CORAL REEF ECOSYSTEMS: AN OVERVIEW OF THEIR STRUCTURE AND FUNCTION

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Summary

Coral reefs are highly diverse, structurally well defined ecosystems, which depend upon high rates of calcification by sessile organisms to build carbonate platforms that support photosynthesis and respiration. High rates of calcification are provided for by warm seawater, high concentrations of calcium and carbonate ions and stimulation of calcification by photosynthesis. On reefs, autotrophy and heterotrophy are tightly coupled so that mature systems exhibit little net organic carbon production and efficient recycling of limited inorganic nutrients. Reef development is primarily dependent on sunlight but growth and community structure are modified by numerous other factors, including proximity to land, hydrodynamics, nutrient availability, sedimentation, disturbance and recruitment. Strong interdependency between different reef organisms and the sessile mode of existence of primary reef-builders renders coral reef ecosystems vulnerable to various types of perturbation, many of which are anthropogenic. Deterioration of coral reef ecosystems is now evident in many parts of the world as a consequence of local, regional and global factors. Loss of corals following El Niño-Southern Oscillation-related excursions above normal summer seawater temperature is approaching a level where the existence of coral reefs may be threatened in coming decades.

1. Introduction

Coral ecosystems can be broadly divided into four categories based upon their proximity to land: fringing reefs, shelf reefs, barrier reefs and atoll reefs. All depend upon the deposition of calcium carbonate by invertebrate animals and calcareous algae to build and maintain a stable platform upon which the processes of photosynthesis and respiration can effectively take place. For reefs to grow, the rate of biogenic carbonate deposition must exceed the rate of carbonate removal by physical and biological agencies. To achieve this rate, several concomitant factors are needed; principally, warm seawater, high concentrations of calcium and carbonate ions and substantial stimulation of calcification by photosynthesis. This requirement for warm water explains why coral reefs do not develop far outside of the tropics. Stimulation of calcification by photosynthesis depends upon there being sufficient sunlight and inorganic nutrients to drive high rates of gross organic production (gross photosynthesis). Photosynthesis raises seawater pH causing changes in the seawater carbonate equilibrium that favor the biological deposition of calcium carbonate. Since both seawater temperature and photosynthesis are governed by solar energy input, we can appreciate that coral reef growth is overwhelmingly controlled by sunlight.

Acting in conjunction with sunlight, however, are numerous other factors that to a greater or lesser extent control the development and species composition of coral reefs. These include both physical (abiotic) and biological (biotic) agents. To gain a general understanding of how such factors variously influence the development of coral reefs, it is perhaps useful to consider the gross differences that occur in reef structure and community composition as we move away from land. It is first necessary, however, to appreciate the physical conditions and chemical processes that are needed for coral reef growth.

2. Reef structure, composition and function (see also *Biological Dynamics of Coral Reefs*)

Reefs are built by sessile organisms. These are organisms which, save for their larval, juvenile, gametangial or sporangial phases, are incapable of moving of their own accord from one location to another. They comprise both invertebrate animals and plants. The main reef-builders are the photosynthetic hermatypic corals and calcareous red and green algae. Once established, such organisms are destined to struggle, exist or flourish under the environmental conditions to which they are exposed. To flourish, they must adapt to their environment. By doing so, they are able to ensure many episodes of reproduction, thus enhancing the chances that their offspring will survive, multiply and evolve across time and space.

Reproduction among corals and algae involves the periodic release of mobile or immobile gametes, spores or larvae into the water column. After spending a variable period of time floating among the plankton, these entities must find or chance upon a suitable place to settle or they will run out of food resources and perish. The probability of this happening is a function of the availability of suitable habitats for settlement. Thereafter, the more favorable the environmental conditions encountered, the greater the likelihood that these progeny will also live long enough to reach maturity and reproduce. This process of adaptation to the surrounding environment is made very much easier if critical conditions, such as ambient light field and hydrodynamic regime, do not vary in a wildly unpredictable fashion. In high energy environments, where coral reefs frequently develop, this can only occur if there are stable platforms to which such reproductive propagules or vegetative fragments can become affixed. Hence, the initial development of reefs depends upon there being a hard, immobile substratum.

Growth of coral reef communities tends to commence once a sufficient number of organisms that secrete carbonate skeletons have accumulated in the same location. This process is known as aggregation and it appears to be a prerequisite for coral reef formation. It results in rapid development of diverse reef communities via construction of a calcified 3-dimensional structure. Development of a durable 3-dimensional structure reduces the likelihood of mechanical destruction, provides suitable habitats for settlement of progeny that live for only brief periods or disperse over short distances and creates refuges for cryptic communities. Settlement and growth of algae and corals encourages development of grazing communities and hence the establishment of predator hierarchies. Inorganic nutrients, extracted from the large volumes of water that pass over the reef surface or from smaller volumes of water that pass through the reef surface, are first fixed into organic compounds by plant life. Organic derivatives are transferred through the higher trophic network from herbivore to carnivore via predation. In the process, substantial amounts of organic nutrients are returned to the benthos in the form of feces. Feces and other organic derivatives released by the benthic community are then broken down into their inorganic components by bacteria, which abound on almost every surface in warm tropical seawater. By this means, inorganic nutrients are again made available for uptake and re-incorporation into organic compounds by the autotrophic community (free-living or symbiotic algae).

In the absence of severe environmental perturbation, these processes of production and consumption are so well coupled that almost all of the food produced on the reef by day is consumed over a 24 h period. For this reason, mature reefs in shallow water have whole day gross photosynthesis to respiration ratios that are close to 1.0. Manifestly, the inorganic mass of a coral reef (i.e., the carbonate framework) increases at a far greater rate than the biomass of its surface tissue. Indeed close inspection of coral reefs shows them to have but thin veneers of living tissue covering massive accumulations of carbonate rock.

2.1. Carbon metabolism (see also *Role of the Oceans in Global Cycles of Carbon and Nutrients*)

Construction of the geological framework of a coral reef by its thin outer layer of living tissue is a product of coupling between photosynthesis and calcification. How this coupling operates is still not properly understood. It is clear nonetheless that since calcification depends upon alkaline pH conditions and yet results in acid production:

$$Ca^{2+} + CO_2 + H_2O \rightarrow CaCO_3 + 2H^+ \qquad (1)$$

elevation of pH by photosynthesis must at least counterbalance the acid produced by calcification. Simply counterbalancing the acid produced by calcification, however, would serve to keep the pH of the calcification environment close to that of the surrounding ocean. Since calcification does not occur spontaneously at normal seawater pH (8.1), the rise in pH associated with photosynthetic carbon dioxide removal must surpass the fall in pH associated with calcification. By this means, a strongly alkaline environment can be maintained, which favors the rapid precipitation of calcium carbonate.

On the highly productive shallow windward slopes of reefs in open water, deposition of calcium carbonate is estimated to occur at a rate of around 10 kg m^{-2} y^{-1}. Given a porosity of 50%, this translates to potential upward reef growth of around 7 mm y^{-1}. While, such rates of upward reef growth are possible, physical and biological agencies frequently remove much of the calcium carbonate precipitated annually. Rates of ~10 kg m^{-2} y^{-1}, moreover, only occur over a small percentage of the reef surface (1-2%). An estimated 4-8% of the surface of a reef calcifies at a more moderate rate of 4 kg m^{-2} y^{-1}, while the remainder is thought to calcify at around 0.5-1 kg m^{-2} y^{-1}. Such spatial heterogeneity in calcification rate is a direct consequence of the distribution and density of reef-building organisms. Shallow fore-reef slopes often have close to 100% cover of corals or calcareous red algae and high surface relief providing a very large relative surface area and the necessary physical and biochemical conditions for rapid calcification. Ninety or so percent of the surface of a reef, however, is composed of sand, rubble, reef rock, filamentous algae or sparse calcareous communities, thus the majority of the reef surface exhibits comparatively feeble rates of calcification.

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Biographical Sketch

John R. M. Chisholm obtained his Batchelor of Science Degree from St. Andrews University, Scotland, in 1981, with 1st Class Honours in Botany. He was awarded the Margaret Laing Bell Prize for Botany in the same year. He obtained his Doctoral Degree from James Cook University, North Queensland, in 1989 for his dissertation on *Photosynthesis, Calcification and Photoadaptation in Reef-Building Crustose Coralline Algae on the Great Barrier Reef*. In 1989-91, he was awarded an Australian Institute of Marine Science Post-Doctoral Research Fellowship for studies on the photobiology of reef organisms, particularly into the effects of ultraviolet radiation on their metabolism. He then led research into methods for enhancing production of naturally occurring anti-cancer substances in tropical marine ascidians at CalBioMarine Technologies, Inc., Carlsbad, California, U.S.A.. In 1994, he joined the Scientific Centre of Monaco, and led research into multiple aspects of the development of the green alga *Caulerpa taxifolia* in the Mediterranean Sea and continued research on the metabolism and ecology of coral reef organisms. He returned to Australia in 1995-1997, as an external consultant to the Australian Institute of Marine Science and the Japanese Association of Marine Sciences and Technologies, to transfer expertise and technology in the field of coral reef community metabolism. Dr. Chisholm returned to the Scientific Centre of Monaco in 1998 as Director of Research into the environmental ecology of *Caulerpa* and coral reef communities.