EFFECTS OF RISING SEAWATER TEMPERATURE ON CORAL REEFS

Thomas J. Goreau
Global Coral Reef Alliance, Cambridge, MA, USA

Raymond L. Hayes
Howard University, Washington, DC, USA

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Summary

Abnormally high temperatures trigger physical, chemical, and biological changes in the oceans that affect coral reefs and fisheries, both directly and indirectly. The mechanisms responsible for those changes are qualitatively reviewed in this chapter. Almost all are potentially detrimental to reef ecosystems. The most dramatic is the uncoupling of symbiosis among corals and their zooxanthellate algae, on which coral reef construction depends. This obligate symbiosis is destroyed by small increases in temperature. Additional increases threaten the viability of corals and their symbionts. Coral reef ecosystems are vulnerable to thermal stress because they live very close to their upper tolerance limit for temperature. Coral reefs throughout the world have already been exposed repeatedly to excessive temperatures starting in the 1980s. Coral mortality has ranged from mild to catastrophic. Continued climate changes, including global warming, will trigger the demise of reef-building corals, leading to the collapse of our most productive, biodiverse, and economically valuable coastal marine ecosystem, the coral reef.

Global reef and pelagic fisheries are also vulnerable to climate change. Reef fisheries are threatened by the loss of habitat, and pelagic fisheries are vulnerable to bottom-up trophic collapse from warm surface waters that block nutrient upwelling. While declines in global fisheries is often blamed on top-down effects from over-fishing, changes in ocean circulation patterns from climate instability pose serious threats from below. Failure to recognize the impacts of these large-scale changes make conventional fisheries management strategies, based on controlling fishing efforts, increasingly irrelevant. Marine protected areas are insufficient to restore these fisheries when habitats have been destroyed or the food chain has collapsed. Reduction of global greenhouse gas concentrations is the *sine qua non* for preservation of coral reef ecosystems and reef fisheries, and for conservation of pelagic fisheries.

1. Introduction

Coral reefs are ancient, majestic, highly productive and exceptionally diverse tropical marine ecosystems. However they are also fragile, sensitive and easily stressed by environmental change. Since the mid 1980s there has been a progressive global decline of robust and dynamic coral reefs into fragmented and degraded communities. This disaster has been driven by impacts of global warming, exacerbated by man-made pollution, destructive fishing practices, over-harvesting and environmental mismanagement. Long-term impacts from sea level rise and oceanic acidity may soon compound other sources of stress. Here we review the physical, chemical, and biological mechanisms by which elevated temperatures affect coral reefs and fisheries, including their interactions with other environmental determinants, and how global warming affects coral reef ecosystems and associated marine fisheries.

2. Direct Thermal Effects

2.1. Sea Level Rise

Increasing temperature causes seawater to expand in volume and at the same time accelerates the melting rate of glaciers and continental ice caps. Both of these processes contribute to rising sea level. The expansion of polar waters due to reduced salinity further promotes sea level rise. Healthy reefs, completely covered with rapidly growing coral colonies, a common sight in tropical waters only a few decades ago, are able to grow upwards faster than the rate of sea level rise. For example, many Jamaican reefs had grown up to 30 meters in thickness since sea level stabilized around 6000 years ago (a rate of about 5 millimeters per year), more than the current rise in sea level of around 2.8 millimeters per year. However the rate of sea level rise rate is accelerating and the degraded reefs that now predominate worldwide have too little live coral cover (often only a few percent to a few tens of a percent), and are growing far too slowly for the reef framework to keep up with sea level rise. These compromised reefs will eventually be drowned, resulting in enhanced rates of coastal erosion.

2.2. The Solubility of Carbon Dioxide and Oxygen in Seawater

Carbon dioxide (CO_2) solubility in water decreases as temperature increases. Consequently warm tropical oceans are a major source of atmospheric carbon dioxide, which dissolves in colder polar waters. As global warming continues, the tropics will become a larger source of carbon dioxide out-gassing, contributing a positive feedback mechanism that amplifies the build-up of greenhouse gases.

Oxygen (O_2) is less soluble in water at higher temperatures. At the same time, dissolved oxygen-dependent respiration rates of most microbes, macrofauna and algae increase markedly. Increasing temperatures exacerbate low oxygen stress and promote the expansion of anoxic dead zones, especially in marine areas with high coastal organic carbon loading from sewage discharge, solid waste disposal, and agricultural waste releases, and in coastal waters and deep basins with poor circulation. Therefore, coral reefs in such regions could die from oxygen deprivation and toxic sulfide accumulations that develop in back reef lagoons during summer nights. For example, after high temperature exposure, many enclosed atolls in French Polynesia experienced severe mortality from anoxia and bacterial infections, wiping out previously flourishing pearl farms. Also, increasing levels of organic pollution loaded into the Pearl River, which drains an area of rapid human population growth in China, caused anoxia and environmental toxicity that killed coral reefs in Hong Kong. Reef mortality will increase in frequency, intensity, and duration as sea temperatures and uncontrolled pollution increase.

2.3. Limestone Solubility in Seawater

Limestone (calcium carbonate or $CaCO_3$) is an exceptional mineral that becomes less soluble as temperature rises. Recent claims have been made that increasing CO_2 may dissolve coral reefs. In fact, tropical coral reefs should not be affected until long after polar waters and the deep sea are affected, because of the decreased solubility of both carbon dioxide and limestone in seawater at elevated temperatures, and because coral reefs have large amounts of exposed limestone sediments which buffer acidity of seawater. Half of all limestone burial in the oceans takes place in coral reefs, which cover only 0.1% of the ocean floor. Ocean acidification from increasing atmospheric CO_2 concentrations will have the least effect at lowering pH in warm tropical surface ocean waters. Thus, coral reefs in the tropical zone will be the last ocean realm to be affected by ocean acidification.

However, increases in CO_2 concentrations at current trends are expected to be much larger than declines in CO_2 and limestone solubility. The CO_2 gas infrared absorption bands are already largely saturated, so higher concentrations of CO_2 will absorb less heat per molecule than lower concentrations. Ocean acidification rises more directly with increases in CO_2 concentration, so the acidity increase will eventually outweigh the thermal impacts of increased CO_2. Acidification of reefs to the point that corals dissolve would take so long compared to the direct thermal impacts on corals themselves that if CO_2 buildup from fossil fuel use continues without control, corals will die from direct thermal bleaching many decades before the limestone reef frame dissolves. Corals are already living near, at, or occasionally beyond their maximum tolerance limit for temperature, but they are still far from having reached any acidity limit.

Biogenic limestone deposition decreases as water becomes more acidic because the concentration of carbonate ions available for calcification is lowered. However, the internal pH of coral tissues can be very different than ambient seawater due to internal production of CO_2 by respiration and its removal by photosynthesis of symbiotic algae. In addition, corals actively pump calcium and hydrogen ions. As coral grows its skeleton, a protected compartment is created between the tissue laying down calcium carbonate crystals and the underlying substrate. Within that compartment, crystal embryos are developed and juvenile skeletal growth ensues by nucleation catalysis. This area of nascent skeletogenesis is isolated from direct exposure to seawater and insulated from ambient acidity. An acidic shift in seawater would not necessarily disrupt skeletal productivity because of the coral soft tissue veneer covering the skeleton. Deep sea corals are able to grow their skeletons slowly even in water that is under-saturated for calcium carbonate.

2.4. Influences of the Hydrological cycle

2.4.1. Salinity

Corals are probably not directly sensitive to evaporation or rainfall per se, but they are highly sensitive to both salinity and light levels, both of which are proportional to the difference between evaporation and rainfall. Corals, adapted to normal ocean salinity (roughly 35 $\pm$ 3ppt) cannot tolerate brackish water exposure for long and may be damaged by excessive salinity. However, there is a species-specific gradient of tolerance in both directions, with a few coral species found in hyper-saline environments (e.g. the Arabian Gulf) and a few species that can grow close to river effluxes.

Evaporation increases sharply with increasing temperature, so as the Earth has warmed in recent decades there has been a measurable increase in tropical lower atmosphere humidity and cloudiness. Although it is clear thermodynamically that ocean evaporation will rise sharply with global warming, most evaporation from the ocean rains out over the ocean, so the net change in surface salinity should be small. However, there has been a minor but detectable increase in the salinity of the tropical oceans due to increased excess of evaporation over rainfall.

Along continental margins, a significant fraction of increased ocean evaporation moisture is transferred by winds to land masses, causing increased rainfall in mountainous coastal areas. Increased rainfall along coastal fringes may be more than balanced by increased drought in the interior areas of large continents. The continental interiors are far from ocean moisture sources that mostly rain out before they reach the interiors, which will get drier as elevated temperatures increase evaporation. Some coastal zones may get more freshwater if the rivers flowing into them originate in mountainous coastal regions, lowering salinity, but regions where rivers originate in continental interiors should have less river runoff due to lower rainfall and increased evaporation, leading to higher coastal zone salinity, especially where river flow is tapped by dams for irrigation. Thus the coastal salinity changes to be expected from climate change will be a very complicated function of regional topography and hydrology, and are very hard to predict accurately from climate models because of the large scale spatial averaging and lack of fine-scale local topographic detail built into such models. Oceanic islands should have increased evaporation and rainfall in much closer balance, and suffer smaller changes in salinity, compared to continental coastal zones.

2.4.2. Light Penetration

Corals require light in the photosynthetically active radiation (PAR) wavelengths for photosynthesis, which controls the rate of coral skeletal growth. PAR is a function of surface solar irradiance, which is largely controlled by cloudiness. While ultraviolet (UV) radiation is a potentially damaging factor, corals have very high levels of ultraviolet screening pigments: even fully bleached corals whose tissues are completely transparent to visible light have so much UV screening pigments that they are opaque to UV light sources. Stratospheric ozone layer depletion leads to increased UV at the surface (if the light is not blocked by increasing cloudiness), but ozone depletion is highest over the poles and there has been little or no statistically significant decline in ozone levels over the tropics.

Due to increases in UV-absorbing atmospheric pollutants, especially sulfur, nitrogen, and hydrocarbon gases that produce haze (that also reflects PAR), a general decline in both UV and PAR at the Earth's surface, known as "global dimming", has been reported. Global dimming has masked the full impact of global climate change and has caused the rate of atmospheric warming to be less than that predicted from greenhouse gas increases alone. However this effect of global dimming is only temporary, because CO_2 has a lifetime of 150 years in the atmosphere, while most aerosols last only days to weeks. Continued masking of the greenhouse effect would require exponential increases in air pollution. As greenhouse gases continue to rise, and as acid rain pollutants and aerosols that contribute to global dimming are controlled for public health reasons, the masking effect has already declined to the point that it has reversed decades of global dimming of PAR and UV caused by atmospheric pollution. As aerosols become far less effective at blocking sunlight, the warming rate is expected to rise even more sharply in the future.

Overall, climate change should result in higher mean ocean cloudiness due to higher evaporation and atmosphere moisture content, which should lower coral growth rates, which are directly dependent on photosynthesis rates. However, this depends strongly on the local details of atmospheric circulation, and increased cloudiness will be greatest in low-pressure equatorial zones and least in high-pressure zones at the latitudinal limits of corals. As a result, the inhibition of coral growth by reduced light should show a latitudinal gradient, being greatest in equatorial zones and being least near the northern and southern limits of coral growth. Predictions of changes in cloudiness and rainfall are the most uncertain predictions made by global general circulation models, due to the great uncertainty in how to parameterize cloud formation and rainfall processes at model sub-grid scales, the great range of mathematical algorithms used in different models, and their poor calibration in terms of empirical data, which make model predicted values poor fits to actually measured values.

2.5. Ocean Thermoclines and Upwelling

Oceans are warmed from the top down by sunlight absorbed by the uppermost layer of the ocean (the photic zone) in which the depth of light penetration depends on water clarity and the high thermal capacity of water. The tropical ocean is the major heat reservoir for the global climate system. Heat transport from the tropics drives global heat budgets of cooler waters and the atmosphere via ocean currents, winds, and thermal changes due to the latent heat of evaporation and condensation. Global warming will expand the cap of warm surface water toward the poles, expanding the tropical area and increasing the potential habitat for corals. Corals are already expanding poleward in the Sea of Cortez and South Africa. Global warming also expands warm water downward by pushing thermoclines to deeper depths.

The maximum depth of coral growth is more often controlled by lack of light than by excessively cold water, so corals would not be expected to increase in depth range in most places unless the water becomes more transparent. Most coastal waters have actually become more turbid due to erosion of soil and sediment from land and because of increased chlorophyll levels following eutrophication from nutrient-loading with domestic sewage, animal waste and agricultural fertilizers. Large, dead reefs can be found in deep offshore sites, for example, along the Caribbean coast of Panama, because once clear, blue water has been replaced by dark, green water due to soil erosion after deforestation.

But the opposite trend takes place in open ocean upwelling zones where the major source of nutrients is not coming from land-based sources but from deep water upwelling. Increasing thickness of warm, nutrient-poor surface layers will push thermoclines deeper and reduce nutrient transport upwards. A decline in phytoplankton chlorophyll and biological productivity has been documented in tropical open ocean waters while a chlorophyll increase in mid latitude open ocean regions has been found. There was an unusually low global ocean net primary productivity in the record hot year of 1998. That productivity rose sharply in the cooler year that followed and steadily dropped in subsequent years as climate change continued. In areas where upwelling is reduced, corals might grow deeper, but they would have less zooplankton for a food supply. Where wind speeds increase, the water will become greener and coral ranges reduced due to decreased light, despite higher food levels. These changes will be strongly affected by shifts in currents and winds, driven by changing temperature gradients.

As the tropical ocean warms, increased warm current heat transport is displaced poleward and increased evaporation results in increased humidity and rainfall. As the heat released when rain condenses drives further convection, wind speed is increasing in many locations. Because the Earth does not heat up at the same rate everywhere due to local topographic factors affecting circulation of air and water, atmospheric pressure differences between areas warming more rapidly and those that are warming more slowly drives increased wind speeds. Increased wind speeds have been documented for most of the ocean, especially around Antarctica, the North Atlantic, and in the mid latitude interiors of the deep ocean basins. These sites are precisely those where the rate of sea surface warming is the lowest. Increases in chlorophyll and productivity in surface water take place where winds have increased and surface water has mixed with deeper water that transport nutrients upwards. In those areas, coral reefs could be overwhelmed by excess nutrients through natural eutrophication as is seen in some open ocean Pacific reefs, for example in the algae dominated reefs of the Northwest Hawaiian Islands and Central Pacific. Coral reefs affected by increased upwelling could change into algae/sponge/tunicate/soft coral communities, such as those found off Cap Vert in Senegal.

Worldwide, all the major upwelling zones have maximum temperatures rising faster than the ocean average, reducing nutrient input to the surface waters and causing food chains to collapse from the bottom up. It is therefore possible that some coastal areas that are now too cold and nutrient rich for corals to survive will become more favorable for them. In those open ocean areas where upwelling appears to be increasing, reducing the regional rates of surface temperature rise, corals may be regionally protected from the direct thermal effects of global warming. However, increased upwelling of cold water also brings increased nutrients, causing a shift away from corals towards algae, sponges, tunicates and soft corals. Indonesia is also warming more slowly than the tropical ocean average, and it appears that increased flow of surface waters from the Pacific to the Indian Ocean (the Indonesian Throughflow), a major regulator of global inter-hemispheric heat exchange, is entraining more cold waters. In areas where the Indonesian Throughflow is strongest, surface water can be as cold as 15 ºC near the equator and the reefs most directly affected by the Indonesian Throughflow are dominated by algae, tunicates and other filter feeding organisms, not by reef-building corals. So while these reefs are spared from exposure to elevated SSTs because of local circulation patterns, they are more vulnerable to eutrophication.

2.6. Dynamics of Reef Frame Growth

Coral skeletal growth rates, as measured by reef frame accretion, rise sharply with increasing temperature, reach a maximum, and then fall even more sharply to zero only slightly above the temperature optimum at which the coral tissues die. Reef coral calcification is proportional to the rate of photosynthesis by symbiotic zooxanthellae. All reef-building corals have an obligate relationship to a specific algal strain, each of which has a distinct temperature optimum and a maximum limit beyond which bleaching ensues. The bleaching threshold is approximately 1.0 ºC above the average monthly temperature in the warmest season. At a molecular level, induction of heat shock protein (HSP) in corals represents the initiation of a thermal stress response. This is the point where normal protein abundances in coral tissues are changed. Studies on the inducible expression of the ubiquitous HSP-70 show that this response initiates at 24 ºC and increases with additional temperature elevation.

2.7. Global Distribution of Coral Reefs

The possibility that coral reefs might extend into areas of sub-optimal temperature as a consequence of changing climate has been often suggested. This implies that corals might rapidly expand their ranges away from the tropical zone. However, this idea ignores the fact that corals quickly die when only slightly above their optimal growth temperature. While new coral colonies may begin growth in some newly warmed areas that are currently too cold to support coral growth, any reefs formed in newly suitable habitat would take thousands of years to mature into ecosystems that could compare to natural reefs that have been killed in warmer areas, and global warming could wipe them out long before large reefs can form. The spread of reefs to higher latitudes would probably be prevented by light limitations or high nutrient levels from coastal upwelling, and sedimentation, and pollution caused by dense coastal populations in temperate zone coastal areas.

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Biographical Sketches

Dr. Tom Goreau, President of the Global Coral Reef Alliance, a non-profit organization for coral reef protection and sustainable management, has dived longer and in more coral reefs around the world than any scientist. His father was the world's first diving marine scientist, and he grew up swimming in coral reefs as soon as he could walk. He was previously Senior Scientific Affairs Officer at the United Nations Centre for Science and Technology for Development, in charge of global climate change and biodiversity issues. He has published around 200 papers in all areas of coral reef ecology, and on global climate change, the global carbon cycle, changes in global ocean circulation, tropical deforestation and reforestation, microbiology, marine diseases, soil science, atmospheric chemistry, community-based coastal zone management, mathematical modeling of climate records, visualizing turbulent flow around marine organisms, scientific photography, and other fields. He developed the method to predict the location, timing, and severity of coral bleaching from satellite data with Ray Hayes. He holds patents with Wolf Hilbertz for new methods for preserving coral reefs from global warming and pollution, restoring marine ecosystems, shore protection, mariculture, and non-toxic methods of preserving wood from marine boring organisms, termites, rot, and fire, in order to increase the lifetime of wood and decrease logging. In 1998 he and Wolf Hilbertz were awarded the Theodore M. Sperry Award for Pioneers and Innovators, the top award of the Society for Ecological Restoration. Dr. Goreau led developing country NGO efforts in marine and climate issues at the United Nations Conference on Environment and Development (Rio de Janeiro, 1992), the UN Summits on Development of Small Island Developing States (Barbados, 1994, Mauritius, 2005), and the UN World Summit on Sustainable Development (Johannesburg, 2002). Dr, Goreau works with tropical fishing communities around the world to restore their coral reefs and fisheries, especially the Kuna Indians of Panama, the only Native people of the

Americas who have preserved their cultural and political independence. He is also a hereditary leader of the Yolngu Dhuwa Aboriginal clan of Arnhem Land, Australia, that preserves the oldest creation myth in the world. Of Panamanian origin, he was educated in Jamaican primary and secondary schools, at MIT (B.Sc in Planetary Physics), Caltech (M.Sc in Planetary Astronomy), Yale, Woods Hole Oceanographic Institution, and Harvard (Ph.D. in Biogeochemistry), and is a certified nuisance crocodile remover.

Dr. Hayes is a Professor Emeritus at the Howard University College of Medicine in Washington, DC, USA. He received his education at Amherst College, Amherst, MA (B.A., cum laude, 1959) and the University of Michigan, Ann Arbor, MI (M.S., 1961, and Ph.D., 1963). He has served on the faculty of several medical schools, including the Harvard Medical School (Boston, MA), the University of Pittsburgh School of Medicine (Pittsburgh, PA), the Morehouse Medical School (Atlanta, GA) , Howard University College of Medicine and the University of the West Indies (Mona, Kingston, Jamaica). He is the immediate past Vice-President of the Association of Marine Laboratories of the Caribbean, a Corporation Member of the Marine Biological Laboratory (Woods Hole, MA), and a Fellow of the American Association for the Advancement of Science. He is also a certified SCUBA instructor, an Associate Member of the Advisory Council on Underwater Archaeology, and a member of the Board of Directors of two international maritime archaeological societies and the Global Coral Reef Alliance. He is currently a volunteer for the American Red Cross (Disaster Relief), the Smithsonian Institution (American History) and the U.S. Naval Historical Center. For many years, he has been a national lecturer for the Undersea and Hyperbaric Medical Society and a congressional advocate for the Physicians for Social Responsibility. He is the co-founder the Human Health and Climate Change Symposium of the International Conference on Global Warming and serves as a moderator and spokesperson for the International Planning Committee for the Global Warming International Center. His bio-medical research contributions have addressed the morphogenesis and differentiation of skeletal muscle *in vitro*, the fibrillogenesis of embryonic connective tissues, the pathogenesis of Progressive Systemic Sclerosis (Scleroderma), and the experimental induction of calcinosis in mammalian soft tissues. His recent marine biological research interests focus upon the cell biology of skeletal formation in stony corals, the histo-pathology of coral reef bleaching, emerging infectious diseases in coral reef organisms, reef and coastal marine ecosystem degradation, and the impacts of and linkages among extreme climate events, elevated ocean temperatures, and global climate change upon human health and marine environmental integrity. Dr. Hayes is married with four adult children.