The reef coral two compartment proton flux model: A new approach relating tissue-level physiological processes to gross corallum morphology

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A B S T R A C T

A comparison of the equations for photosynthesis and calcification in reef corals suggests that the two processes compete for available inorganic carbon; yet reef corals exhibit simultaneous high rates of photosynthesis and calcification during daylight hours. Also, the extreme metabolic activity observed in corals at high irradiance requires a large net efflux of protons at sites of rapid calcification and respiration. Corals have resolved these problems through development of morphologies that separate the zone of rapid calcification (ZC) from the zone of rapid photosynthesis (ZP), with the fixed-carbon energy supply from the ZP being rapidly translocated to the ZC. Translocation of photosynthate from the ZP serves as a means of transporting protons to the ZC, where they are readily dissipated into the water column. Observations on the spatial relationship of the ZC and ZP, analysis of net proton flux, incorporation of photosynthate translocation coupled with an understanding of the importance of boundary layers (BL) leads to a unified hypothesis that describes the processes involved in coral metabolism. The proposed model is based on the observation that reef corals have evolved a wide range of morphologies, but all of them place the ZC between the ZP and the external seawater. This spatial arrangement places the BL in contact with the ZC in order to facilitate efflux of protons out of the corallum. Placement of the ZC between the ZP and the BL maximizes recycling of the metabolic products O₂ and HCO₃⁻. Furthermore, this arrangement maximizes the photosynthetic efficiency of zooxanthellae by producing a canopy structure with the skeletal material in the ZC serving to absorb ultraviolet radiation (UV) while scattering photosynthetically active radiation (PAR) in a manner that maximizes absorption by the zooxanthellae. The ZP is isolated from the water column by the ZC and the BL. Therefore ZP must exchange metabolic materials with the ZC and with the water column through the ZC and its overlying BL. The resulting configuration is highly efficient and responsive to irradiance direction, irradiance intensity, water motion and coral polyp morphology. The skeletons of corals are thereby passively modified in response to physical factors such as light and water motion regime. The model presents a unified theory of coral metabolism and provides explanations for many paradoxes of coral biology, including plasticity of the diverse growth forms and an explanation for coral skeletal growth response to ocean acidification.

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1. Introduction

A recent paper (Jokiel, 2011) describes the “proton flux hypothesis” which states that the decreasing calcification rate observed in corals under increasing conditions of ocean acidification can be attributed to higher \([H^+]\) in the seawater. Increasing \([H^+]\) in the water column will decrease the strength of the diffusion gradient which in turn will slow the efflux of H through the boundary layer and slow the rate of calcification. The initial presentation of the hypothesis regarded the corallum as a “black box” and only considered the inputs and outputs through the boundary layer (BL). The purpose of the present paper is to expand these observations in relation to processes within the “black box” and to synthesize existing data into a corallum-based model. Previous studies have focused on the physiology of coral cells and tissues, without consideration of the immense complexity and diversity of corallum morphologies. The proposed unified model is intended to address the processes of photosynthesis, calcification, and translocation of photosynthate in relation to morphology, irradiance field, hydrodynamic environment and BL conditions of the intact corallum.

Reef corals are coelenterates formed by a surface body wall and a basal body wall that enclose a space called the coelenteron. Terminology used here follows that of Galloway et al. (2007). The surface body wall in contact with sea water consists of two tissue layers—an outer epidermis and an inner gastrodermis separated by a jelly-like substance called mesoglia (Fig. 1). Likewise, the basal body wall consists of the calcicodermis and a gastrodermis separated by mesoglia. The coelenteron connects the polyps of a colony and opens to the external sea water through their mouths. The surface body wall epidermis contains nematocysts. The symbiotic zooxanthellae are located mainly within the cells of the gastrodermis in the surface body wall.

The zooxanthellae are photosynthetic and capable of providing all of the energy needed by the coral symbiosis (Muscatine et al., 1984). The basal wall consists of two cell layers: the cell layer adjacent to the skeleton is called the calcicodermis. A layer of gastrodermis lies between the calcicodermis and the coelenteron and separated from the calcicodermis by mesoglia.

The discovery that calcification in reef corals is enhanced by light (Kawaguti and Sakumoto, 1948) led to development of models that attempted to explain the mechanisms involved. Over the past 50 years a number of observations, hypotheses and reef coral calcification models have been presented (reviewed by Allemand et al., 2011; Cohen and Holcomb, 2009; Gattuso et al., 1999). Goreau (1959) proposed that calcification is accelerated in light due to removal of CO2 from calcification sites by photosynthetic zooxanthellae. This model requires placement of the zooxanthellae at or near the calcification sites, but they actually are located far from the site of calcification.

![Fig. 1. Simplified diagram summarizing the conceptual relationships between various components of reef coral metabolism according to three prominent hypotheses describing photosynthesis and light-enhanced calcification (simplified from Allemand et al., 2004). Zoox = zooxanthellae.](image-url)
Further, the proposed chemical reactions have not been supported by experiential data. The "trans-calcification" model (McConnaughey and Whelan, 1997) proposed that calcification in corals enhances photosynthesis by providing a source of protons that convert seawater HCO₃⁻ to CO₂ and H₂O, thereby supplying some of the CO₂ used in photosynthesis (Fig. 1). Allemand et al. (1998) suggested that OH⁻ produced by photosynthesis facilitate calcification by buffering the H⁺ produced during calcification (Fig. 1). Several studies involved observations on a broader spatial scale. Pearse and Muscatine (1971) showed that carbon is fixed by zooxanthellae on the sides of a coral branch and then transported to the rapidly calcifying branch tip. Coral calcification rate is highest in branch tips where zooxanthellae are not present (Goreau, 1963; Goreau and Goreau, 1959; Pearse and Muscatine, 1971).

Calcification occurs in the space between the calicodermis and the skeleton through a presumed proton transfer process that increases the pH of the fluid to a point where CaCO₃ will crystallize out as aragonite (Allemand et al., 2004; Cohen and Holcomb, 2009; Cohen and McConnaughey, 2003). Calcification in the space between the calicodermis and the skeleton is believed to be controlled by a "proton pump" (Allemand et al., 2004; Cohen and McConnaughey, 2003; Furla et al., 2000a). Such a pump has been demonstrated in sea anemones (Furla et al., 2000b) and is probably present in corals as well. Cohen and Holcomb (2009) suggested that under conditions of increasing OA the corals must expend more energy to remove H⁺ from the calcifying space in order to raise the pH of the contained seawater and convert the plentiful HCO₃⁻ to CO₂⁻ and H⁺. At high pH the CO₂⁻ in the calcifying fluid combines with Ca²⁺ to form the CaCO₃ crystals of the skeleton. Up to 30% of the coral’s energy budget may be devoted to calcification (Allemand et al., 2011).

In localized areas of the corallum undergoing rapid calcification, the gastrodermal layers are absent (Brown et al., 1983; Gladfelter, 1982, 1983; Tambutté et al., 2007). The result is a two-cell layer of very thin tissue that lacks zooxanthellae. Tambutté et al. (2007) conducted a detailed histological study of reef corals and concluded that tissues which calcify at the highest rates, or which initiate calcification, do not possess zooxanthellae. The contemporary four cell layer model of calcification (Allemand et al., 2004; Furla et al., 2000a) is shown in Fig. 2 compared to a modified version representing the two cell layers found in areas of rapid calcification. Previous models of calcification fall short in that they require placement of zooxanthellae near the site of calcification (Fig. 1) when in fact the rapidly calcifying locations lack the gastrodermis that contains the zooxanthellae (Fig. 2).

2. Background information

2.1. The role of carbonic anhydrase (CA) in coral metabolism

The CO₂, HCO₃⁻ and H⁺ involved in coral metabolism are interrelated by the reversible reaction:

$$\text{HCO}_3^- + \text{H}^+ \leftrightarrow \text{CO}_2 + \text{H}_2\text{O}$$

(1)

The reaction described in Eq. (1) is accelerated by CA which facilitates carbon dioxide transport (Enns, 1967). The reaction rate of CA is among the fastest of all enzymes, with a rate that typically is limited by the diffusion rate of its substrates. Coral tissues and zooxanthellae contain large amounts of CA (Graham and Smillie, 1976; Weis et al., 1989). CA undoubtedly plays a major role in controlling transport of CO₂ throughout the coral colony. Al-Horani et al. (2003a) identified three CA localities in corals. The first is CA bound to the membranes of the epidermal cells of the surface body wall, the second is CA bound to the membranes of the gastrodermal cells facing the coelenteron and the third is intracellular. Moya et al. (2008) found this enzyme to be localized in the calicodermis, which controls the precipitation of skeletal material. Wherever the conversion between CO₂ and HCO₃⁻ is very fast in comparison to the rate of diffusion a difference in HCO₃⁻...
concentration corresponding to the CO$_2$ tension difference will be established (Enns, 1967). In this case, HCO$_3^-$ diffusion will supplement CO$_2$ that is being removed by photosynthesis.

2.2. Relationships between coral photosynthesis and calcification

The relationship of photosynthesis to calcification is complex in a coral, but can be reduced to several basic equations. To the extent that CO$_2$ is the substrate, photosynthesis can be represented as:

$$
\text{CO}_2 + \text{H}_2\text{O} \rightarrow \text{CH}_2\text{O} + \text{O}_2
$$  \hspace{1cm} (2)

_Symbiodinium_ possess RUBISCO type II (Rowan et al., 1996) which has high oxygen affinity and uses CO$_2$ exclusively as a substrate. CO$_2$ occurs in very low concentration in seawater and in coral tissues. The CO$_2$ requirement is met by intracellular conversion of the abundant HCO$_3^-$ through the action of CA as described in Eq. (1) within the plant cells. At the typical pH of seawater, most of the total inorganic carbon (C$_T$) is in the form of HCO$_3^-$ (Horne, 1969). Bertucci et al. (2010) identified a H$^+$-ATPase “proton pump” in symbiotic zooxanthellae that appears to be involved in the acidification of the perisymbiotic space, which would promote conversion of the abundant HCO$_3^-$ to CO$_2$. Where HCO$_3^-$ is the primary source of inorganic carbon used in photosynthesis, as is the case of corals (Furla et al., 2000a; Weis et al., 1989), we can combine Eq. (1) and Eq. (2) into the balanced simplified equation:

$$
\text{HCO}_3^- + \text{H}^+ \rightarrow \text{CH}_2\text{O} + \text{O}_2
$$  \hspace{1cm} (3)

However, it is important to keep in mind that rapid interconversion between HCO$_3^-$ and CO$_2$ is occurring and that balanced Eq. (3) combines the processes shown in Eq. (2) and Eq. (1). Respiration can be represented as the reverse reaction of Eq. (3). Consequently, areas where rapid respiration is occurring will be producing large amounts of H$^+$ as well as HCO$_3^-$. The calcification process can be represented as:

$$
\text{HCO}_3^- + \text{Ca}^{++} \rightarrow \text{CaCO}_3 + \text{H}^+
$$  \hspace{1cm} (4)

Eq. (4) shows that the areas of a coral undergoing rapid calcification will precipitate the product CaCO$_3$, but must dissipate H$^+$ away from calcification sites. Eq. (3) and Eq. (4) indicate that both processes would compete for available HCO$_3^-$ if they occurred in the same space. Further, areas of rapid photosynthesis will require a large net influx of H$^+$ while areas of high calcification and respiration will require a net efflux of H$^+$. Thus, photosynthesis and calcification will potentially compete with each other for inorganic carbon if they are not spatially separated, while they have opposite and thus complimentary requirements for H$^+$ flux.

2.3. Spatial relationships

The common Hawaiian coral _Pocillopora meandrina_ (Fig. 3) is a typical branched coral species that represents a basic morphology that is most suitable in the visualization of several important spatial patterns as follows:

2.3.1. Spatial patterns of zooxanthellae distribution

The zooxanthellae-rich tissues of a typical branched coral colony are located in the deeper portions of the corallum, with very few of the photosynthetic zooxanthellae in the tissues of the branch tips. Numerous reports note the general lack of zooxanthellae in rapidly calcifying areas of a corallum (Al-Horani et al., 2005; Brown et al., 1983; Crossland and Barnes, 1974; Fang et al., 2004; Jaubert, 1977; Kajiwara et al., 1997; Lamberts, 1974; Marshall and Wright, 1998; Pearse and Muscatine, 1971; Santos et al., 2009; Tambutté et al., 2007). The zooxanthellae are abundant in the tissues on the sides of the branches of _P. meandrina_, but are largely absent on the growing tips (Fig. 3A). The deeper portions of the colony that contain high densities of zooxanthellae comprise an area that will be termed the zone of rapid photosynthesis (ZP).

2.3.2. Spatial patterns of skeletal growth

Areas of rapid calcification take up alizarin red stain (Lamberts, 1974). A colony of _P. meandrina_ that was grown for 24 h in 20 ppm alizarin red in seawater solution and cleaned of tissue is shown in Fig. 3B. Note that the rapidly calcifying tips incorporated the stain into the skeleton, but not in the deeper portions of the colony that had dense concentrations of zooxanthellae. The outer part of the colony that calcifies rapidly will be termed the zone of rapid calcification (ZC).

2.3.3. Spatial hydrodynamic regimes

The structure of the coral skeleton itself creates friction with moving water and reduces flow through the branched colony (Fig. 4). The branch tips that form the ZC are exposed to high water motion (Fig. 4, black arrows) while the polyps within the colony (ZP) experience a very different environment with low water exchange (Fig. 4, white arrows). The layer of slower flowing seawater adjacent to the coral tissue influences flux of material between the coral and the water column by both advective and diffusive processes and is called the boundary layer (BL). Shashar et al. (1996) evaluated three types of hydrodynamic boundary layers over a coral reef. The diffusion boundary layer (DBL) is related to diffusion-limited processes such as respiration, photosynthesis and calcification at the tissue–water interface and has a spatial scale of a few mm. The momentum boundary layer (MBL) is closely related to the skeletal morphology of a single colony which controls water movement in the proximity of the colony and operates on a scale of cm. The MBL is generally thicker than the
DBL by an order of magnitude. The benthic boundary layer (BBL) controls the interactions of the reef with open seawater and reflects the impact of the overall coral community structure of the reef on material exchange. The BBL is generally on the order of 1 m thick and related to roughness height. However, at the tissue–water interface the DBL is of greatest importance. For most corallum morphologies material exchange between the coral and the water column is controlled by the DBL as modified by the MBL. In some cases, such as massive thickets of the branching reef coral *Acropora*, the BBL may also be important.

As we shall see, the proposed basic model can be applied over multiple levels of organization from tissues (DBL) to colonies (MBL) to massive coral structures (BBL). For purposes of simplicity the term “boundary layer” (BL) will be used for the initial discussion and will include the DBL, MBL and BBL insofar as they influence material exchange between a living reef coral and seawater. For the generalized case (Fig. 5) the relationship between the BL, ZC and ZP in *P. meandrina* is represented in a simplified diagram of three hemispheres. Note the placement of the ZC between the ZP and the BL.

2.3.4. Primary and secondary calcification spatial patterns

Branches are characterized by rapid growth at the tip (extension) followed by secondary calcification (accretion) on the sides of the branches (Gladfelter, 1982, 1983). Density changes in the skeletons of massive corals result from differing rates of extension vs. accretion under different conditions of temperature, irradiance and water motion that occur on a seasonal cycle to produce skeletal banding patterns (Barnes and Lough, 1993). Fig. 6 shows a longitudinal and a transverse section of a branch of the coral *P. meandrina*. The longitudinal section (Fig. 6A) shows low density skeletal material formed at the growing tip in the area of primary calcification (ZC) with dense secondary thickening of the branch occurring deeper in the branched colony (ZP). The transverse section (Fig. 6B) from near the base of the branch shows the original low density material laid down as primary skeleton (labeled P) and dense secondary calcified material (labeled S) that was deposited on the branch sides in the ZP. Primary–secondary calcification is
an important component of coral metabolism that must be included in a universal model.

2.4. Mechanisms controlling material flux

Flux of material between the ZC, ZP and the external water column is controlled by both active and passive processes. The transport of Ca$^{2+}$, CO$_3^-$, HCO$_3^-$, O$_2$, and H$^+$ through the BL is limited by the physical processes of diffusion and advection (e.g., Kaandorp et al., 2005, 2011; Shashar et al., 1993, 1996). Kühl et al. (1995) measured strong pH gradients as well as O$_2$ gradients across the BL of corals. Hurld et al. (2011) showed that various temperate calcifiers show pH gradients within the diffusion boundary layers which appear to act as buffers to mainstream pH. For example, pH at the surface of the coralline algae was ~0.5 units higher in the light and ~0.35 units lower under darkness than in an ambient mainstream seawater. Tambuté et al. (1996) showed that transport of Ca$^{2+}$ across the epidermis and gastrodermis is passive, whereas transport across the calcidermis is active. Ca$^{2+}$ can diffuse from seawater to the coelenteron (Al-Horani et al., 2003b), but metabolic energy is needed for transport of Ca$^{2+}$ across the calcidermis into the enclosed space that forms the skeleton. Ca$^{2+}$ is transported over considerable distances within a colony with the direction of transport toward areas of maximum growth and calcification (Taylor, 1977). Likewise, photosynthate (CH$_2$O) is transported from areas of production toward areas of rapid calcification (Pearse and Muscatine, 1971; Taylor, 1977).

Translocation of metabolic material within the coral has been demonstrated experimentally (Fine et al., 2002; Pearse and Muscatine, 1971; Rinkevich and Loya, 1983; Taylor, 1977). One mechanism for such transport was described by Gladfelter (1983). Polyps of the coral Acropora cervicornis are connected into a complex gastrovascular system, which is lined with flagellated cells that can move the gastrovascular fluid at velocities of more than 2 cm min$^{-1}$. This type of circulation system serves to exchange fluids between the ZP and the ZC.

Proton flux away from the calcification site must occur for calcification to take place (Allemand et al., 1998; Jokiel, 2011; McConnaughey and Whelan, 1997; Smith and Key, 1975). There is an agreement that protons are stripped from bicarbonate and combined with calcium ion to form carbonate at the site of calcification (Fig. 1). Moya et al. (2008) and Furla et al. (2000a) proposed movement of protons away from the calcification site through two cell layers (calcidermis and gastrodermis) into the coelenteron where they are titrated by OH$^-$ produced by photosynthesis in the overlying gastrodermis. However, Brown et al. (1983), Tambuté et al. (2007) and Gladfelter (1982, 1983) have shown that rapidly calcifying areas of the coral (i.e. ZC) such as branch tips, septal margins, etc. have only two cell layers (calcidermis and epidermis separated by mesoglia) between the calcification site and the water column. These tissues are very thin and are missing the gastrodermis and the contained zooxanthellae. In this case the proton flux must be through the epidermal layers directly into the water column through the BL OH$^-$ derived from photosynthesis cannot be involved directly because the zooxanthellae are absent (Fig. 2B). The internal pH of coral animal cells is <6.0 (Venn et al., 2009), so there presumably is a strong diffusion gradient between the coral epidermis and the water column (pH approximately 8.1) and consequent rapid flux of H$^+$ out of the epidermis and into the water column. Regardless of the mechanism of H$^+$ transport and exchange within the coral, proton flux out of the ZC into the water column can ultimately be limited by diffusive and advective processes in the BL (Jokiel, 2011).

Coral show diel oxygen fluctuations that range from supersaturation (373% air saturation) in the light to oxygen depletion at darkness (Shashar et al., 1993), suggesting that diffusion is the dominant process controlling O$_2$ flux throughout the coralium supplemented by transport through the gastrovascular system. During the day high oxygen tension due to photosynthesis will stimulate respiration (Mass et al., 2010). In fact, hyperoxia is required for rapid calcification in corals (Colombo-Pallotta et al., 2010). Respiration at night produces low oxygen tension in the tissues and limits rate of respiration and thus limits rate of calcification.

2.5. Balancing proton flux

A proton centered metabolic model is attractive because [H$^+$] influences all biochemical reactions in the ZC and ZP. Production, uptake and movement of H$^+$ within the coralium influence localized pH within cells and tissues that control biochemical processes. Tracking the flow of protons between the calcification site and the water column is a valuable approach to understanding coral metabolism.

Total alkalinity ($A_T$) is a key concept to the understanding proton flux and is defined as the capacity of a solution to neutralize hydrogen ions. Coral calcification (Eq. (4)) lowers ($A_T$) within the corallium “black box”. However, there is no change in ($A_T$) associated with organic carbon production (Smith and Key, 1975), so photosynthesis and respiration (Eq. (3)) can cause dramatic changes in pH within an enclosed area without changing the capacity of the fluid to neutralize H$^+$. In contrast, calcification rapidly diminishes the ability of the tissues to neutralize protons. A corallum must dissipate approximately 1 mol of protons into the water column for every mole of CaCO$_3$ precipitated as coral skeleton (Eq. (4)). Balance between the coralium and the water column must be achieved either by movement of H$^+$ through the BL into the water column or by movement of additional inorganic carbonate (mostly HCO$_3^-$) from the water column through the BL and into the corallium. The latter is undesirable because HCO$_3^-$ is the major source of inorganic carbon for both photosynthesis and calcification and is in short supply. One additional mole of HCO$_3^-$ would be needed to neutralize the excess H$^+$ for every mole of CaCO$_3$ precipitated in addition to the 1 mol of HCO$_3^-$ needed as reactant plus the additional HCO$_3^-$ needed for photosynthesis that ultimately supplies energy for calcification. Therefore a mechanism for rapid net efflux of H$^+$ from the corallium that does not consume HCO$_3^-$ would be the most efficient means of maintaining a high rate of calcification while still maintaining a high rate of photosynthesis.

3. Synthesis of existing metabolic data into a model

There is a gradient in the density of zooxanthellae from the branch tip to the lower part of the corallium with a consequent gradient in the rates of calcification, respiration and photosynthesis (Goreau, 1959; Pearse and Muscatine, 1971). However, for a first approximation it is useful to simplify coral metabolism into a two compartment (ZP and ZC) model, focusing on proton flux within the two compartments and between the compartments and the water column provides a unifying dynamic principle that greatly simplifies understanding of coral metabolism. Hence it was given the name “two compartment proton flux model”.

3.1. Primary calcification, photosynthesis and translocation of photosynthate

The three dimensional hemispherical layers of the BL, ZC and ZP shown in Fig. 5 are reduced to a two dimensional diagram in Fig. 7. As noted in Section 2.1 the inter-conversion between HCO$_3^-$ and CO$_2$ (Eq. (1)) occurs at an extremely rapid rate during periods of high metabolism due to abundant CA. Therefore the model can be simplified using reversible Eq. (3) to represent photosynthesis and respiration. The proper spatial relationship places Eq. (3) (photosynthesis) in the ZP in the inner hemisphere. Eq. (4) (secondary calcification) also is shown in the ZP, Eq. (4) (primary calcification) along with Eq. (3) (respiration) is shown in the ZC. The major patterns of flux of H$^+$, HCO$_3^-$, O$_2$ and CH$_2$O were added as arrows. In Eq. (4) the HCO$_3^-$ and Ca$^{2+}$ are reactants. The arrow in Eq. (4) represents the calcification reaction that occurs within the corallium and may involve a number of
The products to the right of the reaction arrow are CaCO₃ and H⁺. The transported from the ZP to the ZC where they join protons generated by primary calcification (Eq. (3) and Eq. (4)) are needed to describe the model.

Fig. 7. Simplified model showing the spatial arrangement of the most important chemical reactions and flux of materials with an emphasis on protons. Note that only two equations (Eq. 3 and Eq. (4)) are needed to describe the model.

Important outcomes of this configuration are as follows:

3.1 The high oxygen flux required for respiration in the ZC is readily supplied as a by-product from photosynthetic production in the underlying ZP. Colombo-Pallotta et al. (2010) found that high calcification rate in corals depends on hyperoxic conditions. High oxygen concentration facilitates increased mitochondrial respiration in the ZC which, in turn, generates the large amount of ATP needed to support the rapid deposition of CaCO₃ in the ZC. During daylight hours much of the oxygen produced in the ZP is consumed by the high rate of respiration in the overlying ZC. Al-Horani et al. (2003a) found that gross photosynthesis was approximately seven times higher than net photosynthesis, indicating that respiration consumes most of the O₂ produced by the zooxanthellae. The respiration rate in light was approximately 12 times higher than in the dark. The coupling of gross photosynthesis and light respiration produces intense cycling of internal carbon and O₂. Thus hyperoxia is a key feature of reef coral metabolism that is managed very well by the coral under normal conditions though a variety of mechanisms. However, high oxygen tension can lead to oxidative stress and bleaching in corals exposed to abnormally high temperature and/or extremely high solar irradiance (Lesser, 2011).

3.1.2 High rates of respiration in the ZC produce large amounts of HCO₃⁻ that is available for calcification. Furla et al. (2000a) determined that the major source of C₃ used in calcification is from respiration (70–75% of total CaCO₃ deposition), while only 25–30% originates from the external seawater.

3.1.3 The high flux of H⁺ being generated in the ZC by calcification and respiration can be partially recycled and utilized in the underlying ZP, but most of the H⁺ must be dissipated through the BL as efflux into the surrounding seawater. Placement of the rapidly calcifying areas adjacent to the surrounding seawater facilitates rapid dissipation of the H⁺.

3.1.4 Primary calcification (extension) occurs in the ZC and secondary calcification (thickening) occurs in the NP. Thus the two calcification processes occur in very different physical and chemical environments, so rates of accretion, crystallization pattern and density of skeleton differ.

3.1.5 Positioning of the ZC outside of the ZP results in an optimal photosic environment for the zooxanthellae. The aragonite skeleton of the ZC absorbs damaging ultraviolet radiation (Reef et al., 2009), while transmitting and scattering photosynthetically active radiation (PAR) throughout the ZP [Enriquez et al., 2005]. Multiple scattering of the PAR by the skeleton in the ZC greatly increases absorption by the zooxanthellae in the ZP, leading to very high photosynthetic efficiency.

3.1.6 Placement of the ZC between the ZP and the water column allows for the vertical development of a stratified photosynthetic canopy without disruption of the ZC. If the ZP was located between the water column and the ZC, the coral would cease to calcify as the canopy became more highly developed. Jokiel and Morrissey (1986) report that net primary production as well as production efficiency in the coral Pocillopora damicornis (Fig. 5D) increases to a very high level with increasing canopy height.

3.2. Secondary calcification and photosynthesis

Once the basic framework is produced by rapid extension of the skeleton in the ZC, accretion continues to occur on the sides of the branches. This secondary calcification process occurs in the ZP and can continue for years. Hughes (1987) concluded that primary calcification allows rapid distal growth of branches which are subsequently strengthened by secondary calcification. The proposed model suggests
that secondary calcification has an additional value as a source of protons utilized in the ZP during rapid photosynthesis (Fig. 8).

3.3. Calcification in light and darkness

Photosynthesis ceases in darkness. Oxygen production stops and pH is lowered in the tissues due to respiration. As a result the reactions shown in Fig. 7 will largely be shut down during the night with minimal respiration and calcification. Kühl et al. (1995) report that in the light, photosynthesis resulted in a build-up of O₂ in the photosynthetic tissue of up to 250% air saturation and a tissue pH of up to 8.6, i.e. 0.7 pH units above the pH value of the overlying seawater, due to intense CO₂ fixation. In the dark, O₂ was depleted by the polyp and zooxanthellae respiration, and near anoxic (above the pH value of the overlying seawater, due to intense CO₂ fixation) both O₂ and pH pro-

4. Application of model at the corallum level of organization

4.1. Corallum morphologies

The generalized relationship shown in Fig. 7 is observed over a wide range of configurations and spatial scales (Fig. 9). Branched morphology creates an outer zone of calcifying branch tips exposed to turbulent water where rapid outward growth of the skeleton occurs and where solar irradiation is very high. Rapid photosynthesis occurs largely in the inner quiescent zone of the corallum. In branched colonies (e.g., Fig. 9A, D, and E) the ZC encompasses the outer tips of the branches. Perforate corals replicate the same spatial configuration but at a scale of mm rather than cm (Fig. 9B). Various combinations can be observed. Branched Acropora (Fig. 9A) combines the geometry shown in Fig. 9B and D. Corals with large polyps such as Fungia scutaria achieve layering of the ZC above the ZP by sandwiching dense populations of zooxanthellae in tissues between the septal plates (Fig. 9C), allowing rapid calcification to occur on the outer septal edges that project above the ZP.

At the upper end of the spatial scale (DBL) Kajiwara et al. (1997) studied large thickets of the coral Acropora pulchra and compared growth of outer white-tipped branches (ZC) to growth of brown-tipped branches (ZP) located deeper in the colony. Zooxanthellae concentration in the white-tipped branches was low compared to the dark-tipped branches. The white-tipped branches showed 3 times the skeletal weight increase and 14 times the linear extension increase of the brown-tipped branches. The authors concluded that white-tipped branches with a lightly-calcified skeleton expand the area covered by the coral colony while brown-tipped branches develop a heavily-calcified skeleton that strengthens the colony. Fang et al. (2004) showed higher concentrations of ATP in the white tip compared to the brown stalk, providing the ready supply of the energy needed for rapid calcification.

4.2. Plasticity of corallum growth form in relation to water motion and irradiance

From a topological point of view we can treat the myriad coral growth forms (Fig. 9) as simple hemispheres, with the hemispherical ZC encapsulating the ZP. The ZP is cut off from direct contact with the external seawater column by the ZC. The ZC can be highly porous to external seawater as in the case of loosely branched colony and less porous in tightly branched colonies. In perforate corals (Fig. 9B) and polyps (Fig. 9C) the ZP is isolated from the water column by the ZC. The ZC is isolated from the water column by the BL Flux of materials at the tissue–water interface will respond in a classic hydrodynamic manner. The inner interface of the ZC exchanges materials with the ZP. The ZP contact with the outer seawater column is through the ZC, so influx and efflux of materials responds to changes in the chemistry of the ZC as well as conditions outside of the corallum.

The model as presented in Fig. 7 represents a cross section at a given point on the hemispherical corallum. Water motion and irradiance are not uniform over the surface. Coral reef environments show strong vertical and horizontal gradients of both water motion and irradiance. A simple diagram showing how variation in water motion and
irradiance can influence colony growth form is shown in Fig. 10 for a massive coral and a branched coral. The colonies of many massive and branching coral species become more flattened and plate-like with increasing depth (e.g. Graus and MacIntire, 1976; Jaubert, 1977; Roos, 1967) in response to submarine radiance distribution (direction and intensity). Growth along an axis diminishes with decreasing irradiance. The Hawaiian coral Montipora capitata, for example, is a highly polymorphic species that can display a full range of growth forms from massive to branched to plate-like within a single large colony in response to localized differences in irradiance (Fig. 11A). The colony in the figure lacks zooxanthellae in the growing branch tips (white color) and the outer growing margins of the plates. The mechanism behind this remarkable growth response becomes clear if we examine the results of Jaubert (1977) in studies of the coral Synarea convexa (Fig. 11B) in relation to the proposed model. In shallow water, the zooxanthellae must avoid extreme levels of solar irradiance that would lead to photooxidation of photosynthetic pigments and develop dense concentrations deeper within the branched corallum where irradiance is optimal (Jokiel and Morrissey, 1986). Thus at high light intensity the colonies become hemispherical with branches lacking zooxanthellae at the tips. Irradiance is increasingly attenuated with water depth and the corallum flattens into plates that are oriented perpendicular to the axis of incoming irradiance. Encrusting and plate-like morphologies are simply modifications of the general hemispherical growth form with suppression of calcification along the vertical axis caused by encroachment of the ZP into the ZC (Fig. 10). Jaubert (1977) observed that at high irradiance the reef coral S. convexa grows into a branched morphology with tips that are free of zooxanthellae (Fig. 11). In deeper water the irradiance is diminished and the corals become plate-like, with the zooxanthellae occurring within 1.2 mm of the surface of the perforate corallum (Fig. 11B, “Plate-like a type”). As light diminishes further with increasing seawater depth, the zooxanthellae became more concentrated into a layer of less than 0.4 mm of the surface of the skeletal framework (Fig. 11B, “Plate-like b type”). Thus in low light environments the highest concentrations of zooxanthellae are found near or above the skeleton surface where according to the proposed model they would interfere with calcification by competing for HCO$_3^-$ and disrupting H$^+$ flux. In such cases, growth along the vertical is impaired relative to horizontal growth. Calcification can only continue in the horizontal plane along the margins and underside edges of the plates where irradiance is too low to support zooxanthellae. Such modification of colony growth into a horizontal plate is advantageous because a flat surface (cosine collector) is the most efficient morphology for collecting such vertical down-welling irradiance. Furthermore, formation of a thin skeletal plate requires a minimal expenditure of energy. The massive skeleton found in turbulent shallow waters is not needed in quiescent deep environments. Santos et al. (2009) described the movement of zooxanthellae through the perforate skeleton of M. capitata (Fig. 11A). When flat plates with dense populations of zooxanthellae on the upper surface were overturned, the zooxanthellae migrated or were transported vertically through the perforate skeleton over a period of several days. The zooxanthellae occupied the colorless tissues of the former underside to re-establish the original configuration.

Venn et al. (2011) studied calcification in micro-colonies of the coral Stylophora pistillata that were grown on glass microscope slides. The small corals grew outward rapidly along the margins of the thin flat corallum, allowing observation and measurement of the calcification process under the thin spreading tissues. The tissues growing at the edge of the flat disk were lacking zooxanthellae and thus were transparent. The use of pH indicator dyes confirmed high pH conditions in the calcifying space under the calicodermis. The micro-colonies existed as flat two-dimensional plates with polyps in the center (ZP) and a rapidly growing margin (ZC) that lacked zooxanthellae. According to the proposed model the zooxanthellae rich tissue in the center of the disk-shaped corallum will slow the underlying calcification (secondary calcification) with rapid growth on the edges (primary calcification). Therefore we only see rapid growth along the edges of the "pancake" until slow secondary calcification in the center (ZP) can build enough vertical structure to allow the coral to go into the branching mode of this species with the ZC at the tips. Presumably the rapidly growing edges of the corallum lack gastroderm as well as lacking zooxanthellae. This pattern is typical of the early stages of a newly settled planula larva.

**Fig. 10.** The relationship between the zone of primary calcification (ZC), zone of primary photosynthesis (ZP) and the boundary layer (BL) showing the relative changes across the corallum in relation to the localized changes in irradiance and water motion that occur with increasing water depth for a massive and a branched coral.
4.3. Other responses of the corallum to hydrodynamic regime

Areas between the polyps of certain species contain small spines or projections. Areas of the skeleton covered by the thin colorless tissue are more responsive to changes in water motion than adjacent areas (Jokiel, 1978). Increased water flow reduces the BL over these projections, increasing local skeletal growth and giving rise to the accessory projections (e.g., hoods, papillae, spines) that characterize many species of reef corals (e.g., Fig. 9A and E). In turbulent water these projections grow outward and increase frictional drag and protect the polyp. In calm, low light environments they remain oppressed. In addition to ability to modify their skeletons in response to hydrodynamic conditions, corals show remarkable biochemical plasticity that can augment the delivery of carbon to the site of assimilation. Lesser et al. (1994) showed a significant increase in photosynthesis, respiration and antioxidant enzymes under conditions of increased water motion.

4.4. Irradiance vs. hydrodynamics as forcing functions in computer simulations

Graus and MacIntire (1976) employed a computer simulation based on underwater radiance distribution at different depths and various skeletal growth parameters using the reef coral Montastrea annularis as a model. The resulting computer images are very similar to the actual radiographic images of coral skeletons taken from different light environments, suggesting that direction and intensity of irradiance control skeletal morphogenesis. On the other hand, Kaandorp et al. (2005) performed computer simulation experiments of growth in the coral Madracis mirabilis. Their model is entirely driven by a diffusion-limited BL process and can generate coral growth forms based on advection–diffusion limited absorption of CT in a hydrodynamic field, but will fail to simulate the transitions into the flattened form observed at lower irradiance. Incorporation of the two compartment proton flux model with irradiance associated changes in the position of the ZP relative to the ZC will resolve this issue.

Computer models based on only one of the two factors will still produce relevant output that is partially correct. Hydrodynamic factors impacting the BL will dominate in situations where irradiance is very high and saturates photosynthesis. Deep environments are characterized by low irradiance and low water motion that limits photosynthesis and calcification. The Kaandorp et al. (2005, 2011) model successfully produces three dimensional images of complex coral growth forms based on diffusion-limited CT supply on the reactant side of Eq. (4). This model will result in a prediction of increased coral growth under conditions of increasing OA when actually the opposite will be happening (Jokiel, 2011). The model could be improved by including the effect of diffusion-limited efflux of $[H^+]$ on the product side of the equation in addition to the effect of $C_T$ on the supply side.

4.5. Evolutionary considerations

Early in the evolution of reef corals their energy was obtained primarily through heterotrophic feeding. New possibilities arose once a symbiosis between zooxanthellae and the coral animal was established. Photosynthesis by the zooxanthellae provided the energy needed by the host coral in order to form the fast growing skeletons that give corals a competitive advantage over other sessile organisms. Natural selection favored the ever increasing rates of photosynthesis in shallow tropical seas where plankton is scarce, but where solar radiation is abundant. The evolution of skeletal architectures that place the ZC between the ZP and the surrounding seawater solved the problem of ridding excess protons while providing many other advantages. The success of two important scleractinian coral families (Acroporidae, Poritidae) can be attributed to the innovation of the perforate skeleton, which allows extremely efficient layering of the ZC over the ZP with retention of $H^+$ from secondary calcification in the ZP. Placement of the zooxanthellae within the porous skeleton reduces the importance of the polyps as photosynthetic sites. This in turn allows reduction in polyp size and

![Fig. 11. A. Single large colony of the reef coral Montipora capricornis shows branching morphology in shallow water grading into plate-like growth form in deeper water. B. Illustrations after Jaubert (1977) for the perforate coral Synanthea convexa showing the change in growth form and distribution of zooxanthellae that occur with increasing depth and decreasing irradiance. (Zooxanthellae represented as dots.)](image-url)
5. Conclusions

A synthesis of existing information on coral reef metabolism into a spatially correct coralium model reconciles many paradoxes surrounding reef coral biology and leads to important hypotheses. Spatial separation of the areas of rapid photosynthesis from the areas of rapid calcification reduces competition for HCO₃⁻ between photosynthesis (Eq. (3)) and calcification (Eq. (4)) and simultaneously enhances rapid recycling of materials between the two processes. The model emphasizes the importance of the spatial arrangement of ZP, ZC and BL in regard to proton flux between the compartments, and with the external seawater. Potentially toxic O₂ from photosynthesis in the ZP becomes an asset when consumed by rapid respiration in the ZC to provide the energy for high rates of calcification. In turn, the HCO₃⁻ produced by respiration in the ZC supports the high rate of photosynthesis in the underlying ZP. Placement of the ZC outside of the ZP facilitates rapid efflux of H⁺ into the water column during periods of rapid calcification. Translocation of photosynthetic energy serves a dual role of transporting the waste product H⁺ from secondary calcification as well as photosynthetic energy from the ZP to the ZC where the excess protons can be readily dissipated into the water column. The proposed two compartment proton flux model is consistent with results of diverse reef coral experiments and observations ranging from biochemical to ecological. Furthermore, the proposed scheme provides a means of synthesizing past results to explain many puzzling aspects of coral growth form and function. This model is consistent with the conclusion (Jokiel, 2011) that reduced coral skeletal growth rate under conditions of increasing global OA is caused by diffusion limitation of net H⁺ transport through the barrier due to increasing of [H⁺] in the water column.

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