LIMNOLOGY
and
OCEANOGRAPHY: METHODS

Limnol. Oceanogr.: Methods 3, 2005, 203–210

Measuring surface complexity in ecological studies

Natalie J. Frost[1], Michael T. Burrows[2], Mark P. Johnson[3], Mick E. Hanley[1], and Stephen J. Hawkins[1,4]*
[1]Biodiversity and Ecology Division, University of Southampton, Bassett Crescent East, Southampton, SO16 7PX, United Kingdom
[2]Dunstaffnage Marine Laboratory, Oban, PA34 4AD, United Kingdom
[3]School of Biology and Biochemistry, Queens University Belfast, 97 Lisburn Road, Belfast, BT9 7BL, United Kingdom
[4]Marine Biological Association of the UK, Citadel Hill, Plymouth, Devon, PL1 2PB, United Kingdom

Abstract

Habitat complexity is a potential structuring force in benthic communities. Different studies often estimate complexity in different ways, and it is not always clear how precise the separate techniques are. Here we review three methods of estimating surface complexity: stereo photography, profile gauges, and lengths of chain contoured over the substratum. We derived fractal dimensions for the quadrats in the rocky intertidal zone using each technique. Complexity estimates from chains and profile gauges were related, but neither technique was correlated with the results from stereo photographs. Stereo photographs appeared to overestimate complexity on smooth surfaces. The variance of fractal dimension estimates increased nonlinearly with the mean fractal dimension in each quadrat. Recommendations for the number of replicates needed for a reliable estimate of fractal dimension from a quadrat, therefore, vary as a function of surface complexity. Within the range of complexities typically encountered on rocky shores, as few as three profiles or sets of chains can produce relatively reliable estimates of fractal dimension. The most robust and time effective method, however, would be to sample using as many chain profile sets per quadrat as is logistically feasible. Given the changes in precision with surface complexity, comparisons between studies need to take careful note of the number of replicates and the average level of surface complexity. A null result (no relationship between surface complexity and an ecological variable) could be produced by imprecise estimates of surface complexity based on too few replicate measurements per quadrat.

Considerable interest in ecological research has focused on the importance of habitat architecture and complexity in shaping community structure and function (Floater 2001; Jenkins et al. 2002; Williams et al. 2002). On hard surfaces such as rocky shores, the influences of surface topography on organism abundance, distribution, and behavior have been widely studied (Bergeron and Bourget 1999; Beck 2000; Johnson et al. 2003). However, a clear understanding of the ecological role of habitat complexity is hindered by the problems associated with its measurement (McCoy and Bell 1991; Beck 1998).

A surface can be topographically complex in a number of ways, and there are correspondingly many ways of measuring such complexity. For comparative studies, variation in complexity is usually described with a univariate index. Researchers have a choice of indices with complexity values typically calculated from a transect across the surface. There are essentially two ways in which the complexity of the surface can be translated into an index. The distance traveled along the surface compared to the linear distance between the ends of the transect gives a measure of the extra surface introduced by following cracks and protrusions on the surface. Typically chains are used to follow the surface profile and calculate this type of index (Luckhurst and Luckhurst 1978). As an alternative to surface following techniques, some form of measurement of the surface can be taken, with statistics calculated from the resulting profile. Typically these surface measurements involve recording the different heights of pins in a profile gauge (Underwood and Chapman 1989; McCormick 1994) or the use of a stereophoto to reconstruct heights (Beck 1998). Statistics calculated from these profiles include the sum of consecutive height differences between horizontally adjacent points and indices based on the variance of change in slope angle between consecutive measurements. Separate indices measure slightly different properties of a surface, but tend to be correlated for the same profile (reviewed in McCormick 1994; Beck 1998). One option for both surface following and measurement-based

---

[*]Corresponding author.

Acknowledgments

This work was funded by the Natural Environmental Research Council. We would also like to thank Drs Toby Carter and Malcolm Roberts for technical assistance, and Dr Vladimir Kostylev for discussion at an earlier stage in this work.

estimates of complexity is to calculate a fractal dimension (Beck 1998; Robson et al. 2002). The fractal dimension (*D*) for a surface profile lies between one and two, with values above one indicating greater degrees of surface complexity. If the value for a surface is being reported, the dimension lies between 2 and 3. Commonly roughness is estimated from profiles and transformed to a surface fractal by adding one (assuming an isotropic surface, Petigen and Saupe 1988).

Fractals have a number of advantages as a common currency for surface roughness or environmental heterogeneity. Fractals describe complexity over a range of scales, provide novel descriptions of heterogeneity for ecological theory (Ritchie and Olff 1999), and allow the effects of heterogeneity and area to be separated in biodiversity studies (Johnson et al. 2003). The Euclidian alternatives to fractal measurements of surface complexity are likely to be more useful than fractal measurements of roughness where particular structural components of a surface affect ecological interactions. Euclidian measurements include the number of pits of a certain size. Variations in the number of pits can affect species richness, population density, and larval settlement rates in the absence of variation in *D* (Hills et al. 1999; Beck 2000). A disadvantage of Euclidian measurements is that they will often be specific to a particular system or species, hampering comparative studies. Amongst a range of indices, the "best" predictors of ecological variables, such as species abundances, tend to vary between studies (McCormick 1994; Beck 1998).

Given that fractals have a utility in ecology based on their use as a "common currency," it is important to establish the relative precision of estimates of *D*. As detailed above, both surface following and surface measurement approaches can lead to an estimate of *D*. Chains of different link lengths (Dahl 1973) can provide the variation in step lengths required to estimate a fractal dimension (*see* Materials and procedures). Profiles estimated from gauges or stereo photographs can be measured at different step lengths to determine a fractal dimension (Kostylev 1996; Beck 1998; Johnson et al. 2003). These methods differ in technical complexity, cost, and time required, but it is not clear whether the separate methods produce comparable results and which technique is the most efficient.

The range of values for *D* on rocky shores is of the order of 1 to 1.08 (Beck 2000; Johnson et al. 2003; Davenport 2004). Alarmingly, Russ (1994) states that the precision of methods based on analyzing profiles may be as low as 0.1 (where there are around 100 points in a profile). This apparent lack of precision may therefore swamp the signal attributable to surface roughness, negating fractal dimensions as a useful measurement (Davenport 2004). The methods comparison presented here, therefore, evaluates the signal-to-noise ratio when using the profile gauge, chain, and stereo-photo methods for estimating fractal dimension.

Materials and procedures

Using the fractal dimension *D* as our index of complexity and unit of comparison, we undertook a detailed review of the three methods (profile gauges, stereo-photography, and chains of different link lengths) most frequently used to derive complexity indices. We tested whether the three contrasting measurement techniques would produce comparable indices, and a similar ranking of complexity for randomly sampled 0.0625 m^2 quadrats. Positive correlation of the resulting fractals would suggest that a reliable comparison of habitat complexity between locations is feasible, regardless of the technique employed to measure it. It would also suggest that the simplest and quickest method could be employed in most situations, since the relative complexity index would always be the same whatever the method used. With this possibility in mind, we also examined the efficiency and precision of each technique. Using these approaches, we aimed to determine whether any one method is the most appropriate to quantify habitat complexity in the rocky intertidal, and whether direct comparisons are possible between different approaches.

Profile gauges—Three 300-mm long profiles were taken from each quadrat, two across the diagonals of each quadrat, and the third along one randomly selected side of the quadrat. Profile gauges are easily obtained from hardware stores. The model that we used had 300 plastic pins that can slide independently of each other to conform to surface irregularities, each pin being 1 mm in width and 50 mm in height. The profile gauge was pushed onto the rock so that the pins were molded into the surface. The resulting profile was then traced onto a sheet of paper. Where crevices were too deep for the profile gauge, a note was made on the traced profile of the position of the crevice and the change in vertical height. This was then corrected for, with additional height changes calculated using trigonometry and added to the respective points.

The resulting profiles were scanned and converted into a digital image (using Techdig; Jones 1997). Coordinates were recorded at every point along the profile where there was a change in the vertical dimension. Linear interpolation between adjacent coordinates was used to obtain a continuous line. Fractal dimensions (*D*) were calculated from these profiles using the dividers method (Richardson 1961; Sugihara and May 1990; Cox and Wang 1993) with a geometrically increasing series of step lengths (1, 2, 4, 8, 16, and 32 mm). As the smaller step lengths measure more of the irregularities along a profile, estimated profile length increases with decreasing step size. Fractal dimensions are calculated from the slope of the line relating step size to increases in estimated profile length (following log transformation of the axes, Pennycuick 1992). Example computer code and programs with alternative methods for calculating a fractal dimension can be found in Russ (1994). An average estimate for *D* and the associated variance between estimates were calculated from the three profile measurements taken from each quadrat.

Lengths of chain—Three–hundred millimeter long chains of three different link sizes (10 mm, 20 mm, 45 mm) were laid directly over the substratum such that they conformed as closely as possible to all contours and crevices. The ratio of the horizontal distance covered to the actual chain length gives an estimate of surface roughness (Luckhurst and Luckhurst 1978). Larger values for the chain ratio imply increasingly rougher surfaces. The chain link size is analogous to a divider step length. This allows a fractal dimension to be calculated from the different chain ratios for a profile on the shore using a plot of log distance against log link size. A chain-based fractal dimension was, therefore, calculated for each of three profiles through each quadrat.

Stereo photography—Stereo photography allows the calculation of the three-dimensional coordinates of any photographed point. Location estimates are based on the relative position of a feature on both exposures of a stereo-pair. The basics of the technique require that the distance between the two cameras is known, and that the optical axes of the cameras are parallel (van Sciver 1972) or that images are rectified to represent the same plane. The three-dimensional coordinates of each specified point shared by the images can be calculated based on a series of trigonometric equations (van Rooij and Videler 1996). These photogrammetric techniques have wide applications across a number of scales in environmental science. The increasing availability of digital cameras and the associated technology is reflected in a broad usage of these techniques (Baily et al. 2002).

Stereo photographs of each quadrat were taken with two aligned Ricoh RDC300 digital cameras attached to a portable frame. A tripod was adapted to hold the two cameras at a fixed separation (140 mm), held horizontal to the plane of the rock surface. The base:distance ratio for the photographs was approximately 1:6. Once positioned, the images were taken simultaneously and were downloaded to a computer for viewing. Each stereo-photograph encompassed an overlapping region of 250 mm by 250 mm with a resolution of 0.3 mm per pixel. The accuracy of this system was within a range of ± 20 mm on simple objects in the laboratory (in comparison, the error range was of the same order for the comparative measurements of a stream bed made by Butler et al. 1998).

Points were overlain in stereo photographs using a computer program written in Visual Basic (Burrows unpubl. data unref.; commercially available software for matching points on stereophotos is also available: Chandler and Padfield 1996; Butler et al. 1998). Each of the photographed quadrats was subdivided into 506 grid cells. Within each cell, any identifiable feature such as an irregularity of the rock, was marked in both of the corresponding images from the stereo-photograph pair. The three dimensional coordinates of each point were then calculated using the trigonometric equations in van Rooij and Videler (1996).

Both profile gauge and chain measurements estimate deviations from a plane parallel to the rock surface. Any slope was therefore removed from stereo photograph coordinates to leave a set of points representing deviations from a horizontal plane. Large-scale slopes were estimated from multiple linear regression of z coordinates against the x and y for each quadrat. Residuals from this regression produce a set of z values lying on a horizontal plane. Linear interpolation between these residuals gave an equidistant grid at a resolution of 10 mm that could be used to calculate fractal dimensions. As with the other techniques, fractal dimensions were calculated using the dividers method. A total of 80 interpolated lines (split between x and y axes) were used to calculate an average fractal dimension for each quadrat.

Estimates of precision—The variance and mean for estimates of fractal dimension from each quadrat were positively correlated (following the expectations of Taylor's [1961] power law). Linear regression of natural log transformed mean and variance data were therefore used to interpolate predicted variances for any value of D. These predicted variances led to parametric estimates for confidence intervals with different values of D (using t.SE, where t is the appropriate value from a t-table for a probability of 0.05 and SE is the standard error). The same techniques can be used to interpolate the number of estimates from each quadrat required to estimate D with a set level of precision. Given the relatively low estimates of fractal dimension for rock surfaces in the literature, we used a target precision of ±0.01.

Assessment

Study sites—Data were collected from two moderately exposed shores situated 15 km apart along the southwest coast of England: Heybrook Bay, Devon (UK national grid reference SX 492487) and Portwrinkle, Cornwall (SX 356537). Both shores are biologically similar and have similar underlying geology. At each location 30 (0.25 × 0.25 m) quadrats were examined in the mid inter-tidal zone. Quadrats were selected at random, but with the provision that if the area encompassed greater than 50% of standing water (i.e., a rockpool) it was discarded. Within each quadrat a stereo-pair of photographs were taken, together with three profiles using a profile gauge, and three using chains of different link lengths.

Comparison of complexity estimates between techniques—Fractal dimensions obtained from the stereo photography method (mean $D = 1.06 \pm 0.004$ SE) were consistently higher than those obtained from profile gauges (1.02 ± 0.003), and chains (1.04 ± 0.004). Furthermore, the differences in estimates of D were statistically significant (one-way ANOVA $F = 24.71_{2,87}$, $P < 0.001$, post hoc S-N-K tests $P < 0.01$ for each pair-wise comparison between techniques).

The estimated fractal dimension from stereo photographs did not correlate significantly with estimates from the other techniques (Fig. 1). There was some consistency in the ranking of surfaces between profile gauges and chain methods (Spearman's correlation coefficient = 0.404, $P = 0.027$).

Comparison of precision between estimates—The log variance (v) of D changed with log mean fractal dimension (f) of each quadrat with the following relationships: chains $v = 108.2f + 11.1$; profile gauges $v = 101.0f - 12.8$; stereo photos $v = 29.4f - 9.0$; all significant relationships at $P < 0.05$. These relative

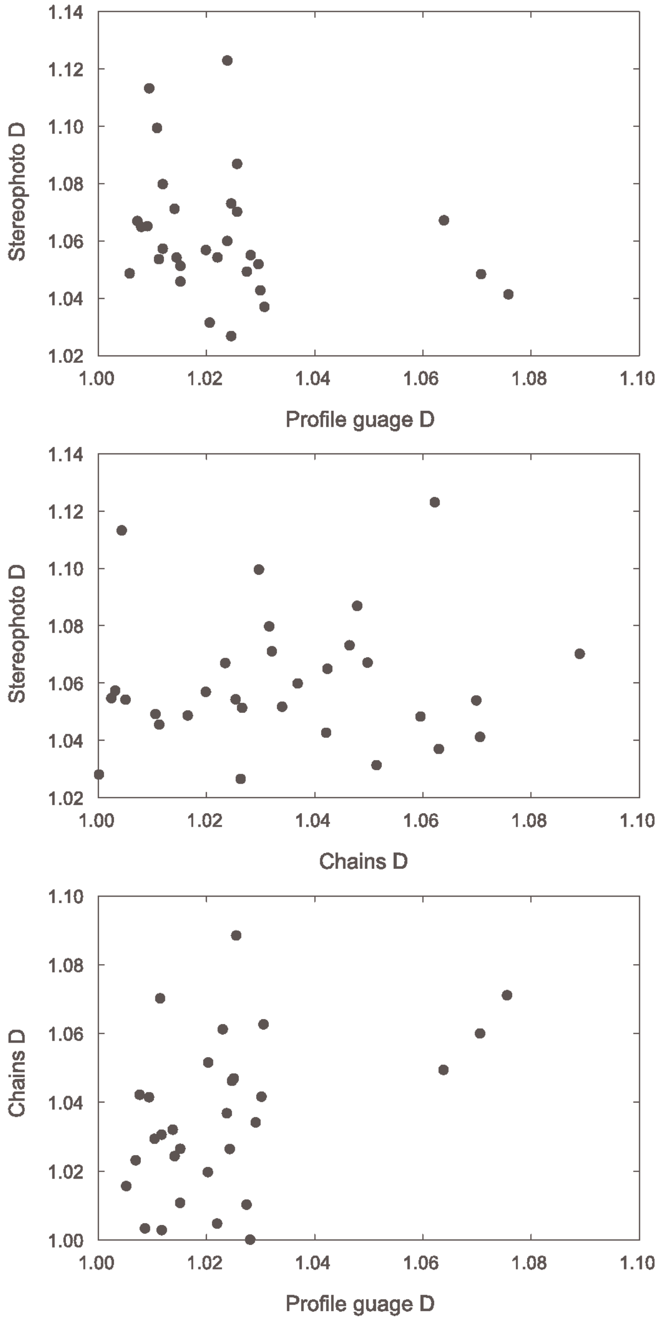

Fig. 1. Pair-wise comparisons of fractal dimension (*D*) estimates from the same 30 quadrats at two sites in southwest England. The three methods (stereo photography, a profile gauge, and chains) are commonly used to quantify habitat complexity in the aquatic systems.

increases in variance with mean fractal dimension resulted in a rapid decrease in the precision of chain and profile estimates (Fig. 2). For quadrats around the mean value for *D*, estimates from profile gauges were relatively precise: the signal of a value of $D = 1.02$ could be significantly distinguished from a smooth surface of $D = 1$. As *D* approaches 1.05, however, the confidence intervals overlap with $D = 1$: for 3 profiles it would be difficult to have much confidence in the repeatability of estimates on rougher surfaces. Chain estimates of fractals have larger confidence intervals than profile estimates, but they follow the same general pattern. Stereo photographs are relatively imprecise if the number of measurements is held constant across different methods (on the basis of 3 estimates of *D* per quadrat). Confidence intervals are initially larger on this basis in stereo photos when compared to the other methods.

The relative precision of the different techniques is further illustrated in Fig. 3. Relatively few profile gauge measurements are needed for an estimated confidence interval of 0.01, as long as the underlying fractal dimension does not rise much above 1.04. Chain estimates for fractals can also be relatively precise, as long as a large number of estimates are taken (approximately 40 at $D = 1.04$). At low values of *D*, more estimates are needed from each stereo photo to achieve the same level of precision as the chain and profile techniques. The intercept at $D = 1$ indicates an estimate of the residual measurement error associated with each technique. This is largest for stereo photos, with an intercept at seven lines per photo.

Discussion

The results indicate that estimates of fractal dimension using different techniques are not always comparable. Reproducible estimates of *D* are, however, attainable with the currently used methods. Relatively few profiles from a quadrat are needed in the range of values of *D* typically encountered on rocky shores.

The different techniques used different step lengths for estimating fractals, and this may reduce the comparability of estimates of *D* if the surfaces were not truly fractal (scale free). We tested for the consistency of fractal estimates across scales by calculating fractals using different step lengths in profiles (5, 10, 20, 40, 80 mm). The average fractal in sampled quadrats was the same regardless of whether the smallest step length was 1 or 5 mm. Comparisons of estimates of D on single profiles confirmed that there were no significant differences between fractals estimated with different step lengths (paired *t* test, $t = 0.28$, $P > 0.7$). The surfaces were therefore fractal across the range of scales measured, and the variation in step lengths did not contribute to the variation between techniques. Beck (1998) also concluded that surfaces were simple fractals in the 0.25 m^2 quadrats that he analyzed.

In comparison to chains and profile gauge measurements, stereo photos lead to relatively high error in estimates of surface complexity as *D* approaches one. Previous studies (Evans and Norris 1987) have found a poor match between the height measurements from stereo photographs and from profile gauges. Furthermore, it is possible that stereo photographs underestimate the complexity on rougher surfaces. As *D* increases, variability between replicate measurements from a quadrat becomes lower in stereo photographs than in the other methods (as shown by the confidence intervals in Fig. 2). These patterns in the results from stereo photographs are the result

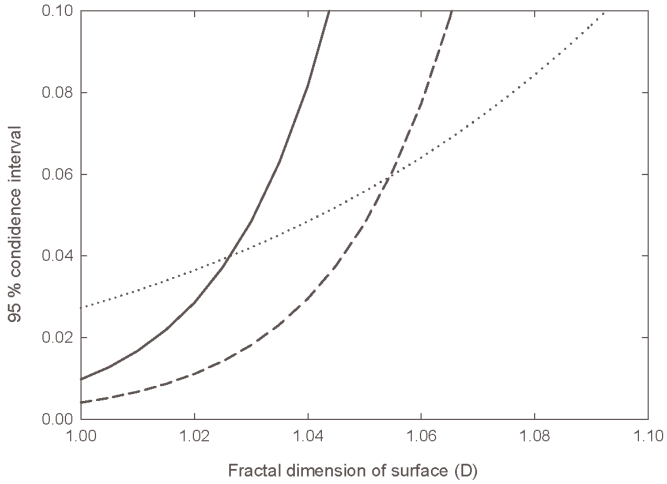

Fig. 2. Estimated error (as 95% confidence intervals ± the mean) when deriving the fractal dimension *D* from three profiles per quadrat using profile gauge (dashed line), chains (solid line), or stereo photography (dotted line).

of both technical limitations of the equipment and intrinsic problems in estimating the topography of complex surfaces. With improvements in the availability of high quality digital cameras and developments in image processing, it will be possible to address some of the technical issues. One area that will have caused underestimation of surface complexity is the interpolation between points required to produce a digital model of the photographed surface. Such interpolation effectively smoothes the surface being measured. While photographs can be analyzed at a higher resolution to reduce the scale of interpolation, good matches between points on stereo images are not always possible (leading to 20% of points being interpolated in the study of stream bed topography by Butler et al. 1998). Hence some degree of interpolation is inherent in current applications of stereo photography in the field.

Other sources of measurement error specific to stereo photos include variations in light levels, the reflective properties of the surface (including surface wetness), the distortions associated with the lens, and the subjective matching of "landmarks" between paired images (Van Rooji and Videler 1996). The need for a properly specified lens model may not be so important at the scale measured (c.f., Butler et al. 1998). A key issue limiting intercomparison of techniques is that surface features may be relatively undersampled in stereo photos (although all techniques can only measure surface complexity and, therefore, underestimate the additional complexity under overhangs; Commito and Rusignuolo 2000). The undersampling hypothesis is partly supported by the negative relationship between profile and stereo photo estimates of *D*. Surface features may be missed in stereo photos when relatively low elevation areas are obscured by surrounding areas (even with a flash, it may not be possible to see the bottom of some cracks and crevices on a photograph, while large changes in height over short distances can obscure the view in stereo photos; Butler et al. 1998). Photographs may, therefore, not record features that other techniques pick up. As these features are not necessarily common on a surface, the final result is more variability with profile gauges and chains (as pits and cracks occur on some, but not all, replicate profiles), while there is less variability with photos (as pits and cracks are can be missed even when they occur on a profile). While improvements in stereo photography can address some of the error at low *D*, further research is needed to address the issues on more complex surfaces. This approach is, however, likely to be specific for particular camera systems, applications, and ranges of *D*.

Chain and profile gauge estimates of fractal dimension appear to be measuring the same properties of the surface. The chains had open links, and slippage of links may have caused the slightly higher mean *D* estimates when compared to profile gauges. This could perhaps be controlled by using chains with fixed link distances (e.g., cycle chain). Estimates of *D* were also correlated with other estimates of surface complexity. For example, individual chain ratios are also estimates of surface complexity, and these were positively related to chain fractal (mean correlation = 0.92, $P < 0.01$) and profile gauge fractal estimates (mean correlation = 0.49, $P < 0.05$) for each quadrat. Such correlations between indices of complexity have been reported previously (McCormick 1994; Beck 1998), implying that there is a property of surface roughness that can be compared between treatments. A note of caution with this conclusion is that sufficient replicate measurements need to be taken in the different studies being compared. The indices are one-dimensional estimates of a complex surface property and hence it is not surprising that there is variation among

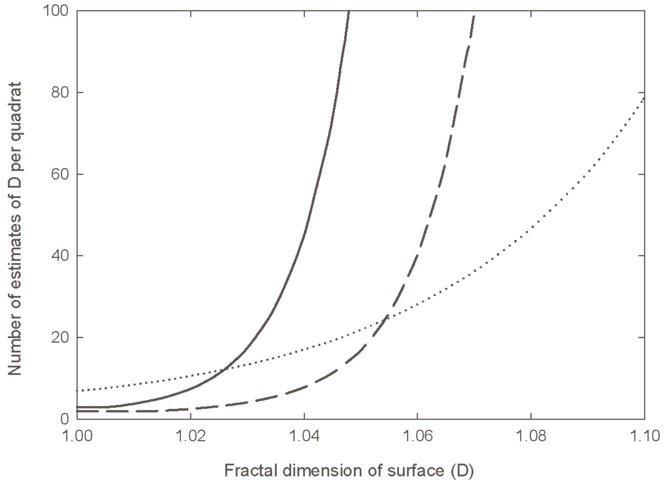

Fig. 3. Number of profiles required to maintain 95% confidence intervals of ±0.01 with increasing surface fractal dimension. Different methods are indicated by a dashed line (profile gauge), a solid line (chains), or a dotted line (stereo photography).

replicate profiles and between techniques. It is highly likely that surface complexity is not perfectly isotropic and that *D* varies with profile orientation. However, information on the orientation of surface roughness is likely to be application-specific and supplementary to the use of indices for most comparative studies of complexity. The variability inherent in complexity estimates implies that studies that conclude "no relationship with surface complexity" may not be reliable if the measurements of complexity were made from relatively few profiles and the surface was complex. For example, at a fractal dimension of 1.05, the error for a chain-based estimate of *D* based on three replicates exceeds 0.05 (Fig. 2). Given this relative level of error, one would expect to find no correlation between measured variables and complexity even if a relationship did actually occur.

The number of profiles sampled in a study is often a compromise between precision and sampling effort. At relatively low values of *D*, profile gauges gave the most reproducible estimates of D. However, this was a time-consuming method, with handling and analysis of each profile taking about 25 minutes. Chain ratios for a profile took about the same time as a profile gauge in the field, but the analysis in the laboratory was quick: no more than 5 min to generate fractal estimates. Even given the higher number of measurements per quadrat needed for a standard level of error (Fig. 3), chains were about four times as quick as profile gauges. In practical terms, however, there are a very large number of chain measurements needed for reproducible estimates at $D > 1.04$ (approximately 50), so profile gauges may be more reliable at the replication level typically used in ecological studies. Where sampling time in the field is restricted (e.g., by tides), it may be more time efficient overall to sample using a profile gauge—even if this results in a longer time spent in the lab.

The cost/benefit efficiency of the different methods can be compared using the product of relative cost and time investment in the different techniques for the same degree for precision (Krebs 1999). As stated above, chains are about four times as quick as profile gauges to generate an estimate of *D*. Stereo photographs were quicker to make in the field than individual profiles, however, the individual processing of images was time consuming (approx 1 h per stereo photo in our system). With commercially available software, this processing would be reduced by a factor of about four. Hence, the relative time investments in generating estimates of *D* are, therefore, 1:4:2 for chains, gauges, and stereo photographs, respectively. This time estimate is based on a single profile for chains and gauges, while stereo photos can be used to generate a large number of profiles from a single digital surface with negligible marginal effort. Given the need to buy software and cameras, the stereo photograph technique is the most expensive to use. A relative costs ratio is 1:5:100 in terms of buying the relevant equipment for chains, gauges, and photogrammetry. Multiplying the number of profiles required for a set degree of precision (95% confidence intervals of ± 0.01; Fig. 3) by the relative costs and time investments indicates how the most efficient technique varies with changes in *D* (Fig. 4). As expected, chains are the most efficient solution at low values of *D*. The line for stereo photos does not change with increasing *D*, as one profile takes virtually the same effort as many profiles from the same digital surface reconstruction. Interestingly, stereo photos can be the more efficient solution on more complex surfaces (still within the range of those typically encountered). As discussed earlier, estimates from stereo photographs may be relatively more precise due to the large number of replicate profiles possible, but there may be underlying error in the process, biasing the estimated values and reducing comparability to other techniques.

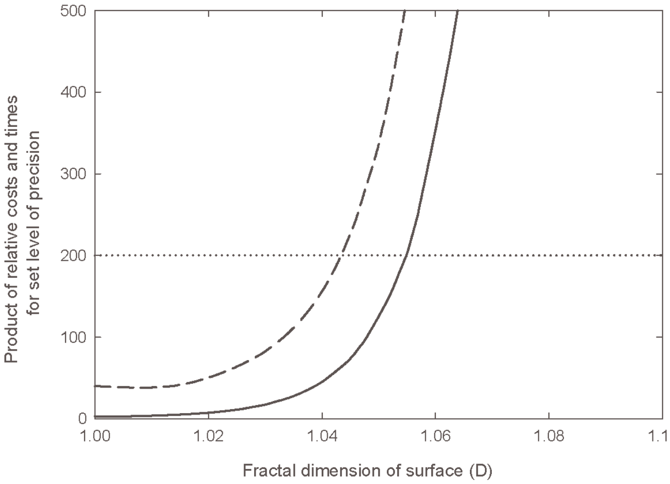

Fig. 4. Comparison of the efficiency of different techniques on surfaces of differing complexity. Efficiency of techniques is estimated as the product of relative cost and time investments for a precision ±0.01 (95% confidence intervals).

Comments and recommendations

It seems clear that one cannot assume consistency in the relative complexity ranking obtained by different measurement techniques. This finding sounds a note of caution for any ecologist wishing to draw generality from separate studies looking at the effects of topographic complexity in the marine intertidal and highlights the need for careful examination of the range of complexities and the number of replicates per estimate in different studies.

Measurements of surface complexity become rapidly more unreliable as *D* increases. Presumably this reflects the variability within quadrats containing complex topographies: a profile may run across a relatively smooth area or a very pitted area even when these areas are centimeters apart. Fortunately, average fractal dimensions on rocky shores are usually of the order of 1.02 to 1.04 (Kostylev 1996; Beck 1998; Johnson et al. 2003), so the lack of precision may not cause too many misinterpretations. If a small number of profiles are to be made, it will be more precise to estimate *D* from a profile gauge as the estimated error curve is less steep than the equivalent curve for chain-based estimates. The chain method is, however, the quickest and easiest technique to use, requiring no specialized equipment and a minimum of subsequent analysis. If this technique is used, our results suggest that surveyors should make as many chain measurements as is logistically feasible. Stereo photographs either did not measure the same elements of complexity as chains or profile gauges, or this was a more error-prone technique. There was evidence for high measurement error on the smoother surfaces sampled. Stereo photographs should, therefore, not be used as the sole source of information on the roughness of a surface without some cross calibration with other techniques. If a stereo photo system can be optimized for a study and the undersampling issue addressed (perhaps by having more than two photographs of the surface), there is evidence from Fig. 4 that photogrammetry is a potentially cost-efficient technique. Of course stereo photos may have other uses in surveys: such as a permanent record of a quadrat, the spatial relationships among different organisms, and the relationships of organisms to topographic features at small scales. Stereo photos are also the most practical method of examining the role of topography at larger scales (meters) on shores (Guichard et al. 2000).

While fractal dimensions remain an important measure of environmental heterogeneity with links to ecological theory, there are serious issues with the derivation and interpretation of fractal dimensions (Russ 1994; Halley et al. 2004). Our results indicate that measurements of fractal dimension can be relatively precise if sufficient replicates are taken. Correlations of ecological variables with such an index of surface roughness are not evidence of causation (Davenport 2004). Hence measurements of surface roughness are likely to be most useful when integrated into broader programs of research that also incorporate measurement and manipulation of specific surface features.

References

Baily, B., P. Collier, P. Farres, R. Inkpen, and A. Pearson. 2003. Comparative assessment of analytical and digital photogrammetric methods in the construction of DEMs of geomorphological forms. Earth Surf. Process. Landforms 28: 307-320.

Beck, M. W. 1998. Comparison of the measurement and effects of habitat structure in gastropods in rocky intertidal and mangrove habitats. Mar. Ecol. Prog. Ser. 169:165-178.

———. 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. J. Exp. Mar. Biol. Ecol. 249:29-49.

Bergeron, P., and E. Bourget. 1986. Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice-disturbed environment. Mar. Ecol. Prog. Ser. 28:129-145.

Butler, J. B., S. N. Lane, and J. H. Chandler. 1998. Assessment of DEM quality for characterizing surface roughness using close range digital photogrammetry. Photogramm. Rec. 16:271-291.

Chandler, J. H., and C. J. Padfield. 1996. Automated digital photogrammetry on a shoestring. Photogramm. Rec. 15:545-559.

Commito J. A., and R. R. Rusignuolo. 2000. Structural complexity in mussel beds: the fractal geometry of surface topography. J. Exp. Mar. Biol. Ecol. 255:133-152.

Cox, B. L., and J. S. Y. Wang. 1993. Fractal surfaces: Measurement and applications in the earth sciences. Fractals 1:87-115.

Dahl, A. L. 1973. Surface area in ecological analysis: quantification of benthic coral reef algae. Mar. Biol. 23:239-249.

Davenport, J. 2004. Fractal dimension estimation in studies of epiphytal and epilithic communities: strengths and weaknesses, p. 245-256. *In* Seuront, L., and P. G. Strutton [eds.], Handbook of scaling methods in aquatic ecology. CRC Press.

Evans, L. J., and R. H. Norris. 1997. Prediction of benthic macroinvertebrate composition using microhabitat characteristics derived from stereophotography. Freshwater Biol. 37:621-633.

Floater, G. J. 2001. Habitat complexity, spatial interference, and 'minimum risk distribution': a framework for population stability. Ecol. Monogr. 71:447-468.

Guichard, F., E. Bourget, and J. -P. Agnard. 2000. High-resolution remote sensing of intertidal ecosystems: A low cost technique to link scale-dependant patterns and processes. Limnol. Oceanogr. 45:328-338.

Halley, J. M., S. Hartley, A. S. Kallimanis, W. E. Kunin, J. J. Lennon, and S. P. Sgardelis. 2004. Uses and abuses of fractal methodology in ecology. Ecol. Lett. 7:254-271.

Hills, J. M., J. C. Thomason, and J. Muhl. 1999. Settlement of barnacle larvae is governed by Euclidean and not fractal surface characteristics. Funct. Ecol. 13:868-875.

Jenkins, G. P., G. K. Walker-Smith, and P. A. Hamer. 2002. Elements of habitat complexity that influence harpacticid copepods associated with seagrass beds in a temperate bay. Oecologia 131:598-605.

Johnson, M. P., N. J. Frost, M. W. J. Mosley, M. F. Roberts, and S. J. Hawkins. 2003. The area-independent effects of habitat complexity on biodiversity vary between regions. Ecol. Lett. 6:126-133.

Jones, R. 1997. Techdig. <http://home.xnet.com/~ronjones/#TECHDIG>

Kostylev, V. 1996. Spatial heterogeneity and habitat complexity affecting marine littoral fauna. PhD thesis, University of Goteborg, Stromstad, Sweden.

Krebs, C. J. 1999. Ecological methodology. 2nd edition. Addison-Welsey Longman.

Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Mar. Biol. 49:317-323.

McCormick, M. I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. Mar. Ecol. Progr. Ser. 112:87-96.

McCoy, E. D., and S. S. Bell. 1991. Habitat structure: the evolution and diversification of a complex topic, p. 3-27. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky [eds.], Habitat structure: The physical arrangement of objects in space. Chapman Hall.

Pennycuick, C. J. 1992. Newton rules biology. A physical approach to biological problems. Oxford Univ. Press.

Petigen, H-. O., and D. Saupe. 1988. The science of fractal images. Springer-Verlag.

Richardson, L. F. 1961. The problem of contiguity: an appendix of statistics of deadly quarrels. Gen. Syst. Yearbk. 6:139-187.

Ritchie, M. E., and H. Olff. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400:557-560.

Robson, B. J., E. T. Chester, and L. A. Barmuta. 2002. Using fractal geometry to make rapid field measurements of riverbed topography at ecologically useful spatial scales. Mar. Fresh. Res. 53:999-1003.

Russ, J. C. 1994. Fractal surfaces. Plenum Press.

Sugihara, G., and R. M. May. 1990. Applications of fractals in ecology. Trends Ecol. Evol. 5:79-86.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189:732-735.

Underwood, A. J., and M. G. Chapman. 1989. Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail *Littorina unifasciata*. J. Exp. Mar. Biol. Ecol. 134:175-196.

Van Rooij, J. M., and J. J. Videler. 1996. A simple field method for stereo-photographic length measurement of free swimming fish. J. Exp. Mar. Biol. Ecol. 195:237-249.

Van Sciver, W. J. 1972. Scale determination of unrecognised undersea objects by stereophotographic photography. J. Mar. Technol. Sci. 6:14-16.

Williams, S. E., H. Marsh, and J. Winter. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. Ecology 83:1317-1329.

Submitted 2 August 2004
Revised 21 February 2005
Accepted 16 March 2005