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Surface Area in Ecological Analysis: Quantification of Benthic Coral-Reef Algae

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Abstract

The surface area of organisms and substrata is shown to be a significant ecological parameter because of its functional importance in the system. Quantification of surface area can be of particular value in morphologically complex environments such as coral reefs. The amount of surface in a reef habitat can be estimated by direct measurements and theoretical approximations, using a surface index (SI) for the amount of surface increase over that of a similarly bounded plane. SI values for a section of the British Honduran barrier reef ranged up to 15 in the reef-crest area at scales significant to macro-organisms. By combining substrate-area measurements with estimates of percent coverage of the major benthic algal components, a reef transect with a horizontal area of 300 m^2 was shown to have over 300 m^2 covered by benthic macroalgae. The potential for the further development of surface estimation techniques is discussed.

Introduction

Surface area is a highly significant, although often neglected, parameter in ecology. The traditional tendency to think in terms of masses and volumes has left surfaces as something to look through rather than at. Yet, in considerations of structure, both form and content are equally important, and surface area is a significant attribute of form. The quantification and classification of surfaces themselves can, therefore, provide a new approach to the structural analysis of communities.

Much of quantitative ecology has taken a functional view of ecosystems, emphasizing the flows of energy and materials between component parts. Surfaces are often the boundaries within which compartments are defined and across which transfers take place, with the amount of surface being a significant rate determinant. The quantification of surface area and the analysis of its significance can, thus, support both structural and functional interpretations of an ecosystem.

This paper discusses quantitative approaches to surface estimation as applied to the specific question of the significance of benthic macroalgae in the coral-reef ecosystem. The complex and varied forms on a reef cannot be explained without reference to surface phenomena and their functional significance. In addition, the generation by the coral-reef ecosystem of its own local environment, and frequently even the underlying geological structure, increases the opportunity for feedback in the evolution of collective as well as individual forms. These same complexities make customary two-dimensional quantitative techniques largely unworkable, requiring new approaches to such problems as determining the amount of benthic algae present.

The following sections discuss surface as a functional concept, with special reference to the marine environment and particularly coral reefs, and explain some approaches to the quantification of surface area both in general theoretical terms and as applied to a specific reef site and problem. The concepts, of course, may be equally useful in other habitats and, indeed, in other fields of research.

Concept of Functional Surface

Surface area has generally been viewed in some specific functional context. Considerations of surface-volume ratios in organisms have emphasized the role of heat loss and other diffusion processes. In plants, where light absorption for photosynthesis and the surface uptake of materials are important, the size-metabolism relationship applies to individual parts such as leaves with their great surface rather than to the whole plant (Odum, 1956). The uptake of phosphorus by algae is proportional to their surface area, and productivity appears similarly related (Odum *et al.*, 1958). This evidence suggests that the recent assertion by McMahon (1973) that weight rather than surface is best correlated with metabolic rate is not generally applicable to plants, or to animals whose surface has an important functional significance (Dahl, 1973).

Aspects of the role of plant form and the resulting surface in light absorption have been discussed by several workers. Jahnke and Lawrence (1965) demonstrated mathematically the greater efficiency of a vertically elongate structure in intercepting light through its greater exposed surface. This concept was expanded by Horn (1971) to a general discussion of the ecological significance of tree forms and their resulting surface, but he dealt only with the outside surface of the form as related to the angle of incident light and not with the detailed surface of each tree structure or leaf where absorption actually takes place. The ability of some algae to vary their form and, thus, their exposed surface in response to local environmental conditions has been demonstrated by Dahl (1971). Monteith (1965), in his work on productivity in field crops, discussed the importance of characteristics of the plant surface such as the angle of leaves and the number of leaf layers relative to the type of incident radiation. The earlier development of a leaf-area index (Watson, 1947), giving the leaf area per unit of ground surface, has provided a useful quantitative and comparative measure of productive plant surface that is being increasingly used in ecological studies (Knight, 1973). While most studies of plant photosynthesis and productivity are quantified on the basis of organism biomass, productive surface may actually be an equally significant measure, since the biomass includes variable quantities of unproductive structural or storage materials.

Surface is of course also important at other levels of biological organization which can only be mentioned here. At the cellular level, the importance of membranes (surfaces) and membrane-bound phenomena is well known. In highly vacuolate plant cells, the cytoplasm itself is largely distributed along the inner cell surface. Various measures of the functional efficiency of plants might be more accurately estimated from a measure of cytoplasmic area or volume derived from the inner surface of the cells, rather than from a dry weight or biomass measure that includes the nonfunctional mass of the walls or a wet weight including the contents of vacuoles.

In ecology, surfaces and substrates are of great importance, as evidenced by the number of measures expressed in terms of units of area. Ecologists deal largely with distributions over a surface, often basing their data on sampling procedures that assume a two-dimensional surface. This assumption can lead to deceptive results if the nature of the surface is not considered. An irregular surface can greatly increase the area present, and to the extent the surfaces sampled depart from the horizontal they will be under-represented or density will be exaggerated. This becomes particularly important as the scale of surface variation approaches the scale of the distribution being measured. Comparisons of such values as patterns of distribution and density of surface-distributed forms based on the assumption of horizontal units of area can be misleading unless corrected for the actual surface.

Surface in the Marine Environment

The multiple functions of surface, especially benthic surface, have been particularly apparent in the marine environment. In the fluid environment of the sea a fixed point of attachment is one of the scarcest and most desirable of resources, particularly in the photic zone. For plants, it permits a stable location and orientation with respect to the incoming light energy. For animals, attachment can mean improved uptake of materials and disposal of wastes without an extra expenditure of energy. Attachment requires substratum, and the more substrate surface available, the greater the potential efficiency of the system in utilizing the energy available in light and water motion. The increased surface generated by the form of the organism becomes equally important, involving a dynamic evolutionary balance between the advantages of increased surface (light absorption, feeding, materials exchange, etc.) and the disadvantages (increased drag, need for structural support, vulnerability, etc.). The functional significance of algal surfaces has recently been described by Neushul (1972). Organism surfaces, in turn, add to the supply of available substrata.

It is no wonder that Connell (1972) has referred to space in such an environment as "the essential resource". Dayton (1971) has demonstrated for one benthic marine habitat, the rocky intertidal, that substrate space is potentially the most important limiting resource, with its utilization controlled by a combination of physical and biological disturbances. Dayton also distinguishes between primary space, the original substratum, and secondary space on organisms attached to the substratum.

Den Hartog (1972), as part of a general discussion of the qualitative importance of substratum (in Kinne, 1972), recently reviewed evidence from temperate marine environments for the importance of substrate topography in benthic plant distribution. He also lists various influences of plants on the substratum, including the hastening or controlling of erosion, and the binding of sediment particles. In the same work, Zobell (1972) states that the densest microbial populations occur on solid substrata.

The Surface of Coral Reefs

In the light of this fundamental importance of surface, the generation by the coral-reef ecosystem of its own substratum takes on an increased significance. The complex reef morphology illustrates the tendency of both organisms and communities under persistent favorable conditions to increase the amount and utilization of surface. The production, occupation, and destruction of surface area are, therefore, basic reef processes, and the balance between them is an essential aspect of the reef ecosystem. The efficient production of surface is a primary function of many reef organisms, and the control of surface by secondary occupants is a basic competitive force and a major determinant of reef communities. Indeed, Dayton's (1971) distinction between primary and secondary space blurs on a coral reef, where organisms often occur in many layers and the substratum itself is organism-generated. The highly porous structure of reefs provides many internal surfaces; the discussion here is restricted to external surfaces, since they are of primary significance to benthic algae.

There have, of course, been frequent references to the importance of surface area on a coral reef, but for lack of quantification this has not always been well understood. Odum and Odum (1955) gave reef biomass per area of horizontal plane covered, but noted that this was much less than the actual surface of the irregular object. Similarly, their chlorophyll values were for horizontal unit areas (because they were perpendicular to the sun's rays), disregarding the absorption of reflected light by other surfaces. For bacterial estimates, they assumed the surfaces of all reef objects to be only three times the horizontal area in complex zones.

Several studies of the standing crop and species diversity of reef fishes have noted the effect of the great sculpturing of the reef and the resulting increased surface on fish populations (Bardach, 1959; Randall, 1963; Talbot, 1965). Randall, in particular, commented on the problem of error introduced in giving fish density and diversity per unit of horizontal area, but concluded that the area of so complex a surface would be difficult to estimate with accuracy. Kohn (1967) used subjective estimates of the heterogeneity and topographic complexity of the reef substratum to estimate the role of habitat complexity in fostering species diversity. More recently, Risk (1972), in another study of fish diversity, attempted to quantify habitat complexity through estimates of surface area based on linear measurements, but while his method of calculation is not fully explained, his values of up to a hundred times the horizontal area seem very high for the types of measurement used.

Marsh (1970) fitted aluminium foil to his coralline algal crusts and then weighed the fitted foil to get surface area values. The technique is only practical, however, for rather simple forms of a reasonable size.

Surface Estimation by Approximation

In approaching the quantification of a complex surface, several factors need to be considered, including the practicality of various types of field methods or data collection, the precision required, the scale of the features of interest, and the units in which the results are to be expressed. As will be apparent in the specific example below, field conditions and the nature and size of the objects can greatly restrict the types of measurements that will be possible. However, absolute accuracy is almost never required, particularly when the areas themselves are so highly variable. What is needed initially is a meaningful basis for comparisons and generalizations, and this can usually be achieved with a careful approximation. The process is much like that used in integral calculus where accuracy is obtained through infinitesimals, reducing the size of each step in the approximation until significant error disappears. For a biological surface or substratum, a geometric approximation of known area can usually be developed to the required level of accuracy. Odum *et al.* (1958) used simple geometric approximations (plates, cylinders, cones) to estimate the surface-volume ratios of several algae. Here, more complex shapes such as those on a reef have been constructed as conservative estimates of actual reef forms; refinements can easily be incorporated as necessary.

Another factor to be considered in quantifying surface is the element of scale. There are multiple levels of surface features depending on the scales at which they are considered. The earth, at one scale a smooth sphere, includes mountains which have boulders covered with microscopic ridges, and so on. The scale of surface variation becomes significant when it approaches the scale of the phenomenon being measured. Surface area is, thus, a relative measure depending on the scale considered. The benthic surface area of significance to a large organism will be different from (and far less than) that important to bacteria. It is possible to simplify a surface-measurement problem by breaking it down into a series of scales which can be treated independently.

Surface variations can conveniently be expressed by means of a surface index (SI), which is here defined as the ratio of the actual surface to that of a plane with similar boundaries, giving a dimensionless number (Stahl, 1962) useful for comparative studies. If a surface has 6 m^2 of area within the limits of 1 m^2, its SI would be 6. The SI, then, measures the amount of surface increase over that of a plane. An SI can be calculated for each significant scale of surface variation, and these are then multiplied to give a total SI for the area being measured.

A consideration of several theoretical surfaces can help to illustrate a number of features of surface estimation. In Fig. 1, SI's are given for surfaces with cubes, papillae, and square, triangular, and curved ridges. Note that the cubes double the amount of surface present, and that there is no difference between the cubed surface and the square ridges of the same size. By comparing a variety of such theoretical surfaces, it becomes apparent that the height of the surface features and their frequency are the most important determinants of the surface index. This can also be demonstrated mathematically. A sinusoidal curve, described analytically by the equation

$$y = a \sin\left(\frac{x\pi}{2p}\right), \tag{1}$$

where a is the amplitude, and p is the periodicity of the curve, can be extended into a third dimension to make a surface of width w (Fig. 2). Using the formula for a

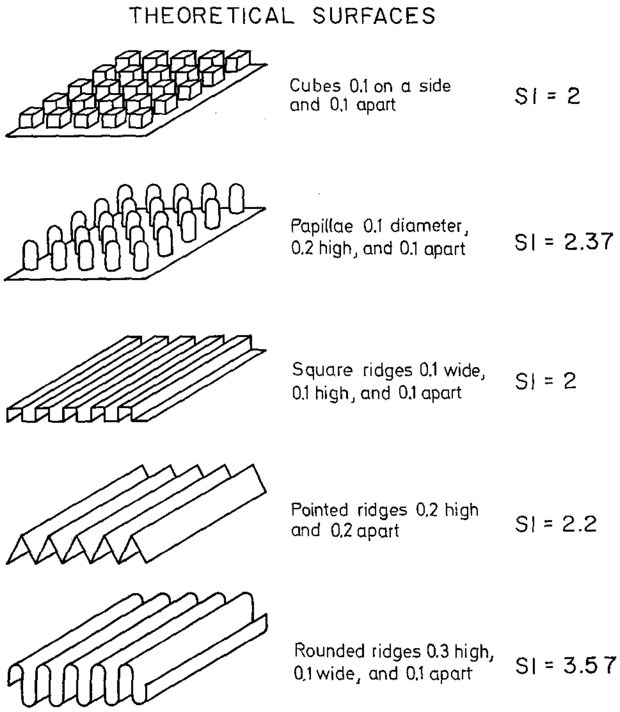

Fig. 1. Theoretical surfaces consisting of cubes, papillae, and various forms of ridges, with proportional dimensions and surface index (SI) for each type

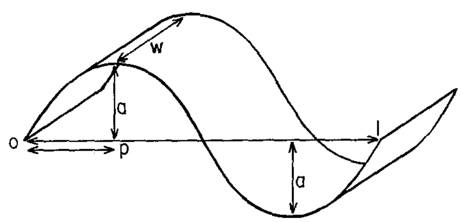

Fig. 2. Sinusoidal surface, with period p, amplitude a, width w, and length l along curve from point of origin o indicated

surface area (Kaplan, 1953), one can show that the area of the above surface is

$$\frac{2w\,l}{\pi}\int_0^{\pi/2}\sqrt{1+\frac{(a\pi)^2}{4\,p^2}\cos^2 v\,dv}\,. \qquad (2)$$

The important point to note in this surface equation is that the ratio $a:p$ increases as the overall area increases, and conversely. Thus, for surfaces of this type it is possible to approximate the area by employing this ratio and the horizontal dimensions. The length along the surface from "o" to "l" (Fig. 2) is the most difficult dimension to calculate, but both this and the height and frequency are relatively easily determined in the field. A transect line laid across the tops of the surface features can give frequency (from interceptions or near interceptions with the line) and height (by measuring vertically down from the line between interceptions). For length along the surface, Risk (1972) simply fitted a chain to the surface in a line across his quadrats, and then measured the length of chain used.

Quantification of Benthic Algal Substratum

These approaches to surface-area quantification have been used to estimate the substratum available for benthic macro-algae on a section of the British Honduran barrier reef near Carrie Bow Cay (16°47′ N; 88°05′ W), as a first step in the quantification of the benthic plant populations. Data were collected along a transect extending from the lagoon bottom inside the reef to the reef crest (Fig. 3). The same transect is being used for a variety of coral-reef ecology studies as part of a Smithsonian Institution program of Investigations of Marine Shallow-Water Ecosystems (IMSWE).

The transect was first surveyed using techniques developed earlier (Dahl, 1972), to provide a description of the reef structure along the line, and to give a rough estimate of the percent coverage of the major distinguishable algal components (Fig. 3). Calculations were then made of the surface area available for each zone or substrate type, at the scales significant to macroscopic benthic algae. Methods varied from direct measurement to theoretical approximation, depending on the types of measurements or sampling possible in the field. The results for each category of substratum are given below.

Thalassia Zone

The *Thalassia* zone (Fig. 4) consisted of a sand bottom covered with plants of *Thalassia testudinum* (density 360/m^2) and scattered *Syringodium filiforme* (80/m^2), with the plant density decreasing seaward. All of the plants in an area of 0.05 m^2 were cut off at the sand surface and measured for length and width of blade and length of each blade densely covered by epiphytic algae. These measurements gave an estimated surface-area contribution from the sea grasses of 3.7 m^2/m^2, of which 1.8 m^2 was occupied by epiphytic algae (the unoccupied area largely comprising young blades and the basal portions of mature blades). Since the sand was too fine and unstable to serve as an algal substrate (for other than unicellular forms) its area contribution was considered as 1 m^2/m^2 for a total surface area in the main part of the *Thalassia* zone of 4.7 m^2/m^2 (SI = 4.7). If microbial populations were being considered, the sand-grain surfaces would, of course, be highly important.

Of this total substratum, only the sea-grass blades provide suitable attachment for macroscopic algae, and of this total area of 3.7 m^2, only 1.8 m^2 of the older

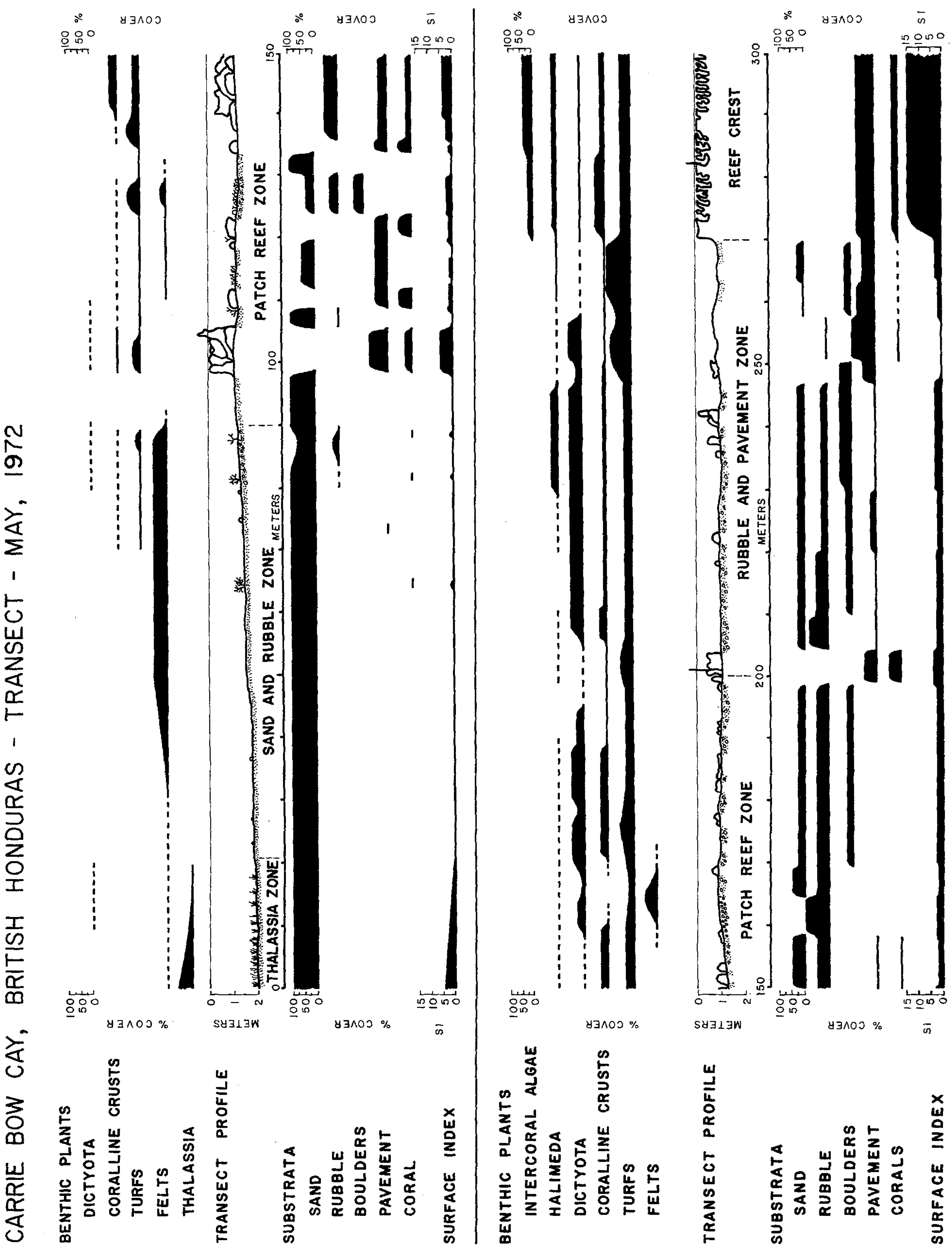

Fig. 3. Transect profile from lagoon bottom to reef crest on the barrier reef near Carrie Bow Cay, British Honduras, showing area coverage of the major plant and substrate types and surface index (SI)

Fig. 4. Lagoon floor in *Thalassia* zone at depth of 2 m, showing density of *Thalassia* and *Syringodium* along transect

Fig. 5. Pieces of coral rubble and associated algae typical of the sand and rubble, patch reef, and rubble and pavement zones

blade surfaces were actually occupied by epiphytic turfs and crusts.

Because of the highly variable nature of the *Thalassia* population, larger samples and repeated sampling in space and time would be necessary to get averages or seasonal extremes of surface.

Sand and Rubble Zone

The substratum in this area, extending along 80 m of the transect, consisted of sand, with scattered chunks of coral rubble toward the seaward end (Fig. 5). To determine the contribution of the rubble to the surface area in this zone, all pieces were collected from a

0.25 m² quadrat near the seaward end of the zone. Each piece was measured, and its area calculated by geometric approximations, using combinations of simple shapes (spheres, cylinders, cones, rectangles, etc.) appropriate to the rubble form, and disregarding cylinder ends and cone bases in calculating area. For each piece of rubble, this gave a conservative approximation of its area. Overall rubble dimensions were also taken for size-class estimates.

Reef Crest and Patch Reefs

For the more complex structure of the reef crest (Figs. 6 and 7) and patch reefs, a theoretical reef surface was constructed to approximate the actual reef features (Fig. 8). The channels, roughly 1 m deep, that passed through the reef crest were represented by a grooved surface (SI = 1.57) of similar dimensions at Scale I (Fig. 8), the largest scale to be considered. At the somewhat smaller Scale II, the variety of corals

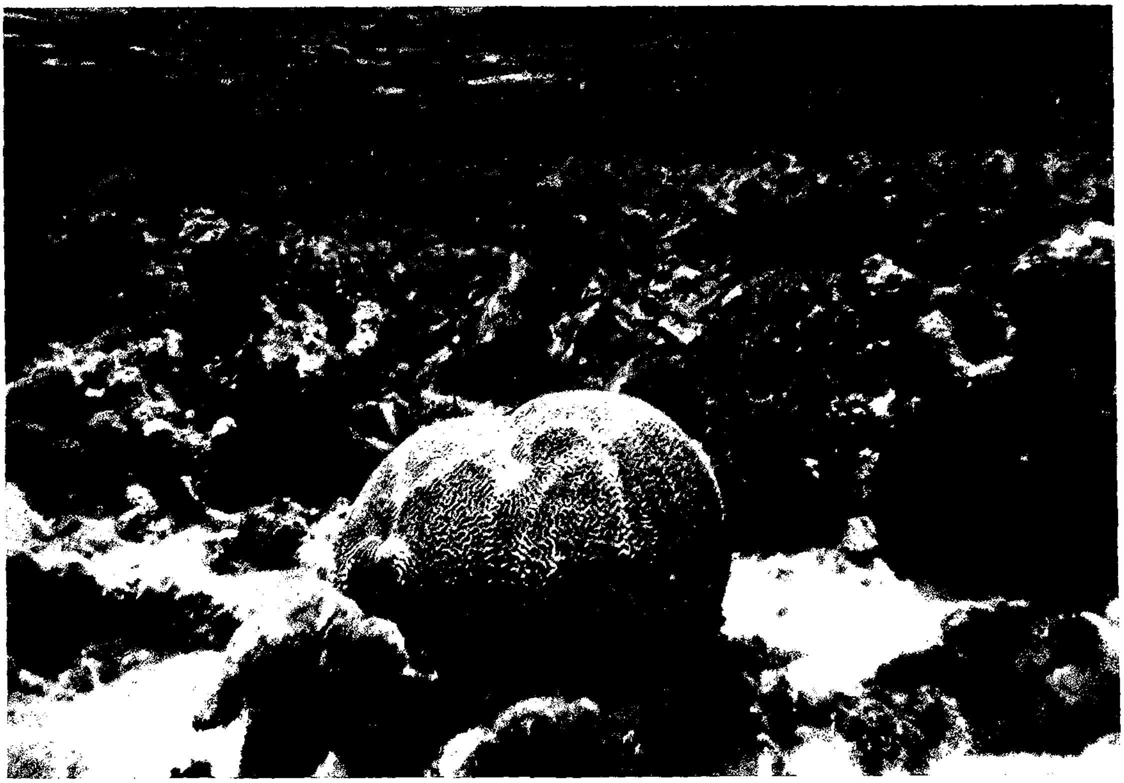

Fig. 6. Back of reef-crest area as viewed from rubble and pavement zone, showing the 1 m high relief and diversity of surface morphologies

Rubble densities of about 100 pieces/m² were observed in this area, with a total surface area of 0.16 m². Halving this, to allow for surface buried in the sand, gives 0.08 m² of additional surface per m², for a total SI = 1.08. The rubble is the only relatively firm substratum in the zone.

Further towards the reef crest, between the patch reefs and in the rubble and pavement zone, the rubble was both larger and more abundant (800 to 900 pieces/m²), with a total surface of nearly 3 m²/m². Allowing for buried surface, a conservative estimate would be SI = 2 to 2.5 in these areas. Most of this rubble was covered by a fine algal turf and crustose corallines.

on and between the ridges were approximated by scattered hemispheres (for the solid and encrusting corals, SI = 1.4), thin ridges (*Agaricia* and *Millepora* spp., SI = 5.6), and branched cylinders (*Acropora palmata*, SI = 3), in percentages roughly that of their area coverage in the field, with the remaining area unoccupied by corals considered to have no relief (SI = 1) at this second scale. Since the surface texture of the corals resulting from the polyp cups adds a third scale of surface, significant for the smaller algal turf forms, geometrical models of polyp cups were created, one of which is shown in Fig. 8. This consists of an inverted cone, 10 mm in diameter, lined with 20 semi-circular plates, giving an SI = 5.25; other

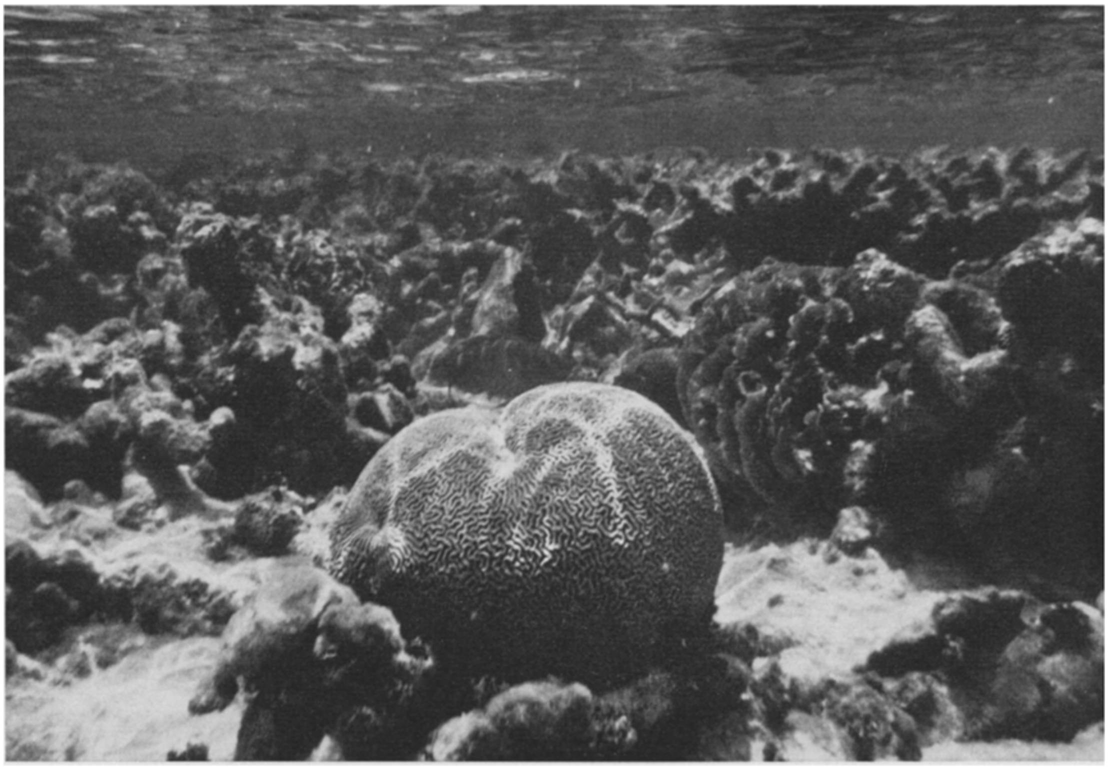

Fig. 7. Center of reef-crest area, with a large branching *Acropora palmata* and various solid and plate-like forms

Table 1. *Estimates of the area covered by benthic algae for each zone along the Carrie Bow barrier-reef transect, giving for each zone the measured width and linear percentage of the zone along the transect, the surface index (SI), the surface area of each zone within a 1 m-wide transect, the percentage of the total area this represents, the estimated area covered by algae, the occupied SI for algae (or the coverage of algae in m^2 per horizontal m^2), and the types of algae found in each zone*

Zone	Width (m)	Linear %	Average SI	Surface area in 1 m-wide transect (m^2)	Area %	Algal coverage (m^2)	Algal occupied SI	Types of algae
Thalassia	20	7	3.5	70	7	24	1.2	Epiphytic turf on *Thalassia*
Sand and rubble	70	23	1	71	7	31	0.4	Light filamentous "felt" on sand; some turf on rubble
Patch reef	110	37	2.5	271	27	167	1.5	Turf on coral rock and rubble; light "felt" and *Dictyota* on sand and rubble
Rubble and pavement	70	23	1.9	136	14	132	1.9	Turf on coral rock and rubble; *Dictyota, Halimeda,* and blue-green algae on sand and rubble
Reef crest	30	10	15	450	45	120	4	Turf, crustose corallines, and many larger algae
Totals	300	100		998	100	374		

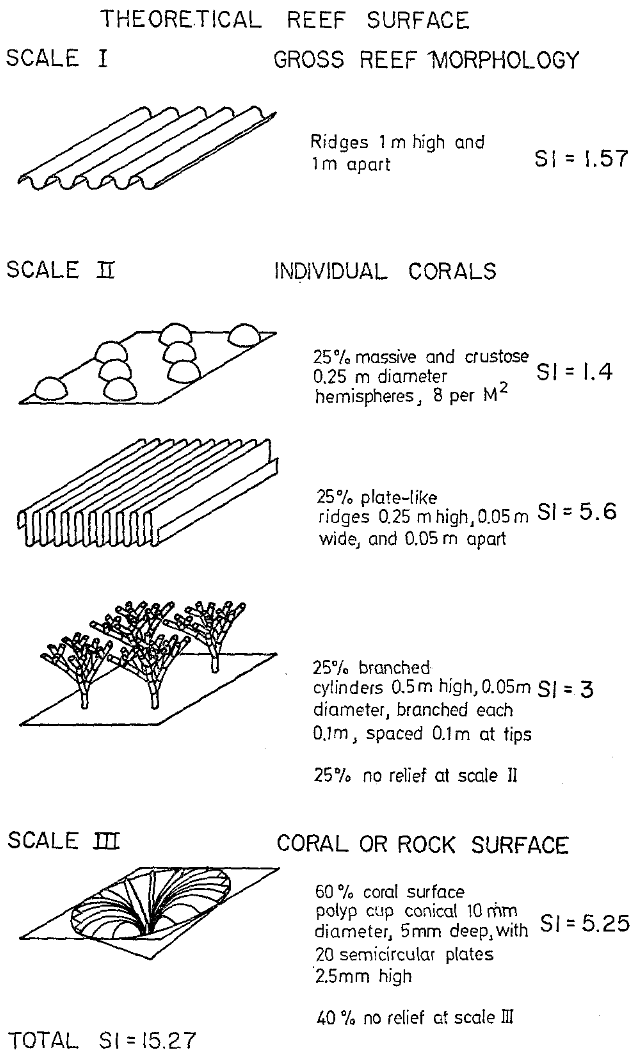

Fig. 8. Elements in the construction of a theoretical reef surface, showing 3 scales of surface features, percentages of different surface types, and dimensions from which the surface index (SI) for each type was calculated. The total SI is the product of all the surface indices at their appropriate percentages and scales

polyp-cup simulations gave similar SI values. Of the total surface at Scale III, 50% was considered to be covered by living coral, and another 10% by recently dead coral, giving 60% of the surface with an SI = 5.25. Multiplying each SI by its percentage, and then multiplying all the SI values at each scale gave a total SI = 15.27. In other words, each square meter of reef crest includes about 15 m^2 of surface (conservatively estimated). Since living coral cover was estimated at 50% of the area (before adding the contribution of Scale III), the amount of surface available for benthic macro-algae equals approximately 4 m^2 out of the total of 15 m^2 available in each horizontal square meter of the reef crest.

For the patch reefs, similar surface indices were used, but the percentages of the Scale-II forms and the percent living coral at Scale III were adjusted to approximate actual conditions in the patch reefs (SI = 4 to 6).

Combining these surface-area estimates with the transect data giving the percent of the difference substrate types and the major algal associations, it is possible to project the amounts and percentages of substrata in each zone and the total substrate area occupied by algae (Table 1).

A number of comments and cautions about these figures are in order. The *Thalassia* zone continues far into the lagoon beyond the transect; the 20 m included here represent the margin of greater significance to reef grazers. Since data from only a single transect are included, and these include many subjective estimates of the percent coverage of algae or substrata, not to mention the approximations involved in deriving the surface indices, the possibilities of error are very great. Measurements in the reef crest are probably the least reliable at present. None of this, however, detracts from the significance of the magnitude of surface increases involved, since the estimates on which these are based are very conservative.

Given these reservations, what is the significance of such surface measurements with respect to benthic algae? The amount of area covered by algae tends to increase from the lagoon to the reef crest, except where the substratum is largely sand. The trend in biomass would be even greater, since more of the area toward the reef crest is occupied by large fleshy algae. The total area covered is somewhat larger than the horizontal plane area of the transect, while the total substrate area is more than 3 times greater, and this is only at scales significant to benthic algae. The estimate of up to 3 times the horizontal area for surfaces of bacterial significance made by Odum and Odum (1955) would appear to be a considerable underestimate, unless the Eniwetok reef flat has much less relief than that in British Honduras.

The figures for algal cover do not, of course, begin to measure all the components contributing to primary productivity. *Thalassia* blades were considered here as a substratum, and algal surfaces occupied by epiphytes were ignored, not to mention the endolithic algal and zooxanthellae. The actual productive surface is probably much closer to the total exposed surface, including the surfaces of all the algae and coral polyps.

Discussion

The concepts of surface area as an ecologically significant parameter, and of the surface index (SI) as a measure of that parameter, are only developed here in a rudimentary form. For various common surface types or shapes, it should be possible either to develop constants by which one or two simple measurements such as height and frequency, or surface length need be multiplied to give the SI, or to prepare tables from which the SI or actual area could be found if the size of the features are known. If the SI is determined for each of the common species at a site, total coral surface could then be derived from a quantitative species measure such as coverage along a transect. The same can be done for other surface forms or groups of organisms. Calculations can also be made for a more detailed breakdown of surface forms, improving precision to whatever extent is necessary.

Once the surface area present has been measured, it can be subdivided or classified on some ecological or functional basis, using parameters such as the surface orientation, level of illumination, occupation by certain organisms, or accessibility to types of grazers. Subsidiary indices or area measures can be used to describe these subdivisions, such as area potentially available to a species, area actually occupied, and their ratio, a measure of competitive effectiveness. The leaf-area index (Watson, 1947), in common use in agricultural research, is a specialized surface index for the amount of productive leaf area per unit of ground. Similar indices would be useful in other ecological contexts.

Appropriate surface measures can also serve as quantitative estimates of spatial heterogeneity, which Pianki (1966) has shown to encourage species diversity. Since great spatial heterogeneity generally results in high species diversity, making traditional methods difficult or inappropriate (Greig-Smith, 1964, 1971), a surface-area analysis and classification can provide an alternative or supplementary quantitative ecological approach by accounting for much of the spatial variability.

Once surface areas have been defined and quantified, it may be possible to treat them on a micro-ecological level as "islands" of substrate, using the methods with which MacArthur and Wilson (1967) have analyzed island populations where, on a larger scale, the amount of area and the extent of its isolation are equally important.

Surface measurements and indices can provide a useful basis for comparisons, both directly, and in conjunction with other measures. Indeed, such comparisons can be made between organisms, communities, or entire systems. What, for instance, are the comparative surface areas or SI's for coral reefs, temperate-shore communities, rain forests, or grasslands, and what might such comparisons say about the efficient utilization of incident radiant energy and other factors? Ratios such as surface area:biomass or surface area:chlorophyll might also be instructive.

For a coral reef, SI or surface-area comparisons can be made within a reef zone, between zones, with other reefs, or with the same reef over time. Since the surface area of a reef is related to the efficiency with which it can utilize certain basic resources, this may prove to be a useful measure of the health of a reef ecosystem; a decrease in surface over time, or a change in the proportions of surface at different scales could signal a decline in environmental quality. For any comparative purposes, however, measurement and computation techniques and scales of features included need to be carefully standardized and explicitly stated.

As surface quantification techniques are refined and more surface data becomes available, it should be possible to approach the quantitative understanding of coral reefs and other ecosystems from a new direction, complementing other techniques now in use. Such an approach to structural analysis can provide a basis, however preliminary, on which small-scale measures of productivity, biomass, etc., can be more accurately projected to give values for the whole community or whole ecosystem. Surface analysis can also contribute to a better understanding of energy and material flows, species diversity and distributions, and other aspects of ecosystems. Hopefully this will lead to a clearer picture of the evolutionary processes that have produced the fantastic diversity of shapes and forms that together comprise a biological community.

Summary

1. Surfaces have a functional significance for many biological and ecological processes.

2. Quantification of surface areas can help to quantify fundamental aspects of the ecosystem.

3. A surface analysis can be particularly useful in studying coral reefs, where the morphological complexity makes other quantitative techniques largely unworkable. The production, occupation and destruction of surface are fundamental reef processes.

4. Complex surface areas can be estimated by selected measurements and theoretical approximations.

5. Different scales of surface features can be analyzed independently and then combined for an estimate of total surface.

6. A surface index (SI) can be used to express the amount of increase in surface area over that of a similarly bounded plane.

7. Simple field measurements such as frequency, height, and length along the surface can be used to estimate the surface area present.

8. For one reef area off British Honduras, the substrate area in the reef crest was more than 15 times that of a horizontal plane.

9. The average benthic algal coverage alone was greater than the horizontal plane area of a reef transect.

10. Surface measurements can provide a useful parameter for comparative studies in ecology.

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Literature Cited

Bardach, J. E.: The summer standing crop of fish on a shallow Bermuda reef. Limnol. Oceanogr. **4**, 77—85 (1959).
Connell, J. H.: Community interactions on marine rocky intertidal shores. A. Rev. Ecol. Syst. **3**, 169—192 (1972).
Dahl, A. L.: Development, form and environment in the brown alga *Zonaria farlowii* (Dictyotales). Botanica mar. **14**, 76—112 (1971).
— Ecology and community structure of some tropical reef algae in Samoa. Proc. int. Seaweed Symp. **7**, 36—39 (1972).
— Biological proportions. Science, N. Y. **181**, p. 469 (1973).
Dayton, P. K.: Competition, disturbance, and community organization. The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. **41**, 351—389 (1971).
Den Hartog, C.: Substratum; plants — multicellular plants *In:* Marine ecology, Vol. 1. Pt 3. pp 1277—1289. Ed. by O. Kinne. London: Wiley-Interscience 1972.
Greig-Smith, P.: Quantitative plant ecology, 2nd ed. 268 pp. London: Butterworths 1964.
— Application of numerical methods to tropical forests. *In:* Statistical ecology, Vol. 3. pp 195—204. Ed. by G. P. Patil, E. C. Pielou and W. E. Waters. University Park, Pa.: Pennsylvania State University Press 1971.
Horn, H. S.: The adaptive geometry of trees, 155 pp. Princeton: Princeton University Press 1971.
Jahnke, L. S. and D. B. Lawrence: Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. Ecology **46**, 319—326 (1965).
Kaplan, W.: Advanced calculus, 679 pp. Cambridge, Mass.: Addison-Wesley 1953.
Kinne, O. (Ed.): Marine ecology. Vol. 1. Environmental factors, Pt 3. 529 pp. London: Wiley-Interscience 1972.
Knight, D. H.: Leaf area dynamics of a shortgrass prairie in Colorado. Ecology **54**, 891—896 (1973).
Kohn, A. J.: Environmental complexity and species diversity in the gastropod genus *Conus* on Indo-West Pacific reef platforms. Am. Nat. **101**, 251—260 (1967).
MacArthur, R. H. and E. O. Wilson: The theory of island biogeography, 203 pp. Princeton: Princeton University Press 1967.
Marsh, J. A., Jr.: Primary productivity of reef-building calcareous red algae. Ecology **51**, 255—263 (1970).
McMahon, T.: Size and shape in biology. Science, N. Y. **179**, 1201—1204 (1973).
Monteith, J. L.: Light distribution and photosynthesis in field crops. Ann. Bot. (N.S.) **29**, 17—37 (1965).
Neushul, M.: Functional interpretation of benthic marine algal morphology. *In:* Contributions to the systematics of benthic marine algae of the North Pacific, pp 47—73. Ed. by I. A. Abbott and M. Kurogi. Kobe, Japan: Japanese Society of Phycology 1972.
Odum, E. P., E. J. Kuenzler, and M. X. Blunt: Uptake of P^{32} and primary productivity in marine benthic algae. Limnol. Oceanogr. **3**, 340—345 (1958).
Odum, H. T.: Efficiencies, size of organisms, and community structure. Ecology **37**, 592—597 (1956).
— and E. P. Odum: Trophic structure and productivity of a windward coral reef community. Ecol. Monogr. **25**, 291—320 (1955).
Pianki, E. R.: Latitudinal gradients in species diversity: a review of concepts. Am. Nat. **100**, 33—46 (1966).
Randall, J. E.: An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. Caribb. J. Sci. **3**, 31—47 (1963).
Risk, M. J.: Fish diversity on a coral reef in the Virgin Islands. Atoll Res. Bull. **153**, 1—6 (1972).
Stahl, W. R.: Similarity and dimensional methods in biology. Science, N.Y. **137**, 205—212 (1962).
Talbot, F. H.: A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa) and its fish fauna. Proc. zool. Soc. Lond. **145**, 431—470 (1965).
Watson, D. J.: Comparative physiological studies on the growth of field crops. 1. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. Ann. Bot. (N. S.) **11**, 41—76 (1947).
Zobell, C. E.: Substratum; bacteria, fungi and blue-green algae. *In:* Marine ecology, Vol. 1. Pt 3. pp 1251—1270. Ed. by O. Kinne. London: Wiley-Interscience 1972.

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