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Coral geometry and why it matters

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Clonal organisms like reef building corals exhibit a wide variety of colony morphologies and geometric shapes which can have many physiological and ecological implications. Colony geometry can dictate the relationship between dimensions of volume, surface area, and length, and their associated growth parameters. For calcifying organisms, there is the added dimension of two distinct ~~material~~ components of growth: biomass production and calcification. For reef building coral, basic geometric shapes can be used to model the inherent mathematical relationships between various growth parameters and how colony geometry determines which relationships are size-dependent or size-independent. Traditionally assumed to be size-independent, linear extension rates can vary as a function of colony size by virtue of its geometry (even with a constant calcification rate). Whether the ratio between mass and surface area remains constant or changes with colony size is the determining factor. For some geometric shapes, the coupling of biomass production (proportional to surface area productivity) and calcification (proportional to volume) can cause one aspect of growth to geometrically constrain the other. The nature of this relationship contributes to a species' life history strategy and has important ecological implications. At one extreme, thin diameter branching corals can maximize growth in surface area and resource acquisition potential, but this geometry requires high biomass production to cover the fast growth in surface area. At the other extreme, growth in large, hemispheroidal corals can be constrained by calcification. These corals grow surface area relatively slowly and may retain a surplus capacity for biomass production which can be allocated towards other anabolic processes. For hemispheroidal corals, the rate of surface area growth rapidly decreases as colony size increases. This ontogenetic relationship underlies the success of microfragmentation used to accelerate restoration of coral cover. However, ontogenetic changes in surface area productivity only applies to certain coral geometries where surface area to volume ratios rapidly decrease with colony size.

1 Coral geometry and why it matters

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16

17 Abstract

18   Clonal organisms like reef building corals exhibit a wide variety of colony morphologies and
19 geometric shapes which can have many physiological and ecological implications. Colony
20 geometry can dictate the relationship between dimensions of volume, surface area, and length,
21 and their associated growth parameters. For calcifying organisms, there is the added dimension
22 of two distinct material components of growth: biomass production and calcification. For reef
23 building coral, basic geometric shapes can be used to model the inherent mathematical
24 relationships between various growth parameters and how colony geometry determines which
25 relationships are size-dependent or size-independent. Traditionally assumed to be size-
26 independent, linear extension rates can vary as a function of colony size by virtue of its geometry
27 (even with a constant calcification rate). Whether the ratio between mass and surface area
28 remains constant or changes with colony size is the determining factor. For some geometric
29 shapes, the coupling of biomass production (proportional to surface area productivity) and
30 calcification (proportional to volume) can cause one aspect of growth to geometrically constrain
31 the other. The nature of this relationship contributes to a species' life history strategy and has
32 important ecological implications. At one extreme, thin diameter branching corals can maximize
33 growth in surface area and resource acquisition potential, but this geometry requires high
34 biomass production to cover the fast growth in surface area. At the other extreme, growth in
35 large, hemispheroidal corals can be constrained by calcification. These corals grow surface area
36 relatively slowly and may retain a surplus capacity for biomass production which can be
37 allocated towards other anabolic processes. For hemispheroidal corals, the rate of surface area
38 growth rapidly decreases as colony size increases. This ontogenetic relationship underlies the
39 success of microfragmentation used to accelerate restoration of coral cover. However,

40   ontogenetic changes in surface area productivity only applies to certain coral geometries where
41   surface area to volume ratios rapidly decrease with colony size.
42
Introduction
44   The colony morphology of clonal organisms varies widely between and within taxa and has
45   many physiological and ecological implications associated with adaptation to environmental
46   conditions (Jackson 1979). For reef building corals, colony morphology has many physiological
47   and ecological implications associated with adaptation to environmental conditions including
48   light, hydrodynamic regime, sedimentation, and subaerial exposure (Jackson 1979; Chappell
49   1980). While many coral species exhibit morphological phenotypic plasticity in response to
50   environmental conditions, their general colony shape is often conserved and can be characteristic
51   within a taxon (reviewed in Todd 2008; Zawada et al. 2019). Coral colony morphology can
52   dictate a coral's internal light regime (e.g., Anthony et al. 2005; Kaniewska et al. 2008, 2014),
53   hydrodynamics and mass transfer (e.g., Hossain and Staples 2019, 2020), and exposure to
54   peripheral processes (Meeters et al. 1997; George et al. 2021). The general geometric shape of a
55   colony can also dictate and constrain the quantitative relationships between various growth
56   parameters which can have additional ecological implications. For corals, these common growth
57   measurements included linear extension rates (length per unit time), areal growth rate (area per
58   unit time), and calcification rate (mass per unit area per unit time) where calcification (G) is
59   related to volume growth rate via average density ($M=\rho V$, where M is mass, V is volume, and ρ
60   is mean density) (Pratchett et al. 2015).
61   For all calcifying organisms including reef building corals, there are two distinct components
62   of growth/production: (1) organic or tissue biomass/biovolume and (2) inorganic or calcium
63   carbonate skeleton (although there is a small fractional component of organic matter in coral
64   skeletons) (DeCarlo et al. 2018). Each aspect of growth requires their own set of elemental
65   resources which have characteristically different levels of availability depending on the habitat.
66   For organisms like reef building corals (and coralline algae and sclerosponges), the growth in
67   biomass (i.e., production) is proportional to growth in surface area (Anthony et al. 2002) while
68   the growth in skeleton mass (i.e., calcification) is proportional to volume (via density).
69   Therefore, biomass production is directly related surface area growth. In contrast, skeletal mass
70   is proportional to volume (assuming a constant mean density), so a constant calcification rate
71   leads to a constant volume growth rate (per unit surface area). The relationship between these
72   two aspects of growth can be influenced by coral geometry may cause one aspect of growth to
73   "geometrically" constrain the other which has important implications for life strategies.
74   For some geometric shapes, the surface area to volume ratio changes with size (Porter 1976)
75   potentially causing ontogenetic changes in the ratio of biomass production to calcification and in
76   the relationship between growth parameters causing them to size-dependent. One of the most
77   common metrics of coral growth across all morphologies is linear extension rate due in part to
78   the relative ease in which it can be measured and used for comparative purposes (reviewed in
79   Pratchett et al. 2015). Linear extensions rates are generally assumed to be characteristics of a

80 species, independent of size (e.g., Hughes and Jackson 1985; Kinzie and Sarmiento 1986), and
81 often used as a foundation of the census-based approach to calculate calcium carbonate reef
82 budgets (e.g., Januchowski-Hartley et al. 2017; Perry et al. 2018, 2019; Molina-Hernandez et al.
83 2020; Cornwall et al. 2021). Changes in linear extensions rates are often interpreted as an
84 environmental signal (e.g., Carricart-Ganivet et al. 2011). However, even with a constant
85 calcification rate, linear extension rates can be colony size-dependent due to the dynamics of
86 surface area to volume ratio which is dictated by the geometry of a coral colony (e.g., Kahng et
87 al. 2023). Therefore, the relationship between linear extension rate and colony size for various
88 geometric shapes is important to quantify and understand.
89   Recent reports have investigated the question whether coral growth is isometric by virtue of
90 the colonial modular design or subject to allometric constraints like non-clonal metazoans
91 (Edmunds 2006; Dornelas et al. 2017; Madin et al. 2020; Carlot et al. 2022; Medellín-
92 Maldonado et al. 2022). If growth is allometric with an ontogenetic decrease in growth rate, there
93 may be important implications for ecosystem function based on the reduction of age/size
94 distributions of coral communities from mass mortality events during the Anthropocene (Dietzel
95 et al. 2020; Carlot et al. 2021). While environmental factors in the form of spatial constraints,
96 competition, or partial mortality due to stress or senescence obviously influence these growth
97 parameters (Barnes 1973; Edmunds 2006), the inherent geometric relationships between growth
98 parameters must be clarified to be able to quantitatively reconcile the different metrics of coral
99 growth which are regularly measured using different techniques under a variety of conditions
100 (Pratchett et al. 2015).
101   In this study, four common reef building coral morphologies are modeled using geometric
102 shapes to illustrate the inherent mathematical relationships between various growth parameters
103 and demonstrate how colony geometry can characteristically alter whether relationships are size-
104 dependent or size-independent. Using previously published empirical values, the geometry-
105 dependent relationships between organic (biomass production) and inorganic (calcification)
106 growth are investigated, and the associated ecological implications are discussed.
107

Materials & Methods

109   To demonstrate the inherent mathematical relationships between various coral growth
110 parameters, four geometric shapes were used to model how a constant calcification rate per unit
111 area (G) affects linear extension rate (C) across time, change in surface area (ΔS), change in
112 planar area (ΔP), and change in volume (ΔV). Surface area productivity (SAP = ΔS/S) and
113 planar area productivity (PAP = ΔP/S) were calculated to demonstrate how quickly a coral
114 generates area (per unit area) across time.
115   • Hemispheroids across the full range of eccentricity values (oblate, circular, prolate)
116   • Flat discs with constant thickness
117   • Branching corals with constant branch diameters (cylinder model)
118   • Conical branch/colony with constant aspect ratio (α = height/basal radius)

119   Size dependent relationships were illustrated by calculating parameters as a function of size
120 (e.g., radius, thickness, length, or height). Average or common empirical values for G and
121 density (ρ) were used from the literature for the various species modeled. To illustrate the effects
122 of geometry independent of G and ρ values, SAP was calculated for all shapes using the same
123 values for G and ρ. For this modeling exercise, favorable growth conditions were assumed with
124 no partial mortality or spatial constraints on growth.
125   A hemispheroid shape was used to model the relationships between these parameters for
126 massive corals (e.g., *Porites* spp.). The effect of the eccentricity (e) was calculated across the full
127 range of possible values from oblate (flattened) to circular to prolate (tall) hemispheroids. For a
128 circular hemisphere (e=0), the calcification rate $\left(G = \frac{\Delta V \rho}{S_t}\right)$ and volume $\left(V = \frac{2}{3}\pi r^3\right)$ equations

129 were used to solve for extension rate $(C_t = r_{t+1} - r_t)$. To calculate SAP $\left(\frac{\Delta S}{S_t} = \frac{S_{t+1} - S_t}{S_t}\right)$, the

130 calcification equations was solved for r_{t+1} and substituted into the equation where surface area S_t

131 $= 2\pi r^2$. PAP $\left(\frac{\Delta P}{S_t} = \frac{P_{t+1} - P_t}{S_t}\right)$ was solved using the equation for planar area $\left(P = \pi a^2\right)$.

132   For a prolate hemispheroid with a circular base (a=b), the polar radius is larger than the
133 equatorial radius (c>a), where c is the polar radius and a and b are the equatorial radii in the two
134 horizontal dimensions. The surface area $\left(S = \pi a^2 + \frac{\pi a c}{e}\sin^{-1}e\right)$ and volume $\left(V = \frac{2}{3}\pi a^2 c\right)$

135 equations were used to solve for SAP using the definition for eccentricity $\left(e = \sqrt{1 - \frac{a^2}{c^2}}\right)$, where

136 c>a. PAP $\left(\frac{\Delta P}{S_1}\right)$ was solved using the equation for planar area $\left(P = \pi a^2\right)$. For an oblate

137 hemispheroid with a circular base (a=b), the polar radius is less than the equatorial radius (c<a).
138 The surface area $\left(S = \pi a^2 + \frac{\pi c^2}{2e}\ln\left(\frac{1+e}{1-e}\right)\right)$ and volume $\left(V = \frac{2}{3}\pi a^2 c\right)$ equations were used to solve

139 for SAP using the definition for eccentricity $\left(e = \sqrt{1 - \frac{c^2}{a^2}}\right)$, where c<a. PAP $\left(\frac{\Delta P}{S_t}\right)$ was solved

140 using the equation for planar area $\left(P = \pi a^2\right)$. For graphing purposes, oblate eccentricity was
141 denoted as negative values to distinguish it from prolate eccentricity. The effects of eccentricity
142 and size (equatorial radius) on SAP and PAP were calculated.
143   A flat circular disk with radius (r) and height/thickness (h) was used to model plate-like
144 corals such as those common in the lower photic zone (i.e., *Leptoseris* spp. and *Agaricia* spp.)
145 (Kahng et al. 2019; Tamir et al. 2019; Gijsbers et al. 2022). The calcification rate $\left(G = \frac{\Delta V \rho}{S_t}\right)$ and

146 volume $\left(V = h\pi r^2\right)$ equations were used to solve for extension rate $(C_t = r_{t+1} - r_t)$. To calculate

147 surface area productivity or SAP $\left(\frac{\Delta S}{S_t} = \frac{S_{t+1} - S_t}{S_t}\right)$, the calcification equations was solved for r_{t+1}

148 and substituted into the equation where surface area $S = \pi r^2$. The effect of skeletal thickness (h)
149 on SAP was calculated within the range of ~~values~~ empirical values reported (Kahng et al. 2020).

150   A cylinder was used to model branching corals with constant average branch radius (r), (e.g.,
151 some branching *Acropora* spp.). As the colony grows, the sum of all branch lengths or total
152 branch length (h_t) can be used to calculate skeletal volume, independent of the number of
153 branches (β_t) or average branch length (h_t/β_t). The surface area ($S_t = 2\pi r h_t + \pi r^2$) can be
154 calculated from the side of the cylinder using total branch length. Since each new branch base
155 covers the side of its parent branch, there is no net increase in surface area from each new branch
156 tip, with the exception of the area of the very first branch tip (πr^2). In this model, the ratios
157 between growth in volume ($\triangle V = \pi r^2[h_{t+1}-h_t]$), surface area ($\triangle S = 2\pi r[h_{t+1}-h_t]$), and total linear
158 extension rate ($C_t=[h_{t+1}-h_t]$) remain constant which is consistent with empirical growth data for
159 *Acropora cervicornis* (Million et al. 2021). The calcification rate $\left(G = \frac{\triangle V \rho}{S_t}\right)$ and volume ($V = h\pi$
160 r^2) equations were used to solve for average branch extension rate $\left(\frac{C_t}{\beta_t}\right)$, where $C_t = h_{t+1} - h_t$. To
161 calculate surface area productivity or SAP $\left(\frac{\Delta S}{S_t} = \frac{S_{t+1} - S_t}{S_t}\right)$, the calcification equations was solved
162 for h_{t+1} and substituted into the equation where surface area. The effect of branch diameter (2r)
163 on SAP was calculated within the range of empirical values reported in the literature.
164   A cone with a constant aspect ratio was used to model a single branch of branching corals
165 with conical branches. Some branching corals have branches that mimic high aspect cones. This
166 same model also applies to some massive corals form colonies that can mimic low aspect cones.
167 A constant aspect ratio ($\alpha = h_t/r_t$) during growth was assumed, where h is branch length/height
168 and r is radius. The calcification rate $\left(G = \frac{\triangle V \rho}{S_t}\right)$ and volume $\left(V = \frac{1}{3}h\pi r^2 = \frac{\pi h^3}{3\alpha^2}\right)$ equations were
169 used to solve for extension rate ($C_t = h_{t+1} - h_t$). To calculate surface area productivity or SAP
170 $\left(\frac{\Delta S}{S_t} = \frac{S_{t+1} - S_t}{S_t}\right)$, the calcification equations was solved for h_{t+1} and substituted into the equation
171 where surface area. The effects of aspect ratio and cone length/height on SAP was calculated.
172
173 **Results**
174   The derivations of the mathematical relationships for each geometric shape are illustrated in
175 Appendix A. Given a constant calcification rate (G) and density (ρ), the size-dependence of the
176 linear extension rate (C_t) for the four geometric shapes depends on whether the surface area to
177 volume ratio remains constant or changes as the coral colony grows in size (Table 1). For a
178 circular hemispheroid, the size-dependent relationship between calcification rate and (radial)
179 linear extension rate can be expressed $G = \frac{\triangle V \rho}{S_t} = \frac{\rho(3C_t r_t^2 + 3C_t^2 r_t + C_t^3)}{3r_t^2}$, so as the colony reaches a
180 larger size ($r_t \to \infty$), $G \to \rho C_t$. Therefore, the linear extension rate increases to an asymptotic
181 maximum value of $C_t \to \frac{G}{\rho}$ (Figure 1). For hemispheroids with nonzero eccentricity, the
182 relationships quantitatively depart from the circular hemisphere (equatorial radial extension rate
183 slower for prolate and faster for oblate) but the asymptotic pattern is qualitatively the same.

184   For a circular flat disc with constant thickness (h), the linear extension rate increases linearly

185   with colony size (radius), $C_t = r_t\left(\sqrt{\frac{G}{\rho h} + 1} - 1\right)$ (Figure 1) and exponentially across time (Kahng

186   et al. 2023).

187   For a cone with constant aspect ratio, the linear extension rate for height increases

188   asymptotically, $C_t = \sqrt[3]{\frac{3G\sqrt{\alpha^2 + 1}}{\rho}h_t^2 + h_t^3} - h_t$, where $C_t = h_{t+1} - h_t$. For high aspect cones (e.g.,

189   α>4), the linear extension rate will not approach the asymptotic maximum value $\left(C_t \to \frac{G\sqrt{\alpha^2 + 1}}{\rho}\right)$

190   until branch length/height become unrealistically long (e.g., h>50 cm) (Figure 1). The linear

191   extension rate for basal radius also increases asymptotically, $C_t = \sqrt[3]{\frac{3G\sqrt{\alpha^2 + 1}}{\rho\alpha}r_t^2 + r_t^3} - r_t$, where

192    $C_t = r_{t+1} - r_t$. For low aspect cones (e.g., α<0.5), the linear extension rate will approach the

193   asymptotic maximum value $\left(C_t \to \frac{G\sqrt{\alpha^2 + 1}}{\rho\alpha}\right)$ at relatively low values (e.g., h>25 cm) (Figure 1).

194   For a branching coral with cylindrical branches of constant diameter, the relationship

195   between calcification rate and total linear extension rate for all branches can be expressed as C_t

196    $= \frac{2Gh_t}{\rho r} + \frac{G}{\rho}$, where h_t is the total lengths of all branches combined. Dividing both sides by the

197   number of branches β_t provides the average branch extension rate $\frac{C_t}{\beta_t} = \frac{2Gh_t}{\rho r \beta_t} + \frac{G}{\rho\beta_t}$, where $\frac{C_t}{\beta_t}$ is

198   average branch extension rate and $\frac{h_t}{\beta_t}$ is average branch length. As the colony grows more

199   branches (i.e., $\rho\beta_t \gg G$), the average branch extension rate decreases asymptotically to a value

200   proportional to average branch length, $\frac{C_t}{\beta_t} \to \frac{2Gh_t}{\rho r \beta_t}$. The proportionality constant decreases with

201   increasing branch diameter.

202   Given a constant calcification rate (G) and density (ρ), the size-dependence of the surface

203   area productivity (SAP) also depends on whether the surface area to volume ratio remains

204   constant or changes as the coral colony grows in size (Table 1). For hemispheroids with constant

205   eccentricity (e), the equations for SAP are listed below:

206   • Circular hemisphere $\frac{\Delta S}{S_t} = \frac{\left(\frac{3Gr_t^2}{\rho} + r_t^3\right)^{2/3}}{r_t^2} - 1$

207   • Prolate hemispheroid $\frac{\Delta S}{S_t} = \frac{\left(\left(a_t^3 + \frac{a_t^2 3G\sqrt{(1-e^2)}}{2\rho}\left(1 + \frac{\sin^{-1}e}{e\sqrt{(1-e^2)}}\right)\right)\right)^{2/3}}{a_t^2} - 1$

208   • Oblate hemispheroid $\frac{\Delta S}{S_t} = a_t^{-2}\left(a_t^3 + \frac{3Ga_t^2\left(1 + \frac{(1-e^2)}{2e}\ln\left(\frac{1+e}{1-e}\right)\right)}{2\rho\sqrt{1-e^2}}\right)^{2/3} - 1$

209   Using average G and ρ values for massive *Porites* (Lough and Barnes 2000; Lough 2008;

210   Lough and Cantin 2014; Lough et al. 2016) were used to calculated SAP as a function of colony

211   size (equatorial radius) and eccentricity (Figure 2). Flatter hemispheroids (i.e., larger c/a ratio)

212 have higher SAP than taller ones. For all hemispheroids, SAP quickly declines asymptotically
213 with increasing size as a coral colony grows.
214   For a cone with constant aspect ratio, SAP is a size dependent and decreases asymptotically
215 with increasing size in a manner analogous to hemispheroids,

216 $\frac{\Delta S}{S_t} = \left(\frac{3G\alpha\sqrt{1+\frac{1}{\alpha^2}}}{\rho h_t} + 1\right)^{2/3} - 1$. Using average G and ρ values for branching *Acropora* (Hughes

217 1987; Morgan and Kench 2012; Pratchett et al. 2015), the SAP for a single conical branch was
218 calculated as a function of branch length and aspect ratio (Figure 3). Aspect ratio is positively
219 correlated with SAP.
220   For a branching coral with cylindrical branches, SAP is a size independent and a function of

221 calcification rate and branch radius/diameter (r), $\frac{\Delta S}{S_t} = \frac{2G}{\rho r}$. SAP declines with increasing branch

222 thickness. Using average G and ρ values for branching *Acropora* spp. (Hughes 1987; Morgan
223 and Kench 2012; Pratchett et al. 2015), the SAP was calculated as a function of branch thickness
224 (Figure 4).
225   For a flat circular disc, SAP is a size independent and is a function of calcification rate and

226 thickness (h), $\frac{\Delta S}{S_t} = \frac{G}{\rho h}$. Thinner colonies have a higher SAP. Using average G and ρ values for

227 deep-water *Leptoseris* spp. from 70-111 m (Kahng et al. 2023), the SAP was calculated as a
228 function of average skeletal thickness (Figure 5).
229   To isolate impact of geometry alone, SAP was calculated using equivalent values for G and ρ
230 for the contrasting shapes (Figure 6). Flat, thin plate-like shapes have the highest SAP which is
231 equivalent to planar area productivity (PAP) by virtue of their horizonal orientation. Cylindrical
232 branching corals with small branch diameters also exhibit high SAP, especially in comparison to
233 their massive coral counterparts (hemispheroids and low aspect cones) which have very low SAP
234 as they reach larger size.
235

Discussion

237
238 **Linear extension rates**
239   Depending on coral colony morphology, inherent mathematical relationships determine
240 which geometries can be expected to have constant (or near constant) linear extension rate (C_t) or
241 size-dependent C_t which changes across time. In general, the stability of the quantitative
242 relationship between calcification rate and linear extension rate depends on the surface area to
243 volume ratio as the colony grows in size. Given a constant calcification rate, linear extension rate
244 ~~to be~~ expected to be nearly constant for large hemispheroid coral colonies (e.g., radius >25 cm)
245 and large branching coral colonies (e.g., >20 branches) with constant branch thickness and
246 average branch length. However, when these colonies are small, decreases in the surface area to
247 volume ratios are significant, so both radial extension rates of hemispheroidal corals and average
248 branch extension rate for branching corals can be expected to decrease significantly during initial

249 growth (if calcification rate remains constant). Given an equivalent calcification rate and branch
250 diameter, longer average branch lengths cause faster average branch linear extension rates.
251 Similarly, thicker branch diameters cause slower average branch linear extension rates.
252   For conical shaped colonies with a constant calcification rate and aspect ratio (α), linear
253 extension rates for both the height/length and the basal radius will decrease asymptotically with
254 increasing height/length or radius respectively. For high aspect cones (e.g., $\alpha > 4$) like those of
255 some branching corals, the natural lengths of conical branches are short relative to the values
256 needed to approach the maximum extension rates. For low aspect cones (e.g., $\alpha < 0.5$) like some
257 flattened morphologies of massive corals, the basal radius extension rates will approach the
258 maximum values quickly relative to the size and longevity of these corals.
259   For disc-like colonies with constant calcification rate and mean thickness (h), radial
260 extension rate can be expected to increase throughout the life of the colony linearly with colony
261 size (radius) and exponentially across time (Kahng et al. 2023).
262   While the actual morphology of coral taxa may deviate considerably from these simple
263 geometric shapes, the key factor which determines whether linear extension rates have a size
264 dependent geometry is whether the ratio of mass (ρV) to surface area changes or remains
265 constant as the colony grows and therefore, whether average density (ρ) remains constant. For
266 massive *Porites* spp., skeletal density varies seasonally on a regular basis, but average density
267 across longer timescales is more stable (Lough et al. 1990, 1992). A small ontogenetic decrease
268 in density (i.e., 4% per 100 yrs) has been reported (Lough 2008). Within a colony, variations in
269 skeletal density across time are generally less than 10% of mean values and several times lower
270 than the percentage variation in calcification and extension rates (Lough and Barnes 2000; Razak
271 et a. 2019). While calcification rate and extension rate correlate with each other, calcification
272 rate does not correlate with density (Lough and Barnes 2000; Lough et al. 2016). With the recent
273 advancements in 3D photogrammetry (e.g., Million et al. 2021) the mass to surface area ratio can
274 be measured empirically for coral taxa that do not conform to a simple geometric shape.
275 Likewise, the stability of skeletal density across time can also be measured empirically (e.g., via
276 x-radiography and computerized tomography).
277   Because calcification rates for a given coral colony can vary considerably across time, the
278 ontogenetic, size-dependent geometric effects on linear extension rate can be overshadowed.
279 Significant interannual variability (e.g., ±25-50% of long-term mean) is commonly reported from
280 retrospective analyses of massive corals (e.g., Kourandeh et al. 2018; Razak et al. 2019;
281 Courtney et al. 2020; etc.). These temporal changes in calcification rate are associated with a
282 variety of biotic and abiotic environmental factors. For hemispheroids and conical massive
283 corals, the asymptotic maximum linear extension rates are directly proportional to calcification
284 rate. For a flat circular disc, linear extension rates are directly proportional size (i.e., radius) and
285 to (roughly) the square root of calcification rate, so size can have an exponentially larger impact.
286   Whether a particular growth metric is naturally isometric or allometric depends on both the
287 individual metric and the colony geometry. Of course, the environmental history of each coral
288 has a dominant effect on *in situ* net growth generating wide variability between conspecifics

289 across time (e.g., Madin et al. 2020). Nonetheless, the character (whether isometric/allometric) of
290 one growth metric can be characteristically different than another due to their inherent
291 mathematical relationship dictated by colony geometry. Likewise, the same growth metric may
292 differ characteristically between coral taxa with contrasting geometries.
293

Organic and inorganic production

294
295   For all calcifying organisms, both biomass production and calcification are required for
296 growth. While both require energy, each aspect of growth has different elemental resource
297 requirements, and the availability of these elemental resources can vary significantly by habitat
298 and depth. In oligotrophic waters associated with shallow coral reef ecosystems the limiting
299 elemental resources for coral biomass production are typically macronutrients like bioavailable
300 nitrogen or soluble reactive phosphorus (Atkinson and Falter 2003; Karl and Church 2017). This
301 limitation of essential macronutrients often results in a surplus and subsequent excretion of
302 organic carbon production (i.e., photosynthate) in well-lit habitats (reviewed in Goldberg 2018).
303 In contrast, the elemental resources for calcification (calcium ions and carbonate alkalinity) are
304 generally not limiting in surface seawater (at normal pH) in tropical habitats. In clear,
305 oligotrophic waters, the depth of the lower photic zone can coincide with the nutricline (or
306 interaction with the nutricline via inertial oscillations) causing inorganic macronutrients to be
307 less limiting or even replete (Kahng et al. 2019). However, available light energy to drive
308 photosynthesis eventually becomes limiting with increasing depth.
309   For reef building corals, coralline algae, and sclerosponges, tissue biomass is limited to a
310 finite layer associated with surface area of their skeleton. This design generates a geometric
311 relationship and potential constraint between the two aspects of growth (skeletal mass and tissue
312 biomass). If average tissue thickness and composition remain constant, the tissue biomass can be
313 expected to be proportional to surface area. Therefore, the surface area productivity (growth of
314 new surface area per unit surface area per unit time) can be a useful metric that can be used as a
315 quantitative proxy for ontogenetic changes in biomass productivity (as the colony grows) and
316 how geometry can constrain it.
317   For calcifying organisms with an external skeleton (i.e., shelled molluscs), calcification can
318 directly relate to the growth of internal volume available for biomass (e.g., Raup and Graus
319 1972; Graus 1974) generating the potential for an analogous geometric constraint. However,
320 ocean acidification studies have demonstrated that reduced calcification can occur without
321 reductions in somatic growth due to reductions in shell thickness and structural integrity
322 (reviewed in Gazeau et al. 2013). Phenotypic plasticity in shell thickness relative to tissue
323 biomass (reviewed in Watson et al. 2012) further suggests that despite the potential geometric
324 relationship between organic and inorganic production, the two aspects of growth are readily
325 decoupled.
326

Ecological Implications of SAP

327
328   For clonal organisms with indeterminate growth, resource acquisition (i.e., energy and
329 elemental resources) can dictate growth rate assuming physiological costs per unit biomass

330   remains constant (Sebens 1987). Within a stable environment in the absence of stress, space
331   limitations, and disturbance, coral resource acquisition can be expected to scale with tissue
332   surface area exposed to light for autotrophy and ambient water for heterotrophy (whether via
333   polyp feeding or direct assimilation) and mass transfer (Porter 1976; Sebens 2003; Monismith
334   2007). Therefore, under optimal conditions maximum rates of production normalized to surface
335   area (i.e., calcification and growth in biomass) can be expected to be independent of colony size.
336   However, depending on colony morphology, portions of a colony's surface area may be subject
337   to self-shading and/or reduced water motion (e.g., feeding and mass transfer) causing reductions
338   and spatial heterogeneity in productivity per unit area (e.g., McFadden 1986).
339   Corals with high SAP can increase their area and therefore resource acquisition capacity
340   quickly to fuel fast growth (both tissue biomass and calcification) when resources are not
341   limiting. However, their growth requires high biomass production to cover the quickly expanding
342   surface area. Therefore, biomass production may limit growth more than calcification with the
343   latter being constrained by the former. This potential constraint has implications for tissue
344   thickness (or biomass reserves) and resilience. The ability of branching corals, especially with
345   species thin branch diameters, to recover from tissue damage or loss without negatively
346   impacting growth can be expected to be less robust than corals with lower SAP. Many branching
347   corals are known to have relative thin tissue thickness (e.g., Loya et al. 2001). These geometry-
348   based predictions are consistent with the life history traits of fast-growing branching corals (e.g.,
349   *Acropora* spp.) and implies that their susceptibility to disturbance such as bleaching-related
350   mortality may be due in part to the inherent tradeoff associated with their geometry (Loya et al.
351   2001; McClannahan et al. 2007; Darling et al. 2012). Where studied, some corals exhibit an
352   inverse correlation between tissue layer thickness and calcification rate which is consistent with
353   this geometric tradeoff (Lough et al. 2016).
354   Several coral taxa (e.g., massive *Porites* spp., etc.) have colonies that mimic a
355   hemispheroidal or a low aspect conical shape. Large colonies with these shapes have very low
356   SAP and grow surface area very slowly. Their biomass growth may be geometrically constrained
357   by calcification thereby giving them a potential surplus in biomass production capacity in excess
358   of growth requirements (Anthony et al. 2002). This slower biomass growth strategy may be tied
359   to their thicker tissues (Loya et al. 2001) and be associated with a geometric tradeoff for greater
360   resilience to bleaching (e.g., Loya et al. 2001; Hughes et al. 2018), a greater capacity to recovery
361   from tissue damage/loss, and higher reproductive output per unit area (Alvarez-Noriega et al.
362   2016). However, during initial growth, their high SAP (and less surplus biomass production
363   capacity) may contribute to the increased mortality rates of juveniles (Meesters et al. 1997).
364   The rapid, initial, ontogenetic change in SAP for massive corals (hemispheroidal or conical)
365   underlies the success of microframentation as a technique for accelerating growth in coral cover
366   (Forsman et al. 2015; Page et al. 2018). When large, massive corals are cut into small fragments,
367   SAP is fundamentally increased by virtue of their geometry. Given an equivalent calcification
368   rate, small colonies grow surface area multiple time faster (per unit surface area) than large
369   conspecifics (Figure 2). Corals with an ontogenetic decrease in SAP likely experience an

370 ontogenetic shift in growth limitation from biomass production to calcification. This geometry-
371 based prediction is consistent with empirical measurements of tissue thickness for massive
372 *Porites* which increases with colony size (Barnes and Lough 1992). Based on geometry,
373 microfragmention will not alter SAP in branching corals (with constant branch diameter), foliose
374 corals (with constant thickness), or thin encrusting corals.
375   Corals with high aspect conical branches appear to have intermediate SAP values depending
376 on their aspect ratio and average branch length. Their SAP values are between those of
377 cylindrical branching corals and hemispheroidal corals with commensurate ecological
378 implications. The aforementioned implications for ontogenetic shift in hemispheroidal coral can
379 also apply to conical branching corals if their average branch length increases with colony size.
380   The coral morphology which naturally enables the highest SAP are thin plate-like shapes. In
381 shallow water exposed to wave stress, sedimentation, and overshading competition, this fragile
382 morphology is not common. However, in the lower photic zone, dominant photosymbiotic coral
383 taxa (e.g., *Leptoseris* spp. and *Agaricia* spp.) are often mimics the shape of a flat circular discs
384 (reviewed in Kahng et al. 2019; Kramer et al. 2022). At these depths offshore, hydrodynamic
385 forces from storm events and exposure to sedimentation is often attenuated. Space competition
386 from fast growing photosynthetic taxa is also attenuated (reviewed in Kahng et al. 2010). Despite
387 the very low calcification rates, the SAP for deep water *Leptoseris* spp. is higher than large,
388 massive *Porites* spp. in shallow-water with their hemispheroidal shape (Kahng et al. 2023).
389   In oligotrophic, shallow-water environments, light available to drive daily photosynthesis is
390 available from a wide range of angles due to scattering and the change in solar angle throughout
391 the day (Kahng et al. 2019). However, in the lower photic zone, the angular width of usable light
392 narrows centered around the vertical axis regardless of time of day. At these depths, horizontal
393 planar area dictates the maximum amount of light that can be harvested by an organism.
394 Therefore, the rate at which planar area is increased (i.e., planar area productivity, PAP) becomes
395 a strategic attribute for phototrophy. The flattening of coral morphology with depth (both
396 interspecies differences and intra species plasticity) reflects an adaptation to increase PAP at
397 depth. For example, the flattening of massive coral colonies with increasing depth (e.g., Grigg
398 2006) increases both SAP and PAP. The coral colony morphology with a geometry that enables
399 the highest PAP is a horizontally flat plate with a very thin skeletal thickness. This morphology
400 is adopted by the deepest photosymbiotic corals around the world (i.e., *Leptoseris* spp.) and is
401 consistent with phototrophic adaptation (Kahng et al. 2012).
402
403 ## Conclusions
404 The geometry of coral taxa can influence the inherent mathematical relationship between the
405 various growth parameters and dictate whether some are size-dependent or size-independent. The
406 size-dependent nature of surface area productivity which underlies the success of
407 microfragmention to accelerate coral cover is colony shape (and species) specific. The geometric
408 coupling between biomass production and calcification differs characteristically between taxa
409 and contributes to the diversity of life history traits of corals.

410

Acknowledgements

411
412
413

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Table 1(on next page)

Table 1

Table 1. Changes in various parameters as coral colony grows in size for each geometric shape. Vertical arrows denote increase/decrease while slating arrows indicate asymptotic increase/decrease. Equal sign denotes constant values which do not change with colony size.

1

	Size metric	Surface area to volume ratio	Linear extension rate	Surface area productivity
Hemispheroid (constant eccentricity)	equatorial radius	↘	↗	↘
Disc (constant thickness)	radius	=	↑	=
Cone (constant aspect ratio)	height/length, basal radius	↘	↗	↘
Branching coral - cylindrical (constant branch diameter)	average branch length	=	↘	=

2
3
4

Figure 1

Figure 1

Figure 1. Size dependent linear extension rates. (*upper left*) Radial extension rate for circular hemisphere (eccentricity = 0) with constant calcification rate (G = 1.6 g cm^{-1} yr^{-1}) and density (ρ = 1.4 g cm^{-3}). (*upper right*) Radial extension rate for circular disc with constant calcification rate (G = 0.06 g cm^{-1} yr^{-1}) and density (ρ = 2.6 g cm^{-3}). (*lower left*) Height/length extension rate for cone with high aspect ratio (α = height/radius = 4) with constant calcification rate (G = 1.6 g cm^{-1} yr^{-1}) and density (ρ = 1.4 g cm^{-3}). (*lower right*) Radial extension rate for cone with low aspect ratio (α = 0.5) with constant calcification rate (G = 1.6 g cm^{-1} yr^{-1}) and density (ρ = 1.4 g cm^{-3}).
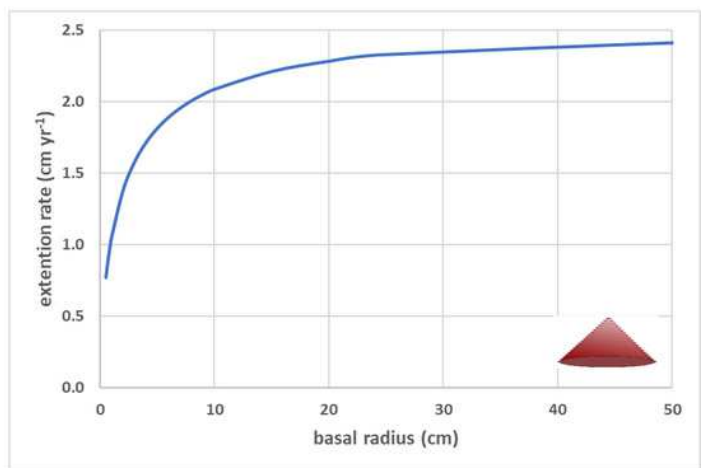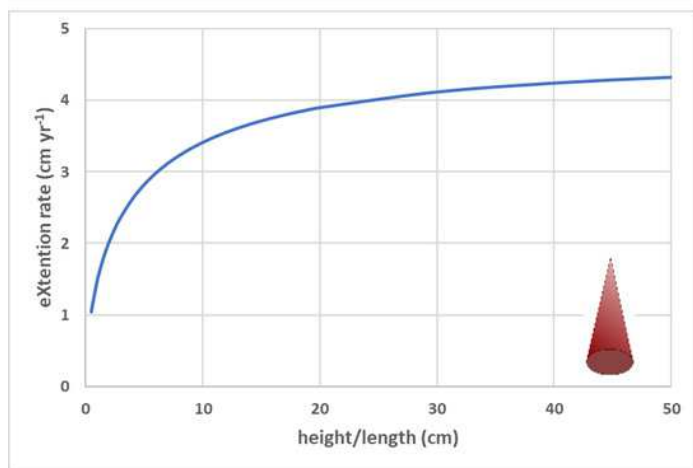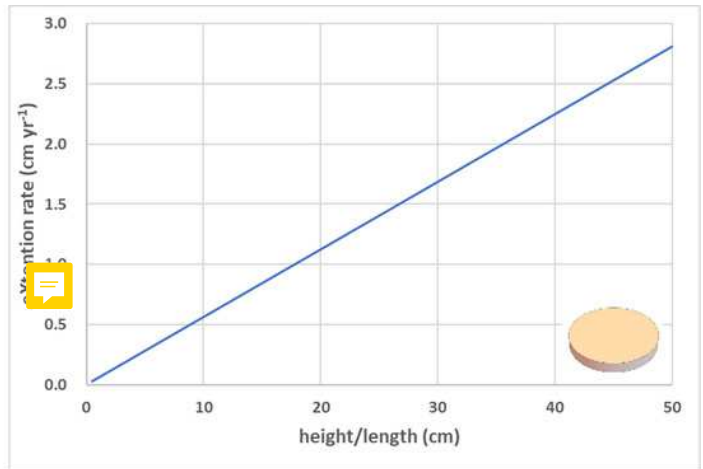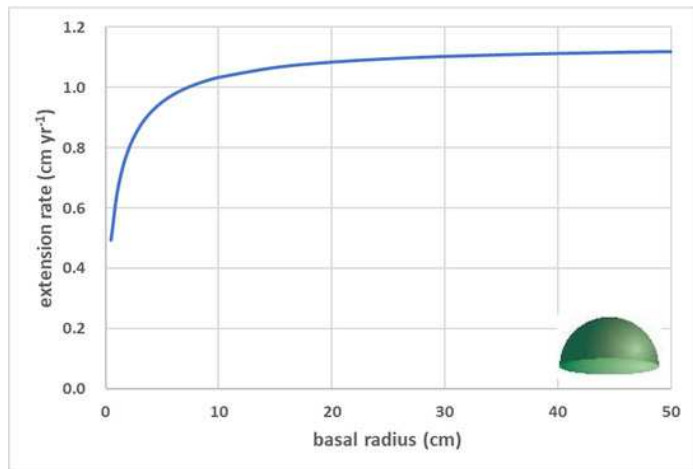
Figure 2

Figure 2

Figure 2. Surface area productivity (yr^{-1}) for a hemispheroid coral colony as a function of colony size (equatorial radius, a) and eccentricity (e) calculated using average values for massive *Porites*: G= 1.64 g cm^{-2} yr^{-1}, ρ= 1.28 g cm^{-3} (Lough 2008). For graphing continuity purposes, eccentricity values for oblate hemispheroids are denoted as negative.
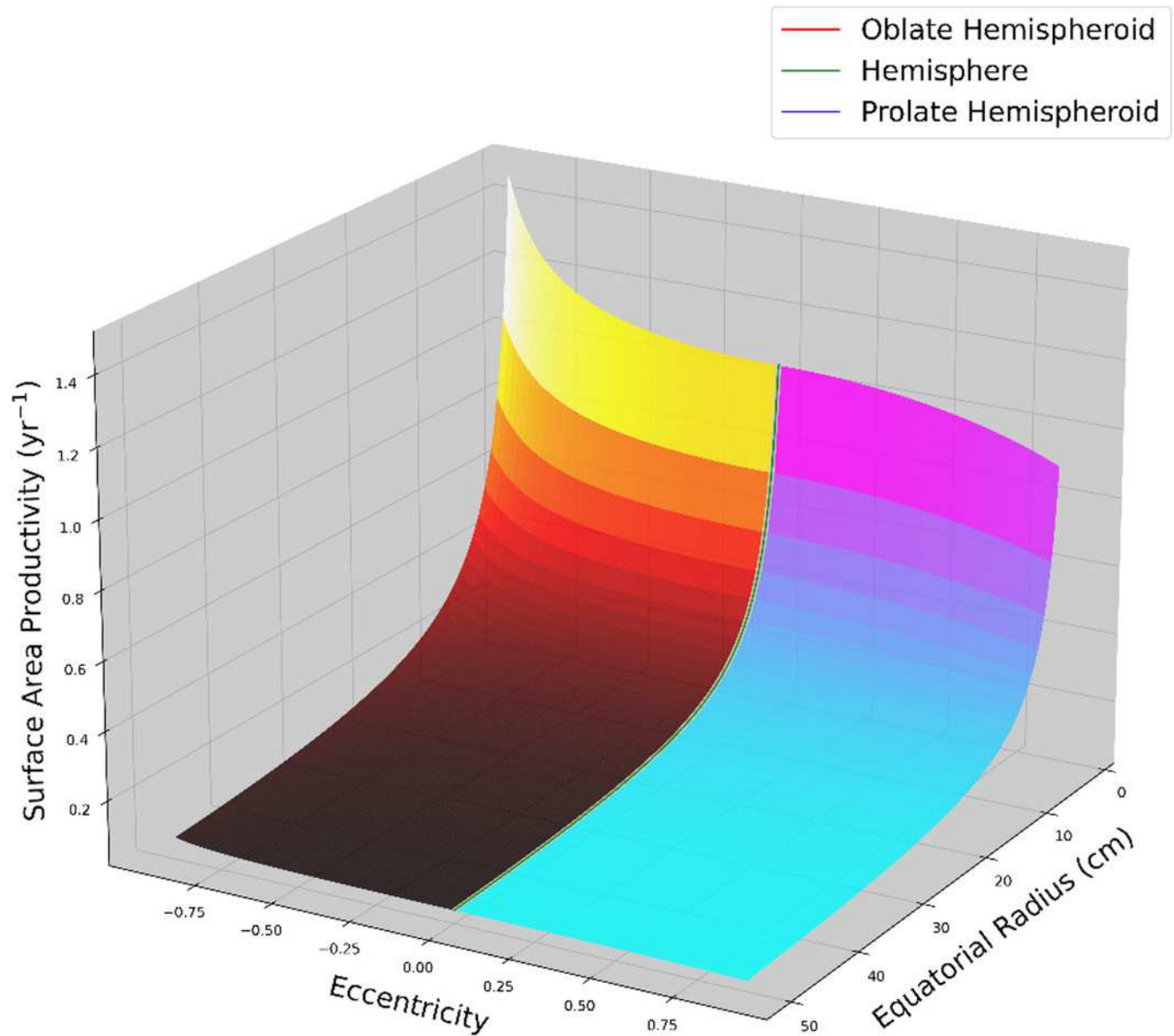
Figure 3

Figure 3

Figure 3. Surface area productivity (yr^{-1}) for a single conical coral colony as a function of height (or a single conical branch) and aspect ratio (α = length/basal radius) using average values for branching *Acropora*: G= 2.5 g cm^{-2} yr^{-1}, ρ= 1.4 g cm^{-3} (Hughes 1987; Morgan and Kench 2012).
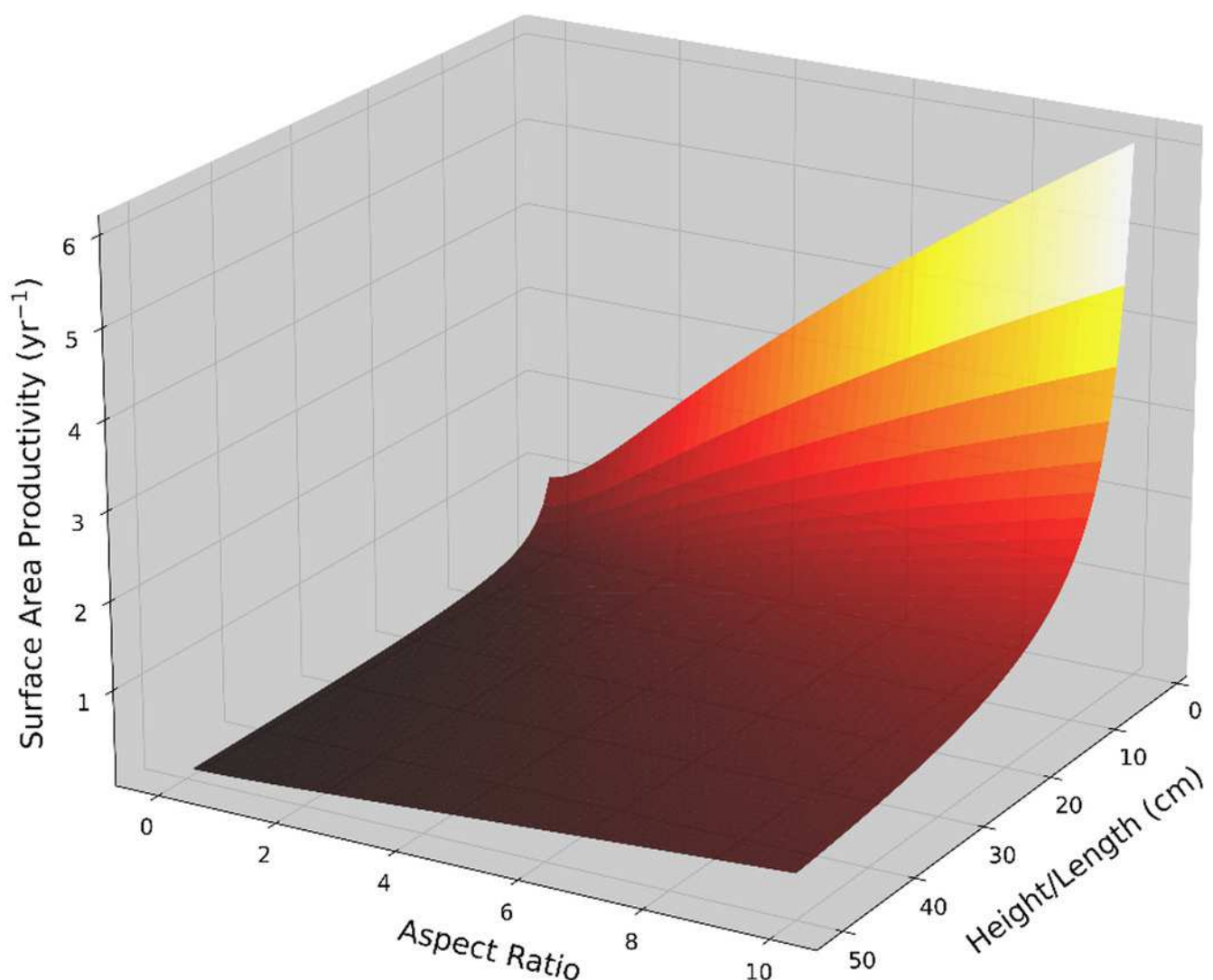
Figure 4

Figure 4

Figure 4. Surface area productivity (yr^{-1}) for a branching coral colony with cylindrical branches as a function of branch diameter using average values for branching *Acropora*: G= 2.5 g cm^{-2} yr^{-1}, ρ= 1.4 g cm^{-3} (Hughes 1987; Morgan and Kench 2012). The yellow shading indicates common values for branch diameter (Nadler et al. 2014).
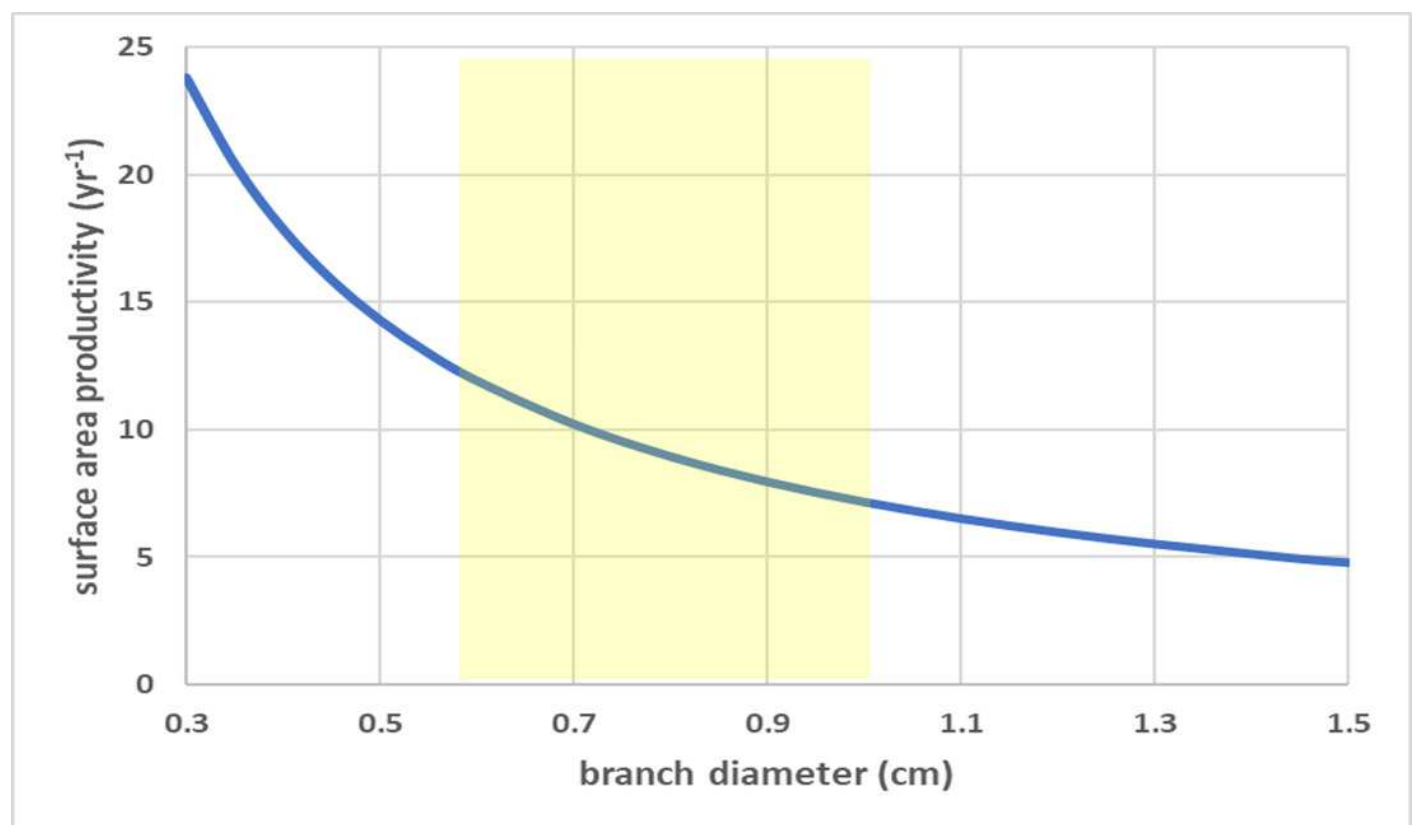
Figure 5

Figure 5

Figure 5. Surface area productivity for a flat plate-like colony as a function of average thickness using average values for branching deep-water *Leptoseris* spp. rom 70-111 m in Hawaii: G= 0.061 g cm^{-2} yr^{-1}, ρ= 2.67 g cm^{-3} (Kahng et al. 2023). The yellow shading indicates common values for skeletal thickness diameter (Kahng et al. 2020).
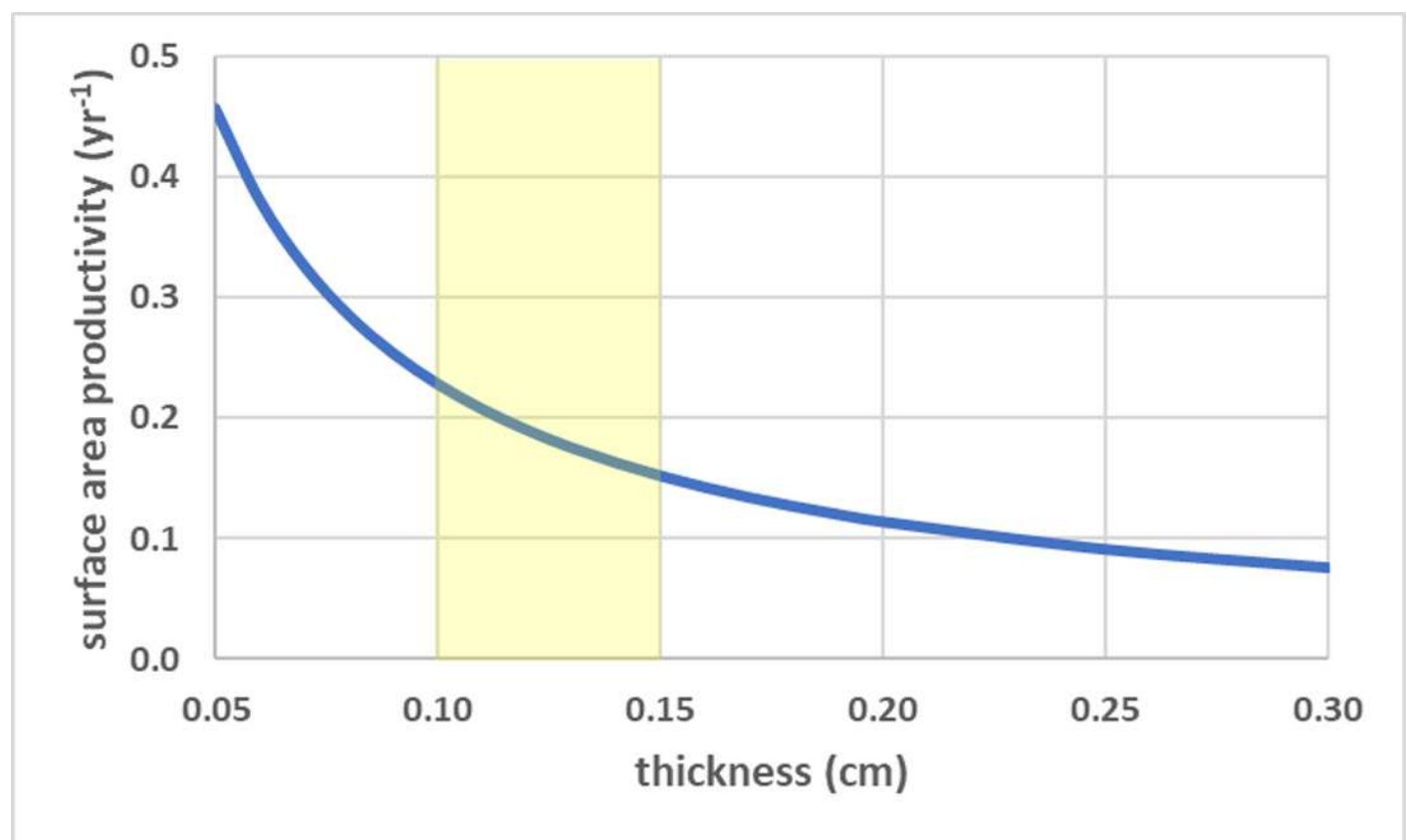
Figure 6

Figure 6

Figure 6. Surface area productivity (yr^{-1}) for three geometric shapes using equivalent values for calcification rate ($G=1.5$ g cm^{-2} yr^{-1}) and density ($\rho= 1.2$ g cm^{-3}). (*upper left*) Flat disc, (*upper right*) cylindrical branching, (*lower left*) single conical branch with a range of aspect ratios (α), and (*lower right*) circular hemispheroid. Yellow shaded areas highlight common values for deep-water *Leptoseris* spp. skeletal thickness (*upper left*) and *Acropora* spp. branch diameter (*upper right*).