

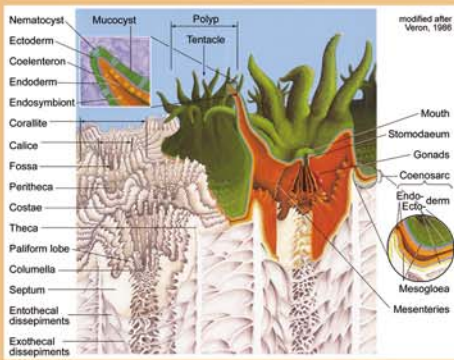


Symbiotic Relationships in Corals

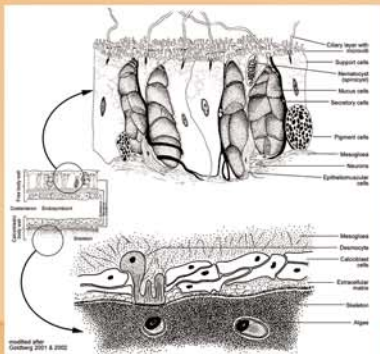
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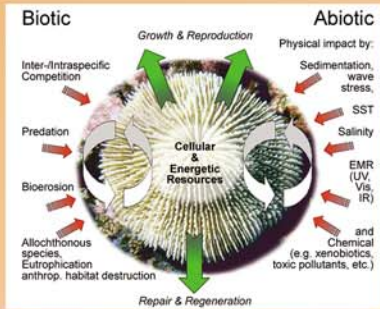
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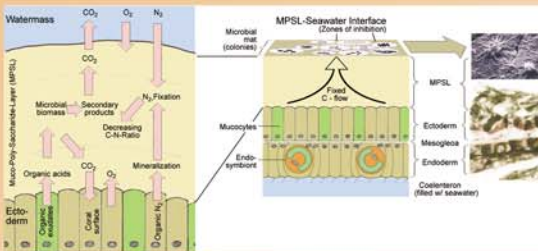
Schematic diagram of the major anatomical elements of the basic skeletal features of scleractinian corals.



Cross-section through the ectodermal layer of the stony coral *Mycetophyllia reesi*. Top: theoretical stratification of the coral surface MPSL. Bottom: Calcioblastic layer in charge of Calcium-carbonate accretion.



Under optimal environmental conditions, reefs oscillate around their climax populations. Thereby each organism (here coral) can accumulate minor energy reserves that enable it to resist certain a/biotic stressors and thereby improve its chance of survival slightly. This net advantage is used to maintain repair-, regeneration, and growth processes and to further strengthen its stress-resisting buffer.



Proposed model of the microbial contribution to coral nourishment. This includes contribution by symbiotic algae, endolithic community, suspension and detritus feeding, and coral mucus microbial community.



A reef section bleached by rising Sea-Surface Temperatures. Due to the build-up of toxic by-products, the coral host expels its endosymbionts. Deprived of energy, bleached colonies die unless temperatures go back to normal and endosymbionts are phagocytized back into the tissue.

Synopsis

All living organisms are equipped with some sort of survival strategies. Each one knows what kind of food it needs and what means to use in order to avoid or defend itself against predators. Under certain circumstances though, organisms of various taxa go even further and establish unique alliances that benefit all participants and even the ecosystem. Yet, because of this relationship and instead of being consumed as a meal, the hosting species enables potential symbionts to thrive within it and to carry out tasks for complementary usage.

An excellent example of this beneficial symbiosis is the coral animal and its associated endosymbionts as well as "exosymbionts". Thereby, neither population could exist without the other with the size of each is determined by that of the other (this is valid for the coral host, but to a lesser extent to its associated symbionts). Rudimentary lineages as a result of evolutionary processes on one side and the constant interaction of living system on the other made it possible that seemingly independent constituents perform tasks that complemented the nutritional spectrum of potential partners. This must have happened in a way that the species involved went into a downward causation and self-organization, which enabled them to co-exist and contribute to benefit the partnership as a whole. At the same time, each component was able to determine the appearance and behavior of this highly organized being. Hence, it is useless to ask whether the coral or the symbionts came first; both were able to go into an evolutionary process, a form of metasystem transition that shaped this co-operation and helped to gain a competitive advantage.

However, we could ask, how can completely different species evolve separately from distinct ancestors, yet depend on each other to exist? The answer is embedded in the trophic status of coral animals. Both production and decomposition processes on coral reefs are exquisitely tied to their structural organization at all levels (in the physiological, physiographic and community sense to underline the holistic principles of community stability). The energetic pools within a reef seem so large, but considering that they are spread over huge areas across the circum-tropical belt in an oligotrophic environment attributes a relativistic momentum to this abundance. Close to the trophic base of this abundance are hermatypic corals living in a symbiotic relationship with endosymbiotic dinoflagellates and exosymbiotic microbial associations. Altogether, the "economic" benefit of these partnerships can be summarized by an increased competitive advantage in viable offspring, resource partitioning and substrate acquisition on an already crowded substrate. However, this partnership restricts physiological tolerances to a rather restricted optimum "window" (i.e. abiotic conditions such as temperature, light, sedimentation, eutrophication, etc.) that suit all participants. Within limits, such a narrow range of tolerance highlight the stenobiotic environmental conditions that must have prevailed over long periods of time to establish the mutual benefits necessary for their establishment and survival.

Introduction

Margulis' fundamental thesis is that organisms are amalgams of several different strains of microorganisms: bacterial endosymbionts are necessary mediators in the creation of complex life forms. Complex organisms cannot exist without the eukaryotic cell-type – likewise the result of the fusion of at least two different kinds of organisms. Symbiogenesis of this kind has been common in the evolutionary history of life and actually accounts for the diversity of living beings, as we know it today. As a result, scientists have proposed the serial endosymbiosis theory (SET), which specifies the relationship between organisms, which live together in a mutual relationship that benefits all parties involved. The evolutionary success of such interactions are thought to be more prevalent in stable, non-seasonal, non-fluctuating environments, and thus more common in the tropics than in temperate regions: e.g. chronic symbiosis is of key importance in reef-building corals. Mutualism of this kind may be regarded as the outcome of "genomic recombinations" in which the resultant phenotypes of the interacting organisms are fitter than each would have been when not interacting. Such genomic recombination had the greatest evolutionary potential in primeval aquatic environments. While Darwin emphasized competition as the driving process of evolution, Margulis places the focus on cooperation. With organisms possessing far greater degrees of freedom than unanimated entities, the rate, the intensity and the outcome of such interactions cannot but accelerate an already induced process. The result of this driving force is most obvious in symbiotic associations, by which independent organisms associate to form a tightly coupled system and eventually merge to establish something that is better suited to cope with the environmental status quo. Thus, symbiosis is a major driving force behind continuously and finely adjusting biota, thereby assigning the organismic world a global dominance.

Corals as the centerpiece in a healthy reef ecosystem

Symbiotic relationships are primarily responsible for the success of benthic reef communities in the tropics. Reef corals in particular not only rely on the important relationship between them and their autotrophic endosymbionts (dinoflagellates of the genus *Symbiodinium* sp., commonly, but incorrectly referred to as zooxanthellae), corals also acquire a substantial amount of their energetic and nutrient requirements by heterotrophy (the in/direct ingestion of zooplankton and other organic particles from the water column and the Mucopolysaccharide Layer (MPSL). The endosymbionts reside within vacuoles in the cells of the host gastrodermis where they serve as primary producers and supply their coral host with up to 95% of their photoassimilates, such as sugars, amino acids, carbohydrates and small peptides making corals autotrophic with respect to carbon. The bacterial exosymbionts cultivated by the coral's own MPSL are likewise used for nutritional requirements. More important though, is their important function in shielding the coral's soft tissue against opportunistic microbial settlers. A third source of resource allocation is the coral's endolithic community that may satisfy 55-65% of the coral's nitrogen requirements. Together these energetic pathways enable the coral to perform its metabolic needs for growth, reproduction, and the deposition of its CaCO₃ skeleton.

Conclusion

The co-specialization of organisms from different taxa and their associated complementary properties culminated in symbiotic relationships and is the result of a system-immanent, self-organized response to stable long-term environmental conditions. In the tropics, many of the recurring benthic fauna "cultivate" symbionts; a trend that extends through most of the marine invertebrate phyla. In fact, these relationships requires that all involved parties do adapt themselves in a way that makes the organismic complex more fit for existence. Hence, only via utilization of the principles of self-organisation are coral-reef ecosystems able to achieve such high levels of productivity in an otherwise hostile and nutrient-deprived environment. Regardless of the change in ecosystem (the biological adaptation in which the genetic composition of the holobiont is altered), it neither involves speciation nor extinction. However, global ecosystem stability faces a reemerging challenge: global climate change. Thereby, the gradually acquired dynamic equilibrium that lead to the establishment of symbiotic relationships is no longer able to respond fast enough to rapidly and frequently occurring stress events (within the lifetimes of the partners). Adaptive change may occur over the course of multiple repetitive stress events, but may take several generations to become established at species, community and ecosystem level. In the meantime ecosystem complexity as we know it will definitely undergo dramatic changes.