c7 Organic reefs indicate a warm shallow-water marine environment < Sractinian corals, red algae, cyanobacteria >

> *¿Por qué yo vivo desterrado / del esplendos de las naranjas?* (Why do I live in exile / away from the brightness of oranges?) —Pablo Neruda (Neftalí Ricardo Reyes Basoalto, 1904-1973).[1]

Atolls and organic-reef cays (pronounced *keys* and spelt so in the Caribbean) (after Spanish *cayos* meaning "small island") are "oases" in the warm blue-seawater "deserts" (nutrient deficient parts) of the oceans. The abundance and diversity of reef life is the more remarkable for its isolation. Reef-building corals are not found where nutrients are abundant in cold-water upwells or where nutrient-rich waters sweep over shelves. Why are the reef corals exiled from this abundance?

Scleractinian corals (aragonite skeleton) live in shallow warm marine water. These true (stony or hard) corals build barrier reefs, fringing reefs, and atolls. Much of these reefs with a glue of sponges is also built by wave-resistant coralline encrusting red algae (commonly *Lithothamnion*).[2] This has long been so. Some corals do live in cold water and others do live in sunless deep water. None of these typically build extensive reefs (***Footnote c7.1***). However, a submerged living patch reef built by *Lophelia pertusa* (an algae-free scleractinian framework forming coral)[3] atop the Sula Ridge of the mid-Norwegian shelf and has dimensions: 13 km length, 0.5 km width, and 10-50 meters height.[4]

Stony corals, sea anemones, sea pens, and jellyfishes belong to the phylum Coelenterata or Cnidaria (which preferred name is pronounced *ni-dar-e-a*, from Gk. *knide* for sea nettle—which explains why the *c*, like *k* in *knife*, is silent). The defining feature of cnidarians are stinging cells (nematocysts).[5] Designed to paralyze fish, these are located on tentacles of the cnidarians. (A grown Australian box jellyfish, *Chironex fleckeri*, has a foot wide bell, sixty, seven-foot long tentacles with 2.5 million nematocysts per inch—a brush against one tentacle can kill a human.) Reef-building stony corals, sea anemones, and sea pens are anthozoans. Anthozoans unlike other cnidarians completely lack a medusa stage and live exclusively as polyps. The hermaphroditic polyps of stony corals, as so of *Acropora*, Elkhorn, *Goniastrea* and Cauliflower, propagate by occasionally venting clouds of sperm and eggs and by budding and fragmentation (thus storms that, and people who, physically break up a reef also propagate it). The platform-reef building anthozoans supplement their ingested diet of fish and small food particles by harboring, in their transparent colorless flesh, colorful symbiotic algae (which, when outside of that habitat, live as dinoflagellates). These harness Sun's energy and in the coral's flesh, in exchange for fertilizer and a home, produce sugars which nutrients the coral absorbs into its bodily fluids. Not all coral cnidarians (anthozoans) are reef building and not all are carnivores. Katharina Fabricius in 1995 described from the Red Sea four soft corals that eat plants. *Dendronzephthya hemprichi* is one. It does not have any symbiotic algae and is not a reef builder. Its stinging cells are less potent than those of stony, reef-building, corals and unlike those it is unable to paralyze and hold on to zooplankton (tiny marine animals) with its tentacles. It does capture, and ingest, phytoplankton (single-celled algae). With a nod (tentacle wave) to Georgyi Frantsevitch Gause's (1910-1986) competitive exclusion rule,[6] by occupying a different niche (pronounced *nitch*, L. for *nest*), vegetarian corals can thrive on reefs built by stony corals but, as so for other soft-bodied reef dwellers, they do not contribute directly to the reef's stony mass.[7]

Platform-reef building stony corals live in shallow-marine water in tropical and subtropical regions where evaporation produces aragonite supersaturation (concentrations of calcium and carbonate ions that exceed calcite-water thermodynamic equilibrium) (***Figure c7.1***). Calcification is also apparently aided by the algae normally present in their flesh. What species of algae does can be a function of sunlight intensity at different depths and in micro-environments in the reef: red light attenuates rapidly with depth; blue light reaches further, lessening in intensity to nothing at the depth of 150 meters in clear water. A pigmented molecule called *rhodopsin* helps many creatures harvest biochemical energy from light. A red-reacting variant of it occurs in shallow water phytoplankton and blue-reacting variant in the deep dwellers of the photic zone. Robert Rowan reported in 1997 that dominant corals of western Atlantic reefs (*Montastraea annularis* boulder star coral, *M. faveolata*, and *M. franksi*) host, in each, three algal symbionts. The proportions of these are found to follow changing environmental factors such as seasonal light intensity and salinity. For these corals, and for mutualisms in general, Rowan finds "the ability to cope with environmental change through changes in symbiont community composition reflects the selective advantage of hosting several distinct symbionts, despite the potential for destabilizing competition among them."[8] Robert W. Buddemeier speculates that the reef-building corals can manipulate, and stay from becoming obligate symbionts of, the algae they host because they retain the same genes that enable their deepwater ahermatypic (not reef building and lacking zooxanthellae) cousins to modestly calcify without the help of algae.[9]

For the last quarter of a billion years the most prominent reef contributing animals have been hexacorals (Scleractinia). These since the Middle Triassic (there are no Lower Triassic corals) have always lived in warm-marine shallow environments, as algal cements between them in their fossil reefs show. Also, paleogeographic reconstructions find that scleractinian coral reefs are always in association with algae-produced sands and evaporites in the lagoons that they fronted.[10]

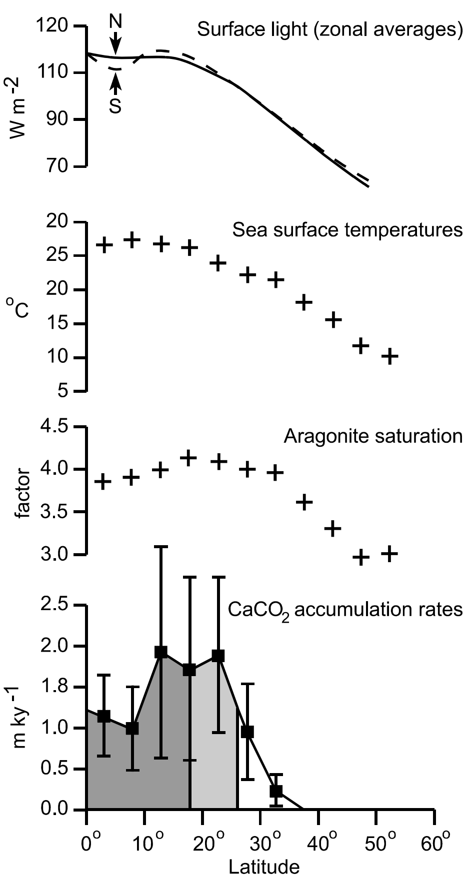

Figure c7.1 [14] Graphs of three factors (light, temperature, and aragonite super-saturation) known to affect coral-algal communities over a range of latitudes: Intensity of gray shading indicates the relative importance of reef contributions.

During the preceding quarter of a billion years (the Paleozoic), various shell-secreting animals—for example, stromatoporoids, brachiopods, bryozoans, bivalvia (clams and oysters, but not the free-swimming scallops and byssus-attached mussels) and extinct tabulate corals and tetracorals (Rugosa, calcite skeleton)—added to the stony mass of organic reefs. Also, beginning some half a billion years ago, calcareous algae (red algae) evolved and have since contributed to the stony framework of organic reefs.

For billions of years before (the Prepaleozoic, more commonly known as the Precambrian) organic reefs were presumably and mostly built by yet reef contributing proteobacterial anoxygenic phototrophs.[11] These most venerable reefs, called *stromatolites*, are mounds of thinly layered hardened calcite mud. In the 1920s, modern analogues (as at Shark Bay in Western Australia)[12] of stromatolites were recognized forming from living mats of cyanobacteria, archaea, and algae. Rare since the appearance of grazing marine invertebrates in the early Paleozoic, stromatolites are the sole megafossils of the Precambrian. Such reefs could only have been built in warm (evaporating to the point that the water is saturated with respect to $CaCO_3$) shallow (sunlit) oceanic water.

As the only abundant visible fossil in the Precambrian, the physical aspects of stromatolites are of use in biostratigraphy (and are so used, particularly in Russia since the 1930s, *see* Chapter *h*).

Undisputed microbial fossils were found in 1954 by Stanley Tyler (1906-1963) and Elso S. Barghoorn (1915-1984) within stromatolites of the Proterozoic Gunflint Iron Formation in Canada. However, no Archean stromatolites indisputably contain fossils of the microorganisms that may have built them.[13]

As reasoned indicators of past environments, the biological aspect of stromatolites has spurred investigations. Caution is necessary: Before one billion years ago, precipitation of aragonite and calcite (both $CaCO_3$) on the seafloor commonly produced sediments with abiotic structures that mimic microbialites (*see* Topic *L8*). Stromatolites as old as three and a half billion years are known.

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