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Essay

Not-so-mutually beneficial coral symbiosis

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The partnership between corals and their intracellular algal symbionts has long been a textbook example of a mutually beneficial association. Here I argue that this view has been made obsolete by a steady accumulation of evidence over the past three decades. The coral–algal relationship is perhaps better viewed as one of domestication — think of it like a cattle farm, in which the coral is the farmer and the algae are the cows. I synthesize old and new evidence in support of this updated view and highlight remaining knowledge gaps, the largest of which continues to be the natural history of algal symbionts.

Coral reefs are in trouble worldwide, largely due to the susceptibility of coral–algal symbioses to rising sea-surface temperatures. Under prolonged heat stress, corals lose their brown-colored algal symbionts and become white (coral bleaching), which can result in widespread coral mortality. This situation urgently calls for a deeper functional understanding of coral–algal symbiosis. At the center of this symbiosis are the dinoflagellate algae of the highly diverse family Symbiodiniaceae[1] that associate with reef-building corals, other Cnidaria (sea anemones, jellyfish), and other marine animals ranging from ciliates (*Euplotes*) to giant clams (*Tridacna*). In the majority of these cases the symbionts are not passed on from the parent to offspring (vertical transmission) but must be acquired by the juvenile host from its environment (horizontal transmission) — this will become important for understanding the dissolution of the symbiosis as well, as we will see below. Once the symbiosis is formed, the classical view posits that the animal host fertilizes the symbiotic algae with nitrogen recycled from its metabolism. This nitrogen promotes algal growth and prompts symbionts to share their energy-rich photosynthetic products with the host coral. Thus, coral helps alga, and alga helps coral. However, there is little experimental evidence for such a harmonious relationship. More than a decade ago, Scott Wooldridge argued[2] that "Far from being unequivocally mutualistic, [coral–algal symbiosis] functioning is best explained in terms of a controlled parasitism whereby the coral host actively 'farms' its domesticated algae in order to optimize the receipt of autotrophic energy." The idea did not take hold at first because many details were still vague. Now, many of the knowledge gaps have been filled by findings based on isotope imaging, gene expression, and genetic manipulation.

Nitrogen

First and foremost, corals and other symbiotic Cnidaria do not 'fertilize' their algae with nitrogen. On the contrary, they make every effort to withhold it from the algae, as a method of controlling their growth and reproduction. The fact that algae in the symbiotic state are nitrogen-limited has been known for some time[3,4]. Recent studies in sea anemones[5,6] and other symbiotic cnidaria, including corals[7,8], have confirmed that the cnidarian host locks up intracellular ammonia in non-essential amino acids through the action of glutamine synthase and associated enzymes (Figure 1A). The energy needed for this 'ammonia scrubbing' comes from carbohydrates that the nitrogen-starved algae produce through photosynthesis, forming a vicious negative feedback loop: the more photosynthetic product the algae give to the host, the more the host limits their growth[8].

What if nitrogen becomes available externally, from the surrounding water? When this occurs, the nitrogen comes mostly in the form of nitrate, which cannot be processed by the host but is readily assimilated by the algae — hardly surprising considering their nitrogen-starved condition. Sub-cellular isotope visualization has revealed that a short pulse of nitrate (or ammonium, for that matter) shows up in algal cells within minutes[9,10]. In the case of external ammonium, the host makes an effort to compete[11], but the algae still get several-fold more. Temporarily freed from their nitrogen limitation, the algae start growing and dividing[4,12], using their photosynthetic product for themselves instead of giving it away to the host.

How does the coral regain control and protect itself from 'cheater' symbionts that do not produce enough carbohydrates? Cheater control is fundamental to any symbiosis[13], but in the case of corals we still don't know how it works. Early studies suggested that those algae that choose to divide instead of 'working' for the host are simply evicted[14]. However, although corals do release more algae when external nitrogen is supplied[4], it is not necessarily the algae that are in the process of dividing[14]. A possible alternative is to digest the algae that don't give away enough photosynthetic product. Conveniently, digesting would simultaneously cull the cheaters and transfer the nitrogen that they have assimilated (the likely cause of cheating!) to the host. A direct investigation of this way of cheater control is still pending, but there are three lines of circumstantial evidence. The first one is that the vacuoles containing photosynthesis-inhibited algae are rapidly labeled by Rab11, the protein that mediates lysosomal fusion, ostensibly targeting them for digestion[15]. The second one is the observation that when a coral hosts an additional algal strain in low abundance, that strain strongly up-regulates its photosynthesis machinery[16]. This suggests that doing more photosynthesis for the host improves your chances as an underdog symbiont. The third line of evidence is based on the observation that, when nitrate and phosphorus are plentiful, about 3.5% of the symbiont population goes missing (likely digested) every day[12]. This matches algal degradation rates directly observed in a coral[17] and would explain efficient transfer of external nitrogen to the host[12]. When the external nitrogen pulse ends, corals seem to continue digesting their symbionts for a while until (presumably) the algae that have assimilated excess nitrogen are gone, nitrogen is limiting again, and the overall symbiont abundance returns to pre-pulse (low) levels[12]. It is interesting to note that both host and the algae grow better under nutrient-replete conditions[12],

contrary to the classical dogma that corals are specifically adapted to nutrient-poor waters.

Carbon

Although the coral doesn't 'fertilize' algae with nitrogen, it does provide them with plenty of carbon dioxide to fix through photosynthesis. The coral uses vacuolar-type H⁺-ATPase (VHA, Figure 1A) to actively pump protons into its algal-containing vacuoles (called symbiosomes), lowering their internal pH to about 4; at this pH, the dissolved bicarbonate is converted to carbon dioxide, which is directly used for photosynthesis[18]. This is a great strategy for the host, because the algae are forced to fix carbon, but without nitrogen they cannot grow, so they have to give up all their photosynthetic product to the host. This is where the analogy with a cattle farm emerges: the coral host ('farmer') tightly controls the reproduction of the symbionts ('cows') through nitrogen limitation while feeding them carbon dioxide ('hay') ad libitum so they keep producing the photosynthetic product ('milk') that the coral uses for its own needs (Figure 1A). The farm analogy is complete with the fact that the coral digests ('slaughters') 1–7% of its symbionts daily[17], as an additional method of population control and to obtain other nutrients (nitrogen and phosphorus) in addition to carbon[12].

A still-missing part of the coral carbon-concentration mechanism is how bicarbonate in symbiosomes is replenished. One promising candidate is SLC4δ, a putative electrogenic sodium-bicarbonate cotransporter[19] that would move bicarbonate inside the symbiosome, following the electrical charge created by VHA. I could not find any reports of this protein's cellular localization or gene expression in the existing literature.

Another missing part of the puzzle is how the coral acquires bicarbonate from seawater. External bicarbonate rapidly equilibrates with the coral's gut cavity, apparently by passive water exchange[20], but it is not clear how it enters the gut cells that contain algal symbionts. The uptake of bicarbonate by coral tissue is highly elevated in the presence of light, and is sensitive to inhibitors of carbonic anhydrase, H⁺-ATPase, and anion transporters[20,21].

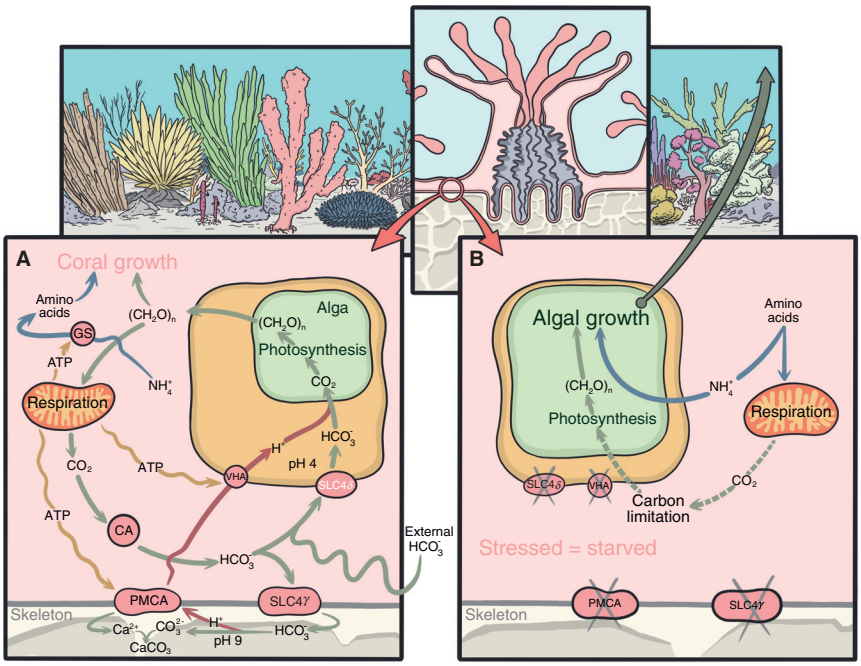

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Figure 1. Metabolic interactions between a coral and its algal symbiont, under normal and stressed conditions.

Under the updated view of coral–algal symbiosis, a coral 'milks' fixed carbon from its symbiotic algae by 'feeding' them CO_2 while withholding nitrogen (via action of glutamine synthase, GS) to prevent algal growth and reproduction. (A) Under normal conditions, the coral V-type H⁺-ATPase (VHA) pumps protons into the vacuole containing an algal symbiont ('symbiosome')[18], which converts bicarbonate (imported via an unknown mechanism, putatively electrogenic and involving the sodium-bicarbonate symporter SLC4δ) to carbon dioxide. At the same time, coral binds all the available nitrogen (NH_4^+) into amino acids[5,8]. The lack of nitrogen prompts algae to give up their photosynthetic product, $(CH_2O)_n$, which the coral uses for its own growth and metabolism, including powering the nitrogen sequestration and carbon concentration mechanisms[8]. Carbon dioxide produced during respiration is recycled into bicarbonate with the help of carbonic anhydrase (CA) and is used for photosynthesis or calcification. Calcification involves the coral-specific bicarbonate transporter SLC4γ[19,26] and plasma membrane calcium ATPase (PMCA). Together, they replenish the protons for the carbon concentration loop and promote deposition of calcium carbonate skeleton[25]. (B) Under stress, the coral is energy-starved, and both the nitrogen-sequestration and carbon-concentration loops stop. The coral starts metabolizing its own amino acids for energy, releasing nitrogen to symbionts[35]. The symbionts begin retaining fixed carbon and growing but their photosynthesis is now carbon-limited[30] because the host's carbon concentration loop is inactive. At this stage they leave the coral (or are evicted by it) in the process known as coral bleaching.

These data are promising, but do not necessarily indicate that these proteins are directly involved in import of external bicarbonate. Instead, the observed sensitivities may reflect the fact that these proteins are the key players in the carbon-concentration loop depicted in Figure 1A. The two likely mechanisms of bicarbonate entry into coral gut cells are via a chloride–bicarbonate exchanger (a good candidate is a protein from the SLC26 family[19]), and/or via the action of membrane-bound external carbonic anhydrase, which would convert bicarbonate into membrane-permeating carbon dioxide[22].

Calcification

Calcification in corals, just like bicarbonate uptake by coral tissues, is greatly enhanced by light[20,23] and appears to be an integral part of the carbon concentration mechanism for photosynthesis. Plasma membrane calcium ATPase (PMCA) pumps protons into the coral tissue from the space underneath it, compensating for the loss of protons due to VHA pumping them into symbiosomes (Figure 1A). At the same time, pH under the tissue increases to about 9, which converts bicarbonate to carbonate and results in calcium carbonate deposition[24]. This idea is essentially a recast of

the 'trans-calcification' hypothesis of McConnaughey and Whelan[25], which postulated that calcification generates protons for bicarbonate assimilation in photosynthesis. Notably, 70–75% of the bicarbonate that serves as a carbon source for calcification (underneath coral tissue) is derived from coral's metabolism[20] and is secreted out of the tissue via the SLC4γ bicarbonate transporter, a protein specific to reef-building (that is, calcifying) corals[19]. In a spectacular recent experiment, the direct involvement of SLC4γ in coral skeleton deposition was shown when a CRISPR/Cas9 knockdown of the gene resulted in fully formed juvenile corals lacking skeleton[26].

Bleaching

It makes sense to assume that coral bleaching — that is, the loss of algal symbionts — occurs when the processes shown in Figure 1A slow down or stop entirely. For symbionts, this slow down primarily means that nitrogen becomes available, giving them a chance to switch to a selfish mode in which they start retaining their photosynthetic product, accumulating lipid stores, and multiplying[27–29]. This situation would be similar to nitrogen-replete conditions described in the previous section, with one important difference: the host does not 'feed' them carbon anymore, so the algae would quickly become carbon-limited. Carbon limitation of the algae might be the actual trigger for the algae to leave, or for the coral to evict the algae — an idea proposed by Wooldridge 15 years ago[30].

What are the initial events that lead to coral bleaching, and who initiates them, host or symbiont? Considering the second question first, it is reasonable to propose that it would be algal symbionts, not the host, that would initiate bleaching. Bleaching does not benefit the coral host in any way — it only exposes it to high risk of mortality and, even under the best scenario, stunts its growth rate for weeks. The highly influential Adaptive Bleaching Hypothesis[31], which proposed that corals drive bleaching to change their symbionts to a better adapted strain, did not receive experimental support: most commonly, bleached corals recover with the same symbiont clone that they had previously[32]. In contrast, from the point of view of a horizontally transmitted symbiont, escaping the stressed host is a perfectly reasonable response to avoid 'going down with the ship' and instead try to infect a new juvenile host[33]. It is important to note that corals mass-spawn during the steepest seasonal temperature ramp-up[34], and so young coral recruits are indeed available for symbiont infection during the hottest months of the year, when bleaching is the most likely. A simple dynamic model predicts that, if bleaching on a thermal cue helps the algae transmit to the next generation of corals and if coral recruits are abundant, then bleaching-susceptible symbionts should prevail over bleaching-tolerant ones[33].

For the symbiont to initiate bleaching upon sensing that the host is stressed (albeit unclear how), it might be sufficient to simply withhold the photosynthetic product, thereby de-powering the host's nitrogen sequestration and carbon concentration loops (Figure 1B)[2]. When only a single symbiont cell out of many retains its photosynthetic product, essentially 'cheating', this would initiate an appropriate local-scale action by the host — probably digestion of the misbehaving alga directly by the gastrodermal cell containing it or after eviction into the gut cavity. But when the whole symbiont population rebels, it should lead to coral-wide energy starvation and a more systemic response. Gene expression analysis indicated that the host indeed looks starved immediately prior to and during bleaching, degrading its own amino acids for energy and making nitrogen available for the algae to use[35].

This view is very different from the currently prevailing 'oxidative theory of bleaching'[36], which postulates that bleaching is primarily the result of oxidative damage to the symbiont's photosystem, which in turn leads to damage to host tissues. This theory implies that, during bleaching, the symbiont should suffer the most damage, an expectation that does not align with the facts that symbionts released during bleaching typically have healthy photosynthesis[27] and show little or no gene expression changes in response to stress[37]. In contrast, the bleaching coral host launches a broad gene-expression response, the same irrespective of whether light was part of the stress — it could be heat, cold, low salinity, or even immune challenge[38].

Overall, it looks as though at the onset of bleaching, the host is stressed, whereas the symbiont is not. Still, the coral host's stress condition includes accumulation of oxidative damage starting several days prior to visible bleaching[35], so it is possible that it ejects the non-productive, carbon-limited (but otherwise healthy) symbionts to avoid further oxidative harm — so in this regard, that part of the oxidative theory of bleaching might yet be true. But at present, the role of reactive oxygen species in bleaching is far from being established[39].

Implications and knowledge gaps

The view presented here calls for one important change in how we study coral biology: we need new ways to monitor the state of coral–algal symbiosis. As of today, the most commonly used measure is the effective quantum yield of algal photosynthesis, because the old paradigm held that disruption of algal photosynthesis is the key trigger of bleaching[36]. Proponents of the new view[35] argue that the state of symbiosis would be better characterized by monitoring the 'farming' effort of the coral — symbiosome acidification and nitrogen scrubbing — as well as signatures of symbionts getting ready to break free by storing lipids and assimilating nitrogen. Establishing quick standardized assays for these processes — ones not requiring gene expression analysis or isotope tracing — is an immediate research priority.

The coral-symbiosis puzzle is still missing many pieces. The mechanism of the host's cheater control, the key element of any symbiosis, remains unknown. Bicarbonate transport into the symbiosome is the central part of the carbon concentration loop (Figure 1A) but we still don't know how it happens (the involvement of the SLC4δ transporter is but a hypothesis). The mechanism delivering external bicarbonate into coral cells is also still unclear. The scheme in Figure 1A deliberately glosses over the fact that coral tissue is composed of several cell layers that all the fluxes shown must somehow navigate. The initiation of bleaching is a process of enormous ecological significance, with numerous possible ways of how it could happen[40]. But arguably the largest knowledge gap

in coral biology that still receives very little attention is the natural history of the algae. What adaptations do they have to thrive, spread, and compete with their peers in such a brutally exploitative setting as the new view presents? Do they really initiate the bleaching process? If so, how do they 'know' that the host is stressed? Can symbionts released during bleaching really infect new coral recruits? How does all of this depend on whether their transmission between coral generations is vertical (from parent to offspring) or horizontal (through environment)? Coral research has thus far been dominated by studies focused on the well-being and survival of the coral host. Perhaps it is time to start looking at variation and evolution of coral symbiosis from the algal perspective, lest we miss half of this complicated — and, it seems, surprisingly shrewd — relationship.

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DECLARATION OF INTERESTS

The author declares no competing interests.

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