants in the low density regions, typically near the left end of the binary subintervals, contribute to the large α side of the curve and their low fractal dimension indicates how few there are. Similarly few in number are those very dense clusters of plants associated with a low scaling exponent α .

Note that when p = 1/2 this binary multiplicative fractal reduces to a uniform distribution of plants on a one-dimensional line, and the multi-fractal spectrum (9–10) collapses to the single point $f = \alpha = 1$.

Figures 14 and 15 illustrate these ideas in two-dimensions rather than one-dimension. Figure 14 shows N = 300 plants on a computer generated multi-fractal; the distribution is the product of two binary multiplicative fractal distributions. The theoretical multi-fractal spectrum, the $f(\alpha)$ curve, for this distribution is also given by equations (9–10) except that the right-hand sides have to be doubled. The distribution ideally has a Hausdorff fractal dimension of D = 2. However, there are many regions of closely clumped plants among regions of sparsely distributed plants, and a multi-fractal description gives more detail of these features. Computing the multi-fractal spectrum, as shown in Figure 15, we see the spread of scaling exponents α ranging from less than 1, characteristic of densely clumped plants, to nearly $\alpha = 5$, characteristic of sparse plants. However, these extremes occur rather rarely as is shown by their low fractal dimension f. Vastly more common are regions associated with a high fractal dimension, here $f \approx 1.8$, and their corresponding scaling exponents $\alpha \approx 2-3$, characteristic of clumps with interspersed dense clumps of plants.

It is important to note that even with N = 300 data plants, the numerically obtained multi-fractal spectrum has only rough quantitative accuracy. Comparing with the theoretical spectrum (dashed), the numerical curve may be judged as follows: for small values of α it is fairly accurate; but the peak height is too low at about 1.85 although reasonably accurately placed; while the right-hand part of the curve is in error by about 10% in α . The inaccuracies for larger α are not surprising as these correspond to the sparse plants in the distribution, and being relatively few in number the results which are heavily based on them are inaccurate. Conversely, the left-hand side of the curve is dictated by the densely clumped plants of which there are a large number and accurate predictions are consequently obtained.

We expect similar accuracy for the multi-fractal spectra based on the experimental data which are shown in Figure 7.



Figure 14: N = 300 points on a two-dimensional multi-fractal. The points are generated by their x and y coordinates being independently chosen at random from the one-dimensional binary multiplicative fractal with p = 0.25. The points are drawn in different shapes to exhibit the variations in the Lipschitz-Hölder exponent α as deduced by the algorithm used for the plant data.



Figure 15: the numerically determined multi-fractal spectrum $f(\alpha)$ for the multi-fractal data displayed in Figure 14. The dashed curve is the theoretical $f(\alpha)$ spectrum. Comparing the two curves, observe that the right-hand part of the numerical curve is unreliable due to the paucity of data in the sparse areas of the plant distribution.