Coral growth modeling

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1 Introduction

Coral growth has been described in several ways. Usually, size is determined using the buoyant weight, the skeleton weight (possibly extrapolated from the buoyant weight), the surface of the frag or of the tissues, or the number of polyps. Buoyant weight can be determined *in vivo* easily and with great precision. however, the determination of the surface of tissues is more difficult and more approximative, even using a 3D scanner, because it is not easy to determine which surface to consider (calicoblastic? oral ectoderm? with polyps retracted or extended?). Yet, it is rather clear that both volume weight of the skeleton produced and surface of the leaving tissues are key aspects in coral growth. We propose, here, a model that derives such data for successive observations of growing corals.

2 Definition of the growth model

In the present coral growth model, we view a zooxanthellate coral colony as a simplified system made of a "sheet" of living tissue which growth essentially in two dimensions on top of an aragonite skeleton that growth in three dimensions. Fig. 1 illustrate this point of view. Skeleton growth is allometric with tissue growth. Allometry coefficient denotes how much energy is dedicated to skeleton formation in comparison with living tissue increase. The higher this coefficient, the more massive the colony.

The skeleton is considered to have a constant density in given conditions. This results into a constant rate between buoyant weight and skeleton volume on one hand, and a constant ratio between the skeleton volume and the moles of $CaCO_3$ it contains, on the other hand.

The sheet of living tissue is considered to have a constant thickness is given conditions, and thus, its surface is directly proportional to its volume (its growth is truly tridimensional). Exchanges on this surface are mediated by flow rate around the coral, which modifies the boundary layer, and the amount of energy the coral dedicates to active transports, modulated by its surface. Energy acquired is also surface dependent, being heterotrophic (plankton capture, ingestion of microbes, or microbial products, pinocytosis of small organic molecules from the seawater column), or autotrophic (mainly, photosynthates translocated from the zooxanthellae). Autotrophic metabolism is dependent on light, density and zooxanthellae and their yield to convert light into chemical energy.

Growth is simply exponential. In given conditions, both the sheet of living tissues and the skeleton are growing exponentially, but with a different rate, quantified in the allometric coefficient. This allometric relationship between skeleton and living tissue growth is not considered for the whole skeleton. Indeed, the whole skeleton is divided into two subparts, one that growth allometrically: the "active" skeleton, i.e., the part of the skeleton that is actually holding living part of the coral colony, and the "idle" skeleton, that is old piece of skeleton that was build by old polyps that have since disappeared. The old skeleton is considered as stable here (constant volume and weight in time), but it is clear that a better model would consider it is bioeroded in time. For the sake of facility, the old skeleton part could also contain any part of the colony that we buoyant weight but that is not part of the growth process, as soon as this part could be considered to have a constant weight in time (piece of rock, cement, fixture, nylon line, etc.). This is then called the "idle part" (IP) in contrast with the active skeleton (AS), on top of which living tissue (LT) is growing.

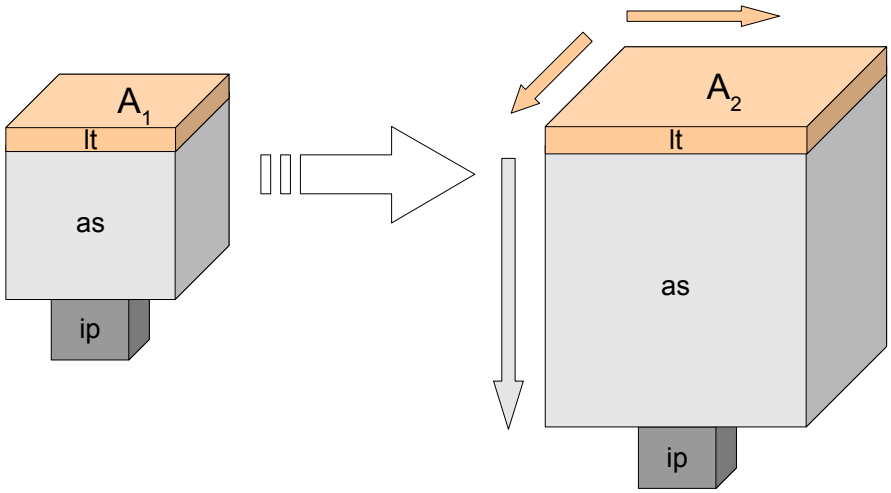

Figure 1: Conceptual coral growth model. The key variable here is the apparent area (A_x) of both the living tissues (lt) and the "active" skeleton (as), which growth in two dimensions with time (from A_1 to A_2 here). In addition, the active skeleton can also grow in the third dimension, on the contrary to living tissue thickness that remains constant over time. A part of the skeleton can eventually by considered as the "idle part" (ip), whose volume remains constant with time. For the sake of facility, ip can also comprise other features like fixture, nylon line, etc. used to hold or manipulate the coral frag. The ip does not take part of the growth process.

Among the aragonite part, it is not easy to determine which is the IP and which is the AS, except if we consider its evolution in time. AS is the fraction that yield an (almost) perfect exponential growth in time. Individual variations can be also eliminated by carefully adjusting the fraction of AS *versus* IP. Hence, we can define AS as the fraction that yield a given growth rate in specified conditions for clone frags (pieces of corals coming from the same coral colony). If these frags are weighed on a nylon line of a negligible weight, it is even possible that AS be actually **higher** that actual skeleton and IP is a **negative** fraction. This can occur when the frag is constituted by smaller than average branches that have a larger tissue/skeleton volume fraction than the average colony. Such frags tend to have a larger growth rate that can only be standardized in one consider AS as higher that actual skeleton they contain!

Carbon fluxes contain both inorganic carbon, used for skeleton building on one hand and used by photosynthesis or produced by respiration on the other hand. It also contains fluxes of organic carbon, produced by autotrophic and heterotrophic activities (with auto/hetero ratio being the ration of autotrophic *versus* heterotrophic source). In the model, as we focus on growth, we simplify the use of inorganic carbon for four purposes: (1) to produce energy, among which a part of it is used for skeletogenesis, (2) to build new somatic tissue, and (3) for other productions that do not lead to increase of the somatic living tissues: mucus production, organic matrix of the skeleton, reproduction, ...

Important parameters are:

- ▷ The αs allometric coefficient that indicates how much the skeleton grow in volume in comparison to living tissue,
- ▷ ρs, the apparent skeleton density, that is the mass of $CaCO_3$ (Ws) per skeleton volume (Vs). Equally important for measuring purposes, but not for the model itself, ρb is the apparent density that can convert buoyant weight into skeleton weight.
- ▷ Apparent living tissue area, At is the key variable here. Its apparent volume Vt is considered proportional to its area, thus with a constant apparent thickness (or height) Ht.

- ▷ Active skeleton area As is considered always equal to the apparent tissue area At (As = At). This is thus collectively called simply as the area (A) of the colony, or frag. The mean active skeleton thickness, Hs is Vs/A (and this is half the mean branches or sheet thickness in case of coral colonies that have leaving tissue on both sides).
- ▷ In given, constant conditions, the area of a colony or frag is growing exponentially with time: $A_{(t)}=A_{(0)}.e^{\beta.t}$, with $A_{(0)}$being the initial area at time t = 0. This is an apparent area that is linked, thus, to the volume or weight of the active skeleton, as derived from buoyant weight or alkalinity anomaly measurement. It is the buoyant weight Wb converted into skeleton weight as (Was +Wis) and derived from Was only.
- ▷ The dark respiration rate is the amount of CO_2 produced by respiration per apparent area (Rd/A in mol CO_2/cm^2), the net photosynthesis rate is the amount of CO_2consumed by photosynthesis in the light phase, considering gross photosynthesis minus light respiration per apparent area (Pn/A in mol CO_2/cm^2). It should be related to illumination per apparent area (hv/A in mol photons/cm^2/s), to zooxanthellae density (Zd/A in nbr of zoox cells / cm^2) and to zooxanthellae yield in the conversion of photons (%).
- ▷ Nitrogen and phosphorus balances are calculated as follows. The amount of organic carbon in the living tissue is proportional to its area as (C/A in mol C/cm^2). Nitrogen and phosphorus amounts are related by their ratio C/N and N/P. Nitrogen assimilation is expressed as the flux of N entering the living tissue per time unit (FN/A in mol N /cm^2/s), and the same for phosphorus (FP/A in mol P/cm^2/s).
- ▷ Hydrogen and oxygen fluxes are not considered in the model, as these atoms comes from the abundant water surrounding the coral. Dioxygen fluxes as simply the opposite as respiration and photosynthesis expressed in CO_2 fluxes.

The model is:

$$y_t = y_0 e^{a.\alpha.t} \tag{1}$$

...

3 Coral growth model - take 2

Here is how this model is obtained:

- ▷ For a given colony, in specified environmental conditions (lightning, water movement, water quality, ...), we make the hypothesis that the colony develops a given shape. It is not unreasonable to consider that the relationship between the volume and surface area of the colony skeleton could be modeled using:

$$Vs = a.As^b \tag{2}$$

- ▷ The surface area of the living tissues is hard to define. For the calicoblastic epidermis, it is very close to *As*, since it has been demonstrated that the tissue is very close to the skeleton. However, for the oral epidermis, the surface area is different and changes depending if the polyps are retracted or extended. In fact, the surface area that interest us is rather related to exchanges between the coral and the surrounding water. So, we consider here a **functional area** *A*, which is defined according to observed exchanges. We make here the double hypothesis that the average thickness or "height" of the living tissue does not changes much with time in given conditions (and thus, the volume of living tissues *Vt* is proportional to its area *At*, at least its "functional" volume *V* and area *A*), and that dark respiration *Rd* is proportional to the functional volume (and thus the functional area) of such tissues. Thus, at a given time, *At* is proportional to the measurable *Rd*:

$$A = c.Rd \tag{3}$$

▷ We could also reasonably think that As is proportional to A, and the weight of the skeleton Ws is proportional to its volume (constant density in given conditions), and thus, allowing the constant a to absorb the proportionality constant, eq 2 can be written:

$$Ws = a.A^b \tag{4}$$

▷ It is reasonable to consider that, for neoformed skeleton in the given conditions, its density ρS is constant, and it is thus easy to know the weight of the skeleton Ws and considering it is pure aragonite (TODO: speak about apparent density here!), the moles of $CaCO_3$ it contains. The actual measure that can be done *in vivo* to estimate the weight of the skeleton is the buoyant weight. It is possible to show that the actual weight can be calculated from the buoyant weight, temperature and salinity of the water, if the skeleton density is known (apparent density, here).

▷ If one measures also skeleton building during Rd measurements, it is possible to know the moles of $CaCO_3$ precipitated in the skeleton per moles O_2 respirated. This value should be recorded for future use. Now if the measurements of both Rd and Ws are repeated in time, one has the following equations:

$$A_t = A_0.e^{kt} = c.Rd_0.e^{kt} \tag{5}$$

4 Nitrogen

Nitrogen cycle essentially involves redox reactions that either provide or require relatively high amounts of energy. Acid-base equilibrium only occurs for $NH_3 + H^+ \Leftrightarrow NH_4^+$. Precipitation/dissolution reactions do not occur in natural seawaters because all ammonium, nitrite or nitrate compounds are very soluble in seawater. In oligothrophic waters that are usual around tropical coral reefs, the most abundant nitrogen species is N_2, a gas that dissolves from the atmosphere where it represents about 78%. However, N_2 is a very stable molecule and only procaryotes, like some cyanobacteria have required biochemical pathways (nitrogenases) to break it and produce amines that can be incorporated in organic matters. Thus, N_2 is largely unavailable as N source for organic matters, except thanks to the key role of cyanobacteria. In organic matter, ammonia or ammonium, N is at the redox stage -3. It can eventually be oxydized into nitrites (NO_2^-at redox stage +3), or nitrate (NO_3^- at redox stage +5) by a series of chemoautotrophic bacteria that use these reactions to get energy. This is called the nitrification process. Finally, other bacteria can perform denitrification (in anoxic conditions) and transform nitrates and nitites back into N_2.

Both algae and corals can use ammonium/ammoniac, nitrites and nitrates as a source of organic nitrogen, with a preference for ammonium/ammoniac which are already at the correct oxydo-reduction stage and requires thus less energy to incorporate into organic matter[1]. Other important sources of nitrogen are urea and aminoacids dissolved in the water column. Aminoacids are produced by all live being but majors produces of dissolved amino acids in the water column around the reef are bacteria. Amino acid uptake by the coral holobiont is a key process, especially for those essential amino acids the coral or zooxanthellae cannot produce themselves (like aspartic acid, to check!?). Urea $CO(NH_2)_2$ is maily produced by terrestrial animals, like mammals. Fishes usually excrete ammonia. however, a few fishes, as well as some invertebrates and even some bacteria can produce urea. . Urea is preferred to nitrate as a source of nitrogen for corals, but not for zooxanthellae. However, urea (or uric acid?) is a mean to store nitrogen in zooxanthellae (see Dubinski & Stambler 2011). The nitrogen cycle, and nitrogen-compound fluxes, centered around the coral and its zooxanthellae is summarized on Fig. 2.

[1]The reduction of nitrates or nitrites to organic matter also result in a stoichiometric consumption of protons, thus rising pH (to check!). On the counterpart, nitrification produces protons and lower pH (check stoechiometry + what about nitrogen fixation and denitrification?)

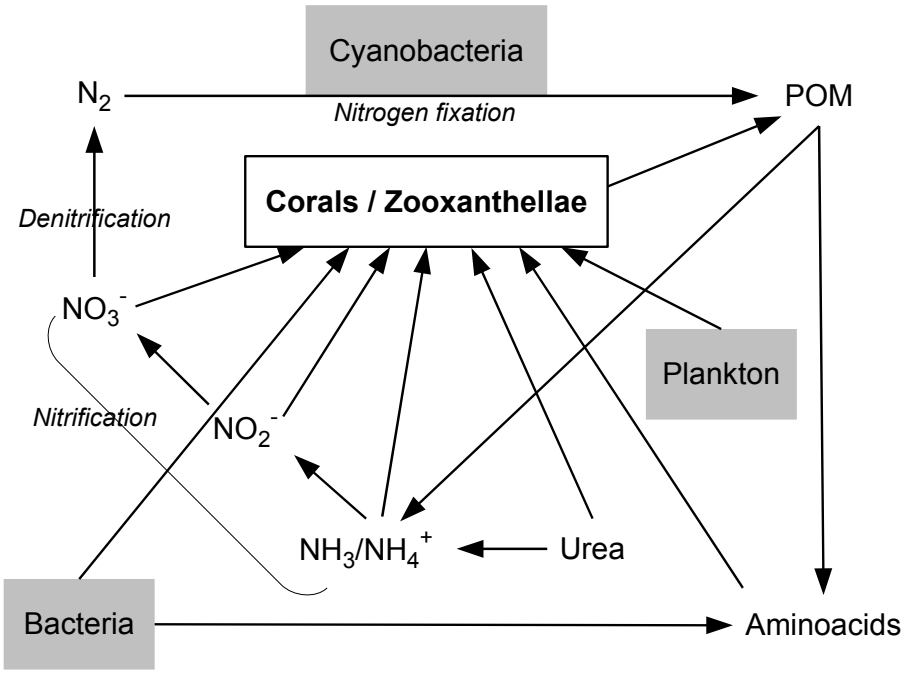

Figure 2: Nitrogen cycle and use of nitrogen sources by the coral or coral zooxanthellae. Plankton comes essentially from the open ocean. It also slightly contributes to POM (particulate organic matter) and ammonia (not shown), but this is negligible in comparison to the contribution of reef organisms. Plankton constitutes the main source of nitrogen from heterotrophic pathway for the coral, although ingestion of bacteria can contribute significantly too. Bacteria degrade POM, urea (not shown) into ammonia and are responsible for recycling of inorganic nitrogen through nitrification and denitrification processes. It has been demonstrated that almost all sources of organic or inorganic nitrogen can be efficiently used by the coral or its zooxanthellae, even at the lower concentration (submicromolar) they exist in the oligothrophic reef waters, except diazote. Only cyanobacteria leaving in the coral skeleton, on or inside the reef substrate can fix nitrogen into assimilable nitrogen compounds for the coral. Cyanobacteria play thus a major, but indirect role in providing nitrogen to the coral in nitrogen-limited conditions. The diagram also show that urea (produced by various reef organisms) can be directly used by the coral or coral zooxanthellae. Finally, the diagram emphasizes the presumed importance of dissolved aminoacids (form the degradation of POM, but mainly produced by bacteria) as a source of essential nitrogen-containing organic compounds for the coral and its zooxanthellae. This is probably true for other organic molecules that could be therefore called "vitamins" for the coral.