Generation of Photosynthetic Surface Area by Coral Reef Algae[1]

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Introduction

The quantification of surface area has proven to be a useful approach to the greater understanding of surface-mediated processes in complex ecosystems such as coral reefs (Dahl, 1973). For plants in particular, it is through surfaces that light is absorbed for photosynthesis and materials exchanged with the surrounding medium, whether gaseous or aquatic. Attachment also requires surface, and in highly productive and mature benthic ecosystems, the generation of substratum is an evolutionary strategy permitting an increase in organism density and diversity.

If a coral reef is viewed as a surface-generating system, it becomes apparent that there is a tendency toward the maximization of surface within the constraints of physical and structural forces. This seems logical, given the importance to the system of the absorption of light energy for photosynthesis, the entrapment of dissolved and particulate matter and plankton for energy and materials, and the release of waste products, all of which are surface-mediated processes. The principal constraint is the need to support the surface and to maintain the integrity of the organism against the force of waves and currents in the most economical fashion. This can be done either with a rigid structure capable of withstanding the external forces, or a pliable form able to adapt to paths of least resistance, or some combination of the two. It is within this basic evolutionary framework that the multiplicity of reef organisms have evolved and developed their own complex patterns of interaction and interdependence.

This paper discusses one dimension of the overall problem of reef surface, that of the "photosynthetic surface", the surface through which light energy is absorbed into organisms and utilized, and in particular the contribution of benthic algae to photosynthetic surface generation. At this point, only external organism surfaces will be considered. Ultimately, it might prove useful to analyze the surface area of cells, plastids, or even thylakoids.

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Methods

The technique used here to estimate the area of a complex form utilizes a combination of simple measurements and geometric approximations at various scales of surface feature (Dahl, 1973). The result is best expressed as a Surface Index (SI), the ratio between the actual area and that of a similarly-bounded plane. This approach accords well with the limitations on obtaining detailed measurements in the field, yet can be developed to any desired level of accuracy much as a curve is integrated mathematically.

The question of accuracy is one frequently raised when approximations are used. In fact, the percent difference in surface area between an irregular form and an appropriate geometric equivalent is usually quite small, and well within the range of error of most initial measurements. For example, an oblate spheroid created by rotating an elipse around its minor axis will have a surface S given by the formula,

$$S=2\pi a^2+\pi\, b^2/e \log e\ 1+\varepsilon/1-\varepsilon$$

where a =major semiaxis, b =minor semiaxis, and ε=eccentricity. For a=5 cm, b=3 cm, and ε=0.8, the surface area is 234.7 cm^2. If, as a very crude approximation, one averaged the maximum and minimum dimensions and determined the area of a sphere of equivalent diameter (8 cm), the resulting area is 201 cm^2, a 17 percent error. Three measurements at right angles (10, 10, and 6 cm) averaged (8.67) give a sphere surface of 236.0 cm^2, reducing the percent difference to 0.5 percent. Similarly, if one takes surfaces generated by sinusoidal curves extended into a third dimension, and approximates then with ridges constructed from flat plates or half cylinders, the error of the approximation is in the 2 to 7 percent range.

Algal Form and Surface

For an alga on a coral reef, the form it will take over evolutionary time will be determined by the following factors: the potential of its developmental system, the physical factors in its particular niche, the requirements for survival from competition and predation, and its capacity to maximize light absorption at an efficient yet safe level under the conditions of illumination available to it. There are more general options available, such as between low specialization with high productivity generally leading to high turn over and often low biomass or standing stock, and high specialization and biomass but generally lower productivity. Before the diverse strategies of algal form can be properly understood, these factors need to be analyzed and quantified where possible. Since the amount of light absorbed is dependent on the area illuminated and the angle of incidence, the measurement and characterization of algal surfaces provides a useful step towards an understanding of the comparative significance of algal forms.

The contribution of benthic algae to the functional surface area of a coral reef can be roughly estimated by determining the surface indices (SI) for the predominant species or association and then combining these in a reconstruction of the basic reef community to calculate their significance to the whole system.

One of the most ubiquitous yet visually insignificant benthic algal components is the turf of small filamentous forms that carpets most reef surfaces not occupied by benthic animals (Dahl, 1972). An average small turf can be simulated with unbranched cylinders 3 mm high and 0.5 mm in diameter at a density of $100/cm^2$. Each filament would have a surface area of 4.7 mm^2, giving a total SI=5.5. A larger turf of 10 mm high branched filaments 1 mm in diameter and spaced 2 mm apart at the tips would have a SI=3. For a more dense turf combining the two types, the SI=8.5.

The brown alga *Dictyota* frequently occurs in mats in some reef areas. Its strap-like branched form is easily approximated. A plant 5 mm wide with 2 cm between dichotomies and a length of 10 cm would have a surface (on both sides) of 62 cm^2. If there are two such plants per 100 cm^2 of bottom, the SI would be 2.2; for a more dense mat of 10 plants per 100 cm^2, the SI=7.2.

Halimeda is a widespread coral reef genus. An average species can be simulated with disks 10 mm in diameter and 1 mm thick, branching dichotomously each two disks to a height of 8 disks, giving a surface area of 57 cm. A cluster of 10 plants in a 100 cm^2 area gives a SI=6.7. For a densely-growing form like *H. opuntia* where the surface density of the disks might be $5/cm^2$, even if only the two most distal disks on each branch are considered to be photosynthetically functional, the SI=19.

An alga like *Caulerpa racemosa* is readily duplicated with cylindrical stolons and erect branches topped with clusters of spheres. A small form with stolons 2 mm in diameter and a total length for stolons and branches of 400 mm in a 100 cm^2 area, with 10 branches each bearing 5 spheres 5 mm in diameter, would have an area of 64 cm^2 and a SI=1.64. A large plant with stolons 3 mm in diameter and 400 mm long, and 6 erect branches each 200 mm long bearing 15 spheres 7 mm in diameter and occupying 100 cm^2 of bottom, would have an area of 174 cm^2 and a SI=2.74.

A small branched coralline alga like *Jania* 0.5 mm in diameter and branching each 2 mm to a total height of 10 mm would have a surface area of 49 mm; at two plants per cm^2, the SI=2. A larger plant like *Amphiroa* 1 mm in diameter and branching each 5 mm might have a SI=3.2 if part of a browsed-over mat 15 mm high, or a SI=7.43 for plants 50 mm high at a density of $4/100\ cm^2$.

Reef Photosynthetic Surface

Surface estimates for individual algal types can be combined with those for other reef features to derive an estimate for the total photosynthetic surface of any part of the reef. Take, for example, a typical buttress area on the barrier reef off Belize (British Honduras) in the vicinity of Carrie Bow Cay. In this area just outside the reef crest, the dominant structures are perpendicular ridges or buttresses built largely by the coral *Agaricia*, rising about 5 m off the bottom from a maximum depth of 10 m, with a 5 m width and spaced about 5 m apart (SI=1.57 for this large scale of feature). About 75 percent of the buttress surface is covered by *Agaricia* (wedge-like plates 15 cm high and 3 cm apart, SI=10), and on about half the surface, the interstices between the *Agaricia* plates are filled with dense algal populations which can be approximated as follows:

20% *Halimeda opuntia*	SI=18
10% *Dictyota*	SI= 2
20% *Amphiroa*	SI= 7
10% small *Caulerpa racemosa*	SI= 1.6
40% dense turf	SI= 8
Total algal	SI= 8.56

Multiplying each SI by its percent occurrence and then summing gives a SI=11.5 for the second scale of features. Since hermatypic corals contain zooxanthellae and are therefore themselves photosynthetic entities, the surface of the polyps should be considered as an additional scale of feature. If about 50% of the coral surface (20% of the total surface) is covered by polyps having, in a typical simulation, a SI=3.2, giving a total SI at this scale of about 1.4, then the total SI for all three scales is about 26, meaning that for each horizontal square meter in this buttress area there are about 26 m^2 of surface (for details, see Table 1).

Table 1. Carrie Bow buttress zone, Surface Index (SI) calculations.

Scale I		
Buttresses		SI=1.57
Scale II		
75% *Agaricia*, SI=10	7.5	
Algae, SI=8.56, minus 1 for *Agaricia* substratum included above, at 50% cover	3.78	
25% no relief at Scale II	.25	
Total SI at Scale II	11.53	11.53
Scale III		
20% polyps, SI=3.2	.64	
80% no relief of Scale III	.8	
Total SI at Scale III	1.44	1.44
Total SI for buttress zone		26.07

Table 2. Carrie Bow buttress zone, photosynthetic surface.

	SI	%
Living coral (Scale II)	5.88	
plus polyps (Scale III)	7.97	
Total living coral	13.85	53
Algae	5.97	23
Total photosynthetic surface	19.82	76
Remainder	6.25	24

It is then possible to subdivide this total surface index to determine the amount of photosynthetic surface (Table 2). Approximately half the total surface at these scales is contributed by living corals, with another quarter from algae, so that about three quarters of the total surface can be considered photosynthetically active (about 20 m^2 per horizontal m^2). The remaining quarter consists largely of sand, rock, and non-photosynthetic animals.

While these estimates are obviously rather crude, with many possibilities for error, they do provide a logical basis for understanding the possible photosynthetic significance of particular reef or plant forms. Also, since these are average figures for the whole buttress zone, the amount of surface in a dense coral and algal clump would be rather higher.

A logical further step in analyses of this type would be to combine surface area quantification of the different components of a community with biomass and productivity measurements, leading to an understanding of the photosynthetic efficiency of different morphologies or organism combinations. The relation of particular forms to the photosynthetic dynamics of both plant and light movement, and the question of maximum photosynthetic rates versus maximum energy utilization, also require exploration. Ultimately, this should result in a clarification of the evolutionary forces determining plant form, and in more accurate and realistic measures of photosynthetic productivity.

References Cited

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