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Lecture Notes

Part 1

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VULNERABILITY OF CORALS TO SEAWATER WARMING

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Introduction

Coral reefs are the most diverse marine habitat, which support an estimated 0.5 to 2.0 million species in the world oceans. They are among the most sensitive of all ecosystems to temperature changes, exhibiting bleaching (a phenomenon in which the symbiotic zooxanthellae are expelled by coral polyps) when stressed by higher than normal sea temperatures. The hypothesis that corals and associated reef organisms might be the first to show adverse effects of global warming has been widely recognized. Coral bleaching is by far the most damaging event in coral reefs and is currently viewed as a major threat to the long-term health of coral reef communities. Although many factors such as acidification, outbreak of diseases, predators, sedimentation, lower salinity, UV radiation, solar radiation, chemical stressors and nutrient inputs are responsible for coral bleaching, rise in seawater temperature causes stress, which leads to expulsion of the symbiotic zooxanthellae by the corals. Bleaching describes the loss of symbiotic zooxanthellae by the coral. Most of the pigments in the usually colorful corals depend on the presence of these symbiotic algae. This phenomenon has been referred to as 'bleaching' due to the fact that corals rapidly lose brown colour (due to the zooxanthellae) and turn a brilliant white. The living tissue of the corals without algae is translucent, so the white calcium carbonate skeleton shows through, producing a bleached appearance. Bleaching is the final manifestation of stress related disorder in corals. It results either in cessation or reduction of growth and a decrease in reproductive output. Various approaches have been employed to understand bleaching, its cause and associated changes occurring in corals. Corals usually recover from bleaching, but they die in extreme cases. Increased frequency of bleaching events will reduce corals' capacity to recover. Bleaching at small local scales has been reported for almost a century. Mass bleaching at larger geographical scales, however, is relatively a new phenomenon. Prior to 1979, there are no formal reports of mass coral bleaching.

Three types of bleaching mechanisms are associated with high temperature and light: animal stress bleaching, algal stress bleaching, and physiological bleaching. Although all the three are important in understanding climate-coral interactions, two are particularly relevant to the present concerns: algal-stress bleaching, an acute response to impairment of photosynthesis by high temperature coupled with high light levels; and physiological bleaching, which reflects depleted reserves, reduced tissue biomass, and less capacity to house algae as a result of the added energy demands of sustained above- normal temperatures.

Reef distribution and global warming

The global distribution of reef-building corals is limited by annual minimum temperature of ~18^{o}C. Global warming might extend the range of corals into areas that are now too cold, the new area made available by warming will be small. Coral reefs require shallow, clear water with at least some hard sea floor, and their propagation depends primarily on ocean currents. The atmosphere and the ocean have warmed since the end of the 19th century and will continue to warm in the future, largely as a result of increasing greenhouse gas concentrations. Evidence of sea surface temperature warming has been found throughout much of the tropics, especially in the northern hemisphere and is correlated to increasing concentrations of carbon dioxide and other greenhouse gases in the earth's atmosphere. Highly significant increases in the sea temperature in the world's tropical oceans have been noted in the past century. While decadal increases in temperature of this magnitude may seem small at first glance, such increases become very significant for corals living close to their thermal limits in oceans where the background temperatures are steadily rising over time. The hypothesis is that corals and other reef organisms might be the first to show adverse effects of global warming. Even slight increase in temperature might push an organism over its physiological limits.

In the Caribbean-wide bleaching event of 1987, however, water temperatures did not exceed normal temperature maxima, but the duration of maximum temperature was much longer than normal. These observations suggested that 'physiological bleaching' rather than 'algal-stress bleaching' played a major role in 1987 in reducing tissue biomass and therefore density of symbiotic dinoflagellates. Such chronic temperature stress may be cause for reef decline, such as low rates of sexual reproduction.

Sea level

Sea level has remained fairly stable for the last few thousand years. And many reefs have grown to the point where they are sea-level-limited. The mean global rate of sea level rise during the 20th century has been nearly 2mm/yr, which is 10-fold higher than the average of the past several millennia. Sea-level rise might drown reefs that are near their lower depth limit by decreasing available light.

El Nino

Depressed sea levels, resulting from El Nino events and other coupled ocean-atmosphere phenomena linked to climate variability, may also contribute to coral bleaching. For instance, coral reefs in the eastern Indian Ocean experienced sea levels 30-40 cm lower than normal for a period of 9 months in 1997-1998. This resulted in a form of algal stress bleaching in shallow reef flat corals in west Thailand between late 1997 and early 1998 termed solar bleaching, because it is primarily triggered by exposure to high solar radiation and not to elevated sea temperature. Mass bleaching of corals in the past two decades has been clearly linked to El Nino events. For example, wide spread bleaching events occurred during the El Ninos of 1982-83,1987-88 and 1997-98. During a typical El Nino event, regions of unusually warm water develop throughout the Pacific and Indian oceans. When these warm water anomalies coincide with seasonal maximum water temperatures, coral bleaching occurs. Mean sea level decreases in the western Pacific during an El Nino event, which can expose shallow reefs, and lead to mass mortalities. Coral bleaching has also occurred during the cold phase of ENSO (La Nina) in regions that tend to have warmer than normal SSTs. El Nino events have increased in frequency, severity, and duration since the 1970s. The severity of bleaching events during El Nino years of the last two decades presents a worst case scenario in predicting the future of coral reef ecosystems, particularly when added to a background of warming sea-surface temperatures.

Precipitation

Increases in precipitation can lower salinity and increase sediment discharge and deposition near river mouths, sometimes leading to mass mortalities on nearby coral reefs. Storms are typical features of tropical seas. Most coral reefs have experienced tropical storms and they usually recover from the damage. Reefs that experience many tropical storms, such as those on Guams and atolls in Pacific develop low profile, wave resistant coral communities. Tropical cyclones may limit reef development, but healthy coral reefs tend to recover from the damage caused by cyclones.

Natural calamities

The 2004 Indian Ocean tsunami damaged coral reefs through 3 mechanisms; wave action which dislodged, smashed, and moved coral and rubble; smothering of corals by increased sediment movement; and mechanical damage and smothering by debris from land. The effects were very localized with some areas seriously damaged, whereas large areas of adjacent coral reef were either slightly affected or undamaged. In most of the countries, the tsunami washed directly over coral reefs, which may have provided some limited protection to the land behind. In India, there was major damage to the coastal areas of southeast coast and especially to the Andaman and Nicobar Islands. The secondary earthquakes occurred in all the islands and all the reefs uplifted vertically out of the ocean (in the northern Andaman), whereas other reefs were thrust downwards several metres (in the southern Andaman and Nicobar). There was major erosion on land, and sediments and debris damaged many reefs. It is anticipated that the majority of the affected reefs will recover within 5 years, assuming that human threats can be minimized by sustainable management and enforcement of legislation.

Factors affecting corals

Factors	Mechanism	Effects
Acidification	Lowering of pH and carbonate ion concentration	Calcification rates reduce
Temperature	Sea surface temperature increase due to greenhouse effect	Coral bleaching
Sea level	Rise in sea level because of warming	Coastal flooding, input of sediments
Storm	Increase in storm frequency and intensity	Species decline or shift
Dust	Iron dust enhances phytoplankton and macroalgal growth; transport of pathogens	Light penetration decrease, macroalgae compete with corals for space

Heat stress and mechanisms of coral bleaching

While localized bleaching can arise as a result of any number of stresses, mass coral bleaching is tightly correlated with short excursions of sea temperature above summer maxima. Over the past 20 years, there have been six major global cycles of coral bleaching (mass coral bleaching events). The link between sea temperature and irradiance in inducing bleaching was recognized two decades ago and reported that 'coral tissues can better withstand temperature extremes at reduced light intensities'. A combination of elevated sea temperature and exposure time predicts mass coral bleaching with great certainty. Not only the intensity, but also the duration of elevated water temperature on a reef, can be an excellent predictor of the strength of a bleaching event. Satellite measurements of sea surface temperature anomalies can be used to predict bleaching events several weeks in advance with more than 90% accuracy

Continued warming of tropical SSTs, as is likely due to the enhanced greenhouse effect, will increase the level of thermal stress to coral reefs. Increased frequency of bleaching events will reduce corals' capacity to recover and may significantly alter the make-up of present day coral reef ecosystems. Sea surface temperature measurements also appear to deliver information on the intensity and outcome of bleaching events. The relationship between SST anomalies, exposure time and coral bleaching and mortality gives strong indications of what the progression will be from bleaching to mortality as heat stress increases over the next century. There is a considerable set of information now on why corals and their zooxanthellae bleach. Corals that are warmer than normal were bleached and died during an investigation made to study the effect of heat effluent flowing from a power plant in reef-building corals in Kaneohe Bay in Hawaii. The physiology of heat stressed corals showed the rapid reduction in photosynthetic activity. Some of this decrease was due to reduced zooxanthellae numbers as the corals bleached. Heat stressed corals develop an increased susceptibility to the phenomenon of photoinhibition, which is very similar to the mechanisms that are faced by all plants when they become temperature stressed. A key observation regarding heat stress in reef-building corals is that not all corals are equally sensitive to temperature. Corals with thicker tissues and more massive growth forms (e.g. *Porites* spp., *Goniopora* spp., *Montipora* spp.) tend to be more tolerant than corals that have thinner tissues (e.g. *Acropora* spp., *Stylophora* spp., *Pocillopora* spp.). Bleaching thus selectively removes certain species from reefs and can lead to major changes in the geographical distribution of coral species and reef community structures.

Zooxanthellae are more sensitive to stress than coral tissue. The thermal threshold above which corals and their symbionts experience heat stress and bleaching also varies geographically, indicating that corals and zooxanthellae have evolved over time to local temperature regimes. Corals closer to the equator have thermal thresholds for bleaching that may be as high as 31°C while those at higher latitudes may bleach at temperatures as low as 26°C. Thresholds may also vary seasonally. Winter maximum upper thermal limit for the ubiquitous coral *Pocillopora damicornis* was 1°C lower than the threshold for the same species of coral in summer. These shifts are evidence of thermal acclimation, a physiological adjustment that can occur in most organisms up to some upper or lower thermal limit.

Heat stress in animals and plants involves breakdown of enzymatic pathways, resulting in biochemical and metabolic dysfunction. The length of stress depends on the absolute temperature, length of exposure, and presence of other environmental factors (light, salinity, water motion). Recent high temperature tolerance experiments conducted on the pacific coral showed a decrease in rate over time of algal symbiont density, coral tissue protein and algal chlorophyll *a* concentrations was greater with increasing temperature.

Reef-building corals that experience thermal stress have reduced growth, calcification and repair capabilities. Coral reproduction is generally sensitive to stress and measures of reproductive output or fecundity can be used as indicators of reactions to various stressors such as mechanical damage, nutrients and oil. Mass coral bleaching has been reported to affect coral reproduction. Examination of corals following a bleaching event in Florida in 1987 showed that bleached colonies did not complete gametogenesis in the season following the bleaching event. Failure of gametogenesis was noticed in a large number of corals that were affected in the southern Great Barrier Reef. The implications for reef dynamics are considerable as recovery of affected reefs can be heavily dependent on larval recruitment. There is growing evidence that low levels of larval recruitment follow periods of thermal stress on coral populations.

Assuming that the reef-building corals like other invertebrates do not have extraordinary rates of genetic adaptation, it can be seen that current thermal tolerances are exceeded annually by the middle of this century. Under these assumptions, corals will bleach more and presumably die more under increasing warming seas. There may be a short period in which populations may see the selection of hardier coral types. However, this period is likely to be short as sea temperatures continue to increase rapidly and the threshold of even these hardy species are exceeded.

Calcification

The oceans absorb about a third of the CO_2 from the atmosphere, resulting in significant changes in seawater chemistry that affect the ability of reef organisms to calcify. Photosynthesis and respiration by marine organisms also affect seawater CO_2 concentration. Changes in the CO_2 concentration alter the seawater pH and the concentrations of carbonate and bicarbonate ions. The net effect of this is that the carbonate alkalinity of seawater will decrease as CO_2 within the earth's atmosphere increase. Projected increases in atmospheric CO_2 reduce the ocean pH to levels not seen for millions of years. Many marine organisms use calcium (Ca^{2+}) and carbonate ($CO_3^{\ 2-}$) ions from seawater to secrete $CaCO_3$ skeletons. Reducing the concentration of either ion can affect the rate of skeletal deposition, but the carbonate ion is much less abundant than calcium, and appears to play a key role in coral calcification. The calcium carbonate saturation state has already decreased since 1880 and it is expected to reduce the calcification rate of corals and calcareous algae on coral reefs and planktonic organisms and organisms in the open ocean. Calcification of coral communities reflects whether corals or calcareous algae dominate the community. Calcification rates of corals depend on other factors such as temperature. The estimated average decline of reef calcification rates are 6-14% as atmospheric CO_2 concentration increased from pre-industrial (280ppmv) to present-day values (370ppmv). Temperature and calcification rates are correlated, corals have responded to increases in water temperature (growing faster through increased metabolism and photosynthetic rates of zooxanthellae) than to decreases in carbonate ion concentration. In order to boost calcification, the temperature increase must remain below the corals' upper thermal limit. A reduction in $CaCO_3$ reduces a reef's ability to grow and to withstand erosion. Some slow growing or weekly cemented reefs may stop accumulating or shrink as carbonate deposition declines and/or erosion increases. Future changes in seawater chemistry will not only lead to decreases in calcification rates, but also to increases in $CaCO_3$ dissolution. Field experiments indicate that the dissolution rate could equal the calcification rate once atmospheric CO_2 concentrations reach double the pre-industrial levels. This points to a slow-down or reversal of reef building and the potential loss of reef structures in the future.

Bleaching of the Indian Reefs

In the Indian Seas, coral reefs are prominent in five regions, *viz.*, Andaman Sea,Nicobar Sea, Lakshadweep Sea, Gulf of Mannar and Gulf of Kachchh. Indian reefs have experienced 29 widespread bleaching events since 1989. The events were recorded in 1989, 1998, 1999 and 2002. Among these, events in 1998 and 2002 were intense. The impacts of 1998 bleaching were worst in the Indian Ocean, where virtually every reef was affected. There are no reports of mass bleaching events prior to 1989. The level of thermal stress at the vast majority of these coral reef regions was unmatched in the period 1901-2002. Sea surface temperature at these coral reef regions have significantly warmed over this period and the frequency of warm events of extreme increase in SST has increased since the late 1980s. A combination of elevated seawater temperature and exposure duration induces coral bleaching and can be used to predict coral bleaching with great certainty. Considering the temperatures that prevailed in 1998, and the predictions on the increase in sea surface temperature in the forthcoming years, the number of future bleaching events and the vulnerability of corals to warming have been projected**.** According to those predictions, bleaching would be an annual event for Indian reefs after two decades. There is substantial scientific evidence that coral reef regions along the Indian EEZ are under severe threat from climate change as well as factors such as over-exploitation and coastal land use. Frequent occurrences of coral bleaching and the ensuing damage to coral reefs have generated interest in documenting stress responses that precede bleaching.

Location	Month/Year	Mortality/Bleaching
Gulf of Mannar	June 1998	60% branching forms lost
Lakshadweep	May 1998	78% mortality
Andaman Islands	May 1998	Up to 50% dead
Nicobar Islands	May 1998	Up to 20% dead
Gulf of Kachchh	May 1998	10-30% bleaching
Palk Bay	April 2002	60% affected

Other factors

Two important factors that enhance the understating of how reefs will respond to climate change.

(i) Adaptation

Adaptation of corals to increasing stress levels might vary the thermal threshold of reef-building corals and modify the projected future. Adaptation at rapid rates is completely lacking for reef-building corals. Adaptation does happen in geological time as seen by the different thermal threshold at different latitudes or habitats across the world's oceans. But, these changes probably took several hundred if not thousands of years to occur. It is important not to forget that the single character of thermal tolerance is actually the meta-character driven by many gene products that have been tuned by selection to a particular mean temperature and which have to be selected. Also, evidence for any form of rapid genetic change in coral populations is currently lacking. Model runs performed to investigate how the changes in mortality affect coral cover and the rapidity to which more thermally tolerant clones will spread across a reef when selection acts against more sensitive clones of a putative species, showed that even the most tolerant clones illustrated slow rate of genetic adaptation.

(ii) Anthropogenic stresses

Destructive fishing practices, overexploitation, pollution, sedimentation from land clearings, and coral mining for lime are seen as threats to the health of Indian reefs. These stresses are critical in determining the rate and extent of the damage caused on the Indian reefs by climate change. The ability of coral reef ecosystems to recover from the influence of medium to catastrophic thermal events will depend on the background stresses that affect the regeneration of coral reef species. In many parts of the world, the influence of humans on reefs has led to deterioration in the capacity of reef systems to absorb perturbations.

The loss of resilience of reefs is another important way the reef systems that have been changed by humans. For example, the loss of herbivores through over-exploitation appears to have been responsible for leading to large scale losses of coral cover from coral reefs around Jamaica and other sites. In this case, herbivory controls algal population growth and ensuring open spaces for the recruitment of juvenile corals. On unperturbed reefs both fish and invertebrate grazers undertake this critical role. However, after fish grazers were removed over the 20th century by fishers, the only grazers left was the sea urchin *Diadema*. This left Caribbean reefs with a reduced capacity to absorb shocks, a fact that was demonstrated when a Caribbean virus decimated sea urchin populations in the 1980s. The result of the loss of the only remaining herbivore was that Caribbean reefs rapidly turned from coral reefs to algal dominated ecosystems.

The preceding example is directly relevant to the impacts of climate change on coral reefs. If catastrophic events like some of those seen on reefs during 1998 occur, coral population is pushed down to very low levels and macro algae (seaweed) dominate the substrate. If high rates of herbivory by fishes and invertebrates are not present, then spaces for new coral recruits are not created and coral migrants are essentially blocked by macro algal and other benthic species. The concept of reef resilience is critically important to how society responds to potential impacts of climate change on coral reefs. While reducing greenhouse gas emissions is an urgent priority, equally important is the need to insure that reefs have the highest resilience possible as they face these challenges. Also the fishing pressure (sedimentation, nutrient loading) would be expected to interact to produce effects on the ability of reef systems to recover from coral bleaching and mortality.

Ramifications of coral reefs to climate change

If there is no adaptation, the reef-building corals will no longer dominate by the middle of this century. Reefs will have progressively lower amounts of reef-building corals. There are several serious ramifications of coral reefs that are no longer dominated by reef-building corals. The first is that much of the productivity and nutrient dynamics of reefs and coastal waters is likely to change as corals become rare. Secondly, due to the combined effects of thermal stress and increased carbon dioxide, the calcification on coral reefs is likely to be much reduced. This may lead to the net erosion of reefs among other issues. The third is that biodiversity of coral reefs will be substantially reduced. And the last is that coral reef associated fisheries are likely to change as waters warm and benthic habitats change.

Suggested reading

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