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Coastal and marine ecosystems

& Global climate change

Potential Effects on U.S. Resources

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Victor S. Kennedy
University of Maryland

Robert R. Twilley
University of Louisiana at
Lafayette

Joan A. Kleypas
National Center for
Atmospheric Research

James H. Cowan, Jr.
LOUISIANA STATE UNIVERSITY

Steven R. Hare
International Pacific
Halibut Commission



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Prepared for the Pew Center on Global Climate Change

by

Victor S. Kennedy
University of Maryland

Robert R. Twilley
UNIVERSITY OF LOUISIANA AT
LAFAYETTE

Joan A. Kleypas
National Center for
Atmospheric Research

James H. Cowan, Jr.
LOUISIANA STATE UNIVERSITY

Steven R. Hare
International Pacific
Halibut Commission

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Foreword Eileen Claussen, President, Pew Center on Global Climate Change

The world's oceans cover approximately 70 percent of the Earth's surface, indicating their importance to the global environment. In addition to having a large influence on global heat transport and precipitation, the oceans are comprised of diverse habitats that support a wealth of marine wildlife. They also provide humans with a wide variety of goods and services including foods, recreational opportunities, and transportation corridors. Based upon current scientific evidence, emissions of greenhouse gases from human activities are projected to cause significant global climate change during the 21st century. Such climate change will create novel challenges for coastal and marine ecosystems that are already stressed from human development, land-use change, environmental pollution, and over-fishing.

"Coastal and Marine Ecosystems & Global Climate Change" is the eighth in a series of Pew Center reports examining the potential impacts of climate change on the U.S. environment. It details the likely impacts of climate change over the next century on U.S. coastal and marine ecosystems, including estuaries, coral reefs, and the open ocean. Report authors, Drs. Victor Kennedy, Robert Twilley, Joan Klepas, James Cowan, Jr., and Steven Hare find:

- Temperature changes in coastal and marine ecosystems will influence organism metabolism and alter ecological processes such as productivity and species interactions. Species are adapted to specific ranges of environmental temperature. As temperatures change, species' geographic distributions will expand or contract, creating new combinations of species that will interact in unpredictable ways. Species that are unable to migrate or compete with other species for resources may face local or global extinction.
- Changes in precipitation and sea-level rise will have important consequences for the water balance of coastal ecosystems. Increases or decreases in precipitation and runoff may respectively increase the risk of coastal flooding or drought. Meanwhile, sea-level rise will gradually inundate coastal lands. Coastal wetlands may migrate inland with rising sea levels, but only if they are not obstructed by human development.
- Climate change is likely to alter patterns of wind and water circulation in the ocean environment. Such changes may influence the vertical movement of ocean waters (i.e., upwelling and downwelling), increasing or decreasing the availability of essential nutrients and oxygen to marine organisms. Changes in ocean circulation patterns can also cause substantial changes in regional ocean and land temperatures and the geographic distributions of marine species.
- Critical coastal ecosystems such as wetlands, estuaries, and coral reefs are particularly vulnerable to climate change. Such ecosystems are among the most biologically productive environments in the world. Their existence at the interface between the terrestrial and marine environment exposes them to a wide variety of human and natural stressors. The added burden of climate change may further degrade these valuable ecosystems, threatening their ecological sustainability and the flow of goods and services they provide to human populations.

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Executive Summary

Since life began on earth, changes in the global climate have affected the distribution of organisms as well as their interactions. However, human-induced increases in atmospheric concentrations of greenhouse gases are expected to cause much more rapid changes in the earth's climate than have been experienced for millennia. If this happens, such high rates of change will probably result in local if not total extinction of some species, the alteration of species distributions in ways that may lead to major changes in their interactions with other species, and modifications in the flow of energy and cycling of materials within ecosystems.

The predicted changes may have a significant effect on coastal ecosystems, especially estuaries and coral reefs, which are relatively shallow and currently under stress because of human population growth and coastal developments. Significant environmental factors that affect the structure (e.g., plant and animal composition) and function (e.g., plant and animal production, nutrient cycling) of estuarine and marine systems and that are expected to be part of global climate change include temperature, sea-level rise, the availability of water and associated nutrients from precipitation and runoff from land, wind patterns, and storminess. Temperature, in particular, influences organism biology, affects dissolved oxygen concentrations in water, and plays a direct role in sea-level rise and in major patterns of coastal and oceanic circulation.

Predictions of the effects of climate change on coastal and marine ecosystems are associated with varying degrees of confidence. There is some confidence in predictions of how increases in temperature will affect plant and animal physiology, abundances, and distributions; aquatic oxygen concentrations; and sea level. There is also some confidence in predictions of the effects of sea-level rise on shallow continental margins, including flooding of wetlands, shoreline erosion, and enhanced storm surges. There is less confidence regarding temperature's influence on interactions among organisms, and even less as to its effects on water circulation patterns. It is also difficult to predict the effects of climate change on precipitation, wind patterns, and the frequency and intensity of storms.

Many species are sensitive to temperatures just a few degrees higher than those they usually experience in nature. A rise in temperature as small as 1°C could have important and rapid effects on mortality of some organisms and on their geographic distributions. Given that temperature increases in the coming century are predicted to exceed 1°C, the major biological change resulting from higher temperatures in U.S. coastal waters may be altered distributions of coastal organisms along the east and west coasts. The geographic ranges of heat-tolerant species such as commercial shrimp on the East Coast may *expand* northward, while the southern range boundaries of heat-intolerant organisms such as soft clams and winter flounder may *retreat* northward. The more mobile species should be able to adjust their ranges over time, but less mobile species may not. Such distributional changes would result in varying and novel mixes of organisms in a region, leaving species

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to adjust to new predators, prey, parasites, diseases, and competitors. Some species would flourish and others would not, and we have no way of predicting at present which species would prevail. Fisheries would also be affected as some species are lost from a region or as others arrive. Warmer conditions would support faster growth or a longer growing season for aquacultured species, but might become too warm for some species in a particular region, requiring a change in the species being cultured.

Because water expands and glaciers melt as temperatures warm, higher temperatures would raise sea levels, inundating coastal lands and eroding susceptible shores. In salt marsh and mangrove habitats, rapid sea-level rise would submerge land, waterlog soils, and cause plant death from salt stress. If sediment inputs were limited or prevented by the presence of flood-control, navigational, or other anthropogenic structures, marshes and mangroves might be starved for sediment, submerged, and lost. These plant systems can move inland on undeveloped coasts as sea levels rise on sedimentary shores with relatively gentle slopes, but seaside development by humans would prevent inland migration. Marshes and mangroves are critical contributors to the biological productivity of coastal systems and function as nurseries and as refuges from predators for many species. Thus their depletion or loss would affect nutrient flux, energy flow, essential habitat for a multitude of species, and biodiversity. Some organisms might thrive (e.g., shrimp, menhaden, dabbling ducks, some shorebirds), at least over the short term as marshes break up and release nutrients or become soft-bottom habitat. Other organisms would be lost from affected areas if their feeding or nesting grounds disappeared and they could not use alternative habitats (e.g., Black and Clapper Rails, some terns and plovers).

Climate change may decrease or increase precipitation, thereby altering coastal and estuarine ecosystems. Decreased precipitation and delivery of fresh water alters food webs in estuaries and affects the amount of time required to flush nutrients and contaminants from the system. Although reduced river flow would decrease nutrient input in estuaries with relatively uncontaminated watersheds, there could be different effects in polluted watersheds that contain point sources of nutrients and contaminants that are not a function of river flow. The combined effects of human development and reduced river flow would degrade water quality conditions, negatively affecting fisheries and human health through such changes as increased presence of harmful algal blooms and accumulation of contaminants in animals and plants. Increased rainfall and resultant freshwater runoff into an estuary would increase stratification of the water column, leading to depleted oxygen concentrations in estuaries with excess nutrients. It would also change the pattern of freshwater runoff in coastal plain watersheds, such as along the southern Atlantic coast and in the Gulf of Mexico. In those regions where water resources are managed by humans, the effects of increased flooding would depend on how managers controlled regional hydrology.

Wind speed and direction influence production of fish and invertebrate species, such as in regions of upwelling along the U.S. West Coast. If upwelling is slowed by changes in wind and temperature, phytoplankton production could be lowered. Where upwelling increases as a result of climate change, productivity should also increase. In some coastal regions, alongshore wind stress and buoyancy-driven density differences help

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produce water movements that transport larval fish and invertebrates to nurseries, such as in estuaries. Climate-related changes in these circulation patterns that hinder such transport might alter the species composition of coastal ecosystems.

Increases in the severity of coastal storms and storm surges would have serious implications for the well-being of fishery and aquaculture industries, as has been demonstrated by the effects of recent intense hurricanes along the U.S. East Coast. Most ecosystems can recover rapidly from hurricanes, but the anthropogenic alteration of coastal habitats may increase the ecological damage associated with more severe storms.

The immense area and the modest extent of our knowledge of the open ocean hamper predictions of how ocean systems will respond to climate change. Nevertheless, it is clear that increased temperature or freshwater input to the upper layers of the ocean results in increased density stratification, which affects ocean productivity. Coupled physical/biogeochemical models predict a net decrease (~5 percent) in global productivity if atmospheric concentrations of carbon dioxide (CO₂) reach a doubling of pre-industrial levels, increasing oceanic thermal stratification and reducing nutrient upwelling. Because productivity varies regionally, simple extrapolation to particular U.S. marine waters is difficult, although some high-latitude areas might benefit from warmer temperatures that lengthen the growing season. Open ocean productivity is also affected by natural interannual climate variability associated with large-scale climate phenomena such as the El Niño-Southern Oscillation. Climate-driven changes in the intensity or timing of any of these phenomena could lead to marked changes in water column mixing and stratification and, ultimately, a reorganization of the ecosystems involved, for better or worse.

Increased CO_2 concentrations lower ocean pH, which in turn changes ocean carbonate chemistry. This may have negative effects on the myriad planktonic organisms that use calcium carbonate to build their skeletons. Some of these organisms appear to play important roles in ocean-atmosphere interactions, but we cannot yet predict any effects that might arise from their diminishment.

Finally, coral reefs, which are already threatened by multiple stressors such as abusive fishing practices, pollution, increased disease outbreaks, and invasive species, would also be at risk from changes in seawater chemistry, temperature increase, and sea-level rise. Lower ocean pH and changed carbonate chemistry would decrease the calcification necessary for building coral reef material. Increased warming would lead to coral bleaching, the breakdown in the symbiotic relationship between the coral animal and the unicellular algae (zooxanthellae) that live within coral tissues and allow corals to thrive in nutrient-poor waters and to secrete massive calcium carbonate accumulations. If sea levels were to rise at a pace faster than corals could build their reefs upward, eventually light conditions would be too low for the zooxanthellae to continue photosynthesis. On reefs near low-lying coastal areas, sea-level rise would likely increase coastal erosion rates, thus degrading water quality and reducing light penetration necessary for photosynthesis and increasing sedimentation that smothers and stresses coral animals. Losses of coral reefs would mean losses in the high biodiversity of these systems as well as the fisheries and recreational opportunities they provide.

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I. Introduction

Environmental change is a fact of life on earth, as is the evolution and extinction of species. However, except for catastrophic events such as massive volcanic eruptions and asteroid strikes, environmental change usually occurs over time scales that range from centuries to millions of years. The predicted rapid changes in climate over the next century (see Box 1) may be such that the subsequent changes in habitat and in species composition and diversity will result in ecosystems that function differently from the way they do now (see Box 2 for further information). Important ecosystem services such as food production, pollution and flood control, and recreational opportunities may be altered — whether positively or negatively is difficult to predict.

For simplicity in thinking about climate changes, we can divide the earth's systems into the atmosphere (air), hydrosphere (water, predominantly the oceans), biosphere (life), geosphere (land, whether above or below the ocean surface), and cryosphere (snow and ice). It is important to realize that climate is affected by interactions within and among all these spheres. The complex processes (e.g., solar input, regional heating and cooling, pressure gradients, circulation) that occur in and affect the atmosphere, sometimes called an "ocean of air," are similar in many ways to the complex processes that occur in and affect the oceans. Biological and chemical processes in the biosphere and geosphere (e.g., production of oxygen by plants and release of carbon dioxide by plants and animals during respiration; release of sulfate aerosols by volcanoes) affect the atmosphere and the oceans, and the atmosphere and oceans affect the biosphere and the geosphere as well as each other. The cryosphere influences the atmosphere, partly because its high albedo reflects radiation back into space, and the hydrosphere, partly because sea ice formation influences freshwater balance. Our knowledge of the intricate, interacting processes in and among these spheres is rudimentary, which makes predictions about the extent and direction of global climate change a grand challenge. In addition, changes may be non-linear (i.e., the output is not directly proportional to the input), so they are not readily predicted from what has been observed in the past, thereby resulting in surprises. Changes may be extreme, and they may be the result of a "flip," or rapid change, from one stable state to another.

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Past and Predicted Changes in Climate Variables

The Third Assessment Report of Working Group I of the Intergovernmental Panel on Climate Change (IPCC, 2001) contains conclusions about recent changes in climate variables and makes predictions based on increasingly sophisticated global climate models that incorporate estimates of future production of greenhouse gases in this century. The models produce simulations of future climate scenarios that might result from the increased emissions of greenhouse gases. The results of different models correspond in varying degrees, so there are various levels of uncertainty for different scenarios of environmental change. However, there is less uncertainty about predicted changes in temperature and sea levels than about predicted changes in precipitation, winds, and storminess. Models produce outputs or results for large geographical regions, but their spatial resolution does not allow them to produce scenarios for smaller regions such as the Chesapeake Bay or San Francisco Bay.

The IPCC report indicates that the average temperature near the surface of the earth has increased by 0.6°C (~1°F) since 1861, with most of the warming occurring from 1910 to 1945 and from 1976 to 2000. The IPCC predicts that by 2100 the earth's near-surface temperature, averaged over the globe, will increase by 1.4 to 5.8°C (2.5 to 10.4°F) from 1990 levels, so sea-surface temperatures would also increase. The greatest warming is expected to occur at high latitudes in winter. The IPCC notes that the predicted global increase is much greater than what was observed in the 20^{th} century and that it is probably greater than any temperature rise that occurred over the past 10,000 years. It is the rapidity of this change that may result in the greatest ecological change in estuarine and marine systems.

The IPCC reports that globally averaged sea level rose between 10 and 20 cm (\sim 4 to 8 in) in the 20th century and predicts a further rise of 9 to 88 cm (\sim 4 to 35 in) between 1990 and 2100. This rise is due to water

expanding as it warms, and to melting from land-based glaciers and ice caps. The amount of snow cover, duration of freshwater ice cover in the Northern Hemisphere, length of non-polar mountain glaciers, and thickness of Arctic sea ice declined during the 20th century. This trend is predicted to continue.

The IPCC reports that precipitation in the Northern Hemisphere probably increased in the 20th century over most mid- to high-latitude and tropical land areas and decreased over sub-tropical (10° N to 30° N) land areas. The frequency of heavy precipitation events in mid- to high-latitude regions may also have increased. The IPCC predicts that globally averaged precipitation will increase in the future, as will winter precipitation and more intense precipitation events over mid- to high-latitudes in the Northern Hemisphere. Predicted changes for low latitude land regions vary regionally (increasing in some and decreasing in others). Alaska is one region for which there is good agreement among the IPCC models in terms of changes in precipitation, with an average change of more than 20 percent expected. This increased precipitation will affect not only streamflow, and thereby salmonid populations both during seaward and spawning migrations, but also the large-scale, nearshore, oceanic currents such as the Alaska Stream and Alaska Coastal Current. This additional freshwater input has the primary effect of increasing stratification in the water column and lowering salinity in the near-surface layer.

The IPCC was unable to find a consistent pattern of tropical and extra-tropical storminess (frequency or intensity) because of variability in the data and could not make firm predictions about future changes in this factor. Warm El Niño-Southern Oscillation conditions (see Box 6) that occurred more often, lasted longer, and were more intense in the mid-1970s than in the past century are not predicted to change over the next century.

This report considers possible influences of climate change on estuarine and coastal marine ecosystems of the United States. It also considers open ocean regions beyond U.S. jurisdiction in which the United States has commercial interests, or in which climate changes may indirectly affect life in this country. It acknowledges that the uncertainties about future emissions and concentrations of greenhouse

gases plus uncertainties associated with constructing scenarios of climate change are accompanied by uncertainties about how sensitive the climate system will be to perturbations (Box 1). Such uncertainties affect our ability to predict the ecological effects of climate change. This report considers the possible effects of changed environmental conditions by beginning with the variables (temperature, sea-level rise) for which there is the most confidence about the direction and extent of change, then examining variables (precipitation, wind, storms) for which there is greater uncertainty as to the direction and extent of change.

The focus here is predominantly on the coastal zone, a region of land margins with dynamic interactions among atmospheric, terrestrial, and aquatic systems. These interactions result in high biological productivity and resources of important economic value. The coasts of the United States and its territories extend for about 80,000 miles and include the coasts of the continental United States as well as Alaska, Puerto Rico, the Pacific islands of Hawaii, American Samoa, and Guam, and a number of smaller island groups in the Pacific and Caribbean (Burke et al., 2001). The narrow coastal strip of the contiguous United States represents 17 percent of the nation's continental land area, but is inhabited by about 53 percent of the population (NOAA, 1998). These are the most heavily developed regions of the nation, with rates of recent population growth that exceed that of the country as a whole. This is important because coastal systems cannot be considered without reference to what is happening on the adjacent land mass. Material washing off land or delivered from the atmosphere with precipitation enters estuaries or the sea, and nutrient and contaminant runoff from densely populated regions stresses coastal ecosystems.

Within the coastal zone, estuaries and their associated wetlands are vital to the well-being of coastal systems and fisheries (Box 3), serving not only as harvest sites, but also as nurseries for commercial species harvested elsewhere. Offshore, the U.S. Exclusive Economic Zone beyond and adjacent to the territorial sea is estimated to be habitat for about 20 percent of all harvestable seafood in the world (Environmental Health Center, 1998). Coastal and offshore systems are currently under heavy harvest pressure, which may threaten not only the fisheries, but also the very existence of some harvested species. Because those species are part of a larger web of feeding and other biological relationships (Box 2), their depletion or loss may have important negative consequences for the ecosystems they inhabit and the reptiles, birds, and mammals that feed on them (Jackson et al., 2001). If climate change adds stress to coastal and offshore systems, that may have major negative effects on some ecosystem components. This situation is analogous to that faced by a human whose immune system is compromised and who may succumb to a disease that would not threaten a healthy person.

Ecological Background

Organisms interact directly and indirectly with each other (e.g., through predation, competition for resources, parasitism) and are influenced by their physical environment. Scientists use food webs (see Figure 1) to encapsulate feeding interactions within different systems, and a multitude of food webs of varying complexity exist in estuarine and marine systems. An organism's role in nature may change as it grows and matures or when it moves to different habitats over time. For example, salmon hatch in freshwater streams, move downstream into estuaries for a time, swim to the ocean where they eventually mature, and return through estuaries to their home stream to spawn. In each of the habitats it lives in during its life cycle, a salmon participates in different food webs, competes for resources (e.g., food, spawning habitat, refuge space) with different species, and is parasitized by different species.

The various linkages among species and feeding groups may provide resiliency so that the loss of a few species may not unravel the web. However, there may be a key species or group of species whose loss would be detrimental to the web's integrity, but our knowledge about such matters is limited for most marine food webs. Even if we knew which species or group was vital to a web's integrity, we would still be hampered in predicting the effects of climate change on most webs. For example, with regard to the estuarine community web (Figure 1), we have data on tolerances to high temperatures for few of the species. We know almost nothing about the effects of high temperature on the microscopic organisms that play significant roles in the "microbial loop" of food webs. Thus we cannot predict how increased temperature might affect webs or systems as a whole. Nevertheless, we can expect that some ecosystems may shift abruptly and with

little warning to an alternative stable state (Scheffer et al., 2001). There is no way at present of predicting if these shifts will be positive or negative in relation to services provided to human endeavors.

A key species does not have to be eliminated from a habitat for there to be resultant changes in its ecosystem. Even if it persists at low numbers, its influence may have been diminished. For example, the eastern oyster, a filter feeder that pumps water over its gills to trap phytoplankton (its floating algal food), was once a significant bottom-dwelling component of the Chesapeake Bay ecosystem. For many reasons, abundances today are about 1 percent of what they were a century ago. As a result, the oyster's ability to filter the bay's water has greatly diminished so that the Chesapeake Bay is no longer a bottom-dominated system. Instead, it is a turbid pelagic system dominated by floating phytoplankton and their zooplankton grazers, and by jellyfish that feed on the zooplankton.

The introduction of a new species into an ecosystem can have an influence as important as the loss or decline of a key species such as the oyster. For example, a filter-feeding clam from Asia has invaded San Francisco Bay. Its introduction and spread has been followed by changes in local food webs so that sections of the bay harboring these clams are now bottom-dominated systems.

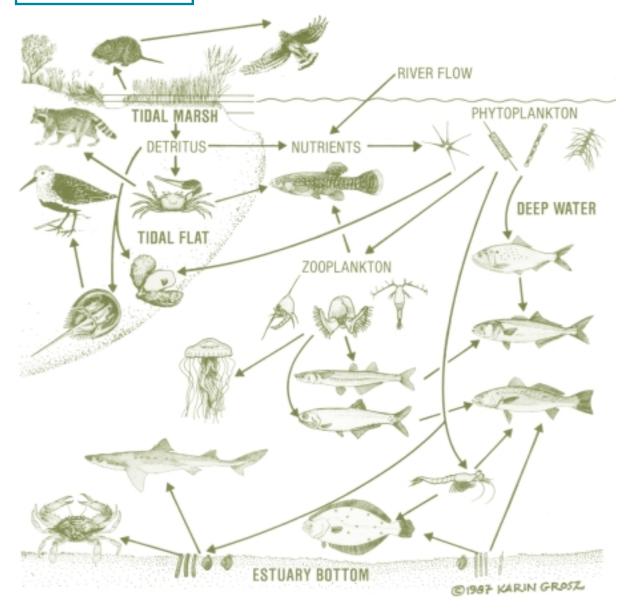
The depleted abundances of oysters and the introduction of the Asian clam have had major effects on their ecosystems. Climate change might have similar effects in ways we are not yet able to predict if key species are affected positively or negatively or if invasions of an exotic species are enhanced. Walther et al. (2002) describe numerous ecological responses to recent climate change.

For an integrated perspective on the possible effects of climate change on aquatic systems in U.S. areas of interest, this report should be supplemented by Frederick and Gleick (1999) on water resources, Wigley (1999) on climate change, Neumann et al. (2000) on coastal resources, and Poff et al. (2002) on freshwater and coastal wetland ecosystems. A number of regional assessments have appeared recently (Najjar et al., 1999; New England Regional Assessment, 2001; Pacific Islands Regional Assessment, 2001; Twilley et al., 2001), and Boesch et al. (2000) have prepared a national overview. Some relevant websites are listed at the end of this report.

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Figure 1

Estuarine Food Web



Schematic diagram of an estuarine food web. The three horizontal lines (upper left) represent low mean tide (bottom line), mean tide, and high tide. Note that the phytoplankton and zooplankton components include members of the "microbial loop" of microscopic organisms that have been discovered recently to serve very important functions in energy flow and nutrient cycling.

Source: Bryant and Pennock (1988).

The Significance of Estuaries

Estuaries are highly productive ecosystems that also play important roles in the productivity of nearshore coastal environments. They are semi-enclosed bodies of water in which freshwater and seawater mix. Changes in freshwater input result in variations in the estuary's salinity, so resident organisms have to be tolerant of such variability.

Ecological processes within estuaries and the types of estuarine habitat are influenced by hydrologic factors of the associated watershed, by the estuary's surface area and volume, and by its freshwater and marine inputs. Drainage from rivers carries dissolved materials (nutrients, contaminants) and particles (soil, sewage) to the estuary. Surface area and volume, coupled with water inflow, influence the residence time of water and associated nutrients and contaminants in an estuary. Freshwater inflow brings particulate material from the watershed that sinks in the estuary as flow decreases. The inflow of seawater from the ocean moves inland along the estuary bottom, retaining these sinking particles and stratifying the water column (see Box 4) and thereby affecting the "health" of the estuary if the retained particles are toxins or contaminants.

Estuaries commonly harbor coastal wetlands or marshes that contain plants tolerant of fluctuating salinity. In temperate and sub-tropical regions, coastal marshes contain predominantly a few species of grasses or grass-like plants, supplemented by microscopic algae that live on the surface of the marsh sediment or marsh organisms. In warmer habitats, swamps or forests of salt-tolerant shrubs or trees called mangroves replace salt marshes in the intertidal zone. Marshes and mangroves depend on sediment washed from the land to grow upward (accrete) in the face of rising sea levels. The presence of extensive tracts of marshes or mangroves can protect the adjacent land and human populations from storm surges of water caused by high intensity coastal storms and hurricanes. Marshes intercept

nutrients and contaminants in runoff and thus combat the effects of excess quantities of these materials, including protecting nitrogen-sensitive seagrasses that play an important role in coastal food webs.

Nutrient runoff supports high estuarine plant production, which in turn supports high animal production, including commercially valuable invertebrates and fish. Houde and Rutherford (1993) note that fish production is influenced by freshwater and nutrient inputs in complex ways. They estimate that whereas estuaries represent only 0.5 percent of the world's marine environment, they support about 5 percent of global fish production. In the United States (Environmental Health Center, 1998), about 75 percent of commercially harvested fish and shellfish as well as species representing up to 90 percent of recreational catches depend on estuaries for spawning and feeding, as nursery habitat for their young, or as migration routes to or from spawning or feeding habitats. Estuaries also serve as economically important recreational venues for boaters, hunters, and birdwatchers. Migrating birds depend heavily on coastal aquatic systems for food. For example, Gulf of Mexico wetlands are vital for the well-being of 75 percent of migrating waterfowl in the Central Flyway (Environmental Health Center, 1998).

Finding space for burgeoning coastal populations (see Neumann et al. (2000) for data on projected population growth) often means encroaching on or destroying wetlands. Over 50 percent of inland and coastal wetlands in the United States have been destroyed since the 1780s (Dahl, 2000). Responses of humans to coastal erosion and sea-level rise may take the form of actions destructive to wetlands such as armoring coastlines with berms or dikes that will prevent biological systems from adjusting naturally (e.g., by inland retreat of wetlands).

II. Effects of Global Climate Change on Coastal Systems

In terms of global climate change, environmental factors that are expected to have the greatest direct effects on estuarine and marine systems are temperature change, sea-level rise, availability of water from precipitation and runoff, wind patterns, and storminess. The state of our knowledge of these environmental factors allows us to make reasonable predictions about some of their effects, but not about others. Temperature influences organism biology (mortality, reproduction, growth, behavior), affects dissolved oxygen concentrations in water, and plays a direct role in sea-level rise and in major patterns of coastal and oceanic circulation. There is some confidence about predicting what would happen to organisms, oxygen concentrations, and sea levels as temperature increases, less confidence as to temperature's influence on interactions among organisms (e.g., predator-prey, parasite-host, competition for resources), and even less as to its effect on water circulation patterns (Box 1).

There is some confidence about predicting the effects of sea-level rise on shallow continental margins, including flooding of wetlands, shoreline erosion, and enhanced storm surges. There is less confidence in the ability to predict the effects of climate change on precipitation, wind patterns, and the frequency and intensity of storms. Precipitation affects runoff into estuaries and therefore influences estuarine circulation, concentrations of nutrients and contaminants, stratification and oxygen deficits, and recruitment of some species (i.e., the addition of new individuals to a species' population). Wind speed and direction influence coastal circulation, including currents that deliver fish and invertebrate larvae from coastal waters into estuaries. Storms and their associated winds can have major negative effects on coastal ecosystems and shoreline structures.

A. Predicted Changes in Environmental Factors

Temperature

Effects on the biology of organisms

Temperature extremes (both high and low) can be lethal to organisms. Because evaporative cooling limits the level to which water temperatures can increase, summer temperatures of tropical waters may not become much higher than they are now as the climate warms. However, temperatures in temperate and boreal regions may rise to levels that are stressful or lethal to resident organisms. Many species are sensitive to temperatures just a few degrees higher than those they usually experience in nature. Indeed, in short-term (days) temperature-tolerance experiments on estuarine invertebrates in the laboratory, a temperature increase of 1°C often raised mortalities from ~0 percent at the lower temperature to ~100 percent at the increased temperature (Kennedy and Mihursky, 1971). Temperature increases in the coming century are predicted to be greater than 1°C (see Box 1).

At sub-lethal levels, temperature influences growth and metabolism, governs animal behavior and distribution patterns of organisms, and acts in concert with other environmental variables such as dissolved oxygen (Box 4). It influences the timing of reproduction and controls rates of egg and larval development. For example, recent declines in the abundance of winter flounder in New England (see below) might be due to the negative effects of warmer winters on egg survival and larval hatching and development (Keller and Klein-MacPhee, 2000).

Higher temperatures also may have positive effects. Some commercially valuable estuarine-dependent species in the lower latitudes have higher growth rates and larger annual harvests when temperatures are higher. For example, shrimp harvest is generally highest in tropical climates and declines northward, so an increase in temperatures could increase the annual yield of shrimp in temperate waters like the Gulf of Mexico, as long as temperatures did not exceed lethal levels. In the mid-Atlantic region, where severe winters are thought to result in low blue crab catches, less severe winters may enhance harvests if other factors do not intervene.

Box 4

Oxygen in Coastal Waters

Oxygen is supplied to the aquatic environment by plant photosynthesis, direct diffusion from the atmosphere, and the mixing of air into water by wind and wave action. Fluctuations in oxygen concentration are caused by diurnal and seasonal changes in light and temperature that influence oxygen production by plants and consumption (respiration) by plants and animals. There may be fluctuations for other reasons. For example, nutrients (nitrogen, phosphorus) support plant production. An excess of nutrients due to atmospheric deposition, runoff from agricultural or other fertilized land, or sewage discharges can lead to very high biological production in the form of algal blooms. The numbers of animals that graze on these blooms will then increase. Damaged and dead algal cells and the feces of the grazers sink to the bottom of the water body. Decomposition of this material by microbes requires oxygen, and the rate of oxygen use by these decomposers may exceed the rate of replenishment by photosynthesis and diffusion or mixing from the atmosphere. Thus deeper water may become hypoxic (low in oxygen concentrations) or anoxic (lacking in oxygen) and this will stress organisms that require oxygen. Also, warm water holds less oxygen than cold water. Organisms whose metabolism has been raised by higher temperatures increase their oxygen demand. The mismatch between supply and demand, if it is high enough, will stress the organisms.

Under some conditions, an aquatic system will become stratified so that a less dense layer of water will lie on top of a denser layer. The stratification prevents oxygen from diffusing into the deeper water, so the deeper

water becomes hypoxic or anoxic until the stratification ends. Thermal stratification occurs when calm surface waters are heated by the sun, become less dense, and blanket the denser, deeper water until the temperature gradient lessens or a storm stirs the water column and mixes the different waters. Salinity stratification occurs in estuaries and shallow shelf waters when freshwater runoff results in a layer of less dense water lying on top of the denser, more saline water in the estuary. Because the freshwater runoff brings land-derived nutrients, an algal bloom may result, with the consequences described above.

A number of coastal regions worldwide are subject to increasing periods of low oxygen concentrations. For example, during periods of high river discharge, a large mass of hypoxic bottom water forms in the northern Gulf of Mexico from April to August as a result of increased density stratification and nutrient loading. Increased precipitation and discharges may exacerbate the already serious problems of eutrophication and hypoxia (Justić et al., 1996). Decreased discharges may reduce the potential for hypoxia by decreasing the frequency and strength of stratification events on the inner continental shelf, as observed during the summer drought in 2000. Thus hydrologic regimes during more intense precipitation will promote hypoxia, whereas periods of drought will reduce the areal extent of hypoxia in nearshore environments. It is also possible that increased mixing by more frequent or more intense storms may alleviate summer hypoxia in regions such as the northern Gulf of Mexico.

Effects on the abundance and distribution of organisms

Temperature directly or indirectly influences population abundances and distributions of organisms. For example, temperature cycles and maximum abundances have been strongly correlated for over 30 commercial fish species in the Gulf of Maine (Dow, 1975), and inshore sea-surface warming and offshore cooling was associated with a period of exceptional fish production on the North American West Coast (Beamish,1993). The distributional limits of southern species in New England moved north as water temperatures increased north of Cape Cod after the 1940s (Taylor et al., 1957), and marine temperature variation explained changes in the north-south distribution of 12 of 36 species of fish in the U.S.

mid-Atlantic region over about 20 years (Murawski, 1993). Higher winter temperatures on a North Carolina inshore reef were associated with greater numbers of 28 species of tropical fish on the reef over a 15-year period (Parker and Dixon, 1998). Similar climate-influenced changes would have positive effects on some fisheries and negative effects on others, presenting a challenge to managers of and participants in particular fisheries.

Although higher temperatures might not result in extinction of a species throughout its range, the species may be eliminated from part of its range. Temperature changes as small as 1°C can have important effects on species distributions in a short time. For example, the number of species of reef fish off

Los Angeles declined by 15 to 25 percent between 1976 and 1977 when temperatures increased abruptly by ~1°C (Holbrook et al., 1997), demonstrating that regional species diversity of mobile organisms can change rapidly. Temperatures in the region remained higher through the 1990s and the proportion of southern species rose while the proportion of northern species fell. As another example, the annual mean water temperature inshore at Monterey Bay, California, increased by ~0.8°C and mean summer maximum temperatures were ~1.9°C higher between the early 1930s and the late 1990s (Sagarin et al., 1999). By 1996, the abundances of 10 of 11 intertidal species with southern (warmer water) distributions were higher than their abundances in the early 1930s, whereas the abundances of 5 of 7 northern (cooler water) species declined in the interim.

Such examples of changed patterns of distribution in concert with warming allow us to develop scenarios of changes in U.S. coastal regions. Thus, species whose southern range ends in the mid-Atlantic region (between Cape Hatteras and Delaware Bay) will be lost from that region if water temperatures reach levels that are lethal or that inhibit successful reproduction and recruitment. For example, the commercially important soft clam in the Chesapeake Bay lives near its southern distribution limit and may be eliminated from the bay if bottom water temperatures approach and remain near 32°C in summer (Kennedy and Mihursky, 1971). Similarly, the commercially important ocean quahog clam lives near its southern limit in the mid-Atlantic region. Weinberg et al. (2002) estimate that an increase of 2°C would extend the period of thermal stress for ocean quahog larvae from the present 167 days to 231 days (May 14-December 31), lowering survival of the larvae and depressing their recruitment to the resident population, which could eventually die out over a period of decades.

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Unfortunately, there are few data on temperature tolerances available for most other species in the mid-Atlantic region (or elsewhere), so data on geographic ranges must be used to predict warming-related shifts in distribution (recognizing that factors other than temperature tolerances also limit distributions). Fish communities in the mid-Atlantic region contain mainly species with either northern or warm-temperate distributions (Musick et al., 1985), so there should be changes in fish distributions if the climate warms. Based on distribution information in Murdy et al. (1997), the southern range limits of cooler-water fish like winter flounder and cunner would retreat northward, whereas warmer-water species like southern flounder and spotted seatrout would range even farther north than they do now.

Similar predictions about expanded distributions northward can be made for some mid-Atlantic invertebrates. For example, pink, white, and brown shrimp support commercial fisheries as far north as North Carolina and range north of Cape Hatteras in noncommercial abundances. If temperature is the factor limiting their northward distribution, climate warming should allow them to become established in the mid-Atlantic region and in the lower Chesapeake Bay in numbers that might support a fishery (although they might face competition for resources from other species).

Based on distribution data in Emmett et al. (1991), similar predictions can be made for Pacific coast organisms. Thus the southern range boundaries of starry flounder, the Dungeness crab, the soft clam, and the fat gaper clam (cooler-water species) may retreat northward as climate warms while the northern range boundaries of Pacific hake, some bass in the genus *Paralabrax*, and the Pacific gaper clam (warmer-water species) may advance northward.

Movement into and colonization of newly suitable (new) habitat depends on many factors: 1) the number of adults available in the original habitat and their ability to produce young (seeds, spores, larvae); 2) an adequate number of potential colonizers (seeds, spores, larvae, migrating juveniles or adults); 3) the ability of potential colonizers to move into the new habitat, including their ability to cross barriers; and 4) the survival of adequate numbers of individuals in the new habitat to ensure genetic diversity to meet environmental challenges and to produce succeeding generations. Poff et al. (2002) emphasized the importance of corridors that link a region where a species is at risk and a more suitable region. Such corridors may not exist for estuarine species that cannot survive the high-salinity marine conditions that occur between estuaries (Kennedy, 1990). Thus, the loss of species from an estuary that has become too warm for those species may reduce species diversity in that estuary in the short term, depending on the

speed of immigration to that estuary of species that can tolerate the warmer conditions. This is especially true of species that have limited abilities to disperse or where there are no dispersal corridors. Mobile organisms like fish, swimming crabs, and shrimp can quickly colonize new habitats by migrating along the coast, but immobile or relatively immobile invertebrates such as clams and oysters will migrate more slowly.

Coastal plants may also be sensitive to changes in air and water temperatures. For example, changes in frequency of freeze events will alter ecosystems of the east and west coasts of the Gulf of Mexico because shoreline vegetation is strongly influenced by the frequency of frost from Texas to south Florida. In south Florida, episodic frost or freezing events help shape ecosystems because tropical plants (including mangrove species) and animals are highly vulnerable to such events. If climate change reduces the frequency of episodic freeze events, over time the coastal red mangrove communities should shift farther north of Tampa Bay on Florida's Gulf of Mexico coast and Laguna Madre on the Texas coast. Greater development of black mangrove forests, whose current infrequent occurrence is associated with the higher frequency of frost, would be expected along the Louisiana coast (black mangroves are the most cold-tolerant of mangrove species and indicate the transition between warm-temperate and subtropical climates). Also, subtropical seagrasses would be more prevalent in warm-temperate coastal habitat where suitable water clarity exists.

Effects on species interactions

Temperatures can also influence changes in species interactions (e.g., predator-prey, parasite-host, competition for resources; see also Box 2) in ecosystems. For example, winter flounder may be negatively affected by the extent of warming predicted for New England (New England Regional Assessment, 2001). As noted earlier, their abundances in southern New England have been declining but the reasons are unclear. An alternative hypothesis to that of Keller and Klein-MacPhee (2000; see above) is that the decline is due to a temperature-mediated shift in the food web that favors organisms that feed in the water column, thus reducing the amount of food available to bottom feeders like winter flounder (New England Regional Assessment, 2001).

Changes in distribution patterns as noted earlier would change the mix of predators, prey, parasites, and competitors in an ecosystem in ways that are not yet understood but that could alter the functions of the ecosystem and the productivity of selected fisheries. Predation pressure in marine ecosystems generally

increases from the poles to the tropics (Vermeij, 1978), so warming due to climate change could cause an ecological shift to increased predation if it led to greater diversity and numbers among predators. For example, warm winter conditions of the past decade have favored predatory game fishes that have become more numerous in the Laguna Madre than elsewhere in Texas (Robinson et al., 1997). In turn, densities of small fishes, shrimps and crabs are lower in Laguna Madre seagrass beds than elsewhere in the Gulf of Mexico (Sheridan and Minello, 2002).

Climate change may also alter species interactions by changing the timing of physiological events (Penuelas and Filella, 2001). For example, altered temperature regimes could advance or retard the timing of reproduction for many species. Where the production of young of a species is synchronized with the presence of their food supply, temperature-induced changes in production of young may result in their being present when their usual food supply, if it does not respond to changed temperature, has not developed or has passed its peak. For example, such "synchronicities" of timing affect migrating waterfowl and shorebirds that depend on the short-term population explosion of invertebrate prey to support food requirements of adults and young on their high-latitude breeding and rearing grounds.

Effects on oxygen concentrations

Temperature influences the amount of oxygen that water can hold (warmer water holds less oxygen than cooler water; see Box 4). Most aquatic organisms extract the oxygen necessary for their metabolic demands and survival from the water in which they live. Interactions between higher temperatures and depleted oxygen could constrict the available habitat for certain aquatic species. For example, striped bass habitat may be "squeezed" along the North American East Coast, especially in Chesapeake Bay, an important spawning and rearing region for this species (Coutant, 1990). The "squeeze" can occur because the surface waters of the striped bass' normal habitat may become so warm that the fish will seek cooler waters. However, the cooler, deeper waters will not contain enough oxygen if hypoxia or anoxia is present (see Box 4) and will be avoided by the fish. Laboratory studies have shown that organisms under stress (as the striped bass would be) pay a metabolic cost in the form of a continued expenditure of energy that may lead to death if the stress does not abate (e.g., Parsons, 1990).

Effects on water circulation

Increased ocean temperatures may alter coastal ocean currents. For example, Gallegos et al. (1993) propose that global climate-induced changes in ocean temperatures might alter circulation patterns of the Gulf of Mexico and Caribbean. This has important implications for coastal south Florida, where the major circulation systems influence the distribution, recruitment, and survival of coastal marine fish and invertebrate communities of the Florida Keys and other areas of south Florida (Lee and Williams, 1999). These coastal boundary currents also influence the residence time of water in nearshore environments and serve as transport mechanisms for materials along the Gulf of Mexico coast. Many recreationally and commercially important fish and shellfish species in the Gulf spawn offshore, especially in winter, but their juveniles depend on coastal and estuarine nursery areas. Alteration of coastal currents and offshore-inshore transport corridors may have negative consequences on the growth and survival of these species (see also Wind, Water Circulation, and Storminess, below).

Sea-level Rise

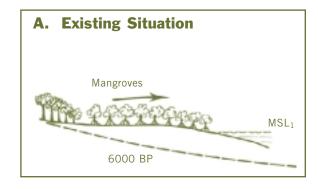
Climate warming will lead to thermal expansion of water and melting of glacier and polar land ice, with a subsequent rise in sea level (Box 1). The effects of sea-level rise will vary with location, speed of the rise, and the geological and biological responses of the affected ecosystems (see Neumann et al. (2000) for a detailed review of the factors affecting the vulnerability of coastal habitat to sea-level rise).

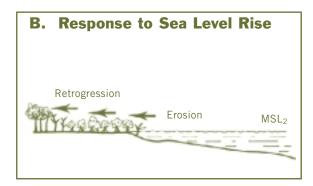
Sea-level rise is a particular threat to the low-lying, shallow-gradient wetlands of the Middle and South Atlantic and Gulf of Mexico. Coastal storms put the two Atlantic regions at further risk from sea-level rise, and the central Gulf Coast region faces an added risk because the deltaic plain is sinking. In general, sea-level rise will inundate coastal lands and erode susceptible shores (Figure 2). In salt marsh and mangrove habitats, sea-level rise may submerge wetlands, waterlog soils, and cause plant death from salt stress. Most wetland habitats can survive sea-level rise by migrating inland to areas of decreasing tidal inundation along undeveloped (by humans) shores with relatively gentle slopes. In the absence of human effects, there would not be a catastrophic effect on most Gulf of Mexico coastal wetlands, at least at the rates of rise currently projected for the next 50 to 100 years.

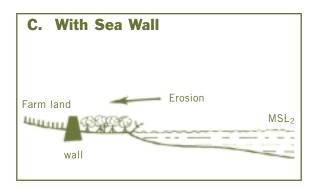
On developed coasts, wetland plant systems cannot move inland as sea level rises on sedimentary shores because seaside development by humans limits that option (Figure 2). If sediment inputs are limited

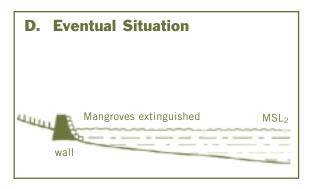
Figure 2

Sea-level Rise Effects on Mangrove Forests









The above figures depict changes in a mangrove forest (could also apply to a salt marsh) that inhabits a depositional terrace that is over 6000 years old (A). In (B), sea level rises at a rate that erodes the foreshore yet allows the forest to retrogress inland. In the presence of human attempts to prevent sea level from inundating the land by building a seawall, the mangrove forest will be eroded away (C and D) and the seawall may have to be strengthened (armored) against wave action that is no longer buffered by the mangroves. BP = before present; MSL = mean sea level.

Source: Bird (1995).

or prevented by the presence of flood-control, navigational, or other anthropogenic structures, marshes and mangroves may be starved for sediment and normal accretion (vertical accumulation of sediment) will be hindered (Figure 3). If inundation outpaces accretion, the marsh or mangrove forest will be submerged, die, and disappear. The continued loss of wetlands in Louisiana indicates that, under the present rate of sea-level rise of 2.3 mm per year and land subsidence of 4 mm per year, total marsh area will be critically reduced as humans alter water and sediment distributions. Estimates of the critical rates of sea-level rise above which south Florida and Caribbean mangrove ecosystems will collapse range from 1.2 mm per year (Ellison and Stoddart, 1991) to 2.3 mm per year (Wanless et al., 1994). However, these rates are only for mangroves in regions with little sediment input, and there has been strong criticism of these threshold

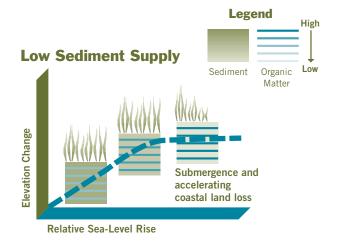
values (Snedaker et al., 1994). The most vulnerable mangrove ecosystems in the Gulf of Mexico include those in micro-tidal limestone settings, and those with extensive inland residential development. For example, the extensive coastal development of south Florida would squeeze many species into smaller habitat spaces, with high risk to vulnerable species such as the endangered American crocodile and perhaps sea turtles (Harris and Cropper, 1992).

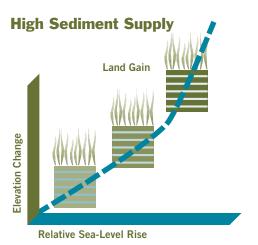
Louisiana is already undergoing high rates of relative sea-level rise because of land subsidence (Neumann et al., 2000). Development of interior wetland margins by humans as well as the relatively steep gradient of the Pleistocene terrace escarpment prevent landward migration of most Louisiana wetlands, so this ecosystem can be maintained only through vertical accumulation of soil. This process is impaired in Louisiana by major human modifications to the hydrology of the Mississippi River deltaic plain. However,

Figure 3

Sediment Supply and Vertical Accretion

of Coastal Marshes





Relationship between extent of sediment supply and persistence of coastal marshes and mangroves as sea level rises. In the top figure, marsh/mangrove ecosystems are starved for sediment and cannot build-up soil (i.e., accrete) to keep pace with sea-level rise, resulting in inundation and land loss. In the bottom figure, soil accretion keeps pace with sea-level rise, allowing continued persistence of the marsh/mangrove ecosystem.

Source: Reed (1999)

where the Mississippi River connects with its deltaic plain, such as in western Terrebonne Bay where the outflow from the Atchafalaya River nourishes adjacent areas, coastal wetlands appear to respond by adequately maintaining their elevation in the face of subsidence (Day et al., 1997). The same is true for

largely unaltered coastal basins such as Pascagoula Bay in Mississippi. It is when sea-level rise is combined with other human land use changes in the drainage basins of the Gulf of Mexico that the consequences may be severe (Cahoon et al., 1998).

Wetland marshes are important contributors to the biological productivity of coastal systems and function as nurseries and as refuges from predators for commercially important shellfish and fish (see Box 5 for some climate-change scenarios for Gulf of Mexico fisheries) and for birds like some rails, gulls, and terns. Rising sea levels will initially increase access to marsh surfaces by fish and invertebrates, perhaps increasing their production in the short term (e.g., Gulf of Mexico shrimp harvests). However, depletion or loss of marshes will have important effects on nutrient flux, energy flows, essential habitat for a multitude of species, and biodiversity (Ray et al., 1992). Such effects will be positive or negative, depending on the species. For example, birds that require the marsh for rearing young (e.g., Black and Clapper Rails, some terns and plovers) will be affected negatively by its loss, whereas birds that feed in shallow water or on intertidal sand and mud flats that replace the marsh (e.g., dabbling ducks, some shorebirds) will be affected positively. Some coastal zones are habitat for rare, threatened, or endangered species of plants and animals and, if the changes threaten rather than enhance their habitat, they may be lost. Such loss represents the loss of much unique and potentially significant genetic information.

Human interference with natural barrier island processes increases the islands' vulnerability to even a small rise in sea level. Many barrier islands move toward the mainland through a process of beach erosion on their seaward flank, overwash of sediment across the island during storms, and deposition of the eroded sediment in the quieter waters of the inland bay. The rate of this natural migration depends largely on the rate of sea-level rise, and also on the frequency and severity of storms and hurricanes. Even a small rise in sea level sets this process in motion. The construction of buildings, roads, bulkheads, seawalls, and any other type of shore hardening disrupts overwash and sediment movement. In response, the beach face and nearshore erode, threatening buildings and narrowing the beach, but the "ribbon of sand" does not grow landward. Eventually, this threatens not only human habitation on barrier islands but also the barrier islands themselves and the habitats they provide.

Finally, accelerated rates of subsidence and sea-level rise may alter the depth and width of shallow estuaries. For example, many estuaries in the Gulf of Mexico are only 1 to 3 meters deep and have little topographical relief, so that small absolute changes in relative sea level will greatly change their relative

bottom area. Because of the strongly wind-driven nature of these estuaries, bottom friction is very important in controlling hydrodynamics. Changes in bottom area will have an immediate and important effect on the pattern of energy dissipation in estuaries (Schroeder et al., 1990). Rapid changes in bottom area and configuration can also have ecological consequences if they bury or scour important fishery nursery habitats such as seagrass meadows and oyster reefs.

Precipitation and Hydrologic Regime

Changes in precipitation (decreases or increases) and hydrologic regimes at the regional level can have important ecological effects on coastal ecosystems. Decreased rainfall and runoff combined with sea-level rise would result in salinity encroachment into the tidal freshwater reaches of an estuary, affecting lower-salinity communities of organisms. Decreased freshwater delivery alters food webs in estuaries and changes the residence time of nutrients and contaminants. Reduced nutrient input during drought can be a major cause of the loss of productivity of a river-dominated estuary during and after drought periods (Livingston et al.,1997). Permanent reductions of freshwater flows due to combined effects of human activities and climate change could lead to major reductions of biological productivity in alluvial bay systems such as the lagoons of Texas, Mobile Bay, Apalachicola Bay, and Tampa Bay.

Whereas reduced river flow would reduce nutrient input in estuaries with rather pristine watersheds, there could be different effects in polluted watersheds. Watersheds next to heavily industrialized or urbanized estuaries have sources of nutrients and contaminants that are not a function of river flow. Many of these estuaries also receive substantial amounts of nutrients such as nitrogen precipitated from the atmosphere. The combined effect of human development, nutrients transported by atmospheric processes, and reduced river flow would produce water quality conditions that would negatively affect fisheries and human health through such changes as accumulation of metals in animals and plants.

Climate change-induced shifts in the recharge of aquifers together with increasing demand by humans on water resources could have important implications for coastal ecosystems. For example, a significant influx of fresh water into several estuaries and bays in the Gulf of Mexico comes from groundwater (Herrera-Silveira, 1996). However, increased upstream consumption of water by agricultural, urban, and industrial users over the last two decades has reduced artesian outflows of groundwater downstream. The combination of increased demand and decreased recharge of this resource as a result of climate change would reduce estuarine productivity in this region and others where estuaries depend on ground water.

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Possible Effects of Climate Change on Coastal Fisheries in the Gulf of Mexico

Projected effects of climate change on Gulf of Mexico fisheries are uncertain and depend on the time horizon that describes subsequent habitat change. Numerous models and review papers from the southeast Atlantic and Gulf attribute survival of young fish, recruitment within estuaries, and fishery yields to such factors as river runoff, salinity and water temperature regimes during critical time periods, percent availability of suitable estuarine nursery habitat, precipitation, favorable wind fields, hypoxia, and sea-level fluctuations. In the short term, warmer water and higher growth rates plus expansion of salt marshes inland with sea-level rise may favor productivity of estuarinedependent marine species. However, this enhanced productivity may be temporary because of long-term negative effects of sea-level rise and wetland loss on fishery habitats (Zimmerman et al., 1991).

For example, many of the predicted climate alterations will influence circulation patterns and transport of salt water within coastal environments. Hydrodynamics in the Gulf of Mexico's shallow estuaries generally are dominated by wind (Lee et al., 1990). Any change in winds will alter existing circulation, especially given the estuaries' relatively small tidal amplitudes and shallow depths and their adjacent shallow coastal shelves. For example, the refilling of estuaries in the northern Gulf after the relaxation of strong northerly winds during a cold frontal passage is probably responsible for the transport of coastal material (e.g., salt water, sediment, eggs, larvae) into the estuaries (Rogers et al., 1993 and papers cited therein). Consequently, changes in the intensity and frequency of frontal passages could severely alter estuarine circulation and recruitment of estuarine-dependent fish species. In addition, changes in rainfall and runoff will alter coastal and estuarine salinity gradients, thus altering circulation and long-term salinity patterns (Wiseman, 1986). Such changes may be sufficient to destabilize shallow coastal habitats, thereby affecting plant and animal species in these habitats.

A clearer understanding of the links between the nursery function of coastal wetlands, hydrology, and climate variation is emerging (Baltz et al., 1993). Interannual

variation in the timing and extent of high water conditions in salt marshes may contribute to annual variation in fishery recruitment. Because many fishes make regular movements onto flooded marsh to feed, marsh access is apparently important to the growth and survival of individuals. Recent studies in Louisiana, where astronomical tides are small, indicate that interannual variability in wind patterns influences the frequency of flooding of salt marsh habitats, and consequently shrimp landings (Childers et al., 1990). In other coastal wetlands with larger, semidiurnal tides, marshes flood more predictably and some fishes may spend as much as one-third of their time in flooded habitats. For species that use high intertidal habitats as nurseries, variability in habitat availability driven by climate change may have a strong influence on recruitment, particularly in the systems of the northern Gulf where tidal range is small.

In the Laguna Madre in a semi-arid region of Texas, the lack of fresh water and the highly saline shorelines limit the development of emergent marshes. Should climate change extend this low rainfall regime northward on the Texas coast, the existing intertidal marshes will diminish in area because of shoreline retreat and enlarged salt barrens landward (similar historical conditions have been observed in the Laguna Madre). Such marsh habitat is unlikely to be replaced by mangroves or seagrasses, at least in the near term. This loss of essential nursery habitat needed to maintain estuarine-dependent fishery productivity may cause fishery yields to decline below historical levels. This prediction is supported by significant declines in shrimp and blue crab commercial yields in south Texas bays and the Laguna Madre during drought and warm winter conditions of the 1990s (Texas Parks and Wildlife Department, 2000). In contrast, Haas et al. (2001) predicted increased shrimp abundance in northern Gulf estuaries with increased estuarine salinity, thus highlighting the uncertainty associated with estimating the effects on fisheries of interacting variation in precipitation and river discharge, salinity, temperature, and hypoxia in climatechange scenarios.

Although the occasional drought year has had a positive effect on the secondary productivity of estuaries in the Gulf of Mexico region, increases in drought intensity or frequency would increase the incidence of coastal hypersalinity, resulting in the decline of valuable habitats such as mangroves, seagrasses, and coral reefs. For example, the release of high salinity waters through the passes of the Florida Keys adversely affects coral reefs offshore. Increased salinity in Florida Bay causes extensive die-offs of seagrasses and stress to mangroves on reef islands. Hypersalinity of south Texas lagoons during an extensive drought in the 1950s contributed to seagrass die-offs and fish kills, particularly in Laguna Madre, where salinities of 80 parts per thousand occurred. Even in the more humid central sector of the Gulf Coastal Plain, a 25-month drought is considered to be a primary cause of severe dieback of about 100,000 acres of salt marshes along coastal Louisiana during the summer of 2000.

Increased rainfall and resultant freshwater runoff into an estuary would shrink estuarine habitat if, at the same time, sea-level rise were moving seawater up an estuary where humans were preventing overflow onto land. This would also increase stratification of the water column, leading to sub-surface hypoxia or anoxia in estuaries with excess nutrients (Malone et al., 1988). If mid-Atlantic estuaries freshened sufficiently, abundances of the sea nettle, a jellyfish species that is negatively affected by low-salinity conditions, would decline. Such a decline in numbers might be ecologically significant because the sea nettle is an important predator of many other species in the food webs of the Chesapeake Bay (Purcell et al., 1999).

Climate change may increase the frequency of intense precipitation events and thereby alter coastal ecosystems, depending on the degree of regional water management. For example, the intra- and inter-annual variability of precipitation has been a major force shaping many coastal ecosystems in the Gulf of Mexico (Twilley et al., 2001). An increase in the intensity of precipitation will change the pattern of freshwater runoff in the coastal plain watersheds. Increased flooding, however, depends on how regional hydrology is managed. For those Gulf of Mexico estuaries that receive much greater inputs of freshwater inflows than they did historically (e.g., southwest Florida's Caloosahatchee estuary), there has been a major shift in their ecological communities to those that are better adapted to lower salinities. By contrast, estuaries and lagoons receiving much lower freshwater inflows than they did historically have shifted to communities better adapted to high-salinity conditions.

Most coastal systems in the Gulf of Mexico would probably experience little direct effect from increased freshwater discharge, except that the estuaries that would receive most of the excess surface water from management canals could experience severe reductions in salinity. Thus, there is potential for adverse consequences. But, again, this depends at least as much on how the water system is managed as on a climate change-induced increase in precipitation. With less precipitation, runoff will decline proportionately in many of the managed systems. The key point is that Gulf of Mexico estuaries may benefit from any degree of increased precipitation, but only a slight decrease in freshwater input may cause severe changes in habitat and water quality. This may be especially evident in regions of large engineered water management systems, or coastal systems in semi-arid conditions. Box 5 describes possible scenarios for Gulf of Mexico fisheries affected by changes in hydrology.

Wind, Water Circulation, and Storminess

The ocean circulation can be divided into two parts – the thermohaline (see Section III C) and the wind-driven circulations. The drag created by wind stress acting on the ocean's surface drives the major ocean surface currents. The winds themselves are created by the unequal heating of the earth's surface. Under most global warming scenarios, polar regions will experience higher temperatures that will reduce the thermal gradient between the poles and equator, which may result in a decrease in wind stress. This would potentially lead to a weakening of the overall wind-driven circulation.

Weaker wind-driven surface currents could seriously affect the structure and function of open ocean and nearshore ecosystems. As an example, the surface waters off the U.S. West Coast can be divided into three oceanographic domains: a coastal upwelling domain off California, a coastal downwelling domain off the southern coast of Alaska, and the Alaska gyre in the Gulf of Alaska. All three of these domains are organized by seasonally varying winds associated with overlying atmospheric pressure cells. Relaxation of the winds would reduce upwelling off California and within the Alaska gyre and reduce downwelling along the coast of Alaska. Transport of nutrients and primary and secondary production would also be reduced.

Wind speed and direction influence productivity of estuarine and marine systems. For example, nutrients that are delivered from deeper waters to the sunlit surface by the upwelling of water support phytoplankton production along coasts. Such upwelling is the result of winds that blow alongshore, and it can be diminished if the water is stratified by differences in temperature or salinity (see Box 4).

If upwelling is slowed by changes in wind and temperature, phytoplankton production will be lowered. Upwelling might continue from shallower waters, but there are fewer nutrients in these waters than in the deeper waters that are normally upwelled. The potential results of decreased upwelling are demonstrated by the 70 percent decline in zooplankton abundances off the California coast between 1951 and 1993 in concert with a warming of the sea surface (up to 1.5°C), which increased stratification and hindered upwelling (Roemmich and McGowan, 1995). Hill (1995) summarizes the apparent negative effects of these depleted zooplankton abundances on other members of the coastal food webs like fish and birds in the region.

There has been some speculation that global warming may result in intensified coastal upwelling in some circumstances (Bakun, 1989). Most greenhouse gas models project more warming over land than over open oceans, resulting in an increased temperature contrast between land and ocean. This increased contrast would strengthen low-pressure cells that typically occur over land adjacent to offshore high-pressure cells. The relative strength and position of these pressure cells results in enhanced alongshore winds that are the driving force behind upwelling.

On the U.S. East Coast, alongshore wind stress and differences in the densities, and therefore buoyancies, of fresher and saltier waters help produce water movements that transport larval blue crabs, menhaden, and bluefish in the Middle and South Atlantic Bights (Epifanio and Garvine, 2001). Climate-related changes in these circulation patterns that hinder such transport may lower abundances of these species within estuaries and along the coast, thereby modifying coastal ecosystems and affecting fishery yields.

Winds may also affect fish production by their role in the large variability that occurs in fish recruitment. A growing consensus suggests that there is an "optimal environmental window" within which larval survival is maximized and outside of which survival is sharply curtailed. Applying this idea to fish recruitment in upwelling regions, Cury and Roy (1989) demonstrated that recruitment is maximized at wind speeds of roughly 5 to 6 meters per second. At lower wind speeds, vertical mixing is weak and food production is low. At higher wind speeds, turbulence in the water column acts to disaggregate food and larvae patches.

There is much uncertainty as to whether coastal storms and hurricanes will increase in number or intensity, or both (see Box 1). Any increase in the number and severity of coastal storms and storm surges

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could have serious implications for the well-being of fishery and aquaculture industries (see below and Neumann et al. (2000) for some estimates of costs of coastal storm damage). An example of problems beyond damage to infrastructure is the deleterious effects of Hurricanes Dennis, Floyd, and Irene on Pamlico Sound, North Carolina, between September and October 1999 (Paerl et al., 2001). About 1 meter of rain from the storms led to 50- to 500-year floods that washed the equivalent of 6-months' supply of nitrogen (much of which resulted from human activities) into the sound. Strong stratification of the water column ensued, bottom waters became hypoxic (low in oxygen concentrations), algal blooms intensified, and fish diseases became more prevalent. The sound takes over a year to flush, so the effects of these hurricanes on ecosystem functions may be prolonged.

The consequences of sea-level rise become acute during storm events because sea-level rise and storms interact to erode beaches and produce high storm surges. Hurricanes and sea-level rise have shaped the coastal topography of the Gulf of Mexico for the last several thousand years (Wanless et al., 1994; Stone et al., 1997). Although it is likely that some Gulf coastal ecosystems would not be damaged by present and even future rates of sea-level rise under average conditions, episodic events like hurricanes and fires may undermine their resilience. Where excessive wind damage stresses mangrove forests and limits their ability to produce peat, forest elevation cannot keep pace with sea level, so additional flooding results in plant mortality and irreversible loss of habitat. If the future frequency of hurricanes were to stay the same as in the past, the ecological consequences of sea-level rise, together with increased coastal development, would be expected to inhibit natural recovery. More frequent storms and hurricanes might lead to increased local damage to mangrove forests, transient increases of sediment and organic load to coastal waters, and increased physical damage to coral reefs.

B. Effects on Aquaculture

Coastal aquaculture has become an important food source, so an understanding of the potential effects of climate change on cultured species is important to the industry. Global aquaculture production (35 percent of which is marine) has increased since the 1950s, attaining a growth rate of ~10 percent annually since 1990 (FAO, 2000); by 2030, aquaculture harvests are expected to be greater than capture harvests. Marine aquaculture production in the United States is expected to continue to grow as well.

Higher temperatures could enhance growth rates of cultured species and allow for the culture of species in areas that are currently too cold for them. On the other hand, a region may become too warm to allow the culture of a heat-sensitive species. For example, high temperatures are associated with summer mortality syndrome in cultivated Pacific oysters on the U.S. West Coast, so increased warming may add to such mortalities. Thus the type of culture in a region may have to change, but that should not be a major problem if it occurs slowly enough so adaptive aquaculture management practices can evolve to prevent or minimize the adverse effects of climate change.

The presence of aquaculture facilities on coasts can affect local ecosystems, in that the concentrated wastes of cultured organisms can pollute or disturb the environment, sometimes supporting harmful blooms of algae. Warm water not only holds less oxygen but also accelerates microbial decomposition of aquaculture wastes, lowering oxygen concentrations and perhaps stressing the cultivated organisms as well as organisms near the facility. Higher temperatures can allow for higher incidences of disease, especially if the organisms in the region are under stress. Finally, an increase in the intensity of coastal storms would threaten culture facilities, especially if the region's sea-level rise results in higher storm surges. Overall, the effects of climate change on fisheries and aquaculture will be region-specific, with some regions benefiting and some not.

C. Effects on Disease and Harmful Algal Blooms

Global climate change may affect the abundance and distribution of pathogens (disease-producing organisms) and harmful algal blooms, thereby influencing diseases of aquatic organisms as well as human health. For example, the protozoan Perkinsus marinus (Dermo) is the most important pathogen threatening the nation's oyster industry. Low temperatures and salinities usually limit infection by this pathogen and higher temperatures and salinities typically increase the incidence of infection. Higher water temperatures in winter have been linked to the northward spread of Dermo into the northeastern states (Cook et al., 1998), so long-term climatic changes may produce shifts in salinity and temperature that favor this oyster pathogen (it is not harmful to humans). Climate change will also affect the distribution of other diseases of aquatic organisms (Harvell et al. 1999).

Warmer coastal waters coupled with eutrophication can also increase the intensity, duration, and extent of harmful algal blooms that damage habitat and shellfish nurseries and that can be toxic to

marine species and humans. These blooms appear to be increasing worldwide, perhaps because of increasing eutrophication. The interaction between eutrophication and climate change in possibly promoting harmful algal blooms represents a major area of uncertainty and is a cause for concern because such blooms can have significant effects on marine ecosystems and on human use of these systems. For example, consumption of shellfish that have ingested harmful algae can cause neurotoxic poisoning in humans.

D. Other Perspectives on Climate Change

There is evidence that marine organisms and ecosystems are resilient to environmental change. Steele (1991) hypothesized that the biological components of marine systems are tightly coupled to physical factors, allowing them to respond quickly to rapid environmental change and thus rendering them ecologically adaptable. Some species also have wide genetic variability throughout their range, which may allow for adaptation to climate change.

There are at least two schools of thought among physiologists and ecologists who have considered possible effects of climate warming on the survival of marine animals (Culotta, 1994). Some believe that marine systems experience fewer extinctions of species compared to terrestrial systems because large numbers of marine species have wide geographic temperature ranges as well as greater capacity to migrate to new habitats through their larvae that drift in the water column. Others counter that the seeming lack of evidence for recent marine extinctions is a result of limited information on biodiversity, that not all marine species have drifting larvae, and that many larvae are short-lived or remain relatively close to the parental population before becoming juveniles.

Paine (1993) argued that immediate marine extinctions in response to climate warming are less likely than as a result of direct human disruption of aquatic systems by overexploitation, introduction of exotic species, and coastal pollution. Similarly, Clarke (1993) proposed that climate warming is unlikely to be a direct cause of extinctions of marine fish and invertebrates and that ecological factors such as interactions with other species may be more significant. Undoubtedly, climate changes will also affect how an organism responds to other environmental stressors.

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III. Effects of Global Climate Change on Open Oceans

A. Effects on Ocean Productivity

Predictions about the effects of climate change on the oceans are often based more on models than observations and are necessarily more general than specific. This is because the immensity of the oceans and the major commitments of shipboard resources necessary for their study have meant that the number of researchers involved and the area covered have been limited. Nevertheless, because the oceans may be affected predominantly by changes in temperature and circulation, predicting the outcome of climate change on the oceans may be somewhat less complicated than for coastal and estuarine systems, where the roles of precipitation and anthropogenic stress are so important.

As noted above for inshore waters, increased temperature or freshwater input to the upper layers of the ocean results in increased density stratification, which affects ocean productivity in two opposing ways. Increased stratification suppresses upwelling of nutrients into the upper, lighted region of the ocean, which leads to decreased production of phytoplankton. At high latitudes, this decrease could be offset somewhat by a lengthened growing season because the mixed layer shallows earlier and deepens later in the year (Bopp et al., 2001). Where phytoplankton production is limited by the length of the growing season, an increase in this length could increase overall system productivity if suitable nutrients are available. Coupled physical/biogeochemical models predict a net decrease (~5 percent) in global phytoplankton productivity under doubled CO₂ conditions that increase oceanic thermal stratification and reduce upwelling of nutrients (Cox et al., 2000). Because productivity varies regionally, simple extrapolation to particular U.S. marine waters is difficult.

Although the effects of global climate change cannot be predicted with certainty, they may mimic certain aspects of the effects of natural climatic variability associated with large-scale climate phenomena such as the El Niño-Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the North Atlantic Oscillation/Northern Hemisphere Annular Mode (NAO/NAM) (Box 6) that occur on decadal to

Modes of Natural Climate Variability

The effects of global climate change cannot be predicted with certainty, but they may mimic certain aspects of the effects of natural climatic variability that occur on decadal to multi-decadal time scales. Thus an understanding of how this natural variability affects ecosystems and fisheries may help us to better predict the consequences of global warming on ecosystem structure and function. These modes of natural climate variability exist independent of anthropogenic climate change, but may act in tandem with (or in opposition to) anthropogenic climate change with consequences that are difficult to predict.

El Niño-Southern Oscillation

One of the greatest sources of interannual variability in worldwide climate and weather is the El Niño-Southern Oscillation (ENSO). During ENSO events, large-scale disruptions that influence global weather patterns occur in the atmosphere and in the tropical Pacific Ocean. There are two phases of ENSO — El Niño (warm ENSO phase) and La Niña (cool ENSO phase). El Niño refers to the appearance of anomalously warm waters extending westward to the International Dateline and sometimes farther. Off the west coast of South America, this results in the disappearance of cool nutrient-rich upwelled water. La Niña represents the appearance of anomalously cool waters in the same region of the Pacific, with upwelling enhanced.

During El Niño events, the main "center of action" in the North Pacific is the Aleutian low-pressure cell that is in an enhanced state (the center of the low has deepened and shifted eastward by several hundred kilometers). The physical effects of this enhanced low in the northeast Pacific include warmer air and sea-surface temperatures, more frequent and severe storm activity, and increased vertical upwelling. ENSO events differ in intensity (regional variations can be substantial), timing, and spatial organization, and the climatological and ecological responses outside the tropics similarly vary from event to event. During La Niña events, atmospheric and oceanic conditions are essentially the reverse of El Niño conditions.

Coastal ecosystems are vulnerable to ENSO cycles because of their effect on the distribution of fresh water. For example, fall and winter seasons are warmer in the Gulf of Mexico during La Niña, followed by little change in spring temperatures and higher temperatures in summer. El Niño is correlated with substantially increased Gulf Coast precipitation in winter. El Niño events appear to strongly affect seabirds along the coast of North America as far north as Alaska. Among the documented effects are declines in the number of eggs produced, changed breeding seasons, decreased juvenile and adult survival, and shifts in distribution.

El Niño events decrease the probability of U.S. land-falling hurricanes, while La Niña events show an increase. Current climate models are insufficient to assess how ENSO cycles might change in the future, although some suggest that they will increase both in frequency and duration.

Pacific Decadal Oscillation

Over much of the past 25 years, the North Pacific climate has been in an almost continuous ENSO-type state despite the absence of ENSO events during most of those years. This change, termed the Pacific Decadal Oscillation or PDO (Mantua et al., 1997), began with the strongly anomalous winter of 1976/77 and has been termed a regime shift. Warm phases of the PDO are correlated with North American temperature and precipitation anomalies similar to those correlated with El Niño: above-average winter and springtime temperatures in northwestern North America, below-average temperatures in the southeastern United States, above-average winter and spring rainfall in the southern United States and northern Mexico, and below-average precipitation in the interior Pacific Northwest and Great Lakes regions. Cool phases of the PDO are simply correlated with the reverse climate anomaly patterns over North America, broadly similar to typical La Niña climate patterns. The PDO-related temperature and precipitation patterns are also strongly expressed in regional snow pack and streamflow anomalies, especially in western North America (Bitz and Battisti, 1999). This has implications for salinity regimes and circulation patterns in estuaries in the region (see Box 3).

North Atlantic Oscillation/Northern Hemisphere Annular Mode

The North Atlantic Oscillation (NAO), an imbalance in atmospheric mass between the North Atlantic and subtropical Atlantic (i.e., the difference in pressure at sea level between Iceland and the Azores) is part of a larger Northern Hemisphere oscillation referred to as the Northern Hemisphere Annular Mode (NAM, Thompson and Wallace, 2001). The NAO/NAM has a strong effect on regional air temperatures and its strongly positive state since 1980 has contributed to much of the observed warming in the Northern Hemisphere over the last 20 years (Wallace et al., 1995), which affects shallow coastal waters. The increase in winter storminess since 1960 has resulted in higher wind speeds and wave heights (Bacon and Carter, 1993). The freshwater balance of the Northern Atlantic gyre may be affected by the NAO/NAM. Ottersen et al. (2001) describe a wide array of ecological effects of the NAO, including effects on marine systems.

multi-decadal time scales. Open ocean productivity is also affected by natural interannual climate variability, and climate-driven changes in the frequency, magnitude, or timing of any of these phenomena may lead to marked changes in water column mixing and stratification, and ultimately a reorganization of the ecosystem (Fasham et al., 2001). For example, El Niño-related stratification of the Pacific Ocean around Hawaii over the past decade resulted in a change from a system controlled by nitrogen concentrations to one controlled by phosphorous concentrations; this signals a significant reorganization of the food webs in the region, with one suite of microorganisms replacing another suite as the dominant primary producers (Karl, 1999).

Elsewhere, the biological and recruitment effects of ENSO warming and cooling events have been documented for a number of West Coast and Alaska fish species. For example, recruitment increased for Pacific hake, Pacific cod, Pacific herring, and Pacific sardine during strong El Niño events, while West Coast rockfish species (*Sebastes* spp.) suffered recruitment failures (Lenarz et al., 1995; MacCall, 1996). Alaska and West Coast sablefish exhibited opposite growth responses, in that Alaskan sablefish had enhanced growth while West Coast sablefish had retarded growth during El Niño events (Kimura et al., 1998); this pattern was reversed during La Niña events. Finally, during the very strong 1982/83 and 1997/98 events, tropical species such as ocean sunfish, Pacific mackerel, and barracuda were found as far north as southeast Alaska. The northward distribution of Pacific mackerel is a particular concern because it is a potential predator of seaward migrating salmon smolts — an example of the potential for food webs to be rearranged by climate change.

Under the PDO, community structure in the Gulf of Alaska ecosystem changed dramatically and abruptly after the climate regime shift of 1976/77 from a cold regime to a warm one (Anderson and Piatt, 1999). Over a 40-year study period, prey species such as pandalid shrimp (three species) and capelin were the dominant species until 1976. After 1977, recruitment of predatory fish increased and, by the 1980s, the prey species had essentially disappeared. Total biomass in the standardized survey catches increased by over 250 percent. In a broader survey of the biological effects of the 1970s climate shift, Francis et al. (1998) documented major changes in the large marine ecosystems of the northeast Pacific, including abrupt population increases (and decreases) for zooplankton, fish, birds, and marine mammals. The NAO/NAM has also been linked to variations in zooplankton and marine fish production on both sides

of the Atlantic. For most commercially important fish species, a positive NAO/NAM results in poor recruitment and growth (Friedland et al., 1993).

The exact mechanism by which these changes occurred is unknown and doubtless differs for many of the species. What appears indisputable, however, is that the driving force behind these widespread ecosystem modifications was climate variability. Anthropogenic climate change can be expected to produce major modifications as well.

B. Effects on Pacific Salmon

Pacific salmon have been shown to be sensitive to changes in climatic conditions. For example, they have been affected by the natural interannual climate variability described above, so it can be assumed that they will be affected by long-term anthropogenic climate change. Salmon spawn in freshwater, and the young live there for a few months to a few years before spending one to several years in the ocean (depending on the species). Attempts to understand the high variability in the abundances of returning salmon populations have focused on the freshwater phase of their life history, but there is increasing awareness that conditions in the ocean play at least as large a role in modulating population levels and perhaps the dominant role in determining size-at-age of the fish. There is general agreement that year class strength of salmon is determined during the early rearing period (Pearcy, 1992), so conditions in the nearshore environment are critical to survival. These conditions are established by climate-driven and ecological processes, with both local and distant climate processes being important. For example, nearshore production of phytoplankton and zooplankton — the food of juvenile salmon — reflects not only local atmospheric heating and upwelling, but also the production transported by currents into the region from hundreds of kilometers farther west in the Pacific.

Both ENSO and PDO strongly affect Pacific salmon production from California to northern Alaska. The influence of ENSO is strongest on West Coast populations and diminishes with increasing latitude. The PDO appears to influence both West Coast and Alaska salmon production, although there is an inverse effect on the salmon of the two regions (Mantua et al., 1997; Hare et al., 1999). The most recent positive phase of the PDO from 1977 to 1998 resulted in sustained high Alaska salmon production and a similarly lengthy period of very poor production of West Coast salmon. During the negative-PDO regime of 1947 to 1976, the relative levels of salmon production between the two regions were reversed; i.e., low in Alaska and high off the West Coast.

The climate signatures of ENSO and PDO are fairly similar in the North Pacific, particularly as they affect sea surface temperatures. One effect of global warming may be an increase in the frequency or intensity, or both, of El Niño events. Warmer waters in the North Pacific have coincided with strong Alaska salmon production but with weak West Coast salmon production. However, the amount of warming has been relatively modest; in their positive phases, both the PDO and ENSO increase temperatures by 1 to 3°C. Whether Alaska salmon would continue to benefit from even higher temperatures is more questionable. Welch et al. (1995) showed that salmon habitat is sharply limited by temperature. Under various global warming scenarios and subsequent heating of the North Pacific, they speculate that the habitable region for some salmon species may shrink to encompass only the Bering Sea and not extend south into the Pacific.

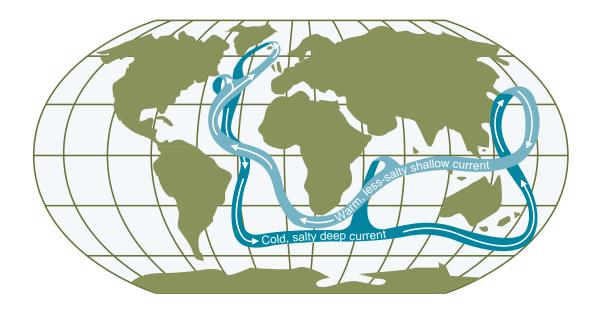
C. Effects on the Thermohaline "Conveyor Belt"

The world's oceans are linked by water movements that are influenced by temperature and salinity (thus the term "thermohaline"). Cold water is denser than warm water, so it sinks below the lighter warm water, and denser high-salinity water sinks below lighter low salinity water. In one instance, this results in a "conveyor belt" system (Figure 4) that slowly moves cold dense seawater from the North Atlantic Ocean surface to deep water and then through the Indian and Pacific oceans and back to the Atlantic Ocean over centuries, with the water gradually warming and becoming less dense and moving back toward the ocean surface. This warm shallow water tempers continental climates as it reaches the eastern Atlantic shores of Europe in the Gulf Stream/North Atlantic current. As the water cools and sinks into the ocean depths in the North Atlantic, it takes with it nutrients, as well as oxygen and CO₂ that it absorbed while at the surface. Deep-sea organisms use the nutrients and oxygen but the CO₂ is not available for use by plants in photosynthesis because of the lack of light in the deep ocean.

A weakening or stoppage of this circulation system would diminish vertical mixing between the ocean surface and the deep sea and would reduce upwelling in temperate and subtropical latitudes. Transport of oxygen from the sea surface to the deep ocean would slow or cease, depriving the deep oceans of their supply of oxygen and slowly (over centuries) rendering them hypoxic (low in oxygen concentrations) or anoxic (lacking in oxygen) as happens now in coastal regions (Box 4). The delivery of nutrients from the upper ocean where plant production occurs to the sunless depths would also be

Figure 4

Global Ocean Circulation



The above figure depicts the global ocean circulation "conveyor belt" that distributes water of different temperatures and salinity throughout the world's oceans over a millennium.

Source: Alley (2000).

modified, affecting deep-sea animals (including commercial fish and squid species) and their communities in the water column and on the ocean floor. Although the present rate of uptake of CO_2 by the ocean could slow, there is disagreement as to whether or not CO_2 would thereby increase in the atmosphere, with a concomitant increase in global air temperatures, or if the increased stratification of the surface waters would affect biological productivity and thus CO_2 uptake.

There is oceanographic evidence that this thermohaline circulation may have slowed or stopped in the distant past over relatively short time intervals (decades). However, our understanding of the mechanisms involved is rudimentary, hampering predictions about the effects of global climate change in the North Atlantic (increased warming of surface water; increased freshening of surface water from melting ice or increased precipitation) on the circulation pattern (Stocker et al., 2001). Coupled general circulation models predict a wide range of responses of the circulation to climate change, from virtually no response to a 40 percent decline sometime in this century (Gent, 2001; IPCC, 2001). Thus these models must be

used cautiously in light of the difficulties with accurately simulating both temperature and salinity (Gent, 2001). Stocker et al. (2001) conclude that changes in the thermohaline circulation are likely with global warming, but that the extent of the changes are uncertain. Based on knowledge to date, Gent (2001) and Sun and Bleck (2001) do not expect a collapse of thermohaline circulation during the 21st century, due to feedbacks that help stabilize circulation in response to warming. However, they caution that we know little about the feedback mechanisms that affect the circulation pattern. Furthermore, these studies assume atmospheric CO₂ concentrations do not exceed a doubling of pre-industrial levels by 2100. Earlier modeling efforts using higher baseline greenhouse gas emissions scenarios for the 21st century did simulate the collapse of thermohaline circulation by 2100 (Manabe and Stouffer, 1994; Stocker and Schmittner, 1997). Thus, the response of thermohaline circulation to global climate change remains uncertain, with predictions being dependent upon assumptions regarding future greenhouse gas emissions and subsequent temperature increases. There has been little study of the potential ecological consequences of any change in this circulation.

D. Effects on Sea Ice

One of the more consistently predicted effects of global warming is on high latitude ice cover. Significantly warmer winters in Alaska during the 1980s and 1990s resulted in less sea ice coverage over the Bering Sea. A retreat in the extent of sea ice diminishes the habitat of ringed seals and polar bears that use the ice for hunting, resting, and rearing young. The seals are the main food item for the bears, so changes in their distributions and populations will affect the bears. Variation in the areal coverage of sea ice and timing of the spring retreat has strong effects on the productivity of the Bering Sea marine ecosystem. For example, the timing of the spring phytoplankton bloom is directly tied to the location of the sea ice edge over the southeast Bering Sea shelf (Stabeno et al., 2001). The presence or absence of a subsurface cold pool, which is better developed and more extensive in summers that follow winters with extensive sea ice coverage, affects the distribution of several commercially important fish stocks, including walleye pollock (Wyllie-Echeverria and Wooster, 1998). Changes in the atmosphere and oceanography of the Bering Sea in the past 20 years have been suggested as driving the tenfold increase in jellyfish biomass over the middle Bering Sea shelf between 1979 and 1997 (Brodeur et al., 1999).

IV. Effects of Global Climate Change on Coral Reefs

Coral reefs are the most biologically diverse of marine ecosystems, and their economic value includes fishery yields, tourism, and shoreline protection.

They occupy 15 to 30 percent of the continental shelf area between 40°N and 40°S (Kleypas, 1997). In the United States and its territories, coral reefs occur in Florida, Texas, Puerto Rico, U.S. Virgin Islands, Hawaii, Johnston Atoll, Commonwealth of the Northern Mariana Islands, American Samoa, Guam, and the U.S.-affiliated Pacific Islands¹ (Republic of Palau, Republic of the Marshall Islands, and the Federated States of Micronesia).

Coral reefs and their associated carbonate environments have been damaged by recent climate changes, so these systems are at risk if climate continues to change. Coral reef degradation has increased greatly over the last few decades: 27 percent of reefs worldwide are considered to be effectively lost (Wilkinson, 2000) through a combination of anthropogenic effects and extensive coral bleaching episodes (see below). Reefs that have experienced the greatest damage are those near population centers. Examples from the United States include "high-risk" reefs (Bryant et al., 1998) in the U.S. Virgin Islands, Puerto Rico, Johnston Atoll, Tutuilla Island of American Samoa, and some of the Mariana Islands, and "moderate-risk" reefs in the Florida Keys and Hawaii. Reefs in these regions are exposed to a variety of local to regional problems such as pollution from urban and agricultural sources, increased sedimentation due to deforestation, and abusive fishing practices such as the use of dynamite or cyanide. Caribbean corals are also experiencing high mortality from an unexplained increase in a variety of diseases (Richardson, 1998).

A. Predicted Changes in Environmental Factors

In terms of global climate change, coral reefs are affected through a variety of mechanisms that are more or less directly related to increased greenhouse gases in the atmosphere (Table 1, Figure 5). We focus on three main consequences of increased anthropogenic greenhouse emissions: seawater chemistry changes, temperature increase, and sea-level rise.

Effects of Increased Atmospheric CO₂ on Coral Reefs,

Listed in Order of Direct Effects

CO ₂ -related Change	Mechanism	Effect on Coral Reefs Reduced availability of carbonate ion [CO ₃ ²⁻] causes reduction in calcification rates in reefbuilding corals and algae.	
Seawater chemistry	Dissolution of CO_2 results in lowering of pH, lowering carbonate ion $[CO_3^{2-}]$ concentrations.		
Seawater temperature	Greenhouse effect leads to higher sea-surface temperatures.	Increase in annual maximum sea-surface temperature of 1–2°C causes coral bleaching.	
Sea level	Global warming leads to melting of ice caps and glaciers, and thermal expansion of oceans, causing sea levels to rise.	Effects largely unknown; some reefs may benefit; others may suffer if coastal flooding causes an increase in nutrient or sediment inputs.	
Storm frequency or intensity	Some climate models indicate an increase in storm frequency or intensity, or both, and a change in storm tracks.	Effects largely unknown; some species may decline while others may benefit.	
Dust deposition	Increased delivery of dust-borne iron may enhance phytoplankton and macroalgal growth; transport of <i>Aspergillus</i> sp. fungus and possibly other pathogens.	Increased phytoplankton production decreases light penetration. Macroalgae compete with corals and calcifying algae for space.	

Changes in Seawater Chemistry

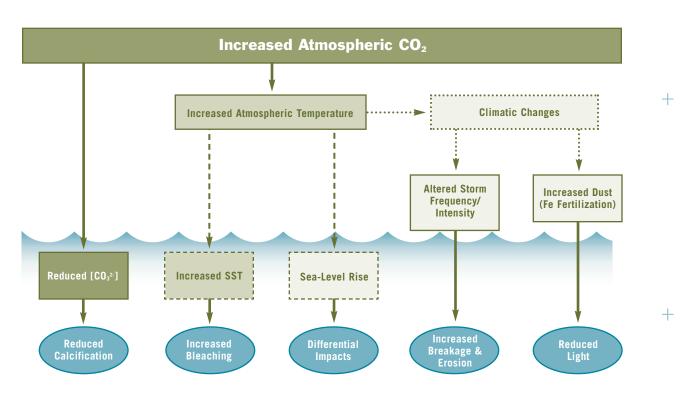
The most direct effect of increased CO₂ concentrations on coral reefs involves changes in surface ocean carbonate chemistry. Gas exchange at the air-sea interface allows the partial pressure of CO2 in the upper ocean to increase proportionately to that in the atmosphere. When carbon dioxide dissolves in water, it forms carbonic acid, a weak acid. An increase in atmospheric CO2 concentration from preindustrial levels (280 ppmv) to the present level (370 ppmv) has led to the surface ocean becoming more acidic, with its carbonate ion concentration reduced by 15 percent. These shifts in ocean chemistry have been documented by extensive field surveys (e.g., Peng et al., 1998).

Recent research in experimental systems and in the field with individual species (see review by Gattuso et al., 1999) and reef communities (Leclercq et al., 2000; Langdon et al., 2000) indicates that calcium carbonate (CaCO₃) precipitation of many reef-building species (corals and calcareous algae) decreases in response to decreased carbonate ion concentrations. Calculations and model results indicate that under double CO₂ conditions, tropical oceans will experience an average 30 percent decrease in

 $CaCO_3$ saturation (a measure of the abundance of calcium and carbonate ions). This will result in an average decrease in coral reef calcification of 20 to 30 percent² (Gattuso et al., 1998; Kleypas et al., 1999; Langdon et al., 2000).

The effects of reduced calcification of reef-building corals and calcifying algae are still speculative but will probably be manifested on reefs in the following ways. First, a reduced capacity to secrete CaCO₃ requires species to form either more compact or less dense skeletons, or both. Changes in coral skeletal morphology or strength will thus change a species' functionality or competitiveness in the community, and will most likely lead to a shift in community structure. Second, reduced CaCO₃ production in a coral reef community lowers its reef-building capacity. Some reefs may cease to accumulate enough CaCO₃ to balance natural erosional processes. Higher latitude reefs such as the northernmost Hawaiian Islands tend to have

Atmospheric CO₂ Effects on Coral Reefs



The above figure depicts the various direct and indirect effects of changes in atmospheric CO_2 concentrations on coral reef ecosystems. Solid lines indicate direct effects, dashed lines indicate indirect effects, and dotted lines indicate possible effects. Fe = iron; SST = sea surface temperature; CO_3^{2-} = carbonate ion.

naturally low carbonate budgets and these reefs are most at risk from reduced reef-building potential.

Third, inorganic cementation (non-biological precipitation of CaCO₃ and related cements) of reefs is likely to be reduced, leaving them more vulnerable to erosion.

Increased Seawater Temperature

The best-known effect of global warming on reefs is coral bleaching, which is a breakdown in the symbiotic relationship between the coral animal and the unicellular algae that live within coral tissues. The algae (called zooxanthellae) produce carbohydrates and other photosynthetic products that the coral can use, and are in turn sustained by the coral's waste products that serve as nutrients — a recycling that appears to enhance the productivity of both organisms. This relationship allows corals to thrive in nutrient-poor waters and to secrete massive CaCO₃ accumulations. When subject to environmental stress, corals (and many other symbiotic reef-dwelling organisms) expel the zooxanthellae or the algal pigments or both, leaving the animals pale to colorless. The symbiotic relationship is thus suspended and the host is weakened until environmental conditions improve and normal zooxanthellae density is regained.

Bleaching occurs under a variety of stresses, but the large-scale bleaching events of the last two decades are strongly correlated with increases in maximum monthly sea-surface temperature (Brown, 1997; Figure 6) and exacerbated by increases in solar radiation (Brown et al., 2000).

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Before the 1980s, coral bleaching events were small-scale phenomena attributed to local stresses such as sudden freshwater influxes or restricted circulation. Regional bleaching events were first noted during the 1982/83 ENSO event when Galápagos reefs suffered severe bleaching and more than 90 percent mortality of coral animals (Glynn, 1984). Since then, large-scale bleaching events have occurred at all latitudes and in all oceans, and are more pronounced during El Niño years (Wilkinson, 2000). The worldwide bleaching event in 1998 was the worst ever noted, and destroyed some 16 percent of the world's coral reefs (Wilkinson, 2000). Nearly all reefs of the United States and its territories have experienced bleaching within the last decade, including significant events in American Samoa (1994), Johnston Atoll (1998), Florida Keys (1990; 1994; 1998) and Puerto Rico (1998). Many corals and reefs can recover from a bleaching event, but the extent of recovery depends on the duration of the event and the severity of the above-normal temperatures. Barring future episodes of mass mortality, even badly damaged reefs can recover through recolonization, and it is expected that about half of those destroyed by bleaching in 1997/1998 will recover (Wilkinson, 2000). Restoration of a coral community usually takes decades and

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is slowed once reef surfaces are taken over by fleshy algae or other non-reef-building species, which in turn can be exacerbated in those areas where overfishing has removed herbivores. Recovery is also hindered where environmental conditions have become degraded by other stressors such as sedimentation and pollution.

Whether coral reefs will survive continued increases in global warming depends on their ability to adapt physiologically, genetically, or ecologically. For example, the hypothesis that coral bleaching may be an adaptive mechanism by which corals can exchange less heat-tolerant symbionts for more heat-tolerant types (Buddemeier and Fautin, 1993) has been supported in experiments (Baker, 2001). Whether this or some similar mechanism will allow corals to adapt to future increases in temperature is uncertain and a topic of debate (Hoegh-Guldberg, 1999).

Increased Sea Levels

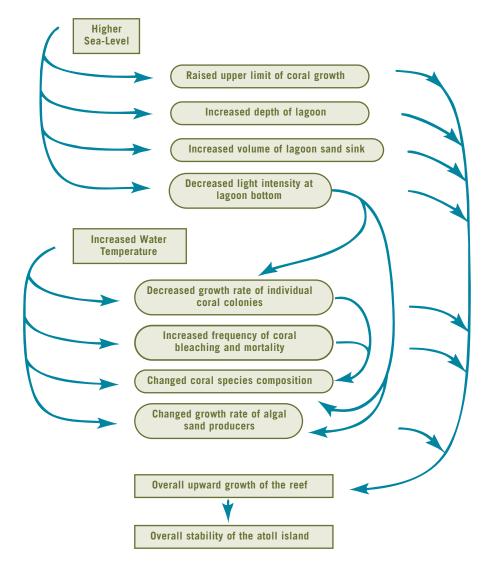
Corals and other reef-building organisms are generally adapted to rising sea levels, and vertical reef growth kept up with a sea-level rise of more than 100 meters since the last glacial period, which included episodic rates exceeding 15 mm/year (Blanchon and Shaw, 1995). Predictions of how well reefs will respond to sea-level rise are mixed because of uncertainties about the magnitude of the rise, local effects of flooding of adjacent lowlands, and complicating effects of other anthropogenic pressures on reefs. Many reefs reached the "growth ceiling" of the sea surface between 6,000 and 3,000 years ago, and have formed expansive reef flats where only the hardiest corals can survive. On some reefs, flooding these shallow areas will provide extra "head-room" for reef organisms to colonize and grow (Figure 6), albeit temporarily until the reef flats once again accumulate to sea level. On reefs that occur near low-lying coastal areas, sea-level rise is likely to increase coastal erosion rates (Leatherman et al., 2000). This would degrade water quality by reducing light penetration necessary for photosynthesis by zooxanthellae and increasing sedimentation that smothers and stresses coral animals (Figure 6).

B. Other Changes

Cyclones and other tropical storms can occasionally inflict serious damage on coral reefs (e.g., reefs in American Samoa were heavily damaged by cyclones in the 1990s). If storms increase in frequency or intensity, some reefs will most likely suffer additional damage (these occurrences are considered local rather than global in scale). If reefs die and are eroded, their role in protecting the adjacent shoreline will be lost, allowing for increased shoreline erosion and silt production during storms. Corals are stressed

Figure 6

Effects of Sea-Level Rise and Temperature on Vertical Growth of Coral Reefs



Source: Pernetta and Elder (1992).

if large amounts of silt are deposited on them. Precipitation lowers the salinity of lagoons, which may stress marine organisms, and affects nutrient runoff from land. Increased silt and nutrient runoff may degrade water quality in island lagoons, perhaps causing shifts in the species of resident algae that may lead to harmful algal blooms. Because many species of fish depend on coral reefs for their existence, damaged reefs may no longer support a fishery for small-scale or commercial use.

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Coastal and marine ecosystems & Global climate change

V. Conclusions

- 1. Global climate change is predicted to affect air and water temperatures, sea-level rise, precipitation, wind patterns, and the frequency and intensity of storms. These environmental variables are of great importance to the structure (e.g., plant and animal composition) and function (e.g., plant and animal production, nutrient cycling) of estuarine and marine ecosystems. Estuarine and coastal marine systems are already under stress from burgeoning human populations whose wastes flow from the land and whose fishing activities are depleting populations of recreational and commercial species. Additional stress from rapid climate change may challenge whatever resiliency a system may have. There may be abrupt, rapid shifts to alternate equilibrium states within affected ecosystems.
- 2. Temperature changes could result in different mixes of species in particular regions compared to the present situation. Higher temperatures would be lethal to some species at the southern end of their range and would allow others to expand the northern end of their range if they were sufficiently mobile. Changed species distributions would result in different mixes of species over time. It is currently impossible to make specific predictions as to how regional food webs would be affected by the different mixes, but energy flow and nutrient fluxes would be modified.
- 3. Warming temperatures would influence reproduction, growth, and metabolism of many species in stressful or beneficial ways, depending on the species. Again, some species would thrive in a region while others declined. In addition to affecting the interactions among species, this would require fishery and aquaculture industries in a region to be flexible in the species that are harvested or cultured.

- 4. Sea-level rise would inundate land, but if marshes and mangroves have enough sediment available to raise the level of the marsh or mangrove forest in concert with rising sea levels, or if they can retreat inland unimpeded by human development, they should continue to exist if sea levels rise at the rates currently predicted. However, if humans build barriers to keep the sea back, then marshes and mangroves would not be able to move inland. Gradually they would be inundated by rising seawater and they (and their ecological services to their associated organisms and to humans) would be lost over time.
- 5. Changes in precipitation could flood coastal systems or leave them in drought. Changes in precipitation would affect runoff from land, stratification of the water column and oxygen concentrations in the deep waters, and water circulation patterns and associated delivery of juvenile organisms to nursery areas, among other things. In concert with sea-level rise, increased runoff from land would shrink estuarine habitat, affecting estuarine organisms and diminishing the very important nursery and maintenance roles estuaries play in supporting animal and plant populations within the estuary and along the coast. This would have negative spillover effects on regional fishing, hunting, and ecotourism enterprises. Decreased precipitation and runoff would reduce nutrient input into coastal ecosystems, degrade water quality in the vicinity of industrialized or urban areas, and increase the risk of harmful algal blooms.
- 6. Changes in wind patterns could affect coastal and estuarine circulation patterns and upwelling or downwelling of water in marine systems. Young organisms of many species are transported into or out of estuaries by nearshore circulation patterns. Changed patterns would affect the normal life cycle of these species, perhaps leading to diminished populations locally, if not to local extinction of the species. This would affect fisheries for some species, and would also modify the mix of species in a region. Decreased upwelling as a result of changes in wind patterns and strength would negatively affect productivity in a region; however, increased upwelling from changes in winds should increase local productivity.
- 7. Changes in the frequency and intensity of storms would affect water circulation processes and threaten coastal aquaculture and fishing industry facilities. In addition, storms and hurricanes accelerate coastal erosion, increase the risk of severe floods that can deliver excessive amounts of nutrients and contaminants into coastal waters, and cause damage to mangrove forests and coral reefs.

- 8. Natural climate variability (ENSO, PDO, and NAO/NAM events) results in changes in open ocean productivity, shifts in the distribution of organisms, and modifications in food webs, foreshadowing what would happen if climate change accelerates. These modes of natural climate variability exist independent of anthropogenic climate change, but may act in tandem with (or in opposition to) anthropogenic climate change with consequences that are difficult to predict.
- 9. Over the coming century, there is a possibility that changes in temperature or salinity of North Atlantic water in the Arctic may slow or shut down the slow-moving thermohaline circulation that delivers cold, dense, oxygenated water to the deep sea. This would affect delivery of oxygen and nutrients from the ocean surface to the deep ocean in coming centuries, with unknown consequences for deep-sea animals and their communities.
- abundance of microscopic open-ocean plants and animals that build calcium carbonate structures. Some of these highly abundant organisms influence ocean-atmosphere interactions, but our knowledge of this influence and these interactions is rudimentary, making it difficult to predict the consequences of any chemical changes.
- episodes of bleaching and high mortality of coral animals have been linked to higher temperatures, and it is not clear if the affected reefs will survive. In the past, corals have been able to build their reef masses upward to keep up with rising sea levels, but the negative effects of increased CO₂ on calcium carbonate precipitation in the ocean may hinder future reef construction. Many coral reefs are stressed by human activities, so they may be more susceptible to climate change than if such stressors were absent.

Endnotes

- 1. Tropical Pacific islands vary from small coral atolls with maximum elevations that are just a few meters above sea level to large islands of Hawaii with high elevations. Their lagoons and coral reefs are diverse and productive ecosystems that support commercial and subsistence fishing and are popular (or potential) tourist destinations. Some islands are fringed by mangrove forests that are important breeding and nursery grounds for fish and birds. On most islands, subsistence fishing provides significant protein for the inhabitants, especially on the smaller islands. Some islands rent fishing rights to U.S. and foreign companies (the western Pacific provides about 70 percent of the world's tuna harvest). The Pacific Islands Regional Assessment (2001) examined the results of various model-based scenarios of climate change in the region and predicted that changes associated with climate change could have profound implications for the region's natural resources.
- 2. Increased acidity of ocean waters and decreased carbonate ion concentrations will also have negative effects on planktonic organisms that use calcium carbonate to build their skeletons. Among such organisms are coccolithophores, single-celled microscopic plants that build external calcium carbonate structures called coccoliths and that form widespread blooms of trillions of individuals. Coccolithophores participate in ocean-atmosphere interactions. They use carbon dioxide in photosynthesis and use bicarbonate ions to build their coccoliths, thereby decreasing the ocean's store of dissolved carbon (it is replenished by diffusion from the atmosphere). When they die, their coccoliths sink to the ocean floor, taking carbon out of circulation for centuries or more. They produce dimethyl sulphide, a chemical that is released when the cells die and that plays a role in cloud formation. Clouds, and the high reflectance from surface blooms of coccolithophores, influence the amount of heat retained in the atmosphere. Any significant loss of coccolithophore populations will probably affect these climate processes.

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Some Relevant Internet Websites

http://www.ipcc.ch/

Intergovernmental Panel on Climate Change

http://www.usgcrp.gov/usgcrp/Library/nationalassessment/default.htm

Online Reports from the U.S. Global Change Research Program on the Potential Consequences of Climate Variability and Change in the United States

http://www.essc.psu.edu/MARA/results/index.html

Mid-Atlantic Regional Assessment

http://www.necci.sr.unh.edu/2001-NERA-report.html

New England Regional Assessment

http://www2.eastwestcenter.org/climate/assessment/climate_draft2a.html

Pacific Islands Regional Assessment of the Consequences of Climate Variability and Change

http://www.cop.noaa.gov/pubs/das/das21.html

COASTAL: The Potential Consequences of Climate Variability and Change. Report of the National Coastal Assessment Group for the U.S. Global Change Research Program

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Pew Center on Global Climate Change 2101 Wilson Boulevard Suite 550 Arlington, VA 22201 Phone (703) 516-4146

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