Contents

Introduction	. 3
Changes in Ocean Conditions	. 3
Lessons Learned from El Niño	. 4
Evidence of Impacts on Marine Life	. 5
1. Polar Regions	. 5
2. Coral Reefs	
3. Salmon and other Fishes	
4. Seabirds and marine mammals	
5. Diseases and Harmful Algal Blooms	
Conclusion	
Acknowledgments	. 7
INTRODUCTION	. 8
GLOBAL CLIMATE CHANGE AND THE OCEANS:	
RISING TEMPERATURES AND SO MUCH MORE	10
Sea Level Rise	11
Wind patterns	
Deep-ocean circulation patterns	
Ocean stratification and primary productivity	
Natural Climate Variability: Lessons from El Niño and Decadal Variation	16
EVIDENCE OF IMPACTS ON MARINE LIFE 1	19
Impacts in Polar Regions	
Coral Reefs	
Shifts in Species' Distribution and the Fate of Pacific Salmon	24
Seabirds and Marine Mammals	
Disease and Harmful Algal Blooms	31
Outbreaks of disease with increasing temperatures	<i>32</i>
Harmful Algal Blooms (HABs)	33
CONCLUSION	35
LITERATURE CITED	36
APPENDIX	47

EXECUTIVE SUMMARY

Introduction

Despite the vast size of the oceans, their phenomenal biological diversity, commercial importance for fisheries and tourism, and intimate role in regulating climate, the impacts of global warming on marine life have rarely been considered. Yet scientific evidence strongly suggests that global climate change already is affecting a broad spectrum of marine species and ecosystems, from tropical coral reefs to polar ice edge communities. While the mechanisms for the changes observed in these complex natural systems are not known with certainty, changes consistent with those expected from climate change across a wide range of geographic locations and types of marine life, coinciding with the warmest years on record, strongly suggest that long-term global warming is now altering marine systems. Recent climate models combined with evidence of past climate indicate that mean global surface air temperatures have already increased 1° Celsius in the past century. Under the models' midrange estimates, temperatures are expected to increase by 3°C (approximately 5.5°F) within the next 100 years if emissions of "greenhouse gases" such as carbon dioxide (CO₂) and methane continue to grow at present rates. To try and fill the information gap and to provide an overview of the current state of scientific knowledge about the impacts of global climate change on marine biodiversity, WWF and Marine Conservation Biology Institute (MCBI) held a workshop on February 1 and 2, 1999 with some of the leading researchers in this field. The information from this workshop, combined with an extensive literature review, provides the basis for this report.

Changes in Ocean Conditions

Rising global temperatures can affect marine life in many ways, both directly and indirectly. Some organisms, such as corals, are intolerant of temperatures just a few degrees warmer than usual. In these cases, higher ocean temperatures can kill

them directly. Increasing temperatures may cause some marine species to shift their distribution poleward, away from the warmest areas. Others may be limited in their dispersal abilities or face physical barriers to migration and may therefore decrease in range or become extinct. Because each species will react to warming temperatures differently, key relationships among species within closely evolved ecosystems could be disrupted. But increasing temperatures will not be the only cause of ecological disruption. Because the ocean and atmosphere are so closely coupled, warming temperatures will be accompanied by numerous other changes in the physical characteristics of the ocean, which will also affect marine life. For example, sea level rise resulting from the expansion of water as it heats and the melting of land-based ice, such as glaciers and polar ice caps, could inundate large areas of coastal wetlands and other habitats important for many commercially significant fishes and other marine life.

Changing temperatures will also alter patterns of ecologically important processes such as upwelling, which bring nutrients from deep waters to the surface where they are used by phytoplankton in photosynthesis. Phytoplankton form the base of the food chain (more appropriately called food web) in many marine ecosystems, and expected declines in their productivity suggest that many other species are likely to be hurt as well. Warming sea surface temperatures can interfere with phytoplankton production by increasing stratification within the water column and increasing the thickness of the warm surface layer. Wind and upwelling will be less able to break through the warm surface waters, reducing availability of nutrients needed for photosynthesis. In general, reduced primary production from phytoplankton under global climate change would mean less overall production in marine ecosystems, including reduced fisheries. Such decreases in productivity may be occurring off the California coast, where scientists have documented a measurable decrease in the abundance of zooplankton, the second level in the food web. Currently the abundance of zooplankton is 70% lower than it was in the 1950s.

Deep ocean circulation patterns are also expected to be altered by global climate change. Currently, cold dense water near the poles sinks and moves toward the equator across the seafloor as warm water from the tropics moves poleward on the surface to replace it. This pattern of turnover in the oceans is called thermohaline circulation because it is driven by differences in water temperature and salinity. Thermohaline circulation performs two essential functions. First, it brings oxygenated surface water down to the deep ocean. Without this constant influx, water along the sea floor would become depleted of the oxygen organisms need to survive. Second, it redistributes heat from the equators towards the poles, as in the case of the Gulf Stream which makes Europe warmer than similar latitudes in North America. But increased precipitation expected in conjunction with global climate change will increase freshwater input in polar regions, reducing the salinity and thus the density of the water there and decreasing thermohaline circulation. Recent evidence has demonstrated that freshwater influx from melting sea ice can significantly reduce thermohaline circulation. From 1968-72 a phenomenon known as the Great Salinity Anomaly was documented during two years when unusually large amounts of Arctic sea ice melted. This amount of freshwater input was sufficient to shut down deepwater formation in the Labrador Sea, a key site for global thermohaline circulation. When this freshwater source was removed, deepwater formation was restored. Future climate change will likely involve alterations of a much greater magnitude and duration, and some climate models predict a total shutdown of thermohaline circulation in the Atlantic will eventually occur. Such a shutdown would likely affect climate in Europe as well as ocean productivity.

Sea level, already rising, is projected to continue to rise during the next century as global temperatures increase. Higher temperatures increase sea level through several mechanisms: thermal expan-

sion of water, melting of glaciers and the Greenland ice sheet, and melting of the Antarctic ice sheet. Considering all these factors, sea levels are predicted to rise an average of 20-40 cm, or approximately 8-16 inches, in the next 50 years, and possibly 15-95 cm (6-37 inches) by 2100. The actual inland area affected by an increase in sea level will be much greater than might appear. A 1-cm rise in sea level can erode a full 1 meter of a beach, and an immediate 1-meter rise in sea level would inundate approximately 20,000 km² (7,000 square miles) of dry land in the U.S. alone, an area roughly the size of Massachusetts. Some regions will be affected more than others, including regions with low-lying areas such as Louisiana. Loss of coastal areas will have a large impact on human populations, as over 20% of the world's population lives within 30 km of the coast and that population is increasing at twice the current global rate. With the minimum sea level rise of 20 cm expected by 2050, an estimated 78 million people will be at risk from flooding.

Lessons Learned from El Niño

Frequent and severe El Niños in the 1980s and 1990s provide glimpses of the types of impacts that might occur with long term global warming. El Niño is a natural phenomenon that results from changes in atmospheric pressures in the Pacific Ocean that concentrate warm waters in the eastern Pacific. Many of the changes that occur in the eastern Pacific during El Niño are similar to those predicted by recent climate models of global warming. Impacts from the severe El Niño in 1982-83 included higher sea surface temperatures and sea levels, lower nutrients, and increased intensity of storms and storm surge. The biological effects of these changes were severe, including the near-extinction of one species of hydrocoral (fire corals) and possibly one species of reef coral from the eastern Pacific. Numerous coral species experienced mass mortalities, with up to 98% of corals killed in some regions. Other marine life such as seabirds, Peruvian anchovy and sardines, marine iguanas, kelp forests off California, and some species of seals and sea lions off South America experienced large die-offs as well. Less severe declines in other species also occurred and some species extended or shifted their geographic ranges, invading areas where they didn't normally occur.

The frequency and duration of El Niño events appears to have changed recently and some scientists are examining whether global climate change has influenced the natural pattern of these events. Evidence indicates that from 15,000 to 7,000 years ago, El Niño events occurred every 15 years or so, and more recently they have occurred every 2 to 8.5 years. But since the 1970s, El Niño events have been even more frequent, with 5 out of 7 years from 1990-1997 experiencing El Niño conditions. Moreover, the most recent El Niño in 1997-98 was the strongest on record, with the highest recorded temperatures. Each month in the last half of 1997 set a high temperature record, and new records were set again a year later in 1998. Recent computer modeling suggests that El Niño events might become more frequent as global temperatures increase. While the impacts of long term global climate change on El Niño patterns may be unclear, this ocean warming phenomenon nevertheless provides valuable insights into the types of ecological changes we might see under global warming.

Evidence of Impacts on Marine Life

1. Polar Regions

Polar regions will experience greater overall temperature change and potentially more biological impacts than areas of lower latitude. Many changes have already been observed. Sea ice is fundamental to polar ecosystems: it provides a platform for many marine mammals and penguins to hunt, escape predators, and breed, and its edges and undersides provide vital surfaces for the growth of algae that forms the base of the polar food web. In areas with seasonal ice cover, spring blooms of phytoplankton occur at ice edges as the ice cover melts, boosting productivity early in the season. But sea ice is diminishing in both the Arctic and the Antarctic. As this area diminishes, so does the food available to each higher level on the web, from zooplankton to seabirds. Higher temperatures predicted under climate change will further diminish ice cover, with open water occurring in areas previously covered by ice, thereby diminishing the very basis of the polar food web.

2. Coral Reefs

These most biologically diverse and beautiful marine ecosystems may also be among the most vulnerable to climate change. Reef corals are extremely sensitive to temperature, and have an upper tolerance only a few degrees above normal high temperatures. If the temperature gets too high, corals bleach, meaning they expel the colorful zooxanthellae – symbiotic photosynthetic algae that produce foods that corals rely on. If temperatures remain too high for too long and bleaching persists, corals eventually die. Massive bleaching has occurred in recent years in response to unusually high water temperatures, particularly in 1997 and 1998, with reports from sites in all the major tropical regions, including the Pacific Ocean, Indian Ocean, Red Sea, Persian Gulf, and Mediterranean and Caribbean seas, with large numbers of corals turning completely white and dying. Some parts of the Indian Ocean had coral mortality of over 90%. Statements from coral reef scientists indicate that, based on current predictions of global warming, there will likely be increased coral bleaching and mortality in the future, with important negative consequences for biodiversity, fisheries, tourism and shore protection.

Recent evidence also shows that coral reefs are directly harmed by increasing levels of CO₂. Living coral reefs are composed of great numbers of coral animals covering a rigid skeleton formed by coral secretions of calcium carbonate. But high levels of atmospheric CO, alter water chemistry and reduce the calcification rate, and hence density, of coral skeletons. Some scientists believe that calcification probably already has decreased on some reefs, and predict that calcification could decrease 17 to 35% from pre-industrial levels by 2100. Reduced density, combined with increased storm activity caused by global climate change and mass mortality of corals from bleaching, can accelerate erosion of reefs. Moreover, this direct effect of CO₂ suggests that coral reefs may not successfully expand into higher latitudes to compensate for increasing sea temperatures in the tropics, as CO, continues to increase globally. By the end of the next century, CO₂ levels in the atmosphere are expected to be at their highest for at least the preceding 50 million years.

3. Salmon and other Fishes

Many fish species are sensitive to temperature, shifting their distribution in response to seasonal or annual changes. Studies now suggest that some fishes and marine invertebrates have shifted their distributions poleward in response to global warming. Studies of reef fish and intertidal invertebrates such as anemones, crabs, and snails at sites in California provide some evidence for this. The abundances of southern species of intertidal marine life increased, while abundances of northern species decreased at a site in Monterey Bay over a 60-year period coincident with warming sea temperatures. Studies of rocky reef fishes in the California Bight show that the proportion of northern species declined, while that of southern species increased over a recent 20-year period.

Drastic declines in some western Alaskan salmon populations in 1997 and 1998 have caused some scientists to wonder whether changes in the marine environment brought about by exceptionally high sea temperatures led to this collapse. The unusual conditions included a rare bloom of phytoplankton typical of low nutrient waters at lower latitudes. These conditions may have contributed to the massive die-offs of seabirds which appeared to have starved, possibly because of less prey in the low nutrient waters. The smaller than usual size of returning salmon, combined with dramatically decreased numbers of those returning, suggests that some fish may have starved, and those that survived had limited food for growth. Canadian and Japanese researchers have found that species such as sockeye salmon are extremely sensitive to temperature. While salmon can withstand higher temperatures in summer when food is abundant, in the winter their tolerance drops considerably. As coldblooded creatures, their metabolism increases in warmer water and keeping up with this high metabolism requires large amounts of food. If sufficient food is not available, salmon can starve. Researchers predict that anticipated increases in water temperature caused by a doubling of CO₂ will eliminate most, if not all, suitable habitat for Pacific sockeye salmon, and possibly for other salmon species as well.

4. Seabirds and marine mammals

Reductions in phytoplankton caused by warming sea temperatures can have devastating effects up the food web. Predators near the top of the web, such as seabirds and marine mammals, are greatly affected by this decline, as observed during recent El Niño events and long-term temperature increases. Scientists have documented decreased reproduction and increased mortality in seabirds and marine mammal populations coinciding with warmer water. Sooty shearwaters off the California coast declined 90% in the late 1980s and early 1990s and Cassin's auklets have declined 50% as zooplankton have plummeted there. In Alaska, the severe decline in shearwaters from 1997 to 1998 was clearly due to starvation, as the abundance of their crustacean prey was dramatically reduced in the unusually warm waters, and common murres died by the tens of thousands as well. Seals and sea lions showed similar declines during El Niño years. Studies showed that females had to dive deeper and were away from their pups longer to find food during the 1983-84 El Niño. As a result, the physical condition of females declined, reducing milk production and pregnancy rates. Young seals and sea lions had reduced growth rates and higher mortality rates as their mothers produced less milk and remained away from them for longer durations. Similar results have been found with polar bears which rely on seasonal sea ice for hunting the seals. As the ice melts sooner in the spring and forms later in the fall with rising temperatures, bears have a shorter hunting season and must rely on fat reserves for a longer period of time. Studies show females and their cubs at the southern edge of their range have lower body weights. Lighter cubs are less likely to survive than heavier ones. Penguins in Antarctica are also feeling the impacts of climate change. Adélie penguins and Crabeater seals dependent on sea ice are declining in some areas as ice cover decreases.

5. Diseases and Harmful Algal Blooms

Some scientists are concerned that global climate change may increase the incidence of harmful algal blooms and disease. Higher temperatures stimulate blooms of toxic or otherwise noxious phytoplankton referred to as harmful algal blooms. Extreme events such as rainstorms or flooding – as expected with climate change – wash sudden pulses of nutrients, chemicals and microorganisms into coastal waters, which may stimulate harmful algal blooms. These blooms are more frequent during El Niño years, which suggests that global climate change may also contribute to increased frequency. Warming of surface waters and decreased vertical mixing can encourage the growth of toxic phytoplankton, as can changes in nutrients in the water column. Species not known to be toxic can also become toxic when nutrient levels are altered.

Temperature increases can act to both weaken the potential host's immune system and stimulate growth of pathogens, thus favoring disease. Changes in water temperature and currents – both of which are predicted by current global climate models – will likely alter the incidence of disease by bringing pathogens into contact with species that had not previously been exposed. Unusually high incidences of diseases attacking marine vertebrates occur during El Niño events or other periods experiencing higher-than-normal sea surface temperatures, although the exact link with temperature is not always clear. Seabird mortalities from avian botulism, Newcastle disease, duck plague, and various strains of influenza also cluster with El Niño events. Greater numbers of whales and dolphins strand themselves during periods of high temperatures, and they often show evidence of sickness. The northward expansion of several diseases is strongly correlated with El Niño events and temperature increases, including MSX and Dermo, two diseases closely associated with aquaculture practices that attack shellfish on the east coast of the U.S. Although causal mechanisms are not always clear, the correlation between elevated temperatures and increased incidence of diseases is an increasing concern for marine biodiversity.

Conclusion

The likely effects of global climate change are particularly troubling given other pressures currently threatening marine biodiversity. Overfishing is a global problem, with almost all of the world's major fishing grounds now overexploited, many economically valuable fisheries devastated, and untargeted fish, seabirds, and marine mammals routinely killed incidentally as bycatch to fishing operations. Coastal development is destroying habitat as human population growth increases disproportionately on the world's coasts, and destructive fishing practices like bottom trawling devastate habitat on the seafloor. Development and land-based activities increase pollution in coastal waters, causing vast "dead zones" where oxygen is depleted, and contribute to the global increase in harmful algal blooms. Alien species are hitching rides in ships' ballast water and invading nonnative waters with increasing frequency, often diminishing or eliminating native species. Global climate change is an additional stress on already stressed species and ecosystems, and may be the "straw that breaks the camel's back" for many types of marine life.

Acknowledgments

Many thanks to numerous people who helped supply information, references, and comments for this report: Jess Adkins, Tundi Agardy, David Ainley, John Allen, Daniel Anderson, Robert Anderson, Ellen Athas, Cheryl Baduini, Richard Barber, Lou Botsford, Raymond Bradley, Barbara Brown, Robert Buddemeier, Scott Burns, Charlotte de Fontaubert, Bill Eichbaum, Max Finlayson, Greg Flato, William Fraser, Robert Furness, Steven Gaines, Thomas Goreau, John Goss-Custard, Tom Hayward, George Hunt, Jochem Marotzke, Adam Markham, Patrick Mazza, Gerald Meehl, Uwe Mikolajewicz, John McGowan, Jennifer Morgan, John Ogden, Brett M. Orlando, Julia Parrish, John Piatt, Jesus Pineda, Stefan Rahmstorf, Marjorie L. Reaka-Kudla, Ted Scambos, Steven Schneider, Mark Spalding, Ian Stirling, Thomas Stocker, Richard Strathmann, William Sydeman, Eli Tziperman, John M. Wallace, Andrew Weaver, Susan Wells, Clive Wilkinson, Margaret Williams and Herbert Wilson. Thanks also to Marijke Unger for workshop logistics, editing and production.

INTRODUCTION

The sea covers 71% of the Earth's surface and is home to unique forms of life found nowhere else on Earth. Of the 33 major types of animal groups in the world, almost all are found in marine waters and 15 are found only there. Marine life is a vital source of food and medicines, and supports millions of livelihoods through tourism and fishing all around the globe. These vast areas of water are intimately connected with the atmosphere and play a major role in shaping our climate on Earth. Despite all of this the impacts of global climate change on marine biodiversity have rarely been considered.1 Yet recent scientific studies strongly suggest that these impacts are likely to be severe, and some appear to be occurring already. To provide an overview of the current state of scientific knowledge about the impacts of global climate change on marine biodiversity, WWF and Marine Conservation Biology Institute (MCBI) held a workshop February 1 and 2, 1999 with some of the leading researchers in this field (see list of participants in the Appendix). These scientists included experts in a wide range of taxonomic groups and geographic areas to provide insights into the likely impacts of climate change throughout the marine realm. This information, combined with an extensive literature review, provides the basis for this report.

For years scientists have documented that natural variability in sea temperatures, and other physical changes associated with changing temperatures, can and do affect marine life. Now, documentation of severe ecosystem impacts from El Niño and other climatic variations, combined with indications of long-term sea temperature rise and associated changes in marine populations, show impacts consistent with predictions of global climate change. These effects are occurring from the trop-

ics to the poles, and they cut across taxonomic groups and travel through food webs – from decreases in phytoplankton to die-offs of seabirds. Because species respond differently to climate, there will be some winners and some losers, and not all marine life will decline. Regardless, such changes indicate significant disruptions of marine ecosystems as we know them, with often unpredictable ripple effects on other forms of marine life and human activities that depend upon them. Small changes now are likely to be precursors of much larger changes in the future.

Information is limited in several ways: first, useful long-term data sets available to study changes are scarce, so much of the marine realm is unexamined. But findings consistent with global warming in those areas that have been examined suggests that many other species and systems are affected as well, but simply have not been recorded. Moreover, the mechanisms for changes observed in these complicated ecosystems are not always clear, and scientists cannot say with certainty that changes are indicative of global climate change. However, changes across a wide range of geographic zones and types of sea life that are consistent with predictions of global warming and coincide with the warmest years on record strongly suggest that increases in global temperature have already, or will in the future, contribute to widespread ecosystem changes.

This is particularly troubling given other pressures currently threatening marine biodiversity. Overfishing is a global problem, with almost all of the world's major fishing grounds now overexploited, many economically valuable fisheries devastated, and untargeted fish, seabirds, and marine mammals routinely killed incidentally as bycatch to fishing

¹For some of the few earlier discussions of this, see the following: Norse, E. A. (1993) Global Marine Biological Diversity: A Strategy for Building Conservation into Decisionmaking, Island Press; Alexander, V. (1992) Arctic marine ecosystems. *In* R.L. Peters and T.E. Lovejoy (Eds.), Global warming and biological diversity. Yale University Press; Ray, G.C., B.P. Hayden, A.J. Bulger, Jr., and M.G. McCormick-Ray (1992) Effects of global warming on the biodiversity of coastal-marine zones. *In* Peters and T.E. Lovejoy (Eds.), Global warming and biological diversity. Yale University Press.

operations. Coastal development is destroying habitat as human population growth increases disproportionately on the world's coasts. Development and land-based activities increase pollution in coastal waters, causing vast "dead zones" where oxygen is depleted, and contribute to the global increase in harmful algal blooms. Alien species are hitching rides in ships' ballast water and invading nonnative waters with increasing frequency, often diminishing or eliminating native species (Norse 1993). Destructive fishing practices like bottom trawling are scouring vast areas of seafloor, crushing, burying, and exposing sea life and devastating their habitat (Watling & Norse 1998). Global climate change is an additional stress on already stressed species and ecosystems, and may be the "straw that breaks the camel's back" for many types of marine life.

Considering existing evidence and knowledge of marine systems, the scientists at the WWF/MCBI workshop suggest that certain types of species and ecosystems may be particularly vulnerable to climate change. Species that are constrained to a particular habitat type or location because of their life history characteristics (such as salmon that return to specific rivers to spawn) and species that are isolated from other suitable areas, might be less able to shift their distribution as climate shifts. For example, species in bays or estuaries, where freshwater from the land meets saltwater in the sea, might be constrained by the saltier water surrounding them. And wildlife at the poles have nowhere cooler to go once warmer temperatures take over their current habitat. Ecosystems that are already impacted by other human activities such as overfishing, pollution, and habitat destruction, might be less likely to absorb additional stress from climate change. Areas that lose much of their natural biota are likely to see increases in opportunistic "weedy" species, that move in and rapidly take over, further reducing biodiversity. The further ecosystems are forced from natural levels of variation, the more likely we are to see surprising effects we have not foreseen. Many of these ecosystems are highly valuable to humans, either directly or indirectly, and perturbations to them may have disastrous effects.

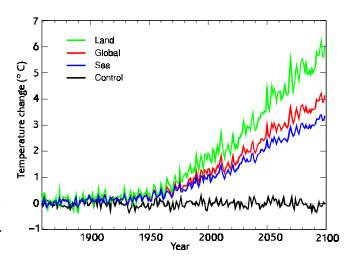
This report is divided into two main sections. The first section discusses current predictions of global climate change, including increases in temperatures and how rising global temperatures can affect marine processes, and hence marine life. The following section synthesizes scientific evidence of the likely impacts of global climate change on some species and ecosystems: polar regions, coral reefs, salmon, other fishes, intertidal invertebrates, seabirds and marine mammals. It also discusses one threat in particular that cuts across many species and ecosystems – the potential for increases in diseases and harmful algal blooms as a result of global climate change.

GLOBAL CLIMATE CHANGE AND THE OCEANS: RISING TEMPERATURES AND SO MUCH MORE

There is no dispute that the greenhouse effect is in place in the Earth's atmosphere – without it, we could not survive. The greenhouse effect refers to the presence of gases such as water vapor, carbon dioxide (CO₂) and methane that trap heat within the lower atmosphere, and is essential for maintaining temperatures that will support life on Earth. Disagreements about the greenhouse effect arise over predictions that increasing concentrations of greenhouse gases caused by human activities will increase global temperatures significantly, and what the impacts of such increases on natural and human systems will be.

The latest ocean-atmosphere models predict that, given the prevailing rate of increase in atmospheric CO₂, average global temperatures for both air and sea will increase in coming decades, and may have already increased (Hadley Centre 1998; Falkowski et al. 1998). Climate models necessarily are a simplification of exceedingly complex natural systems and cannot predict the exact details of future climate changes, but they are increasingly reliable at identifying general trends. With more powerful computers and improved understanding of oceans and climate, new models have more accurately described historical climate and passed other tests of soundness than ever before. Models incorporating greenhouse gases in addition to CO, as well as other factors have been able to replicate the general warming trend that has occurred in the 20th century (A. Weaver, personal communication) and have demonstrated internal consistency. This consistency is necessary for reliable predictions of future climate change. Although sun intensity, volcanic activity, and greenhouse gases have all contributed to climate variation in the past, studies have determined that greenhouse gas concentrations have had the greatest effect on climate variability over the past 400 years (Mann et al. 1998). Researchers are now able to determine the contribution of natural variation to the steady global temperature increases evident since the 1960s (Livezey & Smith 1999), and recent climate models indicate that temperature changes seen since 1945 are largely caused by increases in greenhouse gases (Tett et al. in press).

The Business-as-Usual scenario of the Intergovernmental Panel on Climate Change (IPCC) looks at what is likely to happen if CO₂ emissions continue at their present rate of increase (IPCC 1990). A 1% increase in CO₂ per year (compounded) will double the current CO₂ levels in the atmosphere in approximately 70 years, and quadruple the levels in the next 140 years (Manabe and Stouffer 1993). Under this scenario, a leading climate model from the UK's Hadley Centre calculates that the world has already experienced an increase of almost 1° Celsius (C) in air temperature over the past 50 years, and predicts an additional increase of 3°C (approximately 5.5°F) for the next 100 years (Hadley Centre 1998).



Real-life data support these calculations. Tree rings and ice cores that provide records of climate conditions in the past, indicate that global temperatures decreased by 0.02°C per century for the 900 years previous to the 20th century. But beginning around 1900 this cooling trend was reversed in less

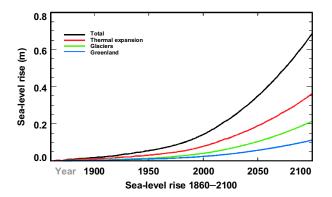
than one century (Mann et al. 1999). Temperatures in the latter 20th century appear to be exceptionally high compared to the preceding 900 years. In December 1998 the World Meteorological Organization confirmed that global temperatures in 1998 were 0.58°C higher than the 1961-1990 average, and 0.7°C higher than temperatures of last century (WMO 1998). The Intergovernmental Panel on Climate Change (an international group of scientists established by the World Meteorological Organization and the United Nations Environment Programme to assess the available scientific, technical, and socioeconomic information in the field of climate change) has stated that the available evidence suggests that the 20th century global mean temperatures are at least as warm as any other century since 1400 AD, and that most climate studies and models show that the observed warming trend over the last century is unlikely to be entirely natural in origin (IPCC 1995). In their 1995 assessment, the IPCC concluded that, while our ability to quantify the human influence on global climate is limited by natural variability in part, "the balance of evidence suggests that there is a discernible human influence on global climate" and that change is expected to continue in the future. But temperatures are not expected to increase uniformly around the globe. Some regions will experience warming much greater than the average global increase, and a few might actually experience cooling (Hadley Centre 1998). Along with the overall trend of temperature rise, there will also be periods of decreasing temperatures due to the natural environmental fluctuations that we have always experienced (Hadley Centre 1998).

While the magnitude of predicted temperature changes may seem small, such changes are known to have far-reaching ramifications on natural systems. Some organisms, such as corals, have very narrow temperature tolerances. If temperatures rise just a degree, individuals can die. In some cases, increasing temperatures may cause marine species to shift their distributions poleward, away from the warmest areas, while others may be limited by their dispersal abilities or physical barriers and decrease in range or become extinct (Breeman 1990; Frank et al. 1990, Lubchenco et al. 1993). But because

each species will react to warming temperatures differently, key relationships within closely evolved ecosystems could be disrupted, such as the local extinction of an important prey species, or an invasion by a voracious predator. Moreover, because the ocean and atmosphere are so closely coupled, global climate change will affect numerous physical characteristics of the ocean, and hence marine life, beyond just temperature. Marine life can be affected directly by higher temperatures, indirectly through changes in other ocean conditions such as sea level, winds, currents, and nutrients, or through interactions with other marine species impacted by environmental changes. Precipitation is predicted to increase at higher latitudes as well (IPCC 1995; Falkowski et al. 1998), which will affect ocean salinities, river runoff, and arctic snowpack. Indeed, the secondary effects from temperature increases may be equally or more influential on marine life than rising temperatures themselves. The complicated nature of climate change, uncertainties about how climate will alter local oceanographic conditions, and the multiple changes in ocean conditions that can occur make precise predictions of impacts on marine life impossible. Nevertheless, general predictions can be made based on the latest understanding of marine systems.

Sea Level Rise

Worldwide sea levels have been rising at varying rates for more than 15,000 years. Estimates of sea level rise over the last 100 years range from 1.0 -2.5 millimeters per year (IPCC 1996; Gornitz 1994). Sea level is projected to rise during the next century as well, as global temperatures increase. Higher temperatures increase sea level through several mechanisms: thermal expansion of water, melting of glaciers and the Greenland ice sheet, and melting of the Antarctic ice sheet (IPCC 1996). Some models predict a sea-level rise from 19 cm in the next 50 years (Mikolajewicz et al. 1990) to 1-2 meters over the next 500 years (Manabe & Stouffer 1993) due to thermal expansion alone. The IPCC estimates that current trends would result in a sea-level rise of about 50 cm by the year 2100 (IPCC, 1996). Although melting of the Antarctic ice sheet hasn't yet played much of a role in sea level rise, its stability may be declining. Three ice shelves have collapsed since 1995 (e.g. Doake 1998; T. Scambos personal communication), and if this continues there could be substantial inputs from Antarctic ice sheets to sea level rise. Runoff from terrestrial ice melt increases erosion and the amounts of sediment and pollutants that enter coastal waters, and increased sedimentation can displace water in the ocean, adding to sea levels as well. Considering all these factors, the Hadley model predicts an average of 20-40 cm, or approximately 8-16 inches, of sea level rise in the next 50 years (Hadley Centre 1998). IPCC (1998) predicts a sea-level rise of 15-95 cm (6-37 inches) by 2100. The amount of sea level rise experienced by any



given coastline will also depend on local geology, local groundwater depletion, and land subsidence (IPCC 1995; Titus & Narayanan 1995).

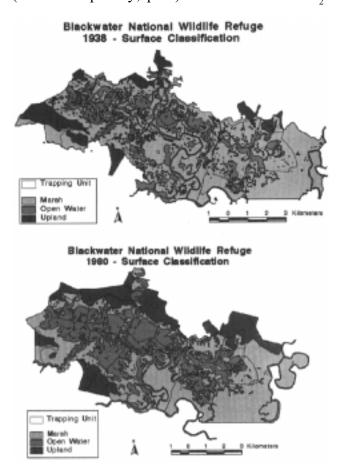
The actual inland area affected by an increase in sea level will be much greater than might appear. A 1-cm rise in sea level can erode a full 1 meter of a beach (Bruun 1962) and storm surge can add up to several meters to local sea level for periods of hours or days (Pittock 1999). An immediate 1meter rise in sea level would inundate approximately 20,000 km² (7,000 square miles) of dry land in the U.S. alone, an area roughly the size of Massachusetts (Titus 1992). Some regions will be affected more than others, including regions with low-lying areas such as Louisiana, which lost approximately 5600 hectares (almost 14,000 acres) per year to sea level rise from 1956-1990 (Barras et al. 1994). Loss of coastal areas will have a large impact on human populations, as over 20% of the world's population lives within 30 km of the coast

and that population is increasing at twice the current global rate. With the minimum sea level rise of 20 cm expected by 2050, an estimated 78 million people will be at risk from flooding (Hadley Centre 1998).

As with temperatures, sea level rise will vary, and some forms of marine life will be impacted more by sea level rise than others. For example, nesting seabirds on low-elevation coral atolls may find their nesting grounds flooded. Coastal wetlands such as salt marshes and mangrove forests are likely to be heavily impacted by sea level rise if they are inundated with sea water and can't migrate inland sufficiently to compensate (Ellison & Farnsworth 1997). These areas are important for stability of the coastline and coastal productivity, and are the nursery grounds for numerous species of invertebrates and fishes, many of them valuable to humans for our consumption. Many commercially valuable species throughout the world rely on coastal ecosystems for some or all of their life cycle (IPCC 1995). Alteration of coastal areas could greatly disturb food webs in marine ecosystems. For example, some hypothesize that eroding marshes and shorelines due to sea-level rise in Chesapeake Bay in the U.S. has increased turbidity in the water and is preventing aquatic vegetation in some locations from obtaining enough light to sustain growth. Concurrently, crab populations which rely on this aquatic vegetation for protection during their early life stages are also declining in the Chesapeake (J.C. Stevenson, personal communication). Eroding Islands in the Chesapeake are rapidly disappearing from sea level rise (Kearney & Stevenson 1991) and many of these islands are important rookeries for nesting birds (J.C. Stevenson, personal communication). Although present estimates are tentative, the world's coastal wetlands already have been disappearing at a rate of 0.5-1.5% per year for the past few decades (IPCC 1995), and climate-induced sea level rise may threaten 20-40% of the rest (IPCC 1995).

Tidal marshes and mangrove forests may have the capacity to keep up with some changes, depending on the amount of sediment washing into the system from land, and the productivity and peat formation of the wetland. If wetland areas can de-

velop inland at a pace that can keep up with sea level rise, these areas may be able to adapt. However, studies at Blackwater Marsh on the Chesapeake suggest that when sea levels become too high (as sediment inputs are not sufficient to offset subsidence) there is very little landward migration because submergence is too rapid for marsh establishment at the landward edge (Stevenson et al. in press). Moreover, coastlines increasingly are being developed, leaving coastal wetlands threatened by sea level rise nowhere to go. Predicted temperature increases may also disrupt peat accumulation: more peat will be broken down under higher temperatures as microbial activity increases (Stevenson et al. 1986). This loss may be offset, however, by increased production of roots and other plant parts (and subsequently, peat) from increased CO₂.



Wind patterns

Global climate change is predicted to affect wind patterns as well as wind intensity. Winds are created from differences in atmospheric pressures, which are largely determined by patterns of surface temperatures. As the Earth's surface is heated, some geographical regions will warm faster than others. Accelerated warming of the planet surface, including the oceans, may produce stronger winds in certain areas, and increase the frequency of extreme events such as storms and hurricanes (Hadley Centre 1998).

Winds determine (in part) water movements such as coastal upwelling – in which deep nutrient-rich waters are brought to the surface - and offshore and alongshore transport. All of these water movements have important consequences for marine species and ecosystems. Upwelling provides much of the necessary nutrients used by phytoplankton for photosynthesis – the first step in the marine food chain or web. Ocean currents play key roles in reproduction of many marine organisms, and a disruption in these currents will affect reproductive success. For example, if larvae or eggs must travel long distances to find suitable habitat, some marine species coordinate their release of larvae or eggs with the presence of offshore currents to increase dispersal. In contrast, other species release their larvae or eggs only when currents are running back onshore, to ensure they settle nearby (Parrish et al. 1983). Increased winds could mean increased transport, sending larvae to areas distant from their targets, or species may fail to spawn if not presented with the appropriate environmental conditions (Peterson et al. 1993). Both of these deviations could be disastrous for the completion of species' life cycles.

Deep-ocean circulation patterns

Ocean water moves around the Earth in several ways. Winds can generate surface currents and induce vertical water movements like upwelling and downwelling. Another important type of circulation is thermohaline circulation, which is driven by differences in density of seawater masses. Density differences are primarily created by differences in temperature (thermo-) and salinity (-haline). The colder a water mass is or the greater its salinity, the greater its density. Water that is more dense sinks below water that is less dense, creating a circulation pattern of turnover in the water column. General thermohaline circulation is driven by the

sinking of the dense water in certain polar regions and its subsequent movement towards the equator across the floor of the ocean basins. On the surface, warmer water from the lower latitudes flows towards the poles to take the place of the water that sank.

Two important functions are maintained by thermohaline circulation. First, this formation of deep water at the poles brings oxygenated surface water down to the deep ocean. There is no other major influx of oxygen into the deep sea. Without the constant influx of oxygen-rich water through this circulation, water along the sea floor would become depleted of oxygen, which would kill much of the existing marine life living on the bottom. Second, thermohaline circulation acts to redistribute heat from the equators towards the poles. Much of the ocean heat transport in the North Atlantic is associated with thermohaline circulation (Rahmstorf, 1997), making average air temperatures in the northeastern Atlantic (e.g. Europe) warmer than those at the same latitude in the Pacific (e.g. Alaska) (Weaver 1995).

Thermohaline circulation patterns are likely to be affected by global climate change, and in turn are likely to affect future climate change. Because thermohaline circulation is driven by density differences of water masses, it is extremely sensitive to influxes of fresh water, of the kind expected to occur from global climate change, due to melting sea ice and increased precipitation (Weaver 1993; Weaver 1995). Fresh water makes ocean water less saline and therefore less dense, so it doesn't sink as quickly. If enough fresh water is added, deep water formation in the North Atlantic may cease altogether, and relatively small amounts may be sufficient to alter thermohaline circulation (Marotzke & Willebrand 1991). Some climate models suggest that, under Business-as-Usual conditions, a complete shutdown of thermohaline circulation in the Atlantic could eventually occur (Manabe & Stouffer, 1993; Stocker & Schmittner 1997). Some models predict recovery of thermohaline circulation patterns in 500 years or so (Manabe & Stouffer 1993) while others show no recovery (Manabe & Stouffer 1993, Stocker & Schmittner 1997).

Recent evidence has demonstrated that freshwater influx from melting sea ice can significantly reduce thermohaline circulation. From 1968 to 1972 a phenomenon deemed the Great Salinity Anomaly was documented. It was a large pool of relatively fresh water (compared to its surrounding sea water) which resulted from two years of anomalously high Arctic sea ice melt. This amount of freshwater input was sufficient to shut down deep-water formation in the Labrador Sea, one of two principal sites of deep-water formation in the North Atlantic. When the ice-melt source was removed, deep-water formation was restored (Weaver 1995). This relatively small amount of fresh water was sufficient to significantly alter deep-water formation in the North Atlantic. Future climate change will likely involve alterations of a much greater magnitude and duration.

Changes to thermohaline circulation could have several impacts. One effect could be to enhance the buildup of atmospheric CO₂ further; if thermohaline circulation were to slow or cease, northward flow of water from the equator will slow, and water at lower latitudes will become warmer. Warm water holds less dissolved CO₂ than cooler water. If the oceans take in less CO₂, more will remain in the atmosphere, enhancing global warming further. Additionally, a slowing of deep-water formation in the Atlantic would likely reduce the transport of oceanic heat to the European continent. European cities along the Atlantic seaboard may begin to cool, approaching the cooler temperatures of their latitudinal counterparts in the Pacific.

Ocean stratification and primary productivity

Primary productivity refers to the synthesis of organic matter (i.e. living material) from inorganic nutrients, and is the foundation of the food chain. In ocean surface waters, phytoplankton – microscopic drifting plant-like cells – are the primary producers, converting inorganic nutrients into phytoplankton biomass through photosynthesis. A "typical" marine food chain could include phytoplankton, which are consumed by zooplankton (small drifting animals), which are consumed by small fishes, which are consumed by predatory fish. Humans may be at the end of this food chain, of-

ten consuming the large predatory fish. The term "food chain" is a simplified description of how energy (e.g. food) is transferred through organisms in an ecosystem. In reality, multiple organisms consuming a variety of other organisms create complex interactions within ecological communities more appropriately referred to as food webs.

Primary productivity is greatly affected by stratification of water in the ocean, which in turn is affected by climatic conditions. During summer months when the ocean's surface is warmed by the sun, the shallow, upper portion of the water column becomes warmer and therefore less dense than the colder water beneath it. The water column is thus described as stratified. The warmer the water on the surface is relative to the colder water beneath it, the more resistant the water column is to mixing by surface winds. In the winter season this stratification breaks down, as the surface waters cool and winter winds break up the density gradients. The surface layer becomes mixed and of uniform temperature. Winter mixing is important for phytoplankton growth because it brings nutrients needed for photosynthesis from deeper water to the surface. Phytoplankton can then utilize the nutrients in the spring and summer, once stratification forms to trap them in the sunlit waters near the surface.

Summer stratification is a normal part of the seasonal pattern of the ocean. But human-induced climate change will affect ocean stratification, and therefore primary productivity. Temperature increases will warm the surface waters beyond expected seasonal temperatures, and the warm layer of surface water will be thicker and more strongly stratified. Wind forcing and upwelling will be less able to break through the warm surface waters to bring nutrient-rich water to the surface, resulting in a reduction of available nutrients in the surface layer. Upwelling may still occur, but if the stratification is strong enough, the upwelled water reaching the surface will come from mid-water regions rather than colder, deeper waters where the nutrient concentrations are greater. This is called shoaling of the upwelled waters. Shoaling has been demonstrated in several cases associated with warmer

surface waters, resulting from natural fluctuations in temperature such as during El Niño events (Peterson et al. 1993; Roemmich & McGowan 1995; Barber et al. 1996; McGowan et al. 1998), and is associated with lowered levels of primary productivity.

In general, less primary production under global warming would mean less overall production in marine ecosystems, which would mean a reduction in resources such as fisheries. Lowered primary production would also remove less CO, from the atmosphere. Surface waters in the oceans now remove CO₂ from the atmosphere through photosynthesis and by exporting of much of the organic material produced into the deep sea. If photosynthesis is reduced with global warming, CO, in the atmosphere could actually increase from the ocean, and further increase global warming. The oceans hold so much more CO, than the atmosphere, approximately 60 times more, that even minor shifts in this equilibrium could have a large effect on atmospheric CO₂ concentrations (Sundquist 1985).

Indirect effects on primary productivity are also likely, given current model predictions and evidence from natural climatic variability such as in El Niño. As ecosystems change due to alterations in nutrient levels and temperature, changes in species composition will be likely. The numbers of phytoplankton cells may not decrease appreciably, but they may be of different species than those currently found in a given region, which can have important effects on the structure and function of ecosystems (Hayward 1997). Phytoplankton species are not all equivalent in their contribution to food webs. Whereas all of them produce organic material through photosynthesis, some are not readily eaten by zooplankton, or are actually toxic. Therefore any change in the species composition at the base of the food web may have significant repercussions for the rest of the marine ecosystem. The replacement phytoplankton species and resulting food webs may not produce the same amount of food resources for fishes and other populations, and hence for human consumption (IPCC 1995).

Changes in species composition of phytoplankton populations may also enhance the buildup of CO₂

in the atmosphere. For example, in the Ross Sea of Antarctica, the species *Phaeocystis antarctica* dominates in areas that are deeply mixed, but the diatom *Nitzschia subcurvata* dominates in areas that are stratified. Although both species photosynthesize, *P. antarctica* draws much more CO₂ from the water, and therefore the atmosphere, than does the diatom *N. subcurvata*. Increased stratification from global warming may make this region much more favorable to diatoms. This shift in species dominance could reduce the amount of CO₂ drawn out of the atmosphere by over a third (Arrigo et al. 1999).

Decreases in productivity may already be occurring off the California coast, where scientists have documented a measurable decrease in the abundance of zooplankton, the second level in the food web. There has been a steady decline in the numbers of zooplankton and larval invertebrates in the California current ever since the 1950s (Roemmich & McGowan 1995). Currently the abundance of zooplankton is 70% lower than it was then. The reason for this may be a decrease in primary production, which the zooplankton rely upon for food, or an increase in predation on the zooplankton, however, the cause is uncertain. No long-term data sets for phytoplankton exist to adequately determine the cause of this decline.

Natural Climate Variability: Lessons from El Niño and Decadal Variation

Climate varies naturally over time. It has changed over geologic time as evidenced by various glacial and interglacial periods, and continues to vary on annual and decadal time scales as well. How species and ecosystems respond to natural variations in climate can provide insights into how they might respond to human-induced global climate change. The El Niño phenomenon is one type of climatic variation that most people have become familiar with in the past two decades. El Niño is caused by a naturally occurring oscillation of atmospheric pressures in the Pacific Ocean that weakens the trade winds that normally move warm water away from the eastern Pacific, and therefore concentrates warmer waters in that region along the equator. Many of the changes that occur in the

eastern Pacific during El Niño are similar to those predicted by current climate models. El Niño climate patterns initially are more extreme and develop more quickly than global climate change, but are usually reversed the following year. Observations of El Niño events may be useful for determining the types of initial short-term changes we can expect as climate change occurs (Castilla et al. 1993).

El Niño events have occurred on average every 2-8 years for the past several thousand years, with a great deal of variation in the intensity and duration of each episode (Rodbell 1999). Two of the strongest events were those in 1982-83 and 1997-98, with impacts on ecosystems around the world. The full effects of the 1997-98 El Niño are not yet known, but initial observations are similar to those from the 1982-83 El Niño and similar to predictions for global warming (McGowan et al. 1998). During the 1982-83 event, physical changes along the eastern rim of the Pacific included higher sea surface temperatures and higher sea levels, lower nutrients and lower salinity (from a shoaling of upwelling) and increased intensity of storms and storm surge. The tropics, around which the majority of El Niño effects are centered, felt effects of the greatest magnitude (Lubchenco et al. 1993). Some of the direct effects of this El Niño included the possible elimination of a species of hydrocoral (fire corals) and possibly one species of reef coral (Acropora valida) from the eastern Pacific, and mass mortalities of coral species, with overall mortality ranging from 50 to 98%, depending on the geographic region (Glynn 1984). There were also mass mortalities in kelp forests off California, which are important habitat for numerous other species. Seabirds such as cormorants and pelicans experienced massive die-offs, as did Peruvian anchovy and sardines, marine iguanas, two seal species (South American and Galapagos fur seals) and two species of sea lions (South American and Galapagos sea lions) (Glynn 1988).

Also associated with El Niño events were many instances of species extending or shifting their geographic ranges when environmental conditions changed, and invading areas where they didn't

normally occur. Many of the El Niño perturbations initiated a host of secondary effects as well. For example, massive kelp die-offs on the California coast eliminated habitat for many species, as well as food for many others (Glynn 1988). Recovering ecosystems were also beset by disease or unexpected predation as neighboring species were disrupted. Such was the case when El Niño eliminated outer reef coral barriers and allowed the coral-eating crown-of-thorns starfish access to previously protected areas, further decimating the remaining corals (Glynn 1991). The recovery of the California kelp forests that were eliminated by El Niño were similarly delayed by a sudden abundance of algae-eating amphipods, probably linked to the reduction of kelp-dwelling fish that preved on these creatures (Tegner & Dayton 1987; Glynn 1988). Clearly, when structure-forming species such as kelps and corals are affected at this magnitude, a host of secondary effects will occur, the extent of which may be difficult or impossible to predict (Lubchenco et al. 1993).

El Niño events occur on a single-year time scale, but a second type of natural climatic variation alternates over decades. In the Pacific, this pattern, termed the Pacific Decadal Oscillation (PDO), involves a shift in the low pressure system off the Aleutian Islands (Hayward 1997). PDO has occurred regularly through the past 2,000 years, influencing the Bering Sea and the North Pacific, down through the California Current and the Peru Current (Hayward 1997). The PDO effects changes in winds, temperatures, rainfall, sea ice, and weather patterns across the U.S. (Trenberth & Hurrell 1994). It changed state in 1925, 1947, and 1976-77 (Mantua et al. 1997), bringing notable changes in weather patterns, such as higher sea surface temperatures off the west coast of North America, as well as changes in species abundances and distributions. Zooplankton off California declined dramatically after the shift in 1976-77 and presumably primary productivity was reduced as well. The increased stratification that results from warmer sea surface temperatures suggests that upwelled water was coming from a shallower depth, and therefore had lower nutrient content than normal (Roemmich & McGowan 1995). Reduced primary productivity would have ripple effects throughout food webs.

While natural climatic variations like El Niño and PDO can provide insights into the biological effects of climate change, they also may be indicating that human-induced climate change is now affecting normal climatic patterns. It is believed that the PDO reversed its state again in the late 1980s or early 1990s, which was expected to cool ocean temperatures (Bering Sea Task Force 1999; E. Venrick personal communication). However, sea level and sea surface temperatures off California have remained higher than average (Hayward 1997) and zooplankton populations remain low (E. Venrick, personal communication). Zooplankton off Southern California that has declined 70% since the 1950s (Roemmich & McGowan 1995) remain at their lowest recorded levels in this region. This decline of secondary production will undoubtedly have effects felt throughout these ecosystems.

The frequency and duration of El Niño events may have changed recently, leading some scientists to examine whether global climate change has influenced this pattern as well. Historical evidence of variation in El Niño frequencies based on South American sediment cores indicates that from 15,000 to 7,000 years ago, El Niño events occurred every 15 years or so. More recently, they have occurred every 2 to 8.5 years (Rodbell et al. 1999). But since the 1970s, El Niño events have been even more frequent, with five out of seven years from 1990-1997 experiencing El Niño conditions. Some consider 1990-1995 to be one continuous El Niño, as the interim temperatures never returned to normal (Trenberth & Hoar 1996). Based on the previous 100 years of climate record, however, the chances of an El Niño event lasting five years is approximately 1 in 1,500 to 1 in 3,000 years (Trenberth & Hoar 1996). Either we are seeing natural climate variability that is not evident from the previous 15,000 years of data, or human-induced climate changes are beginning to occur. Computer modeling suggests that higher global temperatures from greenhouse gases will result in average conditions similar to present day El Niño conditions and that El Niño-like events will become more frequent. Year-to-year variations would also become more extreme, with strong cold events occurring as well (Timmermann et al. 1999). El Niño events are seemingly not influenced by higher CO₂ levels directly (Castilla et al. 1993), but it is possible they are affected by increased greenhouse warming. Higher overall atmospheric and ocean temperatures may mean that threshold temperatures triggering El Niño events are reached more frequently.

The most recent El Niño (1997-98) was the strongest on record, with the highest recorded temperatures. Each month in the last half of 1997 set a high temperature record when compared with values back to the mid-19th century (McPhaden 1999). New records were set again just a year later in 1998 (Mann et al. 1999). The coolest year of the 1990s, 1996, was still nearly as warm as the 1983 El Niño. Temperatures in 1997 off the west coast of North America reached peaks of four standard deviations above the norm. For perspective, this level of deviation is expected by random chance roughly once in 10,000 years. There is no historical context for this type of variation, yet the newest climate models predict much greater temperature increases in the next century (D. Welch, personal communication). Regardless of whether long-term global climate change is altering El Niño patterns, these events provide valuable insights into the types of ecological changes we might see under global warming.

EVIDENCE OF IMPACTS ON MARINE LIFE

Impacts in Polar Regions

The polar regions, particularly the Arctic, are predicted to experience greater overall temperature change than areas of lower latitude (IPCC 1995; Hadley Centre 1998; Bering Sea Task Force 1999). Since some climate change effects are likely to be seen first at higher latitudes, species in those areas may serve as an early warning system for changes to come.

Measurable environmental changes are already occurring in the Arctic and the Antarctic, although the causes aren't yet clear. For example, northward flow through the Bering Strait into the Arctic Ocean appears to have slowed. This implies a reduction of the overall northward flow of nutrient-rich North Pacific Ocean water onto and over the Bering Sea shelf, potentially reducing the overall primary productivity in the region (Bering Sea Task Force 1999). In addition, ocean surface temperatures from British Columbia to the Bering Sea were 5-6°C higher than normal in 1997, and continued to be 2°C warmer through 1998. Deep water temperatures off Seward, Alaska are also 1.5-2°C warmer than normal, indicating temperature changes have occurred through a large portion of the water column (Kruse 1998). Recent measurements of deep Atlantic water moving over the Arctic ridge show an increase in temperature of 1°C since measurements in 1977 and 1983. Compared to a normal background annual variation of 0.05-0.08°C, this is a significant increase (Morison et al. 1998). In late 1997, very little multiyear ice in the Arctic was even 1.5 meters thick, when usually it is 2-3 meters thick at that time of year. (McPhee et al. 1998). A recent report has documented measurable diminishing of Greenland glaciers as well (Krabill et al. 1999). This report indicates some regions of the glacier are thickening, but the southeastern regions, which are most susceptible to climate change, have been thinning at a rate greater than 1 meter per year. The thinning appears to be caused by some ice melt, which then facilitates glacial movement toward the sea. Once in the sea, glaciers melt quickly, increasing freshwater input into the Atlantic to an even greater degree than that predicted by temperature increases alone. Climate models predict substantial decreases in coverage and thickness of arctic sea ice in response to global warming (Tynan & DeMaster 1997).

Although the Antarctic is predicted to experience lesser levels of climate change than the Arctic, measurable warming is also occurring there, accompanied by ecological changes as well. Paleoclimate records as well as modern instruments indicate the western Antarctic peninsula has undergone a warming trend over the past 100 years, particularly in the last half of this century. In the past half-century, the western peninsula has experienced a 4-5°C warming in air temperatures, with 20 of the past 27 years experiencing warmer than average temperatures (Smith et al. in press). A large section of the Larsen A ice shelf collapsed in 1995 over the space of a few days, releasing a large amount of fresh water into the system (Doake et al. 1998). In 1999 scientists from the University of Colorado and the British Antarctic Survey reported that two additional ice shelves, known as Larsen B and Wilkins, lost nearly 3,000 square km of their total area in the previous year as the shelves collapsed (T. Scambos, personal communication). In the past 20 years, the total number of days above the melting point has increased by 2 to 3 weeks in this region, increasing meltwater on the shelves. Large areas of ice shatter as the meltwater percolates into fractures, and deep cracks are forced open to the base of the ice sheet by the weight of the water (T. Scambos, personal communication). Ice shelves are centuries old, and so their recent, rapid disappearance indicates significant climatic changes in this region, and reveals how only a small amount of melting can dramatically reduce ice shelves. Moreover they demonstrate how quickly these changes can occur. Once ice sheets weaken to a critical point, they may collapse very suddenly (Doake et al. 1998).

In both the Arctic and Antarctic, sea ice appears to be retreating. Satellite images of the Arctic measure a 3% decrease in the area of sea ice since the late 1970s, with the rate of ice loss increasing this past decade (McPhee et al. 1998). This reduction has significant implications for marine species and ecosystems: primary productivity is intricately connected to sea ice at the higher latitudes. In ecosystems near the poles with multi-year ice, algae growing attached to and under the ice are responsible for almost all of the primary production on which the entire ecological community depends. At certain latitudes, all marine birds and mammals depend on food webs based on ice communities (Alexander et al. 1996). Higher temperatures predicted under climate change could further diminish ice cover, with open water in areas previously covered by ice, thereby diminishing the basis of the polar food web.

At lower latitudes with seasonal sea ice, ice edge production is also extremely important. Some have estimated that the primary productivity found at the ice edge can be as much as 15 times higher than the productivity in adjacent ice-covered areas or in open water (McRoy & Goering 1976). Massive spring plankton blooms that form at ice edges are a key annual event in areas of seasonal sea ice with productive fisheries (V. Alexander, personal communication). During these blooms, melting ice allows for intense production earlier in the spring than would otherwise occur and contributes a substantial amount of the annual productivity. These blooms support swarms of amphipod crustaceans and other zooplankton – which are then eaten by many species of fishes, seabirds, and marine mammals – and also support seafloor communities as the bloom dies and sinks to the bottom (Alexander et al. 1996; Alexander & Niebauer 1981; Smith & Nelson, 1985). Productivity is further stimulated as algae on the underside of the ice are released into the water as the ice edges melt, and are consumed (Kruse 1998). Marine mammals such as walruses, bearded seals and gray whales forage in seafloor communities for food, and the timing of the bloom is critical to Arctic cod larvae – a key prey species for several seal species, beluga whales, and narwhals (Tynan & DeMaster 1997). Warming would decrease the area covered by seasonal sea ice, decreasing the importance of the spring bloom, and would reduce the length of the growing season by delaying the spring bloom (V. Alexander, personal communication). Sea ice also supports marine mammals like walruses and ringed seals by providing critical breeding and resting areas, and serving as hunting platforms for the polar bears that feed on them (Tynan & DeMaster 1997). In the Bering Sea and in Hudson Bay, evidence of stress in polar bear populations is mounting as sea ice decreases (Bering Sea Task Force 1999; Stirling & Derocher 1993; Stirling 1997). Some native people in the Arctic have reported difficulty hunting marine mammals such as walrus in recent years as sea ice has diminished (C. Pungowiyi, personal communication). In parts of Antarctica, populations of marine mammals and penguins dependent on sea ice are declining, while those that favor open water are increasing (Fraser et al. 1992). Continued loss of sea ice very likely could harm many populations of polar mammals that depend upon it (Tynan & DeMaster 1997).

Changes in the species composition of phytoplankton can also have a marked effect on ecosystems. Northern waters adjacent to the Arctic are beginning to experience phytoplankton species shifts that have never been seen before. The Bering Sea experienced highly unusual marine and atmospheric conditions in 1997-1998; weak winds coupled with strong sunlight created highly stratified, low-nutrient surface waters in the summer of 1997 in the eastern Bering Sea, and a massive bloom of coccolithophores resulted. Coccolithophores are phytoplankton normally associated with low-nutrient areas, and such a large-scale bloom had never before been documented in this area (Vance et al. 1998; Napp et al. 1999). Although the coccolithophores constituted over 98% of the phytoplankton in the water at that time, they did not appear to have been eaten by zooplankton (Wyllie-Echeverria et al. 1999). A second bloom of coccolithophores occurred in the unusually warm waters of 1998, even larger than that of 1997 (Kruse

1998). Significant die-offs of seabirds occurred during this period, with over 190,000 short-tailed shearwaters dying of starvation. Kittiwakes and common murres were also affected (Bering Sea Task Force 1999; Kruse 1998; Vance et al. 1998). It is thought that the milky-white coccolithophores might have made it difficult for the birds to see their prey, or that prey were less available (Kruse 1998; Tynan et al.1999). There was also a decline in euphausiid crustaceans, which are preferred prey for several species of birds and fishes (Napp et al. 1999).

The Bering Sea has exhibited many ecological changes over the past decade. Against the backdrop of a long-term and major decline in populations of Steller sea lions and northern fur seals, populations of other mammals and birds also appear to be stressed. Small forage fish, such as herring, capelin and larval fishes, have been declining for the past 5 years (Brodeur et al. 1999). Species that were previously known from more southern climes have appeared in Alaska including Pacific white-sided dolphins, albacore and yellowfin tuna, and ocean sunfish, and herring spawned earlier than ever before (Kruse 1998). The most visible and dramatic change has been the collapse of major salmon runs in western Alaska in both 1997 and 1998 (Kruse 1998). It is not clear yet to what extent these changes are related to warming, but certainly warmer waters, the reduced nutrients in the area, and the decrease in sea ice cover and delay in ice cover have all played a role (V. Alexander, personal communication). A shift in ocean conditions in the late 1970s resulted in a major reduction in sea ice and increase in temperatures. The unusual conditions in 1997 and 1998 further exaggerated these effects (Niebauer et al. in press).

Some species living in the higher latitudes may be more susceptible to climate warming than those at lower latitudes. Some temperate or tropical species can potentially shift their geographic ranges to stay within suitable climatic ranges. But species that live near the poles have few options for finding higher latitudes, and may not be able to find suitable habitat conditions. Moreover, rela-

tively small changes in climate at the poles can have big effects: ice normally reflects a large percentage of the sunlight that hits it, deflecting its heat away from the Earth's surface. As ice cover is replaced with open water, less sunlight is reflected, and heat trapped in the water under the ice is released, further exacerbating warming.

Coral Reefs

Coral reef ecosystems are among the most productive, diverse ecosystems on earth, but are also among the most vulnerable to global climate change. These "rainforests of the sea" cover much less than 1% of the world's oceans, but include more than a third of the marine species presently described by science, and many species remain undocumented (Reaka-Kudla 1996). Their productivity, diversity and beauty support fishing and tourism throughout the world's tropics, their unique organisms are a promising new source of anti-cancer compounds and other medicines, and reef structures protect coastlines from erosion (Maragos et al. 1996). But many coral reefs worldwide are undergoing unprecedented decline. Multiple stresses, including overfishing and destructive fishing practices, coastal development, nutrient runoff from agriculture and sewage, and sedimentation from logging and development are harming reefs (Bryant et al. 1998; Maragos et al. 1996; Norse 1993; Smith & Buddemeier 1992). By some estimates, 58% of the world's coral reefs are threatened by human activity and 10% have already been severely degraded, although actual conditions for many of the world's reefs are unknown (Bryant et al. 1998). In recent years - most notably 1997 and 1998 - an additional stress has had dramatic results: warmer than average sea surface temperatures.

Found only in warm tropical waters, reef corals are extremely sensitive to temperature, and have an upper tolerance only a few degrees above normal high temperatures (Norse 1993; Smith & Buddemeier 1992; Wilkinson et al. 1999). If the temperature gets too high, corals will bleach, meaning they expel millions of microscopic zooxanthellae – symbiotic photosynthetic algae – that live within their tissues and provide them with food. If temperatures remain too high for too long, corals

cannot recover and eventually die. Other stresses can cause bleaching as well, including increased ultraviolet radiation, prolonged exposure to the air, a reduction in salinity from freshwater, excess silt and other pollution but in recent years, widespread bleaching has been linked largely to high water temperatures (Wilkinson et al. 1999; Glynn 1991; ITMEMS 1998; ISRS 1998). The National Oceanic and Atmospheric Administration (NOAA) of the U.S. Department of Commerce reported that unprecedented coral bleaching and extremely warm waters occurred throughout the tropics during 1998 (NOAA 1998a; NOAA 1998b). Combined landair and sea surface temperatures made 1998 the warmest year of the century (WMO 1998). According to NOAA, coral bleaching was reported throughout the Indian Ocean and Caribbean in 1998, and throughout the Pacific, including Mexico, Panama, Galapagos, Papua New Guinea, American Samoa, and Australia's Great Barrier Reef starting in 1997 (NOAA 1998a). The years 1997 and 1998 brought a very strong El Niño which increased sea surface temperatures in the Pacific with effects felt around the world. While climatologists debate whether the increasing frequency of El Niño's in recent decades is the result of global warming, the effects of unusually warm sea surface temperatures on corals during such periods have been severe, and provide a glimpse of what could happen if global temperatures continue to rise in the future from climate change.

The severity and extent of coral bleaching in 1997-98 was widely acknowledged among coral reef scientists as unprecedented in recorded history, and probably caused by the extreme sea temperatures in those years. Their concern prompted many to make public statements clarifying the likely causes and consequences of this global decline.

The International Society for Reef Studies (ISRS), with 750 members dedicated to promoting the production and dissemination of scientific knowledge and understanding of coral reefs, issued a Statement on Coral Bleaching in October of 1998. In the statement, ISRS concluded that 1997-98 had seen the most geographically widespread bleaching ever recorded, with some areas witnessing ex-

tensive bleaching for the first time in recent history. ISRS scientists recorded reports of bleaching in at least 32 countries and island nations, with reports from sites in all the major tropical oceans of the world, including the Pacific Ocean, Indian Ocean, Red Sea, Persian Gulf, and the Mediterranean and Caribbean Seas. While bleaching can sometimes be a seasonal phenomenon with likelihood of full recovery, ISRS scientists stated that the 1997-98 bleaching episode was exceptionally severe, with a large number of corals turning completely white and dying. One reef on Australia's Great Barrier Reef has been so severely affected that many of the usually robust corals, including one dated over 700 years of age, were badly damaged or had died. Evidence shows that restoration of the reef to its former state may be slow, or if interrupted by human changes, may be diverted to dominance by non-reef-building species. The statement expressed concern about the rate of temperature increases in the future. While corals display impressive acclimation to changes in some environmental conditions, it is unknown whether they could adapt or acclimatize at rates to match the projected rates of seawater temperature increase from climate change. Should seawater temperatures rise, ISRS scientists stated that we might expect the incidence and severity of coral bleaching to increase even further, with the possibility of substantial changes to coral reef community structure. They concluded that the 1997-98 episode of worldwide bleaching is a major cause of concern (ISRS 1998).

The statement directly addressed the question of El Niño: coral bleaching in many parts of the Pacific in the past and in 1997-98 appear to be closely matched to El Niños, however, the connections are not clear-cut for all Pacific locations, and bleaching in the Indian and Atlantic Oceans cannot be directly linked to only El Niño phenomena (ISRS 1998).

Scientists at the International Tropical Marine Ecosystems Management Symposium (ITMEMS) released a similar Statement on Coral Bleaching in November 1998. The Statement noted that tropical sea surface temperatures in 1997 and 1998 were

higher than at any other time in the modern record and stated that the coral bleaching associated with these high temperatures affected almost all species of corals, including some individuals more than 1,000 years old. It stated that this global coral bleaching and die-off is unprecedented in geographic extent, depth and severity, with the Central Pacific the only major reef region spared from major bleaching, and mortality in some parts of the Indian Ocean as high as 90%. While it is unclear how future predicted temperature increases will affect the tropics or whether corals can adapt to these predicted temperature increases, these experts stated that because corals live so near the upper edge of their temperature tolerance, an increase of 2°C as predicted by the IPCC for the next 50 years is of concern. This group concluded that current predictions of global warming suggest there will be increased frequency of coral bleaching and mortality in the future, and that these events eventually will have important negative consequences for biodiversity, fisheries, tourism and shore protection (ITMEMS 1998).

While the unusual conditions of 1997-98 resulted in particularly severe bleaching events, bleaching occurred repeatedly throughout the 1980s in association with unusually high sea temperatures as well. Severe bleaching accompanied the strong 1982-83 El Niño event, with mass mortalities of corals around Costa Rica, Panama, Colombia and Ecuador, and also at sites in the Indo-Pacific and Caribbean (Glynn 1991; NOAA 1998b). During a more moderate El Niño in 1987, bleaching occurred at new sites throughout the Red Sea and the entire extended Caribbean region (Glynn 1991). Studies examining possible causes of these bleaching events concluded that 70% were probably attributable wholly or in part to elevated water temperatures (Glynn 1991; Brown 1987). Other causes included coral exposure caused by sudden sea-level drops and high rainfall reducing salinity as a result of El Niño. Since 1990, some scientists have successfully predicted the location and timing of all large-scale coral bleaching events from satellite temperature data alone (Goreau et al. 1998). In its review of scientific knowledge of coral reefs and global climate change, the U.S. State Department concluded that the mass coral bleaching and mortality events of 1998 cannot be accounted for by localized stressors, natural variability, or El Niño alone. The impacts of these factors was likely accentuated by an underlying global cause; most likely, anthropogenic global warming. Therefore, the State Department concluded, any strategy to maintain coral reefs must include reduction of greenhouse gas emissions (U.S. Department of State, 1999).

Higher sea surface temperatures resulting from global climate change are not the only potential source of damage to coral reefs. Reefs appear to be directly affected by increasing atmospheric CO₂, a primary greenhouse gas. Living coral reefs are built from the limestone skeletons of generation upon generation of corals and other marine life. Each living coral contains up to hundreds of thousands of coral polyps that fashion a rigid skeleton of calcium carbonate over their lifetimes, which can last hundreds of years. But high levels of atmospheric CO₂ alter water chemistry by decreasing pH and carbonate ion concentration, lowering the carbonate saturation state of water, and thereby reducing the calcification rate of corals (Gattuso et al. 1999; Kleypas et al. 1999). Based on decreases in the saturation state already measured in the tropics, some scientists believe that calcification has most likely already decreased on some reefs. They predict calcification could decrease 17 to 35% from pre-industrial levels by 2100 (Kleypas et al. 1999). Reduced calcification can decrease the density of coral carbonate skeletons, as shown in laboratory experiments. Some scientists fear that this reduced density, combined with increased frequency or severity of storms caused by global climate change and mass mortality of corals from bleaching, can accelerate erosion of reefs and potentially favor faster-growing, non-reef building species such as algae and sponges over corals (Done 1999; Smith & Buddemeier 1992; Glynn 1991). Moreover, this direct effect of CO₂ suggests that coral reefs may not successfully expand into higher latitudes to compensate for increasing sea temperatures in the tropics, as CO, continues to increase globally (Kleypas et al. 1999).

To evaluate the scientific basis for growing concerns about the survival of coral reef ecosystems, several scientific societies, including the Working Group 104 of UNESCO's Scientific Committee on Ocean Research, the Society for Integrative and Comparative Biology, the International Society for Reef Studies, and the Ecological Society of America, combined their expertise at a symposium and workshop in January 1998 organized by the Society for Integrative Comparative Biology. This multidisciplinary group included geologists, paleobiologists, climatologists, biogeochemists, aquarists, geneticists, and organismal, ecological, and evolutionary biologists to examine the variety of evidence addressing corals, reefs, and their responses to environmental change. They summarized their findings in a report called "Coral Reefs and Global Change: Adaptation, Acclimation or Extinction? Initial Report of a Symposium and Workshop."2

The group reached several key conclusions about global change and coral reefs, most notably, that coral reef ecosystems appear to be directly threatened by globally increasing atmospheric CO₂. Atmospheric carbon dioxide is expected to double from pre-industrial levels by the year 2070 (despite the Kyoto Protocol), and calcification rates of corals are expected to be reduced by this rising atmospheric carbon dioxide. The group concluded that this change "represents a global, systemic, climate-related threat to the functioning of reef ecosystems" that will interact with the more immediate local stresses such as sedimentation and pollution. Therefore, conservation strategies aimed at removing or mitigating only local environmental stresses are likely to be inadequate, on their own, to maintain the health of coral systems. Regarding sea surface temperature, the group concluded that, although it is difficult to translate predictions of global temperature increases into regional changes, three outcomes from warming water temperatures are probable. First, the temperature zones currently associated with coral reefs will move away from their current latitudes towards the poles. Second, that there will be some rise in sea surface tempera-

tures within current tropical and subtropical latitudes. And third, that there will be some degradation of coral communities from higher temperatures within the present zones. An increase in extreme events may also damage reefs. If significant changes in El Niño and tropical cyclone patterns occur as some predict, tropical cyclones may increase 10 to 20% in intensity by 2070, potentially affecting reefs. Riverine flood frequency and magnitude could increase, causing more sediments and pollutants to wash over coastal reef ecosystems. Projected rates of sea level rise caused by global warming are not likely to be a problem on their own. However, the group concluded that the combination of decreased calcification rates and other stresses may diminish the ability of reefs to keep up with this rising sea level. In general, this synergistic effect of immediate local stresses, combined with global climate stresses was cited as a major concern. Combined impacts are likely to reduce the capacity of reef communities to maintain themselves, and increase the probabilities that major disruptions such as ecosystem collapse or species extinctions will occur.

Regardless of whether the 1997-98 El Niño was influenced by global climate change, the effects of high sea surface temperatures on coral reefs are devastating. As temperatures continue to climb, coral reef ecosystems already under stress from pollution, overexploitation, and other activities will face additional severe threats from climate change that can only be solved through global action.

Shifts in Species' Distribution and the Fate of Pacific Salmon

One of the most intuitive predictions of global warming is a shift in where species are found. Temperature is a fundamental force in the makeup of most ecosystems. As increases in global mean air temperatures of up to 3.5°C by 2100 are predicted by the IPCC (as well as continued increases beyond that), distributions of many species are expected to shift poleward, towards cooler climates (Breeman 1990; Frank et al. 1990, Lubchenco et al. 1993). Numerous studies of marine life have

²Scientific papers from this symposium were published in American Zoologist 39 (1) February 1999.

demonstrated that species respond to changes in temperature, either directly or indirectly, and some indicate that shifts due to global climate change may already have begun.

Some of the most compelling indications of possible shifts in the distribution of marine species due to global warming comes from surveys of rocky intertidal marine life at a location in Monterey Bay. Scientists at the Monterey Bay Aquarium Research Institute and the Hopkins Marine Station of Stanford University compared their 1993-95 survey of life at the site with one completed more than 60 years previously at the same site by an earlier scientist. The location of the original survey was known precisely by the brass bolts fixed to the bedrock in 1930 to position the surveyed transect. The comparison of 46 nonrare species revealed a striking pattern which suggests a northward shift of species ranges during the intervening 60 years: abundances of southern species increased while northern species decreased. Ten of eleven species in the southern geographic range (that is, those with a northern limit south of Cape Mendocino, CA) increased significantly in abundance. Five of seven northern species (those with a southern limit north of Point Conception, CA) decreased significantly. This 60-year period coincided with a period of warming along the coast in which annual mean shoreline temperature increased by 0.75°C, with mean summer temperatures 2.2°C higher. This shift appears to have occurred separately from any effects from El Niño: six of 10 years preceding the original 1930s survey were characterized by moderate to strong El Niño events, while 5 of 10 years preceding the 1993-94 survey were also affected by El Niño events. Southern species far north of their normal ranges were reported for the 1925-27 El Niño, just as in the 1982-83 El Niño that preceded the later survey (Barry et al. 1995; Sagarin et al. in press). Therefore, El Niño events were not the primary factors in the shifts towards southern species between 1931-33 and 1993-94.

Studies in the English Channel show a similar response of planktonic and intertidal organisms to changes in temperatures (Southward 1967; South-

ward et al. 1995). Warm-water species increased in abundance and extended their range, and coldwater species decreased in abundance and retreated during periods of ocean warming in 1920 to 1960, and 1981 to 1995. Species showed the opposite trend during a cooling period from 1961 to 1981. In some cases, these changes were dramatic: some species shifted their latitudinal distribution up to 120 miles, and there were increases or decreases of two to three orders of magnitude in abundance. Based on climate models predicting a mean temperature rise of 2°C over the next 5 decades, these scientists predict shifts of 200-400 miles for marine life in this area, with extensive changes in the structure of ecological communities (Southward et al. 1995).

While some may ask why they should care about the fate of intertidal invertebrates, such shifts indicate that global climate change can dramatically alter natural systems, potentially harming species many people care about for commercial, recreational, or other reasons – such as fish or shellfish. Numerous scientific studies have documented how many fish populations are affected by changes in physical factors like temperature (Francis 1990; Maccall 1996), including walleye pollock (Quinn & Niebauer 1995), capelin (Hamilton 1987), and bluefin tuna and Pacific herring (Mysak 1986). Large variations in sardine abundance off the coast of California appear to be tied to temperature (Lluch-Belda et al. 1992). An analysis of fish and squid species in the northwest Atlantic Ocean revealed that seasonal and annual variation in water temperature strongly affects the latitudinal distribution of many important fish species and their prey, including Atlantic mackerel, scup, Atlantic herring, fourspot flounder, black sea bass, shortfinned squid, and long-finned squid. This study concluded that because different species respond differently to temperature changes, relationships among predators and prey could be disrupted if their ranges no longer overlap as a result of climate change. This could be particularly important for species such as Atlantic cod, which feed on temperature-sensitive species such as mackerel and herring (Murawski 1993). In the northern hemisphere, scientists routinely have documented the

presence of southern species far north of their typical range during El Niño events and paleobiological studies reveal that distributions have shifted in the past as the Earth's climate has changed – moving north when temperatures grew warm and south as they cooled (Fields et al. 1993).

Some studies indicate that this is happening now in some fish populations: that shifts in species distributions and abundances have occurred in response to warmer sea temperatures this century. California researchers compared reef fishes at two different regions off the California coast: one site in the Northern portion of the California Bight, and two sites in the Southern portion. Temperature data for both portions during 1960 through 1995 reveal an abrupt temperature increase consistent with a well-recorded climate shift in the North Pacific in 1976-77. At the Southern sites, researchers found that the number of species present decreased by 15-25% between 1976 and 1977 after the sharp jump in seawater temperature, and remained at that lower level after that. Over the entire 20 year period they examined (1974 to 1993), the proportion of northern species present (those with an affinity for colder water) declined from 50% of all species to about a third of all species, yet the proportion of southern species rose from about a quarter to 35% of all species present (Holbrook et al. 1997) consistent with predictions for warming temperatures. Abundances also changed. By 1991-93, the numbers of individuals of all species in the Northern group, and more than 90% of the species in the Southern group had declined substantially. On average, numbers of fish declined 69%. But not only fish species declined in abundance. At the Northern site, scientists also documented decreases in species lower in the food web on which fish depend, including small crabs and algae. The reasons for this are not entirely clear, but scientists believe it is linked to dramatic declines in zooplankton and overall ocean productivity recorded in this region (Holbrook et al. 1997). Some scientists suggest that a declining nutrient supply to surface layers due to warming waters has caused an overall decline of California marine ecosystems. Nutrients that form the foundation on which the entire food web functions come from cold, deep

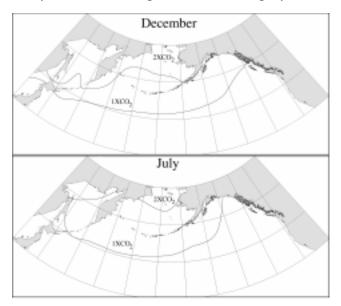
ocean waters that are brought to the surface by upwelling. Roemmich and McGowan (1995) propose that warming of surface layers increases their stratification by making mixing with cooler, deeper layers by wind more difficult. As upwelling comes from shallower, less nutrient-rich waters, smaller amounts of nutrients reach the surface and less is available to support plants and therefore the animals that eat them.

Studies examining Pacific salmon and their precipitous decline in recent years suggest that global climate change could devastate fish populations that millions of people rely upon for food, income, and cultural identity. Very low salmon runs in parts of western Alaska created an economic disaster in that state in 1997 and 1998. Few salmon returned from the ocean to their natal rivers to spawn, those that did return were smaller than usual and arrived later than usual. Water temperatures in 1997 and 1998 were dramatically higher than usual (Kruse 1998). Other unusual events occurred as well, such as a northward shift of the walleye pollock fishery and sightings of southern species such as tuna in Alaskan waters. Even more dramatically, a rare bloom of coccolithophores – a type of phytoplankton more typical of low nutrient waters at lower latitudes – appeared starting in July 1997. These conditions may have contributed to the massive die-offs of seabirds which appeared to have starved to death, either from difficulty in finding prey through the murky bloom, or because less prey was available because of lower nutrients (Kruse 1998). Some scientists are asking whether changes in the marine environment brought about by the warm water temperatures may also have led to the collapse of some Alaskan salmon populations. The unusually small returning salmon, combined with dramatically decreased numbers of those returning, suggests that ocean conditions were extremely poor for growth and survival. It is possible that some fish starved, and those that survived had limited food for growth (Kruse 1998). Similar effects were seen in Fraser River sockeye salmon in British Columbia, Canada (Pacific Salmon Commission 1999). Record coastal sea surface temperatures in 1997 brought subtropical fish species normally found farther south into Canadian waters. Migrating salmon that returned to the river to spawn were the smallest on record. In some runs, fish arrived later than usual, and therefore had already become sexually mature. Some of these fish then spawned in freshwater tributaries below their normal spawning grounds, possibly because they were unable to complete their migration and simply entered nearby streams. Heavy rain throughout the Fraser River watershed, possibly associated with El Niño, resulted in high velocities and extreme turbidity in the river. This, combined with the poor condition of fish, resulted in the largest en-route mortality of Fraser sockeye on record. The Pacific Salmon Commission reported that the 1997 season will rank as one of the most unusual in terms of fish behavior in more than 100 years of commercial fisheries on Fraser River sockeye (Pacific Salmon Commission 1999).

Canadian and Japanese researchers who have reviewed 40 years of data on sockeye salmon throughout the North Pacific suggest it is likely that salmon could be undernourished or starve with high water temperatures. These researchers found that the distribution of sockeye salmon is very strictly limited by water temperature. These limits vary depending on the time of the year, and are likely to be tied to food availability (Welch et al. 1998a). While salmon can withstand higher temperatures in summer when food is abundant – up to 15°C – in the winter their tolerance drops considerably, to no more than 7°C. As cold-blooded creatures, their metabolism increases rapidly in warmer water. Keeping up with this high metabolism requires large amounts of food, and if sufficient food is not available, salmon starve. Researchers predict that anticipated increases in water temperature caused by a doubling of CO₂ could eliminate most, if not all, suitable habitat for Pacific sockeye salmon (Welch et al. 1998a). The other species of Pacific salmon are also known to have equally sharp thermal limits, and their habitat may be significantly reduced by global climate change as well (Welch et al. 1998b; Welch et al. 1995). To stay within these temperature tolerances and avoid incurring large energy losses, salmon will either have to move down into the deep ocean where temperatures are lower, briefly reentering

surface waters to feed, or migrate farther north into the Bering Sea, a greater distance from the freshwater rivers where they spawn. It is unclear whether they could make either of these adaptations. Currently, sockeye spend 70% of their time within the top 10 meters of the ocean's surface (Ogura & Ishida 1995). The evolutionary reason for this behavior may prevent them from successfully moving farther down in the water column without a significant reduction in survival or growth. Increasing migration distances from feeding grounds to native spawning grounds will, at best, result in smaller, more emaciated salmon with lower body fat and fewer eggs. Rivers will also be warmer, increasing the stress on salmon and greater numbers would not survive the long trek. At worst, salmon will not develop the ability to migrate into the Bering Sea at all (Welch et al. 1998a).

Salmon constitute a remarkably large portion of marine life in those surface waters where they are found. Once gone, the ripple effects throughout the ecosystem – both for predators and for prey – will



likely be large. The temperature sensitivity of many other marine species also suggests that few ecological communities will escape disruption from warming sea temperatures.

Seabirds and Marine Mammals

Seabirds and marine mammals are some of the most visible members of marine communities, and some of the most loved. Because they are high in their food webs, however, their populations are likely to be some of the most sensitive to human-induced climate change (Springer, in press). Reductions in phytoplankton associated with climate change can be expected to cascade up the ecosystem, affecting populations of zooplankton, which in turn will affect small fishes, and then larger fishes. Many seabirds and marine mammals which prey on fish are likely to be strongly affected by these changes (Bolin et al. 1986). Evidence from El Niño and from longer term rising sea temperatures indicate this is likely.

Much of the information regarding climate effects on seabird populations comes from the Pacific, where El Niño plays a significant role. Poor reproductive success has been repeatedly documented in warmer years, including El Niño years (Ainley et al. 1995). The frequency of warm sea surface temperatures off California has increased since 1977 (McGowan et al. 1998), and many seabird species in this region have experienced population changes. Seabirds in the Farallon Islands off California laid fewer eggs, and fewer chicks hatched during warmer years (Ainley et al. 1994, 1996b). Many sites and species in the Gulf of California experienced near-zero reproduction during the warm 1997-98 El Niño period. Brown pelicans and Brandt's cormorants in southern California had less than half of their normal numbers of breeding pairs, and consequently, less than half of the expected new chicks (W. Sydeman, symposium presentation at Pacific Seabird Group conference). Brown pelicans and other seabirds in the Gulf of California and off the west coast of Baja California produced almost no offspring during this season (1997-98), and adult mortality was high as well in one area (D. Anderson, symposium presentation Pacific Seabird Group conference). At monitored sites at Point Reyes in north-central California, common murres had total breeding failure in 1998 (J. Boyce, symposium presentation at Pacific Seabird Group conference). Overall, seabird abundance in the California Current declined by 40% from 1987-94, with much of this decline attributable to a 90% reduction in sooty shearwaters, which were previously the most abundant species. Cassin's auklets in the Farallon Islands normally eat zooplankton, but with the decrease in zooplankton, their numbers decreased by 50% as well (Ainley et al. 1996a). However, it appears many of these effects are very localized, with individual populations affected strongly: some species showed none of these extensive losses, and particular sites of some species affected elsewhere sometimes remained unaffected. And some species appeared to do better: offshore species including Leach's storm petrels and Xantus' murrelets in the California Current increased their populations when the temperatures were warmer (Veit et al. 1996). Specific causes of population increases or decreases are not entirely known, but such large-scale population changes most likely have dramatic effects on their respective ecosystems.

Shifts in food supplies associated with El Niño are blamed for reproductive failure in some seabirds, and heavy adult mortality in others. While the massive decline in shearwaters in the California current may have been from altered migration patterns, it is clear their disappearance off Alaska was from starvation. In the fall of 1997, over 10% of the local shearwater population died – approximately 191,000 birds – all showing unmistakable signs of starvation. Shearwaters primarily eat euphausiid crustaceans, and the euphausiid populations declined significantly during this time (C. Baduini, symposium presentation at Pacific Seabird Group conference; Napp et al. 1999). Common murres in Alaska also perished in the spring of 1998, in the tens of thousands, and breeding success was reduced in many locations. At Chisik Island, murres and black-legged kittiwakes arrived at their breeding grounds three weeks late and were stressed from the beginning of the breeding season. These factors combined to yield zero reproductive success at this location (Piatt et al. 1999). The direct effects of low food supplies on seabird populations are also being compounded by indirect ecological interactions: the food shortages affecting common murres off the coast of Washington state during the 1997-98 El Niño also affected the local bald eagle populations. The eagles responded by increasing predation on the murres, further depressing the population (W. Sydeman, symposium presentation at Pacific Seabird Group conference).

Similar effects have been documented in studies of pinnipeds – seals and sea lions – with increased mortality and decreased fertility in many species during the 1982-83 El Niño. Although increased storm frequency and intensity was responsible for the loss of elephant seal pups at some locations, scientists believe the primary cause of declines was a decrease in food availability. During El Niño, the warm water spreading east from the western Pacific affects marine mammal prey in at least two ways: first, reduced primary production of phytoplankton reduces prey availability. Second, some important prey species migrate to cooler waters, either latitudinally or by going into deeper water, making it more difficult for pinnipeds to find adequate prey. Female pinnipeds with young, and the young themselves, were the most greatly affected. Females with young can't travel far in search of food. They must routinely return to the coast to feed their offspring. Studies indicate that female pinnipeds spent more time away from their young, and dove deeper than normal, in their search for food during El Niño years. As a result of expending extra energy but obtaining less food, the physical condition of females declined, reducing milk production, pregnancy rates, and other indications of fertility. Young seals and sea lions suffered with higher than usual death rates and reduced growth rates as their mothers produced less milk and remained away from them for longer durations. In some cases, these impacts were still felt for several years afterwards as weakened and diminished fish populations took time to recover. Thus, prey were still less available than usual (Trillmich et al. 1991).

Some species have shown an ability to shift their food sources when their preferred prey are unavailable, but not all potential food sources are of equal nutritional value to these birds. When the populations of shrimp, capelin and sandfish were largely replaced by pollock, cod and flatfishes in the Gulf of Alaska in the 1980s, fish-eating seabird populations declined and became less productive (Kuletz et al. 1997). Macaroni penguins in the Southern Ocean were able to switch from eating krill to amphipods when the krill populations declined drastically in 1994, but they also experienced

a decrease in breeding success (Croxall et al. 1999). The same effect was seen in marine mammals in the Gulf of Alaska too, with harbor seals, Steller sea lions and Dall's porpoise populations decreasing up to 70% in some cases (Kuletz et al. 1997).

The abundance of prey is only one problem facing marine species as the climate changes – both the timing of peak prey abundances as well as the visibility of prey (due to ocean conditions) are also becoming issues for several seabirds in the northeastern Pacific and the eastern Atlantic. As regional sea surface temperatures increase off the Queen Charlotte Islands in British Columbia, Canada, populations of common murres, tufted puffins, rhinoceros auklets, and Cassin's auklets have all begun breeding earlier. This past season, puffins and auklets started their breeding season two weeks earlier than normal, but the common murres started breeding a full month earlier than the same populations in the 1970s. The earlier breeding season is not a problem in and of itself, however, it means that these birds may be out of synch with their primary prey. Cassin's auklets eat zooplankton, and normally time their breeding cycle so their chicks hatch right after the zooplankton bloom. The zooplankton also respond to higher sea surface temperatures by blooming earlier than normal, but the zooplankton are blooming even earlier than the auklets are hatching, and the birds are unable to catch up. By 1996 the zooplankton bloom was over before the chicks were hatched, translating into reduced survival for both adults and chicks (D. Bertram, symposium presentation at Pacific Seabird Group conference).

Antarctic populations of both birds and mammals are already showing impacts of climate change. Mean annual air temperatures in the Antarctic, and especially winter temperatures in the western Antarctic Peninsula, have been increasing since the 1950s. As a result, during the past five decades, the frequency of cold years has decreased from an average of 4 out of every 5 years, to 1 or 2 out of 5 at present. This in turn has produced a decrease in the availability of winter sea ice, with significant effects on species that rely on this ice, and those who do better without it. Two closely related spe-

cies of penguins demonstrate this effect: in the western Antarctic Peninsula, chinstrap penguin populations have increased over the last four decades, while Adélie penguins have declined. The reason cannot be solely attributed to food supply (they both eat the same prey) but rather, has to do with the fact that they overwinter in completely different habitats. Adélie penguins winter on the sea ice, while chinstraps prefer open water and little ice cover (Fraser et al. 1992). Given the changes in winter sea ice availability over the past several years, chinstrap penguin populations have had the opportunity to increase in numbers. Increased precipitation (snow pack) in some areas, consistent with global warming, also appears to have adversely impacted some Adélie populations as well (Fraser & Patterson 1997). Clearly, despite the close evolutionary relationship of these two penguin species, their different life histories result in different responses to climate change. Antarctic marine mammals have been experiencing similar effects: crabeater seals require pack ice as do Adélie penguins, and their populations have been declining as well (Erickson & Hanson, 1990). Conversely, Southern fur seals, Southern Elephant seals, South Polar skuas and blue-eyed shags, all of which prefer open water, have been increasing in numbers and extending their geographic ranges further south (Fraser et al. 1992).

Some Arctic species near the southern edge of their range may be affected by climate change, where ice floes are melting more quickly in the spring. Researchers from the Canadian Wildlife Service have documented long-term decline in the weight of adult male and female polar bears, and a decline in birthrates in western Hudson Bay since the early 1980s. They believe the earlier breakup of the sea ice in the spring as a result of long-term climate warming may be the cause (Stirling & Derocher 1993; Stirling et. al. 1999). Hudson Bay polar bears rely on the ice floes to provide a platform from which they catch their prey, seals. During the summer months after the sea ice melts, bears are shorebound with less access to seals, and rely heavily on fat reserves to survive. The entire population must fast for at least four months after the ice has broken up, and pregnant females in Hudson

Bay must fast for eight months (Stirling & Lunn 1997; Ramsey & Stirling 1998). When the ice breaks up earlier than usual, bears have less time to build up reserves, and must rely on these reduced reserves for a longer period of time before ice forms again in the fall. Calculations indicate that a mean air temperature increase of only 1°C could bring the ice breakup nearly a week earlier for the western Hudson Bay (Etkin 1991). Less food for the adult bears means females will be lighter and so, in turn, will their cubs. It has been shown that the survival of heavier cubs is greater than of lighter ones (I. Stirling, personal communication). While some believe that bears further north may do better with the breakup of permanent ice that exists in the Arctic, over the short term at least, those populations at their southern limit appear highly vulnerable to warming.

Climate change may have direct effects on seabird and mammal population as well. Sea level rise, increased precipitation, and increased storm activity can directly impact seabird populations by destroying nests, washing fledglings and nests away, or eliminating nesting habitat altogether (Finney et al. 1999). Different populations will be affected to different degrees by sea level rise, depending on their geographic ranges and their life histories. For example, species that rely on low elevation island atolls for reproduction have the least chance of accommodating sea level changes, while birds nesting on rocky cliffs will be the most protected. Those that migrate may find traditional feeding or nesting sites inadequate or entirely nonexistent (IPCC 1998). Studies have shown that storms can significantly impact some bird populations, suggesting that increased storm activity expected from global warming will harm some species (Dunn 1975; Odsjo & Sondell 1976; Blake 1984; Poole 1989). Studies on common guillemot populations in the north Atlantic show that storms appear to impede fishing activities, so chicks either are fed less often (Birkhead 1976) or were brought smaller fish by the adults (Finney et al. 1999). The foraging adults also had to work harder to find their prey, spending more time underwater, and were away from the nest for longer periods of time (Finney et al. 1999). If storms increase in either frequency or

severity as predicted, reproductive success of these birds could diminish.

Seabird populations and many marine mammals currently are threatened by a number of factors beyond climate change, including overfishing, pollution, and bycatch (being caught incidentally through fishing practices). These impacts may compound effects of climate change, reducing populations to the point that they may not recover. It is often difficult to tease apart the different factors involved. Seabirds tend to be relatively long-lived with low recruitment, so their populations remain fairly stable until a critical threshold is crossed. Reduced reproduction will occur before the adult population decreases very much. Usually, the populations that decline during El Niño recover after the event passes. Now, however, some populations are not recovering as expected. It may be that the recovery period between El Niño events is so short in the 1990s that populations don't have the chance to recover. Or more ominously, the ability of our oceans to support life as it does now may be in the process of being permanently altered. Either way, the long-term rapid warming predicted for global climate change may be disastrous for many species that are already stressed from a number of environmental factors, or otherwise unable to adapt quickly.

Disease and Harmful Algal Blooms

Human encroachment on natural systems has increased as the world's population has grown, to the point that very few ecosystems, if any, are "untouched." One result is a steady decline in the health of marine ecosystems due to increased pollution (especially in coastal regions), overfishing, habitat loss, and the introduction of alien species. The effects of climate change are therefore superimposed on ecosystems that are already stressed, and many species and important ecosystem functions may be incapable of adjusting to the additional changes. Moreover, when organisms are stressed their immune systems can become compromised, and this may increase susceptibility to and severity of disease. Some researchers are also examining whether global climate change is increasing the incidence of disease.

Human diseases such as malaria are on the rise with increasing atmospheric temperatures and the incidence of heavy rains and flooding (Morse 1995; McMichael et al. 1996; Epstein 1998); diseases in the marine environment seem to be on the rise as well, as evidenced by both increasing rates of disease in some marine species and the appearance of new diseases. In some cases, new diseases have resulted in near-extinction, such as the mass mortalities of Diadema urchins in the Caribbean in 1982-83. Populations were eliminated from some regions, and reduced to less than 1% of their previous numbers in other regions (Bak et al. 1984; Lessios et al. 1984a; Lessios et al. 1984b). A recent research project has started to track the incidence of marine diseases (the Health Ecological and Economic Dimensions Program (HEED), funded by the National Oceanic and Atmospheric Administration's Office of Global Programs and the National Aeronautics and Space Administration), and links are being drawn between changes in climate and the rate and severity of several types of disease.

Temperature increases can weaken organisms' immune system and stimulate growth of pathogens (Endean 1977; Glynn & D'Croz 1990; Glynn 1993; Kushmaro et al. 1996). A wide variety of chemical pollutants as well as ultraviolet radiation (UV-B) can weaken immune systems and interfere with normal reproduction (Fox 1995; Hanley 1998). Higher temperatures also stimulate blooms of toxic or otherwise noxious phytoplankton referred to as harmful algal blooms, which can have detrimental effects on organisms including shellfishes, fishes, birds, and mammals (Steidinger 1993; Burkholder & Glasgow 1997; Grattan et al. 1998). Extreme events such as rainstorms or flooding – as expected with climate change- wash sudden pulses of nutrients, chemicals and microorganisms into coastal waters, which may change species composition or further stimulate algal growth and harmful algal blooms (Ford & Colwell 1996; HEED 1998). A worldwide reduction of wetlands, which act to filter nutrients out of terrestrial runoff, has further exacerbated the nutrient pollution of coastal waters (Tiner 1984). On top of all of these effects, changes in water temperature and currents – both of which are predicted by current global climate models – will likely alter the incidence of disease by bringing pathogens into contact with species that had not previously been exposed to them.

Outbreaks of disease with increasing temperatures

Unusually high incidences of diseases attacking marine vertebrates occur during El Niño events or other periods experiencing higher-than-normal sea surface temperatures, although the exact link with temperature is not always clear (HEED 1998). Greater numbers of whales and dolphins strand themselves during periods of high temperatures, and they often show evidence of sickness. Seabird mortalities from avian botulism, Newcastle disease, duck plague, and various strains of influenza also cluster with El Niño events (HEED 1998). A major fish kill in the Caribbean in 1980 was coincident with large-scale coral bleaching and disease outbreaks in sea urchins in the same area (Williams & Bunkley-Williams 1990). Although the exact connections between these outbreaks and higher ocean temperatures are not always clear, the increasingly frequent correlation between the two suggest that perhaps there is an association that we have yet to find.

A number of invertebrate epidemics have also been correlated with major temperature shifts: 90% of the green sea urchins in Nova Scotia were believed to be killed in 1980-82 by an amoeba, during a period of record high temperatures (Li et al. 1982; Scheibling & Stephenson 1984). A sudden cold spell in Florida Bay was also associated with urchin deaths, and extreme weather patterns are often associated with invertebrate kills (HEED 1998). The northward expansion of several diseases are strongly correlated with El Niño events and temperatures increases, including MSX and Dermo, two diseases closely associated with aquaculture practices that attack shellfish on the east coast of the U.S. (Cook et al. 1998). A herpes-like virus that has plagued European and Pacific oysters has now spread to U.S. oyster stocks, and is also associated with warm water conditions (LeDeuff et al. 1996). Diseases that are found in aquaculture systems are potential threats to wild stocks that inhabit the same areas (Overstreet et al. 1997).

Perhaps of greatest concern are diseases that attack species that form habitat for many other species, including seagrasses and corals. Seagrasses have been systematically attacked by a number of diseases this century, many of which are correlated with temperature and precipitation extremes and changes in tidal range (Short & Wyllie-Echeverria 1996). In the 1930s, eelgrass beds were decimated by a "wasting disease" that nearly eliminated the species from the North Atlantic (HEED 1998) and caused the extinction of at least one invertebrate species, the eelgrass limpet, whose only habitat was eelgrass blades (Carlton et al. 1991). Recent outbreaks of disease caused by a marine slime mold have hit Florida turtlegrass, and were also associated with high sea surface temperatures and fluctuations in salinity (Durako 1994). Seagrass beds form shelter and feeding grounds for many species of migratory birds, fishes, shrimp, scallops, and other invertebrates, which are all disrupted when the seagrass beds disappear.

Coral reefs are increasingly plagued by a number of newly identified diseases with disturbing names including Black Band, White Band, White Pox, Dark Spot, Coral Plague, and Rapid Wasting Syndrome. A wide range of species are affected and the diseases seem to be spreading rapidly. In most cases the causative agents are unknown (Richardson 1998). Some coral bleaching has been associated with bacterial infections of Vibrio sp. (relatives of bacteria responsible for cholera), and these infections are exacerbated by high water temperatures (Kushmaro et al.1996). Sea fan disease has been linked to a terrestrial fungus (Smith et al. 1998), and increasing runoff from land could easily contribute to a higher incidence of the disease. Pollution and other human impacts may be contributing factors to coral diseases, in addition to high water temperatures. Bleaching caused by high temperatures would certainly weaken coral colonies, and may make them more susceptible to the increasing occurrence of disease (Fitt et al. 1993; ISRS in press). Bleaching was reported in at least 32 different countries during 1997-98, during one of the strongest El Niño events on record (ISRS 1998), and bleaching is predicted to increase as global temperatures rise (ITMEMS 1998; ISRS 1998). If this is the case, the already increasing rate of disease in corals may increase even further.

Harmful Algal Blooms (HABs)

Blooms of toxic phytoplankton commonly referred to as "red tides" or "brown tides" are not technically diseases, but they can have highly detrimental effects on marine ecosystems and human health. Algal toxins can cause a variety of conditions in humans exposed to them, ranging from rashes, to memory loss, to jaundice and death (Grattan et al. 1998). While some of these phytoplankton are toxic when ingested, others have spines or other physical attributes that can damage fish gills. They are often associated with heavy terrestrial runoff or coastal pollution, or sudden changes in water temperature or ocean currents (Franks & Anderson 1992; Hallegraeff 1993; Humborg et al. 1997). Toxic blooms can cause the closure of fishing beaches as well as swimming beaches and other recreational areas and have been implicated in mortalities of marine species, including green sea turtles (Landsberg 1998), several species of seabirds (HEED 1998), Mediterranean monk seals in 1997 (Hernandez et al. 1998), manatees in Florida in 1996 (HEED 1998), menhaden fish on the Carolina coast since the early 1980s (Burkholder & Glasgow 1997), sponges and spiny lobsters in Florida Bay (Butler et al.1995). In each of these cases, algal toxins were ingested by zooplankton, other invertebrates and fishes, which were then eaten by these other species. The toxins become concentrated as they are passed up the food web, so the amount of toxins ingested by birds and marine mammals could easily be sufficient to cause death.

Mortality can also occur following the crash of large algal blooms. Blooms occur when marine conditions allow one species of phytoplankton to dominate the water column. Often their numbers are so great that the water becomes colored (i.e. red tides or brown tides) and the phytoplankton can block much of the light. When the phytoplankton cells die, bacterial decomposition may remove much of the oxygen from the water column, harm-

ing marine life by depleting their oxygen supply (Graneli et al. 1989).

The occurrence of HABs has increased in the past several decades, both in frequency and extent and in the prevalence of toxicity (Smayda 1990; Anderson 1995). There are many possible reasons for this, but warming of sea surface temperatures and the increase in extreme weather events may be contributing factors. Novel phytoplankton species and local species that were not previously known to bloom are now causing toxic blooms, and are occurring in areas not previously experiencing HABs (Smayda 1990; Hallegraeff 1993). Temperature changes can affect phytoplankton distributions just as they affect distributions of other species. HABs are more frequent during El Niño years (Hallegraeff 1993), and outbreaks of Ciguatera fish poisoning from algal toxins in Pacific islands are correlated with El Niño and sea surface temperatures (Hales et al. 1999). This suggests that if global climate change is accompanied by more El Niño events as simulations suggest (Timmermann et al. 1999) or if El Niño events are an indication of what we can expect from global warming, climate change may help increase the frequency of toxic blooms in the future.

Warming of surface waters and decreased vertical mixing can encourage the growth of toxic phytoplankton, as do changes in nutrients in the water column (Valiela 1984; Smayda 1990; Humborg et al. 1997). Species not known to be toxic can also become toxic when nutrient levels are altered (Smayda 1990; Hallegraeff 1993). Such changes in nutrient regimes and ocean temperatures are predicted by current global change models, which suggests that the occurrences of HABs will become increasingly problematic as climate change progresses.

Many marine ecosystems are currently under siege from a number of agents, including pollution, overexploitation and damaging fishing practices, coastal development and increased runoff, and the introduction of alien species (Norse 1993). Plants and animals under stress are weakened, and thereby more susceptible to parasitism and disease. Populations reduced in number by overfishing are less

able to rebuild their numbers after an epidemic. Anthropogenic climate change will be acting on systems that are not as resilient as they have been in the past, and those systems may not be able to adjust accordingly. The increasing incidence of harmful algal blooms and disease we are seeing now will likely become worse through time, as a warming climate adds additional stresses on already overstressed marine coastal systems.

CONCLUSION

Increasingly, scientists are recognizing that in the 1990s we have already entered the period of global warming: despite recognition of the natural variability inherent in the world's climate system, climatologists believe that the recent global warming trend is at least partially caused by increased emissions of greenhouse gases to the atmosphere. The main source of these gases is from the burning of fossil fuels such as coal and oil for energy production and transportation. The expected rate of warming in coming decades will be even greater than we are now experiencing, and scientists fear that the rate of climate change will be too fast for some organisms to adapt. With such widespread changes already observed in marine life, the implications for even more dramatic changes in the near future are serious.

While scientists cannot say with certainty that the widespread and disturbing ecosystem changes observed in recent years are caused by global warming, and cannot precisely predict the wide range of biological changes possible, changes recently observed are consistent with what we expect to see with increasing global warming in coming decades. Increasingly, scientists are stating that current limitations in our understanding of all the connections in our remarkably complex natural world should not stop policymakers from taking action: in other words, our current levels of understanding are sufficient to warrant concern. Numerous biologists have publicly stated their concerns about the biological impacts of climate change on coral reefs, and some physical scientists are making similar statements about global changes. For example, in December 1998, the American Geophysical Union (AGU), an international scientific society of 35,000 geophysicists, geologists, and other earth scientists, issued a statement proclaiming that "[t]here is no known geologic precedent for the transfer of carbon from the Earth's crust to atmospheric carbon dioxide, in quantities comparable to the burning of fossil fuels, without simultaneous changes in other parts of the carbon cycle and climate system. This close coupling between atmospheric carbon dioxide and climate suggests that a change in one would in all likelihood be accompanied by a change in the other." They concluded by stating that "AGU believes that the present level of scientific uncertainty does not justify inaction in the mitigation of human-induced climate change and/or the adaptation to it" (American Geophysical Union 1998).

Perhaps most compelling of all are the conclusions of the Intergovernmental Panel on Climate Change (IPCC), an international group of scientists established by the World Meterological Organization and the United Nations Environment Programme to assess climate change. In their 1995 assessment they summarized several key points: (1) greenhouse gas concentrations have continued to increase, (2) climate has changed over the past century, (3) the balance of evidence suggests a discernible human influence on global climate, and (4) climate is expected to continue to change in the future.

Clearly, altering our Earth's atmosphere through excessive fossil fuel use is a massive experiment with uncertain outcomes. The risks associated with such systemic global change are high. Given the compelling evidence from multiple scientific corners, action should be taken now to reduce emissions of greenhouse gases and subsequent climate change. The longer we wait to act, the fewer our options will be.

LITERATURE CITED

- Ainley, D.G., L.B. Spear and S.G. Allen (1996a) Variation in the diet of Cassin's auklet reveals spatial, seasonal, and decadal occurrence patterns of euphausiids off California, USA. Marine Ecology Progress Series 137:1-10.
- Ainley, D.G., W.J. Sydeman, S.A. Hatch and U.W. Wilson (1994) Seabird population trends along the west coast of North America: causes and extent of regional concordance. Studies in Avian Biology 15:119-133.
- Ainley, D.G., W.J. Sydeman and J. Norton (1995) Upper trophic level predators indicate interannual negative and positive anomalies in the California Current and food web. Marine Ecology Progress Series 118:69-79.
- Ainley, D.G., W.J. Sydeman and J. Norton (1996b) Apex predators indicate interannual negative and positive anomalies in the California Current food web. Marine Ecology Progress Series 137:1-10.
- Alexander, V. (1992) Arctic marine ecosystems. *In* R.L. Peters and T.E. Lovejoy (Eds.), Global warming and biological diversity. Yale University Press, 386 pp.
- Alexander, V., S.M. Heinrichs and H.J. Niebauer (1996) Bering Sea Ice Dynamics and Primary Production. Proc. NIPR Symp. Polar Biol. 9:13-25,
- Alexander, V. and H.J. Niebauer (1981) Oceanography of the eastern Bering Sea ice-edge zone in spring. Limnol. Oceanogr. 26(6): 1111-1125.
- American Geophysical Union (1998) AGU Position Statement Climate Change and Greenhouse Gases. www.agu.org/sci_soc/policy/sci_pol.html.

- Anderson, D.M. (Ed) (1995) ECOHAB the ecology and oceanography of harmful algal blooms, a national research agenda. National Science Foundation and National Oceanographic and Atmospheric Administration, Washington DC.
- Anderson, D., J. Keith, E. Palacios, E. Velarde, F. Gress and K.A. King (1999) El Niño 1997-98: seabird responses from the southern California Current and Gulf of California. Pacific Seabird Group conference, Blaine, WA, February 24-28, 1999.
- Arrigo, K.R., D.H. Robinson, D.L. Worthen, R.B. Dunbar, G.R. DiTullio, M. VanWoert and M.P. Lizotte. (1999) Phytoplankton community structure and the drawdown of nutrients and CO₂ in the southern ocean. Science 283:365-367.
- Baduini, C.L., K.D. Hyrenback and G.L. Hunt, Jr. (1999) Anomalous weather events in the southeastern Bering Sea: the condition of short-tailed shearwaters in 1997 and 1998. Pacific Seabird Group conference, Blaine, WA, February 24-28, 1999.
- Bak, R.P.M., M.J.E. Carpay and E.D. de Ruyter van Steveninck (1984) Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. Marine Ecology Progress Series 17:105-108.
- Barber, R.T., M.P. Sanderson, S.T. Lindley, F. Chai, J.Newton, C. C. Trees, D.G. Foley and F.P. Chavez (1996) Primary productivity and its regulation in the equatorial Pacific during and following the 1991-1992 El Niño. Deep-Sea Research Part II 43(4-6):933-969.
- Barras, J.A., P.E. Bourgeois and L.R. Handley. (1994) Land loss in coastal Louisiana 1956-1990. National Biological Survey, Fish and Wildlife Service, U.S. Dept. of Interior, National Wetland Center Open File Report 94-01, 10 color plates, 4 pp.

- Barry, J.P; C.H. Baxter, R.D. Sagarin and S. E. Gilman (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. Science 267:672-675.
- Bering Sea Task Force (1999) Status of Alaska's Oceans and Marine Resources. Bering Sea Task Force Report to Governor Tony Knowles. March 1999.
- Bertram, D.F. (1999) Ocean climate changes mismatch prey and breeding seabird populations. Pacific Seabird Group conference, Blaine, WA, February 24-28, 1999.
- Birkhead, T.R. (1976) Effects of sea conditions on rates at which Guillemots feed chicks. British Birds 69:490-492.
- Blake, B.F. (1984) Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. Journal of Experimental Marine Biology and Ecology 76:89-103.
- Bolin, B, B.R. Doos, J. Jager and R.A. Warrick (Eds.) (1986) The greenhouse effect, climate change and ecosystems. Wiley, London, 541 pp.
- Boyce, Jennifer A., Michael W. Parker, Stephen W. Kress, Harry R. Carter and Richard T. Golightly (1999) The impacts of the 1998 El Niño-southern oscillation on nearshore common murre colonies in central California. Pacific Seabird Group conference, Blaine, WA, February 24-28, 1999.
- Breeman, A.M. (1990) Expected effects of changing seawater temperatures on the geographic distribution of seaweed species. *In* J.J. Beukema et al. (Eds.) Expected Effects of Climatic Change on Marine Coastal Ecosystems, pp. 69-76, Kluwer Academic Publishers, Netherlands.
- Brodeur, R.D., G.H. Kruse, P.A. Livingston, G. Walters, J. Ianelli, G.L. Swartzman, M. Stepanenko and T. Wyllie-Echeverria (1999) Living marine resources (groundfish, salmon, and

- crabs) *In* S.A. Macklin (Ed). Report of the FOCI International Workshop on Recent Conditions in the Bering Sea. Seattle, WA November 9-10, 1998. Contribution 2044 from NOAA/Pacific Marine Environmental Laboratory, Contribution B358 from Fisheries-Oceanography Coordinated Investigations.
- Brown, B.E. (1987) Worldwide death of Corals natural cyclical events or man-made pollution? Marine Pollution Bulletin 18(1): 9-13.
- Bruun, P. (1962) Sea level rise as a cause of shore erosion. Journal of Waterways and Harbors Division (ASCE) 88:116-130.
- Bryant, D., L. Burke, J. McManus and M. Spaulding (1998) Reefs at risk: a map-based indicator of threats to the world's coral reefs. World Resources Institute, Washington DC.
- Burkholder, J.M. and H.B. Glasgow, Jr. (1997) *Pfiesteria piscicida* and other *Pfiesteria*-like dinoflagellates: behavior, impacts and environmental controls. Limnology and Oceanography 42(5):1052-1075.
- Butler, M.J. IV, J.H. Hunt, W.F. Herrnkind, M.J. Childress, R. Bertelsen, W. Sharp, T. Matthews, J.M. Field and H.G. Marshall (1995) Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Marine Ecology Progress Series 129:119-125.
- Carlton, J.T., G.J. Vermeij, D.R. Lindberg, D.A. Carlton and E. Dudley (1991) The first historical extinction of a marine invertebrate in an ocean basin: the demise of the eelgrass limpet *Lottia alveus*. Biological Bulletin 180 (1):72-80.
- Castilla, Juan Carlos, Sergio A. Navarrete and Jane Lubchenco (1993) Southeastern Pacific coastal environments: main features, large-scale perturbations, and global climate change. *In* Earth systems responses to global change. Academic Press, Inc., San Diego, CA, p. 167.

- Cook, T., M. Folli, J. Klinck, S. Ford and J. Miller (1998) The relationship between increasing sea-surface temperature and the northward spread of *Perkinsus marinus* (Dermo) disease epizootics in oysters. Estuarine, Coastal, and Shelf Science. 46:587-597.
- Coral Reefs and Global Change: Adaptation, Acclimation or Extinction? Initial Report of a Symposium and Workshop. http://coral.aoml.noaa.gov/themes/coral_cg.html
- Croxall, J.P., K. Reid and P.A. Prince (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Marine Ecology Progress Series 177:115-131.
- Doake, C.S.M., H.F.J. Corr, H. Rott, P. Skvarca and N.W. Young (1998) Breakup and conditions for stability of the northern Larsen Ice Shelf, Antarctica. Nature 391:778-780.
- Done, T.J. (1999) Coral community adaptability to environmental change at the scales of regions, reefs, and reef zones. American Zoologist 39 (1): 66-79.
- Dunn, E.K. (1975) The role of environmental factors in the growth of tern chicks. Journal of Animal Ecology 44:743-754.
- Durako, M.J. (1994) Seagrass die-off in Florida Bay (USA): changes in shoot demographic characteristics and population dynamics in *Thalassia testudinum*. Marine Ecology Progress Series 110:59-66.
- Ellison, A.M. and E.J. Farnsworth (1997) Simulated sea level change alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). Oecologia 112:435-446.
- Endean, R. (1977) Destruction and recovery of coral reef communities. *In* O.A. Jones and R. Endean (Eds.), Biology and Geology of Coral Reefs. Academic Press, New York, NY, pp. 215-254.

- Epstein P.R. (Ed.) (1998) Extreme Weather Events: The Health and Economic Consequences of the 1997/98 El Niño and La Niña. Center for Health and the Global Environment. Harvard Medical School.
- Erickson, A.W. and M.B. Hanson (1990) Continental estimates and population trends in Antarctic ice seals. In Kerry K.R. and G. Hempel (Eds.) Ecological change and the conservation of Antarctic ecosystems. Proc. 5th SCAR Symp. Antarct. Biol. Hobart. August-September 1988. Springer Berlin Heidelberg New York.
- Etkin, D.A. (1991) Break-up in Hudson Bay: its sensitivity to air temperatures and implications for climate warming. Climatological Bulletin 25(1):21-34.
- Falkowski, Paul G., Richard T. Barber and Victor Smetacek. (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281:200-206.
- Fields, P.A., J.B. Graham, R.H. Rosenblatt and G.N. Somero (1993) Effects of expected global climate change on marine faunas. Trends in Ecology and Evolution 8(10): 361-367.
- Finney, S.K., S. Wanless and M.P. Harris (1999) The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. Journal of Avian Biology 30: (in press).
- Fitt, W.K., H.J. Spero, J. Halas, M.W. White and J.W. Porter (1993) Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 Caribbean "bleaching event." Coral Reefs 12:57-64.
- Ford, T.E. and R.R. Colwell (1996) A Global Decline in Microbial Safety of Water: A Call for Action. A report from the American Academy of Microbiology. Washington DC.
- Fox, G.A. (1995) Tinkering with the tinkerer: pollution versus evolution. Environmental Health Perspectives 103(Suppl. 4):93-100.

- Francis, R.C. (1990) Climate change and marine fisheries. Fisheries 15(6): 7-9.
- Frank, K.T., R.I. Perry and K.F. Drinkwater (1990)
 Predicted response of Northwest Atlantic invertebrate and fish stocks to CO₂-induced climate change. Transactions of the American Fisheries Society 119:353-365.
- Franks, P.J.S. and D.M. Anderson (1992) Alongshore transport of a toxic phytoplankton bloom in a buoyancy current: *Alexandrium tamarense* in the Gulf of Maine. Marine Biology 112:153-164.
- Fraser, W.R. and D.L. Patterson (1997) Human disturbance and long-term changes in Adélie Penguin Populations at Palmer Station, Antarctic Peninsula. *In* B.Battaglia, J. Valencia and D.W.H. Walton (Eds.) Antarctic Communities. Cambridge University Press. pp. 445-452.
- Fraser, W.R., W.Z. Trivelpiece, D.G. Ainley, S.G. Trivelpiece (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biology 11:525-531.
- Gattuso, J.P., D. Allemand and M. Frankignoulle (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review on interactions and control by carbonate chemistry. American Zoologist 39 (1): 160-183.
- Glynn, P.W. (1984) Widespread coral mortality and the 1982/83 El Niño warming event. Environmental Conservation 11:133-46.
- Glynn, P.W. (1988) El Niño-Southern Oscillation 1982-1983: nearshore population, community, and ecosystem responses. Annual Review of Ecology and Systematics 19:309-45.
- Glynn, P.W. (1991) Coral reef bleaching in the 1980s and possible connections with global warming. Trends in Ecology and Evolution 6: 175-179.

- Glynn, P. (1993) Coral reef bleaching in the 1980's and possible connections with global warming. Trends in Ecology and Evolution 6:175-179.
- Glynn, P.W. and L. D'Croz (1990) Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. Coral Reefs 12:1-7.
- Goreau, T.J., R. Hayes, A. Strong, E. Williams, G. Smith, J. Cervino and M. Goreau (1998) Coral reefs and global change: Impacts of temperature, bleaching, & emerging diseases. Sea Wind 12(3):2-6.
- Gornitz, V. (1994) Sea-level rise: a review of recent past and near-future trends. Earth Surface Processes and Trends 4: 316-318.
- Graneli, E., P. Carlsson, P. Olsson, B. Sundstrom, W. Graneli and O. Lindahl (1989) From anoxia to fish poisoning: the last ten years of phytoplankton blooms in Swedish marine waters. *In* E.M. Cosper, V.M. Bridelj and E.J. Carpenter (Eds.). Novel Phytoplankton Blooms. Springer-Verlag, New York, pp. 407-427.
- Grattan, L.M., D. Oldach, T.M. Perl, M.H. Lowitt, D.L. Matuszak, C. Dickson, C. Parrott, R.C. Shoemaker, C.L. Kaufman, M.P. Wasserman, J.R. Hebel, P. Charache and J.G. Morris, Jr. (1998) Learning and memory difficulties after environmental exposure to waterways containing toxin-producing *Pfiesteria* or *Pfiesteria*-like dinoflagellates. Lancet 352:532-539.
- Hadley Centre model report (1998). Climate change and its impacts. http://www.meto.gov.uk/sec5/CR_div/Brochure98/
- Hales, S., P. Weinstein and A. Woodward (1999) Ciguatera (fish poisoning), El Niño, and Pacific sea surface temperatures. Ecosystem Health 5:20-25.
- Hallegraeff, G.M. (1993) A review of harmful algal blooms and their apparent global increase. Phycologia 32(2):79-99.

- Hamilton, K. (1987) Interannual environmental variation and North American fisheries. Bulletin American Meteorological Society 68(12):1541-1548.
- Hanley, K.A. (1998) Polar exposure: environmental threats to arctic communities. Swiss Coalition for the Protection of Whales, Wadenswil, Switzerland; Global Survival Network, Washington, DC.
- Hayward, Thomas L. (1997) Pacific Ocean climate change: atmospheric forcing, ocean circulation and ecosystem response. Trends in Ecology and Evolutions 12(4):150-154.
- HEED (1998) Marine ecosystems: emerging diseases as indicators of change. Health Ecological and Economic Dimensions of Global Change Program (HEED), Paul R. Epstein principal investigator. Boston, Massachusetts, 85 pp.
- Hernandez, M., I. Robinson, A. Aguilar, L.M.Gonzalez, L.F. Lopez-Jurado, M.I. Reyero, E. Cacho and J. Franco (1998) Did algal toxins cause monk seal mortality? Nature 393:28-29.
- Holbrook, S.J., R.J. Schmitt and J.S. Stephens Jr. (1997) Changes in an assemblage of temperate reef fishes associated with a climate shift. Ecological Applications 7(4):1299-1310.
- Humborg, Christoph, Venugopalan Ittekkot, Adriana Cociasu and Bodo v. Bodungen (1997) Effect of Danube River dam on Black Sea biogeochemistry and ecosystem structure. Nature 386:385-388.
- IPCC (1990) Warrick, R.A. and H. Oerlemans. Sea Level Rise. *In* Houghton, J.T., G.J. Jenkins and J.J. Ephraums (Eds.). Climate Change: The IPCC Assessment, 1990, Cambridge University Press.
- IPCC (1995) Watson, Robert T., Marufu C. Zinyowera, Richard H. Moss (Eds.). Climate Change 1995. Impacts, adaptations and miti-

- gation of climate change: scientific-technical analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge. 879 p.
- IPCC (1996) Houghton, J.T., L.G. Meira Filho,B.A. Callendar, N. Harris, A. Kattenberg, K.Maskell (Eds.). Climate Change. 1995. TheScience of Climate Change. Cambridge University Press, Cambridge. 572 p.
- IPCC (1998) Watson, Robert T., Marufu C. Zinyowera, Richard H. Moss (Eds.). The regional impacts of climate change: an assessment of vulnerability. A Special Report of IPCC Working Group II.. Cambridge University Press, Cambridge. 518 pp.
- ISRS (1998) International Society of Reef Studies Statement on Coral Bleaching. Reef Encounter. Newsletter of the International Society for Reef Studies: 24:19-20.
- ISRS (In press) International Society of Reef Studies Statement on Diseases on Coral Reefs (in press). Reef Encounter. Newsletter of the International Society for Reef Studies 25.
- ITMEMS (1998) International Tropical Marine Ecosystems Management Symposium Statement on Coral Bleaching. Unpublished. November, 1998.
- Kearney, M. and J.C. Stevenson (1991) Island land loss and marsh vertical accretion in rate: Evidence for historical sea-level change in the Chesapeake Bay. Journal of Coastal Research 7:403-415.
- Kleypas, J.A., R.W. Buddemeier, D. Archer, J.P. Gattuso, C. Langdon and B.N. Opdyke (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284: 118-120.

- Krabill, W., E. Frederick, S. Manizade, C. Martin, J. Sonntag, R. Swift, R. Thomas, W. Wright, and J. Yungel (1999) Rapid thinning of parts of the Southern Greenland ice sheet. Science 283:1522-1524.
- Kruse, Gordon H. (1998) Salmon run failures in 1997-1998: A link to anomalous oceanic conditions? Alaska Fishery Research Bulletin 5(1):55-63.
- Kuletz, K.J., D.B. Irons, B.A. Agler and J.F. Piatt (1997) Long-term changes in diets and populations of piscivorous birds and mammals in Prince William Sound, Alaska. *In* Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems, November 13-16, 1996, Anchorage, AK, pp. 703-706. Alaska Sea Grant Program.
- Kushmaro, A., Y. Loya and M. Fine (1996) Bacterial infection and coral bleaching. Nature 380:396.
- Landsberg, J.H. (1998) The potential role of biotoxins in sea turtle fibropapillomas. Proceedings of the Second Sea Turtle Fibropapilloma Workshop, Hawaii, December 1997. NOAA Technical Memorandum.
- LeDeuff, R.M., T. Renault and A. Gerard (1996) Effects of temperature on herpes-like virus detection among hatchery-reared larval Pacific oyster *Crassostrea gigas*. Diseases of Aquatic Organisms 24:149-157.
- Lessios, H.A., J.D. Cubit, D.R. Robertson, M.J. Shulman, M.R. Parker, S.D. Garrity and S.C. Levings (1984a) Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. Coral Reefs 3:173-182.
- Lessios, H., D.R. Robertson and J.D. Cubit (1984b) Spread of *Diadema* mass mortality through the Caribbean. Science 226:335-337.
- Li, M.F., J.W. Cornick and R.J. Miller (1982) Studies of recent mortalities of the sea urchin (*Strongylocentrotus droebachiensis*) in Nova Scotia. Int. Council Explor. Mer CM 1982/L:46.

- Livezey, R.E. and T.M. Smith (1999) Covariability of aspects of North American climate with global sea surface temperatures on interannual to interdecadal timescales. Journal of Climate 12(1):289-302.
- Lluch-Belda, D., S. Hernandez-Vazquez, D.B. Lluch-Cota, C.A. Salinas-Zavala and R.A. Schwartzlose (1992) The recovery of the California sardine as related to global change. CalCOFI Rep. 33:50-59.
- Lubchenco, J., S.A. Navarrete, B.N. Tissot and J.C. Castilla (1993) Possible ecological responses to global climate change: Nearshore benthic biota of northeastern Pacific coastal ecosystems. *In* Harold A. Mooney, Eduardo R. Fuentes and Barbara I. Kronberg (Eds.), Earth system responses to global change. Academic Press, Inc., San Diego, CA, p. 147-166.
- Maccall, A.D. (1996) Patterns of low-frequency variability in fish populations of the California current. CalCOFI Rep. 37: 100-110.
- Manabe, S. and RJ. Stouffer (1993) Century-scale effects of increased atmospheric CO₂ on the ocean-atmosphere system. Nature 364: 215-218.
- Mann, M.E., R.S. Bradley and M.K. Hughes (1998) Global-scale temperature patters and climate forcing over the past six centuries. Nature 392:779-787.
- Mann, M.E., R.S. Bradley and M.K. Hughes (1999) Northern hemisphere temperatures during the past millenium: inferences, uncertainties, and limitations. Geophysical Research Letters 26(6):759-762.
- Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78(6):1069-1079.

- Maragos, J.E., M.P. Crosby and J.W. McManus (1996) Coral Reefs and Biodiversity: A Critical and Threatened Relationship. Oceanography. 9 (1): 83-99.
- Marotzke, J. and J. Willebrand (1991) Multiple equilibria of the global thermohaline circulation. Journal of Physical Oceanography 21(9):1372-1385.
- McGowan, J.A., D.R. Cayan, L.M. Dorman. (1998) Climate-ocean variability and ecosystem response in the northeast Pacific. Science 281:210-217
- McMichael, A.J., A. Haines and R. Sloof (Eds.) (1996) Climate Change and Human Health. World Health Organization, World Meteorological Organization, United Nations Environment Programme, Geneva, Switzeland.
- McPhaden, Michael J. (1999) Genesis and evolution of the 1997-98 El Niño. Science 283:950-954.
- McPhee, Miles G., Timothy P. Stanton, James H. Morison, Douglas G. Martinson (1998) Freshening of the upper ocean in the Arctic: Is perennial sea ice disappearing? Geophysical Research Letters 25(10):1729-1732.
- McRoy, C.P. and J.J. Goering (1976) Annual budget of primary production in the Bering Sea. Mar. Sci. Commun. 2:255-267.
- Mikolajewicz, U., B.D. Santer, E. Maier-Reimer (1990). Ocean response to greenhouse warming. Nature 345:589-593.
- Morison, J., M. Steele and R. Anderson (1998) Hydrography of the upper Arctic Ocean measured from the nuclear submarine U.S.S. *Pargo*. Deep-Sea Research I, 45: 15-38.
- Morse, S.S. (1995) Factors in the emergence of infection diseases. Emerging Infections Diseases 1:7-15.

- Murawski, S.A. (1993) Climate change and marine fish distributions: forecasting from historical analogy. Transactions of the American Fisheries Society 122(5): 647-658.
- Mysak, L.A. (1986) El Niño, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci. 43:464-497.
- Napp, J.M., K.O. Coyle, T.E. Whitledge, D.E. Varela, M.V. Flint, N. Shiga, D.M. Schell and S.M. Henrichs (1999) Nutrients and lower trophic level response. *In* S.A. Macklin (ed). Report of the FOCI International Workshop on Recent Conditions in the Bering Sea. Seattle, WA November 9-10, 1998. Contribution 2044 from NOAA/Pacific Marine Environmental Laboratory, Contribution B358 from Fisheries-Oceanography Coordinated Investigations.
- NOAA (1998a) 1998 Coral reef bleaching in Indian Ocean unprecedented, NOAA announces. News Release. National Oceanic and Atmospheric Administration. July 1, 1998.
- NOAA (1998b) Record-breaking coral bleaching occurred in tropics this year NOAA reports. News Release. National Oceanic and Atmospheric Administration. October 15, 1998.
- Niebauer, H.J., N. Bond and L.P. Yakunin (In press) On the climatology and ice of the Bering Sea *In* The Dynamics of the Bering Sea. University of Alaska Sea Grant, Fairbanks, AK.
- Norse, E.A. (1993) Global Marine Biological Diversity: A Strategy for Building Conservation into Decisionmaking. Island Press.
- Odsjo, T. and J. Sondell (1976) Reproductive success in ospreys *Pandion haliaetus* in southern and central Sweden, 1971-1973. Ornis Scandinavica 7:71-84.
- Ogura, M. and Y. Ishida (1995) Homing behaviour and vertical movements of four species of Pacific salmon (Oncorhynchus spp.) in the central Bering Sea. Canadian Journal of Fisheries and Aquatic Science 52:532-540.

- Office of Science and Technology Policy (1997). Climate Change: State of Knowledge. Executive Office of the President, Washington, DC. 18p.
- Overstreet, R.M., D.V. Lightner, K.W. Hasson, S. McIlwain and J. Lotz (1997) Susceptibility to Taura syndrome virus of some panaeid shrimps native to the Gulf of Mexico and the Southeastern United States. Journal of Invertebrate Pathology 69: 165-176.
- Pacific Salmon Commission (1999) Report of the Fraser River Panel to the Pacific Salmon Commission on the 1997 Fraser River sockeye and pink salmon fishing season. Prepared by the Pacific Salmon Commission, March 1999.
- Parrish, R.H., A. Bakun, D.M. Husby and C.S. Nelson (1983) Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. FAO Fisheries Report 291(v. 3):731-777.
- Peterson, C.H., R.T. Barber and G.A. Skilleter. (1993) Global warming and coastal ecosystem response: How northern and southern hemispheres may differ in the Eastern Pacific Ocean. *In* Harold A. Mooney, Eduardo R. Fuentes, and Barbara I. Kronberg (Eds.), Earth system responses to global change. Academic Press, Inc., San Diego, CA, 1993, pp. 17-34.
- Piatt, J.F., G. Drew, T. Van Pelt, A. Abookire, A. Nielsen, M. Shultz and A. Kitaysky (1999) Biological effects of the 1997/1998 ENSO event in lower Cook Inlet, Alaska. PICES Scientific Report No. 10:93-100.
- Pittock, A.B. (1999) Coral reefs and environmental change: adaptation to what? American Zoologist 39 (1): 10-11.
- Poole, A.F. (1989) Ospreys. A natural and unnatural history. Cambridge University Press, Cambridge. 246 pp.

- Quinn, T.J. and H.J. Niebauer (1995) Relation of eastern Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment to environmental and oceanographic variables. *In* Climate Change and Northern Fish Populations. R.J. Beamish (ed) Canadian Special Publication of Fisheries and Aquatic Sciences. pp. 497-507.
- Rahmstorf, S. (1997) Risk of sea-exchange in the Atlantic. Nature 388:825-826.
- Ramsey, M.A. and I. Stirling (1998) Reproductive biology and ecology of female polar bears (*Ursus maritimus*) J. Zool. Lond. 214:601-634.
- Ray, G.C., B.P. Hayden, A.J. Bulger, Jr., and M.G. McCormick-Ray (1992) Effects of global warming on the biodiversity of coastal-marine zones. *In* Peters and T.E. Lovejoy (Eds.), Global warming and biological diversity. Yale University Press, 386 pp.
- Reaka-Kudla, M.L. (1996) The global biodiversity of coral reefs: A comparison with rainforests. *In* Reaka-Kudla, M.L., D.E. Wilson, and E.O. Wilson (eds.) Biodiversity II: Understanding and Protecting our Natural Resources, pp. 83-108. Joseph Henry/National Academy Press, Washington DC.
- Richardson, L.L. (1998) Coral diseases: what is really known? Trends in Ecology and Evolution 13 (11): 438-443).
- Rodbell, D.T., G.O. Seltzer, D.M. Anderson, M.B. Abbott, D.B. Enfield, J.H. Newman. (1999) An ~15,000-year record of El Niño-driven alluviation in southwestern Ecuador. Science 283:516-520.
- Roemmich, D. and J. McGowan. (1995) Climatic warming and the decline of zooplankton in the California current. Science 267:1324-1326.
- Sagarin, R.D., J.P. Barry, S.E. Gilman and C.H. Baxter. (in press). Climate related changes in an intertidal community over short and long time scales. Ecological Monographs.

- Scheibling, R.E. and R.L. Stephenson (1984) Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. Marine Biology 78:153-164.
- Short, F.T. and S. Wyllie-Echeverria (1996) Natural and human-induced disturbance of seagrasses. Environmental Conservation 23(1):17-27.
- Smayda, T.J. (1990) Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. Pp. 29-40. In: Edna Graneli, Bo Sundstrom, Lars Edler, and Donald M. Anderson (Eds.). Toxin Marine Phytoplankton. Elsevier Science Publishing Co., Inc., New York.
- Smith, G.W., C.D. Harvel and K. Kim (1998) Response of sea fans to infection with *Aspergillus* sp. (Fungi). Rev. Biol. Trop. 46 Supl: 5: 205-208.
- Smith, R.C., E. Domack, S. Emslie, B. Fraser, D. Ainley, K. Baker, J. Kennett, A. Leventer, E. Mosley-Thompson, S. Stammerjohn and M. Vernet (in press). Marine ecosystem sensitivity to historical climate change: Antarctic Peninsula. BioScience.
- Smith S.V., and R.W. Buddemeier. (1992) Global Change and Coral Reef Ecosystems. Annu. Rev. Ecol. Syst. 23:89-118.
- Smith, W.O. and D.M. Nelson (1985) Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. Science 227: 163-166.
- Southward, A.J. (1967) Recent changes in abundance of intertidal barnacles in south-west England: a possible effect of climatic deterioration. Journal of the Marine Biological Association: U.K. 47: 81-95.
- Southward, A.J., S.J. Hawkins and M.T. Burrows (1995) Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. Journal of Thermal Biology 20: 127-155.

- Springer, A.M (in press) Is it all climate change? Why marine bird and mammal populations fluctuate in the North Pacific. In Biotic impacts of extra tropical climate change in the Pacific. Aha Huliko'a Proceedings, University of Hawaii.
- Steidinger, K.A. (1993) Some taxonomic and biological aspects of toxic dinoflagellates. Pp. 1-28. *In* Falconer, Ian R. (Ed.) Algal Toxins in Seafood and Drinking Water, Academic Press, London, UK.
- Stevenson, J.C., J.E. Rooth, M.S. Kearney and K. Sundberg. (In press) The health and long term stability of natural and restored marshes in Chesapeake Bay. 36 Pages in D. Krieger and M. Weinstein (editors): Concepts and Contoversies in Tidal Marsh Ecology. Klewer Press, The Netherlands.
- Stevenson, J.C., L.G. Ward and M.S. Kearney (1986) Vertical Accretion in marshes with varying rates of sea-level rise. Pages. 241-259 in D. Wolfe (editor): Estuarine Variability. Academic Press, New York
- Stirling, I., Lunn, N.J. and Iacozza, J. (in press) Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. Arctic 52.
- Stirling, I., and N.J. Lunn (1997) Environmental fluctuation in arctic marine ecosystems as reflected by variability in reproduction of polar bears and ringed seals. *In* Woodlin, S.J., and Marquiss, M. (eds) Ecology of Arctic Environments. Oxford: Blackwell Science Ltd. pp. 167-181.
- Stirling, I. (1997) The importance of polynyas, ice edges, and leads to marine mammals and birds. Journal of Marine Systems 10:9-21.
- Stirling, I. and A.E. Derocher (1993) Possible impacts of climate warming on polar bears. Arctic 46(3):240-245.

- Stocker, T.F. and A. Schmittner (1997) Influence of CO₂ emission rates on the stability of the thermohaline circulation. Nature 388:862-865.
- Sundquist, E.T. (1985) Geological perspectives on carbon dioxide and the carbon cycle. P. 5-59 in E. T.Sundquist and W. S. Broecker (Eds.) The carbon cycle and atmospheric CO₂: natural variations archean to present. American Geophysical Union Geophysical Monograph 32. Washington, DC. 627 pp.
- Sydeman, W.J., J.K. Parrish, P. Martin, F. Gress, M.M. Hester, K.K. Hastings, A.J. Hebshi, J.A. Thayer, J. Buffa and N. Nur (1999) Spatial and temporal trends in reproductive dynamics of seabirds in the California Current marine ecosystem: response to El Niño and lower frequency marine climate change. Pacific Seabird Group conference, Blaine, WA, February 24-28, 1999.
- Tegner, M.J. and P.K. Dayton (1987) El Niño effects on southern California kelp forest communities. Adv. Ecol. Res. 17:243-79.
- Tett, S.F.B., P.A. Stott, M.R. Allen, W.J. Ingram and J.F.B. Mitchell (in press) Causes of twentieth century temperature change. Nature.
- Timmermann, A., J.Oberhuber, A. Bacher, M. Esch, M. Latif and E. Roeckner (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398: 694-697.
- Tiner, R.W. Jr. (1984) Wetlands of the United States current status and recent trends. U.S. Dept. of Interior, Fish and Wildlife Service, Washington, DC.
- Titus, J.G. (1992) Greenhouse effect and coastal wetland policy. How Americans could abandon an area the size of Massachusetts at minimum cost. Environmental Management 15(1):39-58.
- Titus, J.G. and V. Narayanan (1995) The probability of sea level rise. U.S.. Environmental Protection Agency, EPA 230-R95-008, Washington, D.C., 186 pp.

- Trenberth, K.E. and T.J. Hoar (1996) The 1990-1995 El Niño-Southern Oscillation event: longest on record. Geophysical Research Letters 23(1):57-60.
- Trenberth, K.E. and J.W. Hurrell (1994) Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9(6):303-319.
- Trillmich, F., K.A. Ono, D.P. Costa, R.I. DeLong, S.D. Feldkamp, J.M. Francis, R.L. Gentry, C.B. Heath, B.J. LeBoeuf, P. Maljuf and A.E. York (1991) The effects of El Niño on pinniped populations in the eastern Pacific. *In* Pinnipeds and El Niño: Responses to Environmental Stress. Fritz Trillmich and Kathryn Ono (eds.) Pp. 247-270. Springer-Verlag,
- Tynan, C.T., G.L. Hunt, Jr., E.H. Sinclair and C. Pungowiyi (1999) Seabirds and marine mammals. *In* S.A. Macklin (ed). Report of the FOCI International Workshop on Recent Conditions in the Bering Sea. Seattle, WA November 9-10, 1998. Contribution 2044 from NOAA/Pacific Marine Environmental Laboratory, Contribution B358 from Fisheries-Oceanography Coordinated Investigations.
- Tynan, C.T. and D.P. DeMaster (1997) Observations and predictions of Arctic climatic change: potential effects on marine mammals. Arctic 50(4): 308-322.
- U.S. Department of State (1999) Coral bleaching, coral mortality, and global climate change. Report presented by Rafe Pomerance, Deputy Assistant Secretary of State for the Environment and Development to the U.S. Coral Reef Task Force. Released by the Bureau of Oceans and International Environmental and Scientific Affairs, U.S. Department of State, March 5, 1999.
- Valiela, I. (1984) Marine Ecological Processes. Springer-Verlag. New York, NY

- Vance, T.C., J.D. Schumacher, P.J. Stabeno, C.T.
 Baier, T. Wyllie-Echeverria, C.T. Tynan, R.D.
 Brodeur, J.M. Napp, K.O. Coyle, M.B. Decker,
 G.L. Hunt, Jr., D. Stockwell, T.E. Whitledge,
 M. Jump and S. Zeeman (1998) Aquamarine
 waters recorded for first time in eastern Bering
 Sea. EOS 79(10):121, 126.
- Veit, R.R., P. Pyle, J.A. McGowan (1996) Ocean warming and long-term change in pelagic bird abundance within the California Current system. Marine Ecology Progress Series 139:11-18.
- Watling, L. and E.A. Norse (1998) Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. Conservation Biology 12(6): 1180-1197.
- Weaver, A.J. (1993) The oceans and global warming. Nature 364:192-193
- Weaver, A.J. (1995) Driving the ocean conveyor. Nature 378:135-136.
- Welch, D.W., A.I. Chigirinsky and Y. Ishida (1995) Upper thermal limits on the oceanic distribution of pacific salmon (Onchorhynchus sp.) in the spring. Can. J. Fish. Aquat. Sci. 52:489-503.
- Welch, D.W, Y. Ishida and K. Nagasawa (1998a) Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. Can. J. Fish. Aquat. Sci. 55:937-948.
- Welch, D.W., Y. Ishida, K. Nagasawa and J.P. Eveson (1998b) Thermal limits on the ocean distribution of steelhead trout (*Oncorhynchus mykiss*). N. Pac. Anadr. Fish Comm. Bull. No. 1: 396-404.
- Wilkinson, C., O. Linden, H. Cesar, G. Hodgson, J. Rubens and A.E. Strong (1999) Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: An ENSO impact and a warning of future change? Ambio: 28: 188-196.

- Williams, E.H. Jr. and L. Bunkley-Williams (1990) Recurring mass mortalities of Caribbean herrings: implications for the study of major marine ecological disturbances. Journal of Aquatic Animal Health 2:230-236.
- WMO (1998) World Meteorological Organization Annual Statement on the Global Climate. http://www.wmo.ch/index.html.
- Wyllie-Echeverria, T., E.D. Cokelet and S.A. Macklin (1999) Conclusions of working groups. *In* S.A. Macklin (Ed.). Report of the FOCI International Workshop on Recent Conditions in the Bering Sea. Seattle, WA November 9-10, 1998. Contribution 2044 from NOAA/Pacific Marine Environmental Laboratory, Contribution B358 from Fisheries-Oceanography Coordinated Investigations.

APPENDIX

List of Workshop Participants:

Vera Alexander School of Fisheries and Ocean Sciences University of Alaska-Fairbanks

James P. Barry Monterey Bay Aquarium Research Institute

Terence J. Done
Australian Institute of Marine Science

Paul R. Epstein Center for Health and the Global Environment Harvard Medical School

Raphael D. Sagarin Department EEMB University of California, Hopkins Marine Station

Vassili Spiridonov WWF Russia Program Office

J. Court Stevenson Horn Point Laboratory University of Maryland Center for Environmental Sciences

Elizabeth Venrick Scripps Institute of Oceanography UC San Diego

Sarah Wanless ITE Banchory Research Station

David W. Welch Dept. of Fisheries and Oceans Pacific Biological Station Facilitators:

Elliott A. Norse Ewann A. Berntson Amy Mathews-Amos Marine Conservation Biology Institute

Adam Markham World Wildlife Fund