# **Species Extinction**

#### 8. Species Extinction

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### Introduction

The Intergovernmental Panel on Climate Change (IPCC) claims "new evidence suggests that climatedriven extinctions and range retractions are already widespread" and the "projected impacts on biodiversity are significant and of key relevance, since global losses in biodiversity are irreversible (very high confidence)" (IPCC-II, 2007, p. 213). The IPCC even claims to know that "globally about 20% to 30% of species (global uncertainty range from 10% to 40%, but varying among regional biota from as low as 1% to as high as 80%) will be at increasingly high risk of extinction, possibly by 2100, as global mean temperatures exceed 2 to 3°C above pre-industrial levels" (Ibid.).

These claims and predictions are not based on what is known about the phenomenon of extinction or on real-world data about how species have endured the warming of the twentieth century, which the IPCC claims was unprecedented in the past two millennia. Because we addressed the impact of rising  $CO_2$ concentrations and rising temperatures on plants in detail in the previous chapter, we only briefly recap the evidence concerning terrestrial plants here, finding no evidence of a wave of temperature-driven extinctions, and in fact evidence of just the opposite. We then devote the largest part of the chapter to the effects of global warming on two species to which the IPCC devotes special attention, coral reefs and polar bears.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/e/extinction.php</u>.

#### References

IPCC. 2007-II. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.D. Hanson. (Eds.) Cambridge University Press, Cambridge, UK.

### 8.1. Explaining Extinction

There is a large gap between what scientists understand about the definition and causes of extinctions and what is reported in the popular press and even in some headline-seeking scientific journals. We start our analysis by asking what we know about the causes of past extinctions, the shortcomings of popular predictions of pending extinctions due to climate change, and the phenomenon of rapid evolutionary change.

### 8.1.1. Defining Extinction

Looking at the research papers selected to support the theory of massive warming extinctions, we are struck by many biologists' apparent misunderstanding of extinction. Some biologists seem to believe that effective conservation means every local population of butterflies and mountain flowers must be preserved. This is obviously impossible on a planet with continual, massive climate changes and human impacts. Some biologists try to define more and more local populations as separate species—a subterfuge.

A recent article in *Science* amply illustrates the conflicted feelings and biologists' frantic desire to protect everything. In an article titled "All Downhill from Here," Krajick (2004) laments the supposed danger to pikas (rodents, cousins to rabbits) that live on treeless mountaintops:

As global temperatures rise, the pika's numbers are nose-diving in far-flung mountain ranges ... researchers fear that if the heat keeps rising, many alpine plants and animals will face quick declines or extinctions ... creatures everywhere are responding to warming, but mountain biota, like cold-loving polar species, have fewer options for coping. ... Comprising just 3% of the vegetated terrestrial surface, these islands of tundra are Noah's ark refuges where whole ecosystems, often left over from glacial times, are now stranded amid un-crossable seas of warm lowlands.

Krajick himself seems to forget the words in his own opening paragraph: pikas "are also some of the world's toughest mammals." As for his "un-crossable seas of warm lowlands," pikas may not be able to thrive in the lowlands competition, but it does seem likely they could find enough vegetation there during their travels to tide them over until they find other, cooler mountaintops.

Parmesan and Yohe (2003) also present a distorted version of the term "extinction." They counted Edith's checkerspot butterflies at 115 North American sites with historical records of harboring the species and then classified the sites as "extinct or intact." They found local checkerspot populations in much-warmer Mexico were four times more likely to be "locally extinct" than those in much-cooler Canada. Similarly, Ian Stirling, an expert on polar bears who is widely quoted in the debate over whether global warming may reduce polar bear populations, was quoted by the World Wide Fund for Nature in 2002 as saying "polar bear numbers will be reduced in the southern portions of their range [and] may even become locally extinct" (WWF, 2002). However, "locally extinct" is not a scientific term. Extinct means "no longer in existence; died out." Gone forever. Parmesan and Yohe are using it in reference to butterfly populations that have simply moved-and even left forwarding addresses farther north. Polar bears, too, are known to migrate to different areas in response to changes in climate and

competition for food. This is not extinction, but extirpation—the loss of a population in a given location. The butterflies are responding effectively to climate change—which is certainly what we would hope a butterfly species would do on a planet with a climate history as variable as Earth's. Parmesan and Yohe found populations of Edith's checkerspot butterflies thriving over most of western North America, but fewer of them at the southernmost extremity of their range—in Baja California and near San Diego—than in the past. However, parts of Canada have been warming into their preferred climate range.

Species resist extinction strongly and they often persist even when humans think they've been wiped out. The supposedly extinct ivory-billed woodpecker was recently found in two forests in eastern Arkansas (Arkansas Game and Fish Commission, 2005). The Nature Conservancy recently found three "extinct" snails in Alabama and California. Botanists have found the Mount Diablo buckwheat plant for the first time since 1936. At least 24 other "extinct" species have been found during natural heritage surveys in North America since 1974 (Holloway, 2005).

### References

Arkansas Game and Fish Commission. 2005. Ivory-billed woodpecker found in Arkansas. News release. 5 August.

Holloway, M. 2005. When extinct isn't. Scientific American, 9 August.

Krajick, K. 2004. All downhill from here. *Science* **303**: 1600–1602.

Parmesan, C. and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

World Wide Fund for Nature, 2002. *Vanishing Kingdom— The Melting Realm of the Polar Bear*. World Wide Fund for Nature. Gland, Switzerland.

### 8.1.2. Past Extinctions

Most of the world's major species "body types" were laid down during the Cambrian period 600 million years ago (Levinton, 1992), so we know the major species have dealt successfully through the ages with new pest enemies, new diseases, ice ages, and global warmings greater than today's. Most wild species are at least one million years old, which means they have all been through at least six hundred 1,500-year climate cycles. Not the least of the warmings was the Holocene Climate Optimum, which was warmer than even the predictions of the IPCC for 2100 (IPCC, 2007). That very warm period ended less than 5,000 years ago.

Environmentalists argue that the speed of today's climate change is greater than previous warmings and will overwhelm the adaptive capacities of plants and animals. Yet history and paleontology agree that many of the past global temperature changes arrived very quickly, sometimes in a few decades. For example, 12,000 years ago, the Younger Dryas event suddenly and violently swung from warm temperatures back to Ice Age levels by the shutdown of the Gulf Stream as melting water from the extra trillion tons of ice built up in the glaciers and ice sheets over the previous 90,000 years of frigid climate was released into the oceans. The shutdown of the oceans' Atlantic Conveyor quickly triggered another thousand years of Ice Age. How did wild species deal with Mother Nature's sudden, sharp reversals then? In another example, starting about 1840 a Wyoming glacier went from Little Ice Age cold to near presentday warmth in about a decade (Schuster et al., 2000). There's no evidence of any local species being destroyed by that rapid temperature change.

In contrast to the missing evidence of past climate changes having caused extinctions, we already know how most of the world's extinct species were lost, and in what order of magnitude (Singer and Avery, 2007). The first cause is huge asteroids striking the planet. The web sites of such universities as the University of California-Berkeley, Smith, and North Carolina State are replete with evidence of these "big bangs." Earth's collisions with massive missiles from outer space explode billions of tons of ash and debris into the planet's atmosphere, darken the skies, and virtually eradicate growing seasons for years at a time. There apparently have been more than a dozen such collisions in the Earth's past and they have destroyed millions of species, most of which we know about only through the fossil record.

In 2004, researchers announced that geological evidence suggests an object crashed at the shoreline of what is now Australia's northwestern coast 251 million years ago, creating climate changes and other natural catastrophes. Gugliotta (2004) filed the following report on the discovery for the *Washington Post*:

Scientists said yesterday they have found evidence that a huge meteorite or comet plunged into the coastal waters of the Southern Hemisphere 251 million years ago, possibly triggering the most catastrophic mass extinction in Earth's history. The researchers said that geological evidence suggests that an object about six miles in diameter crashed at the shoreline of what is now Australia's northwestern coast, creating climate changes and other natural catastrophes that wiped out 90 percent of marine species and 70 percent of land species.

The second known cause of extinctions is hunting. For a million years or so, humans along with Homo erectus in Southeast Asia and Neanderthals in Europe have hunted whatever they could kill. If it went extinct, we hunted something else. In this sense, the last Ice Age did cause some indirect species extinctions. During that extremely cold period, so much of the world's water was trapped in ice caps and glaciers that sea levels dropped as much as 400 feet below today's levels. Stone Age hunters walked across the Bering Strait from Asia and found hordes of wild birds and mammals that did not fear man. More than 40 edible species were wiped out in a historical eye-blink, including North America's mammoths, mastodons, horses, camels, and ground sloths (Diamond, 1997).

A similar spate of human-hunter extinctions recently has been confirmed in Australia by the discovery of a cave full of fossils beneath the Nullabor Plain. The new fossils disarm the claim that a huge number of Australian species-including its marsupial lion, claw-footed kangaroo, giant wombat, and the Genvornis, the heaviest bird ever knownwent extinct 46,400 years ago because of climate change. The discovery team said the species found in the cave died during a dry climate similar to today's, which hadn't changed in 400,000 years. However, the fire-sensitive woodlands, to which the species were adapted, disappeared suddenly about 46,000 years ago-apparently because the newly arrived aboriginal people burned the woods to drive game into the arms of club-wielding hunters. The landscape was reshaped by fire from woods to shrubbery (Western Australian Museum, 2007).

Third: Man learned to farm. Farming for food made us less likely to hunt wild animals and birds to extinction, but eventually we claimed one-third of all the Earth's land area for agriculture. The saving grace was that the best land for farming tended to have few species; instead it had large numbers of a few species, such as bison on the American Great Plains and kangaroo in the Australian grasslands. In contrast, researchers have found as many species in five square miles of the Amazon as in the whole of North America. Fortunately, man tended to farm the best land for the highest sustainable food yields, leaving much of the poorer land (with its diversity) for nature (Avery, 2000).

Fourth: Alien species. Mankind's ships, cars, and planes transport species across natural barriers, enabling them to reproduce and compete with native species. This has made the survival competition among species much more global. Island species, in particular, have found themselves in more intense competition and many have gone extinct.

These four explanations for the major extinctions of the past are each now well documented and understood. The claim that changes in temperature during the twentieth century—which the IPCC calls unprecedented in the past two millennium—are causing extinctions is much more dubious, as we see in the next section.

### References

Avery, D.T. 2000. Saving the Planet With Pesticides and Plastics: The Environmental Triumph of High-Yield Farming. Hudson Institute, Indianapolis, IN. 36–37.

Diamond, J. 1997. Guns, Germs and Steel. W. W. Norton & Company, New York. 46–47.

Gugliotta, G. 2004. Impact crater labeled clue to mass extinction. *Washington Post*, 14 May.

IPCC. 2007-II. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. and Hanson, C.E. (Eds.) Cambridge University Press, Cambridge, UK.

Levinton, J. 1992. The big bang of animal evolution. *Scientific American* **267**: 84–91.

Schuster, P.F., *et al.* 2000. Chronological refinement of an ice core record at Upper Fremont Glacier in South Central North America. *Journal of Geophysical Research* **105**: 4657–666.

Singer, S.F. and Avery, D. Unstoppable Global Warming Every 1,500 Years. Rowman & Littlefield Publishers, Inc.

Western Australian Museum. 2007. Ancient Nullabor megafauna thrived in dry climate. Media Alert, 25 January.

### 8.1.3. Theories of Contemporary Extinctions

In striking contrast to the four known causes of past extinctions, which are backed by extensive fossil and archeological evidence, Thomas et al. (2004) simply asserted the *theory* that raising or lowering the Earth's temperature would cause major wildlife extinctions on a linear model. Accordingly, small temperature changes lead to relatively small reductions in species numbers while larger temperature increases drive more species to extinction. The team first defined "survival envelopes" for more than 1,100 wildlife species-in Europe, the Brazilian Amazon, the wet tropics of northeastern Australia, the Mexican desert, and the southern tip of South Africa. Then they used a "power equation" to link loss of habitat area with extinction rates. If the equation showed that a species' potential habitat was projected to decline, it was regarded as threatened; the greater the expected habitat loss, the greater the threat. There was no provision for species adaptation or migration.

One of the Thomas team's "moderate" scenarios was an increase in Earth's temperature of 0.8° C in the next 50 years. The researchers said this would cause the extinction of roughly 20 percent of the world's wild species, perhaps one million of them. Fortunately, this prediction can easily be checked. The Earth's temperature has already increased 0.8° C over the past 150 years. How many species died out because of that temperature increase? None that we are aware of.

The Thomas paper tells us in its opening sentence: "Climate change over the past 30 years has produced numerous shifts in the distributions and abundances of species, and has been implicated in one species-level extinction." The scientists who are predicting that 0.8° C of warming would cause hundreds of thousands of wildlife species extinctions over the next 50 years concede that this level of temperature increase over the past 150 years has resulted in the extinction of *one* species.

Reality takes away even that one extinction claim. Thomas *et al.'s* single cited example of a species driven extinct by the recent warming is the Golden Toad of Costa Rica. That was based on a 1999 paper in *Nature* by J. Alan Pounds and coauthors (Pounds *et al.*, 1999) describing research conducted at the Monteverde Cloud Forest Preserve in Puntarenas, Costa Rica. Pounds *et al.* claimed that, due to rising sea surface temperatures in the equatorial Pacific, 20 of the 50 species of frogs and toads (including the Golden Toad) had disappeared in a cloud forest study area of 30 square kilometers. (Cloud forests are misty habitats found only in the mountains above 1,500 meters, where the trees are enclosed by cool, wet clouds much of the time. The unusual climate serves as a home to thousands of unique plants and animals.) Pounds and a coauthor explained his thesis to a scientific conference in 1999:

In a cloud forest, moisture is ordinarily plentiful. Even during the dry season ... clouds and mist normally keep the forest wet. Trade winds, blowing in from the Caribbean, carry moisture up the mountain slopes, where it condenses to form a large cloud deck that surrounds the mountains. It is hypothesized that climate warming, particularly since the mid-1970s, has raised the average altitude at which cloud formation begins, thereby reducing the clouds' effectiveness in delivering moisture to the forest. ... Days *without* mist during the dry season ... quadrupled over recent decades (Pounds and Schneider, 1999).

Pounds said at least 22 species of amphibians have disappeared from the cloud forest. Although the other species that disappeared were known to exist in other locations, the Golden Toad lost its only known home. However, two years after Pounds hypothesized that the amphibians lost their cloud forest climate to drying from sea surface warming, another research team demonstrated that it was almost certainly the clearing of lowland forests under the cloud forest of Monteverde that changed the pattern of cloud formation over the Golden Toad's once-mistier home. Lawton et al. (2001) noted that trade winds bringing moisture from the Caribbean spend five to 10 hours over the lowlands before they reach the Golden Toad's mountain home in the Cordillera de Tileran. By 1992, only about 18 percent of the original lowland vegetation remained. The deforestation reduced the infiltration of rainfall, increased water runoff, and thus reduced soil moisture. The shift from trees to crops and pasture also reduced the amount of water-holding canopy.

In March 1999, the Lawton team got satellite imagery showing that late-morning dry season cumulus clouds were much less abundant over the deforested parts of Costa Rica than over the nearby still-forested lowlands of Nicaragua. To check their conclusion, the Lawton team simulated the impact of Costa Rican deforestation using Colorado State University's Regional Atmospheric Modeling System. The computer modeling showed that the cloud base over pastured landscape rose above the altitude of the Cordillera peaks (1,800 meters) by late morning. Over forests, the cloud base didn't reach 1,800 meters until early afternoon. Lawton says these values "are in reasonable agreement with observed cloud bases in the area." That puts the blame for the cloud forest dryness squarely on the farmers and ranchers who cleared the lowlands. Pounds' own paper noted deforestation as a major threat to mountain cloud forests. The Lawton study leaves the Thomas team's big computerized study of mass species extinction without any evidence that moderate climate changes—even when abrupt—cause species extinctions.

The two other articles in Nature also failed to report any evidence of extinctions caused by the recent warming trend. The closest thing to an extinction threat in the Root et al. studies was the expansion of red foxes into the southern former range of arctic foxes in North America and Eurasia. However, this is displacement/ replacement, not extinction. Hersteinsson and Macdonald (1992) concluded that the changes in fox ranges were driven by prey availability. The arctic foxes are found primarily in the treeless regions of the Arctic, where they feed on lemmings and voles in the summer and eat heavily from seal carcasses in the winter. The larger red foxes eat a wider range of prey and fruits and are regarded as stronger competitors in forest and brush land. However, they are less well camouflaged for the winters in the treeless tundra than the arctic foxes in their blue-white winter pelts. Warming temperatures have allowed trees, brush, and red foxes to move farther north in the past 150 years-but they also have allowed arctic foxes to retain enough land and prey to succeed north of the red foxes. We do not know what would have happened if there had been no northern habitat and prey to support the arctic foxes during a red fox expansion, but the foxes already have survived more radical warming than they have faced recently. In earlier parts of the interglacial period, the Arctic temperatures were 2° to 6° C higher than they are now (Taira, 1975; Korotsky et al., 1988).

Returning to the study of Thomas *et al.* one more time, it is interesting to note that an earlier study by Thomas contained findings that completely discredit the thesis on which the 2004 claim rests—that species have readily defined "survival envelopes" outside which they cannot survive. The Thomas team began its 2001 paper by restating the long-believed and broadly held concept that many animals are "relatively sedentary and specialized in marginal parts of their geographical distributions." Thus, creatures are "expected to be slow at colonizing new habitats." Despite this belief, however, the Thomas team cites its own and many other researchers' studies showing that "the cool margins of many species' distributions have expanded rapidly in association with recent climate warming." This mildly undercuts their thesis. Much worse was to come. The two butterfly species the authors studied "increased the variety of habitat types that they can colonize" and the two species of bush cricket they studied showed "increased fractions of longer-winged (dispersive) individuals in recently founded populations." The longer-winged crickets would be able to fly farther in search of new habitat.

As a consequence of the new adaptations, the Thomas authors report, "Increased habitat breadth and dispersal tendencies have resulted in about 3 to 15fold increases in [range] expansion rates, allowing these insects to cross habitat disjunctions that would have represented major or complete barriers to dispersal before the expansions started." The changes in the butterfly and cricket populations render Thomas's entire thesis of "survival envelopes" inadequate at best and quite likely irrelevant. Yet this paper was not only written before the Root analysis, it was included in the Root analysis as one of the select few research studies supporting the mega-extinction theory.

Buried in the IPCC report are admissions that the computer models based on the dubious notion of "survival envelopes" that it relies on produce "a picture of potential impacts and risks that is far from perfect, in some instances apparently contradictory" (p. 239) and "climate envelope models do not simulate dynamic population or migration processes, and results are typically constrained to the regional level, so that the implications for biodiversity at the global level are difficult to infer," citing Malcolm *et al.*, 2002 (IPCC, 2007-II, p. 240). We agree, which is why, in the following sections, we present more reliable theories and evidence that paint a much different, and more accurate, picture of the fate of wildlife in a warming world.

### References

Hersteinsson, P. and Macdonald, D.W. 1992. Interspecific competition and the geographical distribution of red and Arctic foxes, *Vulpes vulpes* and *Alopex lagopus*. *Oikos* 64: 505–15.

IPCC. 2007-II. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. and Hanson, C.E. (Eds.) Cambridge University Press, Cambridge, UK.

Korotky, A.M., *et al.* 1988. Development of Natural Environment of the Southern Soviet Far East (Late Pleistocene-Holocene). Kauka, Moscow, Russia.

Root, T., *et al.* 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**: 57–60.

Lawton, R.O., *et al.* 2001. Climatic impact of tropical lowland deforestation on nearby mountain cloud forests. *Science* **294**: 584–87.

Malcolm, J.R., et al. 2002. Habitats at Risk: Global Warming and Species Loss in Globally Significant Terrestrial Ecosystems. World Wide Fund for Nature, Gland, Switzerland.

Pounds, J.A., *et al.* 1999. Biological response to climate change on a tropical mountain. *Nature* **398**: 611–15.

Pounds, J.A. and Schneider, S.H. 1999. Present and Future Consequences of Global Warming for Highland Tropical Forests Ecosystems: The Case of Costa Rica. Paper presented at the U.S. Global Change Research Program Seminar, Washington, DC. 29 September.

Taira, K. 1975. Temperature variation of the 'Kuroshio' and crustal movements in eastern and southeastern Asia 700 Years B.P. *Palaeogeography, Palaeoclimatology, Palaeoecology* **17**: 333–338.

Thomas, C.D., *et al.* 2001. Ecological and evolutionary processes at expanding range margins. *Nature* **411**: 577–81.

Thomas, C.D., *et al.* 2004. Extinction risk from climate change. *Nature* **427**: 145–48.

# 8.1.4. Data on Contemporary Species

What does real-world data say about rates of 2002. the United extinction? In Nations Environmental Program (UNEP) published a new World Atlas of Biodiversity (Groombridge and Jenkins, 2002). It reported that the world lost only half as many major wild species in the last three decades of the twentieth century (20 birds, mammals, and fish) as during the last three decades of the nineteenth century (40 extinctions of major species). In fact, UNEP said the rate of extinctions at the end of the twentieth century was the lowest since the sixteenth century-despite 150 years of rising world temperatures, growing populations, and industrialization.

There is a wealth of data to support the fact that

many species have prospered during the twentieth century, starting with research conducted by those who claim rising temperatures have caused a rise in extinctions. Parmesan and Yohe (2003) examined the northern boundaries of 52 butterfly species in northern Europe and the southern boundaries of 40 butterfly species in southern Europe and North Africa over the past century. Given the 0.8° C warming of Europe's temperatures over that period, it is striking to have Parmesan and Yohe tell us that "nearly all northward shifts involved extensions at the northern boundary with the southern boundary remaining stable." Thus, in the researchers own words, "most species effectively expanded the size of their ranges."

Chris Thomas and a coauthor in a study published in 1999 documented changes in the distribution between 1970 and 1990 of many British bird species (Thomas and Lennon, 1999). He found that the northern margins of southerly species shifted northward by an average of 19 km, while the southern margins of northerly species remained unchanged.

On 26 high mountain summits in the middle part of the Alps, a study by Grabherr *et al.* (1994) of the plant species found "species richness has increased during the past few decades, and is more pronounced at lower altitudes." In other words, the mountaintops show little loss of biodiversity at upper elevations, and increased species richness at lower elevations, where plants from still-lower elevations extended their ranges upward.

Pauli *et al.* (1996) examined the summit flora on 30 mountains in the European Alps, with species counts that ranged back in history to 1895. They report that mountaintop temperatures have risen by 2° C since 1920, with an increase of 1.2° C in just the last 30 years. Nine of the 30 mountaintops showed no change in species counts, but 11 gained an average of 59 percent more species, and one mountain gained an astounding 143 percent more species. Did historic species get crowded out by the flood of new warmerzone plants? The 30 mountains showed a mean species loss of 0.68 out of an average of 15.57 species. There was no documentation that any of the species "lost" on particular mountains represented extinctions rather than local disappearances.

Vesperinas *et al.* (2001) reported that native heatsensitive plant species have responded to temperature increases in the Iberian Peninsula and the Mediterranean coast over the past 30 years by expanding their ranges "towards colder inland areas where they were previously absent."

Van Herk et al. (2002) reported that the number

of lichen species groups present in the Central Netherlands increased from 95 in 1979 to 172 in 2001 as the region warmed. The researchers found the average number of species grouped per site increased from 7.5 to 18.9. Again, more warmth produced increased species richness.

Looking at the distribution of 18 butterfly species widespread and common in the British countryside, "nearly all of the common species have increased in abundance [during the warming], more in the east of Britain than in the west" according to a research team led by Emie Pollard of Britain's Institute of Terrestrial Ecology (Pollard *et al.*, 1995).

Warm-water species of plankton rapidly responded to warming and cooling in the western English Channel, shifting latitudinally by up to 120 miles, and increasing or decreasing their numbers by two to three-fold over 70 years, according to research by A.J. Southward of Britain's Marine Biological Association (Southward, 1995).

In the Antarctic, Adelie penguins need pack ice to thrive, whereas chinstrap penguins prefer ice-free waters. R.C. Smith *et al.* (1994) found that the Adelie penguins in the West Antarctic Peninsula are declining because the warming on the peninsula favors the chinstraps. Meanwhile the chinstraps in the Ross Sea region are suffering because 97 percent of Antarctica—the part that isn't the peninsula—is getting colder. This can hardly be surprising. Two varieties of a highly mobile species have moved to the sites that favor their respective feeding and breeding requirements while their populations decline in the unfavorable sites.

The Antarctic's only two higher-level plant species have responded to the Antarctic Peninsula's warming by increasing their numbers at two widely separated localities (Smith, 1994). Fortunately, it would take thousands of years of increased warming to melt all the Antarctic ice and a very long period of extended cold to close all the open water around the Antarctic Peninsula. The 1,500-year climate cycle makes it almost certain that Antarctica's plants and penguins will continue to adapt rather than disappear.

Invertebrates in a rocky intertidal site at Pacific Grove, California can't move, but their populations change. The invertebrates were surveyed by Saragin *et al.* (1999) in 1931–1933 and again in 1993–1996 after a warming of 0.8° C. Ten of the 11 southern species increased in abundance, whereas five of seven northern species decreased.

New photographs were taken by Sturm *et al.* (2001) to match a set of 1948–1950 photographs of

the Brooks Range and the Arctic coast of Alaska. At more than half of the matched locations, researchers found "distinctive and, in some cases, dramatic increases in the height and diameter of individual shrubs ... and expansion of shrubs into previously shrub-free areas."

Western American bird species are pioneering and expanding their ranges over vast areas and huge climatic differences as the climate warms. N.K. Johnson of the University of California-Berkeley compiled records for 24 bird species from Audubon Field Notes, American Birds and other sources (Johnson, 1994). He found "four northern species have extended their ranges southward, three eastern species have expanded westward, fourteen southwestern or Mexican species have moved northward, one Great Basin-Colorado Plateau species has expanded radially, and two Great Basin-Rocky Mountain subspecies have expanded westward."

Brommer (2004) studied the birds of Finland, which were categorized as either northerly (34 species) or southerly (116 species). Brommer quantified changes in their range margins and distributions from two atlases of breeding birds, one covering the period 1974-79 and one covering the period 1986-89, in an attempt to determine how the two groups of species responded to what he called "the period of the earth's most rapid climate warming in the last 10,000 years." Once again, it was determined that the southerly group of bird species experienced a mean poleward advancement of their northern range boundaries of 18.8 km over the 12year period of supposedly unprecedented warming. The southern range boundaries of the northerly species, on the other hand, were essentially unmoved, leading once again to range expansions that should have rendered the Finnish birds less subject to extinction than they were before the warming.

Similar results were obtained in a study by Hickling *et al.* (2005) of changes in the northern and southern range boundaries of 37 non-migratory British dragonfly and damselfly species between the two 10-year periods 1960-70 and 1985-95. All but two of the 37 species increased the sizes of their ranges between the two 10-year periods, with the researchers reporting that "species are shifting northwards faster at their northern range margin than at their southern range margin," and concluding that "this could suggest that species at their southern range margins are less constrained by climate than by other factors," which surely appears to be the case.

Chamaille-Jammes et al. (2006) studied four unconnected populations of a small live-bearing lizard that lives in peat bogs and heath lands scattered across Europe and Asia, concentrating on a small region near the top of a mountain in southeast France at the southern limit of the species' range. There, from 1984 to 2001, they monitored a number of lifehistory traits of the populations, including body size, reproductive characteristics, and survival rates, during which time local air temperatures rose by approximately 2.2°C. In doing so, they observed that individual body size increased dramatically in all four populations over the 18-year study period in all age classes and, in the words of the researchers, "appeared related to a concomitant increase in temperature experienced during the first month of life." As a result, since fecundity is strongly dependent on female body size, they found that "clutch size and total reproductive output also increased." In addition, they learned that "adult survival was positively related to May temperature."

In discussing their findings, the French researchers say that since all fitness components investigated responded positively to the increase in temperature, "it might be concluded that the common lizard has been advantaged by the shift in temperature." This finding, as they describe it, stands in stark contrast to what they call the "habitat-based prediction that these populations located close to mountaintops on the southern margin of the species range should be unable to cope with the alteration of their habitat." They conclude that "to achieve a better prediction of a species persistence, one will probably need to combine both habitat and individual-based approaches," noting, however, that individual responses, such as those documented in their study (which were all positive), represent "the ultimate driver of a species response to climate change."

The Audubon Society (2009) released a report in February 2009 calling attention to the correlation between the movement of North American bird populations and an increase in average January temperatures in the lower 48 U.S. states from 1969 to 2005. The report breathlessly recounted the expansion of the northern boundaries of the habitats of 58 percent of observed species of birds over the past four decades and concluded that "we must act decisively to control global warming pollution to curb the worst impacts of climate change, and take immediate steps to help birds and other species weather the changes we cannot avoid." But the study did not ask whether the warming that occurred during this period

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benefitted or hurt most bird populations by moving poleward the northern edge of their habitats. One might suppose the net effect would be beneficial, and in fact this is what Audubon itself found but failed to mention in the body of the report. In a data table presented in an appendix to the report, one finds that 120 of the 305 species reported in the study (39 percent) showed statistically significant population increases, 128 (42 percent) showed no change, and only 57 (19 percent) showed statistically significant declines. These numbers suggest that North American bird species overall benefited from the modest warming from 1969 to 2005.

Many, and probably most, of the world's species have benefited from rising temperatures in the twentieth century. There is very little evidence of *any* extinctions. What should be plain is that, despite predictions of extinctions based on theories and computer models, real-world observations confirm that a warmer world is more, not less, hospitable to wildlife.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/r/rangeexpanimals.php</u> and <u>http://www.co2science.org/subject/e/extinction.php</u>.

### References

Audubon Society. 2009. Birds and Climate Change: On the Move — A Briefing for Policymakers and Concerned Citizens. National Audubon Society, New York, NY. February.

Brommer, J.E. 2004. The range margins of northern birds shift polewards. *Annales Zoologici Fennici* **41**: 391-397.

Chamaille-Jammes, S., Massot, M., Aragon, P. and Clobert, J. 2006. Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Global Change Biology* **12**: 392-402.

Grabherr, G. et al. 1994. Climate effects on mountain plants. Nature **369**: 448.

Groombridge, B. and Jenkins, M.D. 2002. World Atlas of *Biodiversity*. United Nations Environmental Program (UNEP) and University of California Press, Berkeley, CA.

Hickling, R., Roy, D.B., Hill, J.K. and Thomas, C.D. 2005. A northward shift of range margins in British Odonata. *Global Change Biology* **11**: 502-506. Johnson, N.K. 1994. Pioneering and natural expansion of breeding distributions in western North American birds. *Studies in Avian Biology* **15**: 27-44.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.

Pauli, H. *et al.* 1996. Effects of climate change on mountain ecosystems—upward shifting of mountain plants. *World Resource Review* **8**: 382-390.

Pollard, E. *et al.* 1995. Population trends of common British butterflies at monitored sites. *Journal of Applied Ecology* **32**: 9–16.

Saragin, R.D. *et al.* 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* **69**: 465–90.

Smith, R.C. *et al.* 1999. Marine ecosystem sensitivity to climate change. *BioScience* **49**: 393–404.

Smith, R.I.L. 1994. Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia* **99**: 322–28.

Southward, A.J. 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 temperatures. *Journal of Thermal Biology* **20** (1): 127–55.

Sturm, M. *et al.* 2001. Increasing shrub abundance in the Arctic. *Nature* **411**: 546–47.

Thomas, C.D. and Lennon, J.J. 1999. Birds extend their ranges northwards. *Nature* **399**: 213.

Van Herk, C.M. *et al.* 2002. Long-term monitoring in the Netherlands suggests that lichens respond to global warming. *Lichenologist* **34**: 141–54.

Vesperinas, E.S. *et al.* 2001. The expansion of thermophilic plants in the Iberian Peninsula as a sign of climate change. In G. Walther *et al.* (Eds.) *"Fingerprints" of Climate Change: Adapted Behavior and Shifting Species Ranges.* Kluwer Academic/ Plenum Publishers, New York. 163–84.

### 8.1.5. Rapid Evolutionary Change

Skelly *et al.* (2007) critiqued the climate-envelope approach to predicting extinctions used by Thomas *et al.* (2004), citing as their primary reason for doing so the fact that this approach "implicitly assumes that species cannot evolve in response to changing climate." As they correctly point out, "many examples of contemporary evolution in response to climate change exist," such as populations of a frog they had studied that had "undergone localized evolution in thermal tolerance (Skelly and Freidenburg, 2000), temperature-specific development rate (Skelly, 2004), and thermal preference (Freidenburg and Skelly, 2004)," in less than 40 years. Similarly, they report, "laboratory studies of insects show that thermal tolerance can change markedly after as few as 10 generations (Good, 1993)."

Adding that "studies of microevolution in plants show substantial trait evolution in response to climate manipulations (Bone and Farres, 2001)," the researchers further noted that "collectively, these findings show that genetic variation for traits related to thermal performance is common and evolutionary response to changing climate has been the typical finding in experimental and observational studies (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001)."

Although evolution will obviously be slower in the cases of long-lived trees and large mammals, where long generation times are the norm, the scientists say the case for rapid evolutionary responses among many other species "has grown much stronger," citing, in this regard, the work of six other groups of researchers comprised of two dozen individuals (Stockwell et al., 2003; Berteaux et al., 2004; Hairston et al., 2005; Bradshaw and Holzapfel, 2006; Schwartz et al., 2006; Urban et al., 2007). As a result, they write, "on the basis of the present knowledge of genetic variation in performance traits and species' capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as other environmental changes (Stockwell et al., 2003; Grant and Grant, 2002; Balanya et al., 2006; Jump et al., 2006; Pelletier et al., 2007)."

Much the same conclusion has been reached by still other groups of scientists. In a study of the field mustard plant, for example, a group of three researchers (Franks *et al.*, 2007) found evidence for what they describe as "a rapid, adaptive evolutionary shift in flowering phenology after a climatic fluctuation," which finding, in their words, "adds to the growing evidence that evolution is not always a slow, gradual process but can occur on contemporary time scales in natural populations."

Likewise, another group of researchers who published in 2007 (Rae *et al.*, 2007)—who worked with hybrids of two *Populus* tree species—obtained results which, as they phrased it, "quantify and identify genetic variation in response to elevated  $CO_2$ and provide an insight into genomic response to the changing environment." The results, they wrote, "should lead to an understanding of microevolutionary response to elevated  $CO_2$  ... and aid future plant breeding and selection," noting that various research groups have already identified numerous genes that appear sensitive to elevated  $CO_2$ (Gupta *et al.*, 2005; Taylor *et al.*, 2005; Ainsworth *et al.*, 2006; Rae *et al.*, 2006).

Life in the sea, in this regard, is no different from life on land. In another study published in 2007, for example, a team of four marine biologists (Van Doorslaer et al., 2007) conducted an experiment with a species of zooplankton in which they say they "were able to demonstrate a rapid microevolutionary response (within 1 year) in survival, age at reproduction and offspring number to elevated temperatures," and they state that "these responses may allow the species to maintain itself under the forecasted global warming scenarios," noting that "strongly indicates rapid what they learned microevolution of the ability to cope with higher temperatures." Many other studies, some of them cited in Section 8.3, have produced analogous results with respect to increases in temperature on corals (Kumaraguru et al., 2003; Willis et al., 2006) and increases in CO2 on freshwater microalgae (Collins et al., 2006).

In conclusion, many species have shown the ability to adapt rapidly to changes in climate. Claims that global warming threatens large numbers of species with extinction typically rest on a false definition of extinction (the loss of a particular population rather than entire species) and speculation rather than real-world evidence. The world's species have proven to be very resilient, having survived past natural climate cycles that involved much greater warming and higher  $CO_2$  concentrations than exist today or are likely to occur in the coming centuries.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/e/subject\_e.php</u> under the subheading Evolution.

### References

Ainsworth, E.A., Rogers, A., Vodkin, L.O., Walter, A. and Schurr, U. 2006. The effects of elevated CO<sub>2</sub> concentration on soybean gene expression. An analysis of growing and mature leaves. *Plant Physiology* **142**: 135-147. Balanya, J., Oller, J.M., Huey, R.B., Gilchrist, G.W. and Serra, L. 2006. Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science* **313**: 1773-1775.

Berteaux, D., Reale, D., McAdam, A.G. and Boutin, S. 2004. Keeping pace with fast climatic change: can arctic life count on evolution? *Integrative and Comparative Biology* **44**: 140-151.

Bone, E. and Farres, A. 2001. Trends and rates of microevolution in plants. *Genetica* **112-113**: 165-182.

Bradshaw, W.E. and Holzapfel, C.M. 2006. Evolutionary response to rapid climate change. *Science* **312**: 1477-1478.

Collins, S., Sultemeyer, D. and Bell, G. 2006. Changes in C uptake in populations of *Chlamydomonas reinhardtii* selected at high CO<sub>2</sub>. *Plant, Cell and Environment* **29**: 1812-1819.

Franks, S.J., Sim, S. and Weis, A.E. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences USA* **104**: 1278-1282.

Freidenburg, L.K. and Skelly, D.K. 2004. Microgeographical variation in thermal preference by an amphibian. *Ecology Letters* **7**: 369-373.

Good, D.S. 1993. Evolution of behaviors in *Drosophila melanogaster* in high-temperatures: genetic and environmental effects. *Journal of Insect Physiology* **39**: 537-544.

Grant, P.R. and Grant, B.R. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**: 707-711.

Gupta, P., Duplessis, S., White, H., Karnosky, D.F., Martin, F. and Podila, G.K. 2005. Gene expression patterns of trembling aspen trees following long-term exposure to interacting elevated  $CO_2$  and tropospheric  $O_3$ . New Phytologist **167**: 129-142.

Hairston, N.G., Ellner, S.P., Gerber, M.A., Yoshida, T. and Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters* **8**: 1114-1127.

Hendry, A.P. and Kinnison, M.T. 1999. The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**: 637-653.

Jump, A.S., Hunt, J.M., Martinez-Izquierdo, J.A. and Penuelas, J. 2006. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology* **15**: 3469-3480. Kinnison, M.T. and Hendry, A.P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112-113**: 145-164.

Kumaraguru, A.K., Jayakumar, K. and Ramakritinan, C.M. 2003. Coral bleaching 2002 in the Palk Bay, southeast coast of India. *Current Science* **85**: 1787-1793.

Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S. and Coulson, T. 2007. The evolutionary demography of ecological change: linking trait variation and population growth. *Science* **315**: 1571-1574.

Rae, A.M., Ferris, R., Tallis, M.J. and Taylor, G. 2006. Elucidating genomic regions determining enhanced leaf growth and delayed senescence in elevated CO<sub>2</sub>. *Plant, Cell & Environment* **29**: 1730-1741.

Rae, A.M., Tricker, P.J., Bunn, S.M. and Taylor, G. 2007. Adaptation of tree growth to elevated CO<sub>2</sub>: quantitative trait loci for biomass in *Populus*. *New Phytologist* **175**: 59-69.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N. and O'Connor, R.J. 2006. Predicting extinctions as a result of climate change. *Ecology* **87**: 1611-1615.

Skelly, D.K., Joseph, L.N., Possingham, H.P., Freidenburg, L.K., Farrugia, T.J., Kinnison, M.T. and Hendry, A.P. 2007. Evolutionary responses to climate change. *Conservation Biology* **21**: 1353-1355.

Skelly, D.K. and Freidenburg, L.K. 2000. Effects of beaver on the thermal biology of an amphibian. *Ecology Letters* **3**: 483-486.

Skelly, D.K. 2004. Microgeographic countergradient variation in the wood frog, *Rana sylvatica*. *Evolution* **58**: 160-165.

Stockwell, C.A., Hendry, A.P. and Kinnison, M.T. 2003. Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* **18**: 94-101.

Taylor, G., Street, N.R., Tricker, P.J., Sjodin, A., Graham, L., Skogstrom, O., Calfapietra, C., Scarascia-Mugnozza, G. and Jansson, S. 2005. The transcriptome of *Populus* in elevated CO<sub>2</sub>. *New Phytologist* **167**: 143-154.

Thomas, C.D., *et al.* 2004. Extinction risk from climate change. *Nature* **427**: 145–48.

Urban, M.C., Philips, B., Skelly, D.K. and Shine, R. 2007. The cane toad's (*Chaunus* [*Bufo*] *marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society of London B*: 10.1098/rspb.2007.0114.

Van Doorslaer, W., Stoks, R., Jeppesen, E. and De Meester, L. 2007. Adaptive microevolutionary responses to simulated global warming in *Simocephalus vetulus*: a mesocosm study. *Global Change Biology* **13**: 878-886.

Willis, B.L., van Oppen, M.J.H., Miller, D.J., Vollmer, S.V. and Ayre, D.J. 2006. The role of hybridization in the evolution of reef corals. *Annual Review of Ecology, Evolution, and Systematics* **37**: 489-517.

## 8.2. Terrestrial Plants

The IPCC's global warming extinction scenario is that if it gets "too hot" for a species of plant or animal where it currently lives, individuals of the heatstressed species would have to move to a cooler location in order to survive. In many cases, however, acclimation can adequately substitute for migration, as has been demonstrated by several studies in which the temperatures at which plants grow best rose substantially (by several degrees Centigrade) in response to increases in the air temperature regimes to which they had long been accustomed (Mooney and West, 1964; Strain *et al.*, 1976; Bjorkman *et al.*, 1978; Seemann *et al.*, 1984; Veres and Williams, 1984; El-Sharkawy *et al.*, 1992, Battaglia *et al.*, 1996).

How does acclimation happen? One possible way is described by Kelly et al. (2003). In reference to the view of the IPCC, they note that "models of future ecological change assume that in situ populations of plants lack the capacity to adapt quickly to warming and as a consequence will be displaced by species better able to exploit the warmer conditions anticipated from 'global warming'." In contrast to this assumption, they report finding individual trees within a naturally occurring stand of Betula pendula (birch) that are genetically adapted to a range of different temperatures. As they describe it, they discovered "the existence of 'pre-adapted' individuals in standing tree populations" that "would reduce temperature-based advantages for invading species," which finding, they say, "bring[s] into question assumptions currently used in models of global climate change."

Another perspective on the adaptation vs. migration theme is provided by the work of Loehle (1998), who notes (using forests as an example) that the  $CO_2$ -induced global warming extinction hypothesis rests on the assumption that the growth rates of trees rise from zero at the cold limits of their natural ranges (their northern boundaries in the Northern Hemisphere) to a broad maximum, after which they decline to zero at the warm limits of their natural ranges (their southern boundaries in the Northern Hemisphere). Loehle demonstrates that this

assumption is only half correct. It properly describes tree growth dynamics near a Northern Hemispheric forest's northern boundary, but not its southern boundary.

Loehle notes that in the Northern Hemisphere (to which we will restrict our discussion for purposes of simplicity), trees planted north of their natural ranges' northern boundaries are able to grow to maturity only within 50-100 miles of those boundaries. Trees planted south of their natural ranges' southern boundaries, however, often grow to maturity as much as 1,000 miles further south (Dressler, 1954; Woodward, 1987, 1988). Loehle reports that "many alpine and arctic plants are extremely tolerant of high temperatures, and in general one cannot distinguish between arctic, temperate, and tropical-moist-habitat types on the basis of heat tolerances, with all three types showing damage at 44-52°C (Gauslaa, 1984; Lange and Lange, 1963; Levitt, 1980; Kappen, 1981)."

What Loehle finds from his review of the literature and his experience with various trees in the Unites States is that as temperatures and growing degree days rise from very low values, the growth rates of boreal trees at some point begin to rise from zero and continue increasing until they either plateau at some maximum value or drop only very slowly thereafter, as temperatures rise still higher and growing degree days continue to accumulate. Trees from the Midwest, by comparison, do not begin to grow until a higher temperature or greater accumulation of growing degree days is reached, after which their growth rates rise considerably higher than those of the colder-adapted boreal species, until they too either level out or begin to decline slowly. Lastly, southern species do not begin to grow until even higher temperatures or growing degree day sums are reached, after which their growth rates rise the highest of all before leveling out and exhibiting essentially no decline thereafter, as temperatures and growing degree days continue to climb.

In light of these observations, it is clear that although the northern range limit of a woody species in the Northern Hemisphere is indeed determined by growth-retarding cool growing seasons and frost damage, the southern boundary of a tree's natural range is not determined by temperature, but by competition between the northern species and more southerly adapted species that have inherently greater growth rates.

Whenever significant long-term warming occurs, therefore, earth's coldest-adapted trees are presented

with an opportunity to rapidly extend the cold-limited boundaries of their ranges northward in the Northern Hemisphere, as many studies have demonstrated they have done in the past and are doing now. Trees at the southern limits of their ranges, however, are little affected by the extra warmth. As time progresses, they may at some point begin to experience pressure from some of the faster-growing southern species encroaching upon their territory; but this potential challenge is by no means assured of quick success. As Loehle describes it:

Seedlings of these southern species will not gain much competitive advantage from faster growth in the face of existing stands of northern species, because the existing adult trees have such an advantage due to light interception. Southern types must wait for gap replacement, disturbances, or stand break up to utilize their faster growth to gain a position in the stand. Thus the replacement of species will be delayed at least until the existing trees die, which can be hundreds of years ... Furthermore, the faster growing southern species will be initially rare and must spread, perhaps across considerable distances or from initially scattered localities. Thus, the replacement of forest (southern types replacing northern types) will be an inherently slow process (several to many hundreds of years).

In summing up the significance of this situation, Loehle says "forests will not suffer catastrophic dieback due to increased temperatures but will rather be replaced gradually by faster growing types."

Another possibility that must be seriously considered is that northern or high-altitude forests will not be replaced at all by southern or low-altitude forests in a warming world. Rather, the two forest types may merge, creating entirely new forests of greater species diversity, such as those that existed during the warmer Tertiary Period of the Cenozoic Era, when in the western United States many montane taxa regularly grew among mixed conifers and broadleaf schlerophylls (Axelrod 1944a, 1944b, 1956, 1987), creating what could well be called super forest ecosystems, which Axelrod (1988) has described as "much richer than any that exist today."

Possibly helping warmer temperatures to produce this unique biological phenomenon during the Tertiary were the higher atmospheric  $CO_2$  concentrations of that period (Volk, 1987), as has been suggested by Idso (1989). As documented extensively in Chapter 7, elevated concentrations of atmospheric  $CO_2$  significantly stimulate plant growth rates (Kimball, 1983)—especially those of trees (Saxe *et al.*, 1998; Idso and Kimball, 2001)—and they also greatly enhance water use efficiency (Feng, 1999). Even more important, however, is how atmospheric  $CO_2$  enrichment alters plant photosynthetic and growth responses to rising temperatures.

It has long been known that photo-respiration which can "cannibalize" as much as 40 percent to 50 percent of the recently produced photosynthetic products of C<sub>3</sub> plants (Wittwer, 1988)-becomes increasingly more pronounced as air temperature rises (Hanson and Peterson, 1986). It also has been established that photorespiration is increasingly more inhibited as the air's CO2 content rises (Grodzinski et al., 1987). Hence, there is a greater potential for rising CO<sub>2</sub> concentrations to benefit C<sub>3</sub> plants at higher temperatures, as was demonstrated by the early experimental work of Idso et al. (1987) and Mortensen (1987), as well as by the theoretical work of Gifford (1992), Kirschbaum (1994) and Wilks et al. (1995). In an analysis of 42 experimental datasets collected by numerous scientists. Idso and Idso (1994) showed that the mean growth enhancement due to a 300-ppm increase in atmospheric CO<sub>2</sub> concentration rises from close to zero at an air temperature of 10°C to 100 percent (doubled growth) at approximately 38°C, while at higher temperatures the growth stimulation rises higher still, as also has been shown by Cannell and Thornley (1998).

Several studies have additionally demonstrated that atmospheric  $CO_2$  enrichment tends to alleviate high-temperature stress in plants (Faria *et al.*, 1996; Nijs and Impens, 1996; Vu *et al.*, 1997); and it has been proven that at temperatures that are high enough to cause plants to die, atmospheric  $CO_2$  enrichment can sometimes preserve their lives (Idso *et al.*, 1989; Idso, 1995; Baker *et al.*, 1992; Rowland-Bamford *et al.*, 1996; Taub *et al.*, 2000), just as it can often stave off their demise in the very dry conditions that typically accompany high air temperatures (Tuba *et al.*, 1998; Hamerlynck, *et al.*, 2000; Polley *et al.*, 2002).

#### Box 1: The CO<sub>2</sub>-Temperature-Growth Interaction

The growth-enhancing effects of elevated  $CO_2$  typically increase with rising temperature. This phenomenon is illustrated by the data of Jurik *et al.* (1984), who exposed bigtooth aspen leaves to atmospheric  $CO_2$  concentrations of 325 and 1,935 ppm and measured their photosynthetic rates at a number of different temperatures. In the figure below, we have reproduced their results and slightly extended the two relationships defined by their data to both warmer and cooler conditions.



At 10°C, elevated CO<sub>2</sub> has essentially no effect on net photosynthesis in this particular species, as Idso and Idso (1994) have demonstrated is characteristic of plants in general. At 25°C, however, where the net photosynthetic rate of the leaves exposed to 325 ppm CO<sub>2</sub> is maximal, the extra CO<sub>2</sub> of this study boosts the net photosynthetic rate of the foliage by nearly 100 percent; and at 36°C, where the net photosynthetic rate of the foliage by nearly 100 percent; and at 36°C, where the net photosynthetic rate of the leaves exposed to 1,935 ppm CO<sub>2</sub> is maximal, the extra CO<sub>2</sub> boosts the net photosynthetic rate of the foliage by a whopping 450 percent. The extra CO<sub>2</sub> increases the optimum temperature for net photosynthesis in this species by about 11°C, from 25°C in air of 325 ppm CO<sub>2</sub> to 36°C in air of 1,935 ppm CO<sub>2</sub>.

In viewing the warm-temperature projections of the two relationships, it can also be seen that the transition from positive to negative net photosynthesis—which denotes a change from life-sustaining to life-depleting conditions—likely occurs somewhere in the vicinity of  $39^{\circ}$ C in air of 325 ppm CO<sub>2</sub> but somewhere in the vicinity of  $50^{\circ}$ C in air of 1,935 ppm CO<sub>2</sub>. Hence, not only was the optimum temperature for the growth of bigtooth aspen greatly increased by the extra CO<sub>2</sub> of this experiment, so too was the temperature above which life cannot be sustained increased, and by about the same amount, i.e.,  $11^{\circ}$ C.

A major consequence of these facts is that the optimum temperature  $(T_{opt})$  for plant growth—the temperature at which plants photosynthesize and grow best—generally rises with atmospheric CO<sub>2</sub> enrichment (Berry and Bjorkman, 1980; Taiz and Zeiger, 1991). An example of this phenomenon is presented in Box 1, where it can be seen that the increase in atmospheric CO<sub>2</sub> concentration utilized in this particular study increases the optimum temperature for photosynthesis in this species from a

broad maximum centered at  $25^{\circ}$ C in ambient air to a well-defined peak at about  $36^{\circ}$ C in CO<sub>2</sub>-enriched air.

How much is plant optimum temperature typically increased by an extra 300 ppm of CO<sub>2</sub>? Based largely on theoretical considerations, Long (1991) calculated that such an increase in the air's CO<sub>2</sub> concentration should increase  $T_{opt}$ , in the mean, by about 5°C, while McMurtrie and Wang (1993) calculated the increase at somewhere between 4° and 8°C.

The implication of the finding that plant optimum temperature rises so dramatically in response to increasing atmospheric CO<sub>2</sub> concentration is that if the planet were to warm in response to the ongoing rise in the air's CO<sub>2</sub> content—even to the degree predicted by the worst-case scenario of the IPCC (6.4°C by 2100)—the vast majority of earth's plants would likely not need to migrate towards cooler parts of the globe. Any warming would provide them an opportunity to move into regions that were previously too cold for them, but it would not force them to move, even at the hottest extremes of their ranges; for as the planet warmed, the rising atmospheric  $CO_2$ concentration would significantly increase the temperatures at which most of earth's C<sub>3</sub> plants which comprise fully 95 percent of the planet's vegetation (Drake, 1992)-function best, creating a situation where earth's plant life would actually prefer warmer conditions.

With respect to the C<sub>4</sub> and CAM plants that make up the remaining 5 percent of earth's vegetative cover, most of them are endemic to the planet's hotter environments (De Jong et al., 1982; Drake, 1989; Johnson et al., 1993), which according to the IPCC are expected to warm much less than the cooler regions of the globe. Hence, the planet's C<sub>4</sub> and CAM plants would not face as great a thermal challenge as earth's C<sub>3</sub> plants in a warming world. Nevertheless, the work of Chen et al. (1994) suggests they too may experience a modest increase in their optimum temperatures as the air's CO<sub>2</sub> content rises (a 1.5°C increase in response to a 350-ppm increase in atmospheric CO<sub>2</sub> concentration). Consequent-ly, and in view of the non-CO<sub>2</sub>-related abilities of earth's vegetation to adapt to rising temperatures discussed in the previous section, plants of all photosynthetic persuasions should be able to successfully adapt to any future warming that could be caused by the enhanced greenhouse effect. So obvious is this conclusion, in fact, that Cowling (1999) has bluntly stated, "maybe we should be less concerned about rising CO<sub>2</sub> and rising temperatures and more worried about the possibility that future atmospheric CO<sub>2</sub> will suddenly stop increasing, while global temperatures continue rising."

James Hansen, in testimony to a U.S. House of Representatives committee, has claimed that life in alpine regions is "in danger of being pushed off the planet" because of rising temperatures. In July and August 2003, a team of three researchers investigated this scenario by resurveying the floristic composition of the uppermost 10 meters of 10 mountain summits in the Swiss Alps (Walther et al., 2005), applying the same methodology used in earlier surveys that were conducted there in 1905 (Rubel, 1912) and 1985 (Hofer, 1992). This analysis covered the bulk of the Little Ice Age-to-Current Warm Period transition, and it revealed that plants of many species had indeed marched up the sides of the mountains, as the earth in general-and the Swiss Alps in particular-had warmed. Of even greater significance, however, was the fact that not a single mountaintop species was "pushed off the planet." Between 1905 and 1985 the mean number of species observed on the 10 mountaintops rose by 86 percent, while by 2003 it had risen by 138 percent, providing, in the words of the researchers who conducted the work, "an enrichment of the overall summit plant diversity."

Another research team studied the same phenomenon on 12 mountaintops in the Swiss Alps (Holzinger et al., 2008), making complete inventories of vascular plant species that were present there in 2004, while following-"as accurately as possible," in their words-the same ascension paths used by other researchers in 1885, 1898, 1912, 1913, and 1958, after which they compared their findings with those of the earlier studies. By these means, they detected upward plant migration rates on the order of several meters per decade, which phenomena increased vascular plant species richness at the mountains' summits by 11 percent per decade over the 120-year study period. This finding, in their words, "agrees well with other investigations from the Alps, where similar changes have been detected," and they cited, in this regard, four additional studies (Grabherr et al., 1994; Pauli et al., 2001; Camenisch, 2002; Walther, 2003).

Another pertinent study was conducted by a researcher who analyzed altitudinal shifts in the ranges of alpine and subalpine plants in the mountains of west-central Sweden (Kullman, 2002), where air temperature had risen approximately 1°C over the past hundred years. This work revealed that since the early twentieth century, alpine and subalpine plants had migrated upslope by an average of 200 m. Most importantly, it also indicated, according to the scientist who did the work, that "no species have yet become extinct from the highest elevations," which finding was said by the researcher to "converge with observations in other high-mountain regions worldwide," in support of which statement five more new studies were cited (Keller et al., 2000; Kullman, 2002; Klanderud and Birks, 2003; Virtanen et al., 2003; Lacoul and Freedman, 2006).

In light of these many real-world findings, it is clear that warmer temperatures have not led to an increase in plant extinctions, and in fact have led to the opposite effect: greater plant growth and diversity in larger areas of the globe. Nor did the warming of the past century—which the IPCC claims was unprecedented over the past millennium—push any upward-migrating plants "off the planet" at the tops of its mountains. One of the most highly promoted hypothetical scenarios of the IPCC is contradicted by real-world data.

### References

Axelrod, D.I. 1944a. The Oakdale flora (California). *Carnegie Institute of Washington Publication* **553**: 147-166.

Axelrod, D.I. 1944b. The Sonoma flora (California). *Carnegie Institute of Washington Publication* **553**: 167-200.

Axelrod, D.I. 1956. Mio-Pliocene floras from west-central Nevada. University of California Publications in the Geological Sciences **33**: 1-316.

Axelrod, D.I. 1987. The Late Oligocene Creede flora, Colorado. University of California Publications in the Geological Sciences **130**: 1-235.

Axelrod, D.I. 1988. An interpretation of high montane conifers in western Tertiary floras. *Paleobiology* **14**: 301-306.

Baker, J.T., Allen Jr., L.H. and Boote, K.J. 1992. Response of rice to carbon dioxide and temperature. *Agricultural and Forest Meteorology* **60**: 153-166.

Battaglia, M., Beadle, C. and Loughhead, S. 1996. Photosynthetic temperature responses of *Eucalyptus globulus* and *Eucalyptus nitens*. *Tree Physiology* **16**: 81-89.

Berry, J. and Bjorkman, O. 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* **31**: 491-543.

Bjorkman, O., Badger, M. and Armond, P.A. 1978. Thermal acclimation of photosynthesis: effect of growth temperature on photosynthetic characteristics and components of the photosynthetic apparatus in *Nerium oleander*. *Carnegie Institution of Washington Yearbook* **77**: 262-276.

Camenisch, M. 2002. Veranderungen der Gipfelflora im Bereich des Schweizerischen Nationalparks: Ein Vergleich uber die letzen 80 Jahre. *Jahresber nat forsch Ges Graubunden* 111: 27-37. Cannell, M.G.R. and Thornley, J.H.M. 1998. Temperature and  $CO_2$  responses of leaf and canopy photosynthesis: a clarification using the non-rectangular hyperbola model of photosynthesis. *Annals of Botany* **82**: 883-892.

Chen, D-X., Coughenour, M.B., Knapp, A.K. and Owensby, C.E. 1994. Mathematical simulation of  $C_4$  grass photosynthesis in ambient and elevated  $CO_2$ . *Ecological Modelling* **73**: 63-80.

Cowling, S.A. 1999. Plants and temperature—CO<sub>2</sub> uncoupling. *Science* **285**: 1500-1501.

De Jong, T.M., Drake, B.G. and Pearcy, R.W. 1982. Gas exchange responses of Chesapeake Bay tidal marsh species under field and laboratory conditions. *Oecologia* **52**: 5-11.

Drake, B.G. 1989. Photosynthesis of salt marsh species. *Aquatic Botany* **34**: 167-180.

Drake, B.G. 1992. Global warming: The positive impact of rising carbon dioxide levels. *Eco-Logic* 1(3): 20-22.

Dressler, R.L. 1954. Some floristic relationships between Mexico and the United States. *Rhodora* **56**: 81-96.

El-Sharkawy, M.A., De Tafur, S.M. and Cadavid, L.F. 1992. Potential photosynthesis of cassava as affected by growth conditions. *Crop Science* **32**: 1336-1342.

Faria, T., Wilkins, D., Besford, R.T., Vaz, M., Pereira, J.S. and Chaves, M.M. 1996. Growth at elevated CO<sub>2</sub> leads to down-regulation of photosynthesis and altered response to high temperature in *Quercus suber* L. seedlings. *Journal of Experimental Botany* **47**: 1755-1761.

Feng, X. 1999. Trends in intrinsic water-use efficiency of natural trees for the past 100-200 years: A response to atmospheric  $CO_2$  concentration. *Geochimica et Cosmochimica Acta* **63**: 1891-1903.

Gauslaa, Y. 1984. Heat resistance and energy budget in different Scandinavian plants. *Holarctic Ecology* **7**: 1-78.

Gifford, R.M. 1992. Interaction of carbon dioxide with growth-limiting environmental factors in vegetative productivity: Implications for the global carbon cycle. *Advances in Bioclimatology* **1**: 24-58.

Grabherr, G, Gottfried, M. and Pauli, H. 1994. Climate effects on mountain plants. *Nature* **369**: 448.

Grodzinski, B., Madore, M., Shingles, R.A. and Woodrow, L. 1987. Partitioning and metabolism of photorespiratory intermediates. In: Biggins, J. (Ed.) *Progress in Photosynthesis Research*. W. Junk, The Hague, The Netherlands, pp. 645-652.

Hamerlynck, E.P., Huxman, T.E., Loik, M.E. and Smith, S.D. 2000. Effects of extreme high temperature, drought and elevated  $CO_2$  on photosynthesis of the Mojave Desert

evergreen shrub, Larrea tridentata. Plant Ecology 148: 183-193.

Hanson, K.R. and Peterson, R.B. 1986. Regulation of photorespiration in leaves: Evidence that the fraction of ribulose bisphosphate oxygenated is conserved and stoichiometry fluctuates. *Archives for Biochemistry and Biophysics* **246**: 332-346.

Hofer, H.R. 1992. Veranderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. *Ber. Geobot. Inst. Eidgenoss. Tech. Hochsch. Stift. Rubel Zur* 58: 39-54.

Holzinger, B., Hulber, K., Camenisch, M. and Grabherr, G. 2008. Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. *Plant Ecology* **195**: 179-196.

Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric  $CO_2$  enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153-203.

Idso, S.B. 1989. Carbon Dioxide and Global Change: Earth in Transition. IBR Press, Tempe, AZ.

Idso, S.B. 1995. *CO*<sub>2</sub> and the Biosphere: The Incredible Legacy of the Industrial Revolution. Kuehnast Lecture Series, Special Publication. Department of Soil, Water & Climate, University of Minnesota, St. Paul, MN.

Idso, S.B., Allen, S.G., Anderson, M.G. and Kimball, B.A. 1989. Atmospheric CO<sub>2</sub> enrichment enhances survival of *Azolla* at high temperatures. *Environmental and Experimental Botany* **29**: 337-341.

Idso, S.B. and Kimball, B.A. 2001. CO<sub>2</sub> enrichment of sour orange trees: 13 years and counting. *Environmental and Experimental Botany* **46**: 147-153.

Idso, S.B., Kimball, B.A., Anderson, M.G. and Mauney, J.R. 1987. Effects of atmospheric  $CO_2$  enrichment on plant growth: The interactive role of air temperature. *Agriculture, Ecosystems and Environment* **20**: 1-10.

Johnson, H.B., Polley, H.W. and Mayeux, H.S. 1993. Increasing  $CO_2$  and plant-plant interactions: Effects on natural vegetation. *Vegetatio* **104-105**: 157-170.

Jurik, T.W., Weber, J.A. and Gates, D.M. 1984. Short-term effects of  $CO_2$  on gas exchange of leaves of bigtooth aspen (*Populus grandidentata*) in the field. *Plant Physiology* **75**: 1022-1026.

Kappen, L. 1981. Ecological significance of resistance to high temperature. In: Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H. (Eds.) *Physiological Plant Ecology. I. Response to the Physical Environment*. Springer-Verlag, New York, NY, pp. 439-474. Keller, F., Kienast, F. and Beniston, M. 2000. Evidence of response of vegetation to environmental change on highelevation sites in the Swiss Alps. *Regional Environmental Change* **1**: 70-77.

Kelly, C.K., Chase, M.W., de Bruijn, A., Fay, M.F. and Woodward, F.I. 2003. Temperature-based population segregation in birch. *Ecology Letters* **6**: 87-89.

Kimball, B.A. 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**: 779-788.

Kirschbaum, M.U.F. 1994. The sensitivity of  $C_3$  photosynthesis to increasing  $CO_2$  concentration: a theoretical analysis of its dependence on temperature and background  $CO_2$  concentration. *Plant, Cell and Environment* **17**: 747-754.

Klanderud, K. and Birks, H.J.B. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* **13**: 1-6.

Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* **90**: 68-77.

Kullman, L. 2007. Long-term geobotanical observations of climate change impacts in the Scandes of West-Central Sweden. *Nordic Journal of Botany* **24**: 445-467.

Lacoul, P. and Freedman, B. 2006. Recent observation of a proliferation of *Ranunculus trichophyllus* Chaix. in highaltitude lakes of Mount Everest Region. *Arctic, Antarctic and Alpine Research* **38**: 394-398.

Lange, O.L. and Lange, R. 1963. Untersuchungen uber Blattemperaturen, Transpiration und Hitzeresistenz an Pflanzen mediterraner Standorte (Costa Brava, Spanien). *Flora* **153**: 387-425.

Levitt, J. 1980. Responses of Plants to Environmental Stresses. Vol.1. Chilling, Freezing, and High Temperature Stresses. Academic Press, New York, NY.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography* **25**: 735-742.

Long, S.P. 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric  $CO_2$  concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**: 729-739.

McMurtrie, R.E. and Wang, Y.-P. 1993. Mathematical models of the photosynthetic response of tree stands to rising  $CO_2$  concentrations and temperatures. *Plant, Cell and Environment* **16**: 1-13.

Mooney, H.A. and West, M. 1964. Photosynthetic acclimation of plants of diverse origin. *American Journal of Botany* **51**: 825-827.

Mortensen, L.M. 1987. Review: CO<sub>2</sub> enrichment in greenhouses. Crop responses. *Scientia Horticulturae* **33**: 1-25.

Nijs, I. and Impens, I. 1996. Effects of elevated CO<sub>2</sub> concentration and climate-warming on photosynthesis during winter in *Lolium perenne*. *Journal of Experimental Botany* **47**: 915-924.

Pauli, H., Gottfried, M. and Grabherr, G. 2001. High summits of the Alps in a changing climate. The oldest observation series on high mountain plant diversity in Europe. In: Walther, G.R., Burga, C.A. and Edwards, P.J. (Eds.) *Fingerprints of climate change—Adapted behaviour and shifting species ranges*. Kluwer Academic Publisher, New York, NY, USA, pp. 139-149.

Polley, H.W., Tischler, C.R., Johnson, H.B. and Derner, J.D. 2002. Growth rate and survivorship of drought:  $CO_2$  effects on the presumed tradeoff in seedlings of five woody legumes. *Tree Physiology* **22**: 383-391.

Rowland-Bamford, A.J., Baker, J.T., Allen Jr., L.H. and Bowes, G. 1996. Interactions of CO<sub>2</sub> enrichment and temperature on carbohydrate accumulation and partitioning in rice. *Environmental and Experimental Botany* **36**: 111-124.

Rubel, E. 1912. Pflanzengeographische Monographie des Berninagebietes. Engelmann, Leipzig, DE.

Saxe, H., Ellsworth, D.S. and Heath, J. 1998. Tree and forest functioning in an enriched  $CO_2$  atmosphere. *New Phytologist* **139**: 395-436.

Seemann, J.R., Berry, J.A. and Downton, J.S. 1984. Photosynthetic response and adaptation to high temperature in desert plants. A comparison of gas exchange and fluorescence methods for studies of thermal tolerance. *Plant Physiology* **75**: 364-368.

Strain, B.R., Higginbottom, K.O. and Mulroy, J.C. 1976. Temperature preconditioning and photosynthetic capacity of *Pinus taeda* L. *Photosynthetica* **10**: 47-53.

Taiz, L. and Zeiger, E. 1991. *Plant Physiology*. Benjamin-Cummings, Redwood City, CA.

Taub, D.R., Seeman, J.R. and Coleman, J.S. 2000. Growth in elevated CO<sub>2</sub> protects photosynthesis against hightemperature damage. *Plant, Cell and Environment* **23**: 649-656.

Tuba, Z., Csintalan, Z., Szente, K., Nagy, Z. and Grace, J. 1998. Carbon gains by desiccation-tolerant plants at elevated CO<sub>2</sub>. *Functional Ecology* **12**: 39-44.

Veres, J.S. and Williams III, G.J. 1984. Time course of photosynthetic temperature acclimation in *Carex eleocharis* Bailey. *Plant, Cell and Environment* 7: 545-547.

Virtanen, R., Eskelinen, A. and Gaare, E. 2003. Long-term changes in alpine plant communities in Norway and Finland. In: Nagy, L., Grabherr, G., Korner, C. and Thompson, D.B.A. (Eds.) *Alpine Biodiversity in Europe*. Springer, Berlin, Germany, pp. 411-422.

Volk, T. 1987. Feedbacks between weathering and atmospheric CO2 over the last 100 million years. *American Journal of Science* **287**: 763-779.

Vu, J.C.V., Allen Jr., L.H., Boote, K.J. and Bowes, G. 1997. Effects of elevated  $CO_2$  and temperature on photosynthesis and Rubisco in rice and soybean. *Plant, Cell and Environment* **20**: 68-76.

Walther, G.R. 2003. Plants in a warmer world. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 169-185.

Walther, G.-R., Beissner, S. and Burga, C.A. 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* **16**: 541-548.

Wilks, D.S., Wolfe, D.W. and Riha, S.J. 1995. Simple carbon assimilation response functions from atmospheric CO<sub>2</sub>, and daily temperature and shortwave radiation. *Global Change Biology* **1**: 337-346.

Wittwer, S.H. 1988. *The Greenhouse Effect*. Carolina Biological Supply, Burlington, NC.

Woodward, F.I. 1987. *Climate and Plant Distribution*. Cambridge University Press, Cambridge, UK.

Woodward, F.I. 1988. Temperature and the distribution of plant species and vegetation. In: Long, S.P. and Woodward, F.I. (Eds.), *Plants and Temperature. Vol. 42, The Company of Biologists Limited*, Cambridge, UK, pp. 59-75.

# 8.3. Coral Reefs

the IPCC, "many studies According to incontrovertibly link coral bleaching to warmer sea surface temperature ... and mass bleaching and coral mortality often results beyond key temperature thresholds" (IPCC 2007-II, p. 235). "Modelling," the IPCC goes on to say, "predicts a phase switch to algal dominance on the Great Barrier Reef and Caribbean reefs in 2030 to 2050." The IPCC further claims that "coral reefs will also be affected by rising atmospheric CO<sub>2</sub> concentrations ... resulting in declining calcification" (Ibid.).

In the following pages we review the scientific literature on coral reefs in an effort to determine if the ongoing rise in the air's  $CO_2$  content, rising temperatures, or rising sea levels pose a threat to

these incomparable underwater ecosystems. Because the fate of the earth's corals has become so prominent in the debate over climate change and because our findings are so entirely at odds with those of the IPCC, we present a brief summary of our key findings here:

- There is no simple linkage between high temperatures and coral bleaching.
- As living entities, corals are not only acted upon by the various elements of their environment, they also react or respond to them. And when changes in environmental factors pose a challenge to their continued existence, they sometimes take major defensive or adaptive actions to ensure their survival.
- A particularly ingenious way coral respond to environmental stress is to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode by one or more varieties of zooxanthellae that are more tolerant of the stress that caused the bleaching.
- The persistence of coral reefs through geologic time—when temperatures were as much as 10°-15°C warmer than at present, and atmospheric CO<sub>2</sub> concentrations were two to seven times higher than they are currently—provides substantive evidence that these marine entities can successfully adapt to a dramatically changing global environment. Thus, the recent die-off of many corals cannot be due solely, or even mostly, to global warming or the modest rise in atmospheric CO<sub>2</sub> concentration over the course of the Industrial Revolution.
- The 18- to 59-cm warming-induced sea-level rise that is predicted for the coming century by the IPCC—which could be greatly exaggerated if predictions of CO<sub>2</sub>-induced global warming are wrong—falls well within the range (2 to 6 mm per year) of typical coral vertical extension rates, which exhibited a modal value of 7 to 8 mm per year during the Holocene and can be more than double that value in certain branching corals. Rising sea levels should therefore present no difficulties for coral reefs. In fact, rising sea levels may have a positive effect on reefs, permitting increased coral growth in areas that have already reached the upward limit imposed by current sea levels.

- The rising CO<sub>2</sub> content of the atmosphere may induce changes in ocean chemistry (pH) that could slightly reduce coral calcification rates; but potential positive effects of hydrospheric CO<sub>2</sub> enrichment may more than compensate for this modest negative phenomenon.
- Theoretical predictions indicate that coral calcification rates should decline as a result of increasing atmospheric CO<sub>2</sub> concentrations by as much as 40 percent by 2100. However, real-world observations indicate that elevated CO<sub>2</sub> and elevated temperatures are having the opposite effect.

#### References

IPCC, 2007-II. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson. (Eds.) Cambridge University Press, Cambridge, UK.

### 8.3.1. Indirect Threats

Coral bleaching ranks as probably the most frequently cited indirect negative consequence believed to result from  $CO_2$ -induced global warming. It is a phenomenon that is characterized by a loss of color in certain reef-building corals that occurs when the algal symbionts, or *zooxanthellae*, living within the host corals are subjected to various stresses and expelled from them, resulting in a loss of photosynthetic pigments from the coral colony. If the stress is mild, or short in duration, the affected corals often recover and regain their normal complement of zooxanthellae. However, if the stress is prolonged, or extreme, the corals eventually die, being deprived of their primary food source.

We begin our review of the subject by discussing the many suspected causes of coral bleaching, almost all of which have been attributed (often implausibly) to CO<sub>2</sub>-induced global warming. Then, we examine the possibility that corals can adapt to the various environmental threats they face, after which we explore whether the widespread bleaching events seen in recent decades are indeed caused by global warming. We conclude our discussion of the major indirect threats facing modern coral reefs by examining the threat of rising sea levels, which the IPCC predicts will occur over the course of the twenty-first century.

### 8.3.1.1. Coral Bleaching

### 8.3.1.1.1. Temperature Effects

One of the most frequently cited causes of coral bleaching is anomalously high water temperature (Linden, 1998). The origin of this attribution can be traced to the strong El Niño event of 1982-83, in which widespread bleaching was reported in corals exposed to unusually high surface water temperatures (Glynn, 1988). Since that time, a number of other such observations have been made (Cook *et al.*, 1990; Glynn 1991; Montgomery and Strong, 1994; Brown *et al.*, 1996); and several laboratory studies have demonstrated that elevated seawater temperatures can indeed induce bleaching in corals (Hoegh-Guldberg and Smith, 1989; Jokiel and Coles, 1990; Glynn and D'Croz, 1990).

However, just as anomalously high seawater temperatures have been found to be correlated with coral reef bleaching events, so too have anomalously low seawater temperatures been identified with this phenomenon (Walker et al., 1982; Coles and Fadlallah, 1990; Muscatine et al., 1991; Gates et al., 1992; Saxby et al., 2003; Hoegh-Guldberg and Fine 2004; Yu et al., 2004). These observations suggest that the crucial link between temperature and coral reef bleaching may not reside in the absolute temperature of the water surrounding the corals, but in the rapidity with which the temperature either rises above or falls below the temperature regime to which the corals are normally adapted. Winter et al. (1998), for example, studied relationships between coral bleaching and nine different temperature indices, concluding that although "prolonged heat stress may be an important precondition for bleaching to occur," sharp temperature changes act as the "immediate trigger."

In a related study, Jones (1997) reported coral bleaching on a portion of Australia's Great Barrier Reef just after average daily sea water temperature rose by 2.5°C over the brief period of eight days. Likewise, Kobluk and Lysenko (1994) observed severe coral bleaching following an 18-hour *decline* of 3°C in seawater temperature. Because the corals studied by the latter researchers had experienced

massive bleaching two years earlier as a result of an anomalous 4°C *increase* in water temperature, the authors concluded that coral bleaching is more a function the rapidity of a temperature change than it is of the absolute magnitude or sign of the change, i.e., heating or cooling.

Further evidence that high or low seawater temperatures *per se* are not the critical factors in producing coral bleaching is provided by Podesta and Glynn (1997), who examined a number of temperature-related indices of surface waters in the vicinity of Panama over the period 1970-1994. Their analysis revealed that for the two years of highest maximum monthly sea surface temperature, 1972 and 1983, coral bleaching was reported only in 1983, while 1972 produced no bleaching whatsoever, in spite of the fact that water temperatures that year were just as high as they were in 1983.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/c/bleachingtemp.php</u>.

### References

Brown, B.E., Dunne, R.P. and Chansang, H. 1996. Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years. *Coral Reefs* **15**: 151-152.

Coles, S.L. and Fadlallah, Y.H. 1990. Reef coral survival and mortality at low temperatures in the Arabian Gulf: New species-specific lower temperature limits. *Coral Reefs* **9**: 231-237.

Cook, C.B., Logan, A., Ward, J., Luckhurst, B. and Berg Jr., C.J. 1990. Elevated temperatures and bleaching on a high latitude coral reef: The 1988 Bermuda event. *Coral Reefs* **9**: 45-49.

Gates, R.D., Baghdasarian, G. and Muscatine, L. 1992. Temperature stress causes host cell detachment in symbiotic enidarians: Implication for coral bleaching. *Biological Bulletin* **182**: 324-332.

Glynn, P.W. 1988. El Niño-Southern Oscillation 1982-83: Nearshore population, community, and ecosystem responses. *Annual Review of Ecology and Systematics* **19**: 309-345.

Glynn, P.W. 1991. Coral bleaching in the 1980s and possible connections with global warming trends. *Ecology and Evolution* **6**: 175-179.

Glynn, P.W. and D'Croz, L. 1990. Experimental evidence for high temperature stress as the cause of El-Niñocoincident coral mortality. *Coral Reefs* **8**: 181-190.

Hoegh-Guldberg, O. and Fine, M. 2004. Low temperatures cause coral bleaching. *Coral Reefs* 23: 444.

Hoegh-Guldberg, O. and Smith, G.J. 1989. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper. and *Seriatopora hystrix* Dana. *Journal of Experimental Marine Biology and Ecology* **129**: 279-303.

IPCC 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Jokiel, P.L. and Coles, S.L. 1990. Response of Hawaiian and other Indo-Pacific reef corals to elevated sea temperatures. *Coral Reefs* **8**:155-162.

Jones, R.J. 1997. Changes in zooxanthellar densities and chlorophyll concentrations in corals during and after a bleaching event. *Marine Ecology Progress Series* **158**: 51-59.

Kobluk, D.R. and Lysenko, M.A. 1994. "Ring" bleaching in Southern Caribbean *Agaricia agaricites* during rapid water cooling. *Bulletin of Marine Science* **54**: 142-150.

Linden, O. 1998. Coral mortality in the tropics: Massive causes and effects. *Ambio* **27**: 588.

Montgomery, R.S. and Strong, A.E. 1994. Coral bleaching threatens oceans life. *EOS* **75**: 145-147.

Muscatine, L., Grossman, D. and Doino, J. 1991. Release of symbiotic algae by tropical sea anemones and corals after cold shock. *Marine Ecology Progress Series* **77**: 233-243.

Podesta, G.P. and Glynn, P.W. 1997. Sea surface temperature variability in Panama and Galapagos: Extreme temperatures causing coral bleaching. *Journal of Geophysical Research* **102**: 15,749-15,759.

Saxby, T., Dennison, W.C. and Hoegh-Guldberg, O. 2003. Photosynthetic responses of the coral Montipora digitata to cold temperature stress. *Marine Ecology Progress Series* **248**: 85-97.

Walker, N.D., Roberts, H.H., Rouse Jr., L.J. and Huh, O.K. 1982. Thermal history of reef-associated environments during a record cold-air outbreak event. *Coral Reefs* 1: 83-87.

Winter, A., Appeldoorn, R.S., Bruckner, A., Williams Jr., E.H. and Goenaga, C. 1998. Sea surface temperatures and coral reef bleaching off La Parguera, Puerto Rico (northeast Caribbean Sea). *Coral Reefs* **17**: 377-382. Yu, K.-F., Zhao, J.-X., Liu, T.-S., Wei, G.-J., Wang, P.X. and Collerson, K.D. 2004. High-frequency winter cooling and reef coral mortality during the Holocene climatic optimum. *Earth and Planetary Science Letters* **224**: 143-155.

#### 8.3.1.1.2. Solar Radiation Effects

The link between solar radiation and coral reef bleaching goes back more than a century to when MacMunn (1903) postulated that ultraviolet radiation could be potentially damaging to corals. It wasn't until half a century later, however, that scientists began to confirm this suspicion (Catala-Stucki, 1959; Siebeck, 1988; Gleason and Wellington, 1995).

Many investigators of the solar irradiance-coral reef bleaching link have studied the phenomenon by transplanting reef corals from deep to shallow waters. Gleason and Wellington (1993), for example, transplanted samples of the reef-building coral Montastrea annularis from a depth of 24 meters to depths of 18 and 12 meters. Using sheets of acrylic plastic to block out ultraviolet radiation on some of the coral samples, they found that the shielded corals experienced less bleaching than the unshielded corals, and that the unshielded corals at the 12-meter depth had significantly lower amounts of zooxanthellae and chlorophyll per square centimeter than all other treatment and control groups. Likewise, Hoegh-Guldberg and Smith (1989) reported bleaching in the corals Stylophora pistillata and Seriatopora hystrix when they were moved from a depth of 6 meters to 1.2 meters. Vareschi and Fricke (1986) obtained similar results when moving *Plerogyra sinuosa* from a depth of 25 meters to 5 meters. As in the case of temperature stress, however, Glynn (1996) notes that artificially reduced light levels also have been observed to cause coral bleaching.

A number of laboratory studies have provided additional evidence for a link between intense solar irradiance and coral reef bleaching, but identifying a specific wavelength or range of wavelengths as the cause of the phenomenon has been a difficult task. Fitt and Warner (1995), for example, reported that the most significant decline in symbiont photosynthesis in the coral *Montastrea annularis* occurred when it was exposed to ultraviolet and blue light; but other studies have reported coral bleaching to be most severe at shorter ultraviolet wavelengths (Droller *et al.*, 1994; Gleason and Wellington, 1995). Still others have found it to be most strongly expressed at longer photosynthetically active wavelengths (Lesser and Shick, 1989; Lesser *et al.*, 1990; Brown *et al.*, 1994).

As additional studies provided evidence for a solar-induced mechanism of coral reef bleaching (Brown *et al.*, 1994; Williams *et al.*, 1997; Lyons *et al.*, 1998), some also provided evidence for a solar radiation-temperature stress synergism (Gleason and Wellington, 1993; Rowan *et al.*, 1997; Jones *et al.*, 1998). There have been a number of situations, for example, in which corals underwent bleaching when changes in both of these parameters combined to produce particularly stressful conditions (Lesser *et al.*, 1990; Glynn *et al.*, 1992; Brown *et al.*, 1995), such as during periods of low wind velocity and calm seas, which favor the intense heating of shallow waters and concurrent strong penetration of solar radiation.

This two-parameter interaction has much to recommend it as a primary cause of coral bleaching. It is, in fact, the mechanism favored by Hoegh-Guldberg (1999), who claimed—in one of the strongest attempts made to that point in time to portray global warming as the cause of bleaching in corals—that "coral bleaching occurs when the photosynthetic symbionts of corals (zooxanthellae) become increasingly vulnerable to damage by light at higher than normal temperatures." As we shall see, however, the story is considerably more complicated.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/c/bleachingsolar.php</u>.

### References

Brown, B.E., Dunne, R.P., Scoffin, T.P. and Le Tissier, M.D.A. 1994. Solar damage in intertidal corals. *Marine Ecology Progress Series* **105**: 219-230.

Brown, B.E., Le Tissier, M.D.A. and Bythell, J.C. 1995. Mechanisms of bleaching deduced from histological studies of reef corals sampled during a natural bleaching event. *Marine Biology* **122**: 655-663.

Brown, B.E., Le Tissier, M.D.A. and Dunne, R.P. 1994. Tissue retraction in the scleractinian coral *Coeloseris mayeri*, its effect upon coral pigmentation, and preliminary implications for heat balance. *Marine Ecology Progress Series* **105**: 209-218.

Catala-Stucki, R. 1959. Fluorescence effects from corals irradiated with ultra-violet rays. *Nature* **183**: 949.

Droller, J.H., Faucon, M., Maritorena, S. and Martin, P.M.V. 1994. A survey of environmental physico-chemical parameters during a minor coral mass bleaching event in Tahiti in 1993. *Australian Journal of Marine and Freshwater Research* **45**: 1149-1156.

Fitt, W.K. and Warner, M.E. 1995. Bleaching patterns of four species of Caribbean reef corals. *Biological Bulletin* **189**: 298-307.

Gleason, D.F. and Wellington, G.M. 1993. Ultraviolet radiation and coral bleaching. *Nature* **365**: 836-838.

Gleason, D.F. and Wellington, G.M. 1995. Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Marine Biology* **123**: 693-703.

Glynn, P.W. 1996. Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology* **2**: 495-509.

Glynn, P.W., Imai, R., Sakai, K., Nakano, Y. and Yamazato, K. 1992. Experimental responses of Okinawan (Ryukyu Islands, Japan) reef corals to high sea temperature and UV radiation. *Proceedings of the 7<sup>th</sup> International Coral Reef Symposium* **1**: 27-37.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866.

Hoegh-Guldberg, O. and Smith, G.J. 1989. The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper. and *Seriatopora hystrix* Dana. *Journal of Experimental Marine Biology and Ecology* **129**: 279-303.

Jones, R.J., Hoegh-Guldberg, O., Larkum, A.W.D. and Schreiber, U. 1998. Temperature-induced bleaching of corals begins with impairment of the  $CO_2$  fixation mechanism in zooxanthellae. *Plant, Cell and Environment* **21**: 1219-1230.

Lesser, M.P. and Shick, J.M. 1989. Effects of irradiance and ultraviolet radiation on photoadaptation in the zooxanthellae of *Aiptasia pallida*: Primary production, photoinhibition, and enzymatic defense against oxygen toxicity. *Marine Biology* **102**: 243-255.

Lesser, M.P., Stochaj, W.R., Tapley, D.W. and Shick, J.M. 1990. Bleaching in coral reef anthozoans: Effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* **8**: 225-232.

Lyons, M.M., Aas, P., Pakulski, J.D., Van Waasbergen, L., Miller, R.V., Mitchell, D.L. and Jeffrey, W.H. 1998. DNA damage induced by ultraviolet radiation in coral-reef microbial communities. *Marine Biology* **130**: 537-543. MacMunn, C.A. 1903. On the pigments of certain corals, with a note on the pigment of an asteroid. Gardiner, J.S. (Ed.) *The fauna and geography of the Maldive and Laccadive Archipelagoes*. Cambridge, UK: Cambridge University Press. Vol. 1, pp. 184-190.

Rowan, R., Knowlton, N., Baker, A. and Jara, J. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* **388**: 265-269.

Siebek, O. 1988. Experimental investigation of UV tolerance in hermatypic corals (Scleractinian). *Marine Ecology Progress Series* **43**: 95-103.

Vareschi, E. and Fricke, H. 1986. Light responses of a scleractinian coral (*Plerogyra sinuosa*). *Marine Biology* **90**: 395-402.

Williams, D.E., Hallock, P., Talge, H.K., Harney, J.N. and McRae, G. 1997. Responses of *Amphistegina gibbosa* populations in the Florida Keys (U.S.A.) to a multi-year stress event (1991-1996). *Journal of Foraminiferal Research* **27**: 264-269.

### 8.3.1.1.3. Other Causes

In a review of the causes of coral bleaching, Brown (1997) listed (1) elevated seawater temperature, (2) decreased seawater temperature, (3) intense solar radiation, (4) the combination of intense solar radiation and elevated temperature, (5) reduced salinity, and (6) bacterial infections. In a similar review, Meehan and Ostrander (1997) additionally listed (7) increased sedimentation and (8) exposure to toxicants. We have already commented on the four most prominent of these phenomena; we now address the remaining four.

With respect to seawater salinity, Meehan and Ostrander (1997) noted that, as with temperature, both high and low values have been observed to cause coral bleaching. Low values typically occur as a result of seawater dilution caused by high precipitation events or storm runoff; high values are much more rare, typically occurring only in the vicinity of desalinization plants.

A number of studies also have clearly delineated the role of bacterial infections in causing coral reef bleaching (Ritchie and Smith, 1998); this phenomenon, too, may have a connection to high seawater temperatures. In a study of the coral *Oculina patagonica* and the bacterial agent *Vibrio* AK-1, for example, Kushmaro *et al.* (1996, 1997) concluded that bleaching of colonies of this coral along the Mediterranean coast has its origin in bacterial infection, and that warmer temperatures may lower the resistance of the coral to infection and/or increase the virulence of the bacterium. In subsequent studies of the same coral and bacterium, Toren *et al.* (1998) and Kushmaro *et al.* (1998) further demonstrated that this high temperature effect may operate by enhancing the ability of the bacterium to adhere to the coral.

In discussing their findings, Kushmaro et al. (1998) commented on the "speculation that increased seawater temperature, resulting from global warming or El Niño events, is the direct cause of coral bleaching." In contradiction of this presumption, they cited several studies of coral bleaching events that were not associated with any major sea surface temperature anomalies, and they explicitly stated, "it is not yet possible to determine conclusively that bleaching episodes and the consequent damage to reefs is due to global climate change." Likewise, Toren et al. (1998) noted the extensive bleaching that occurred on the Great Barrier Reef during the summer of 1982 was also not associated with any major sea surface temperature increase; they stated, "several authors have reported on the patchy spatial distribution and spreading nature of coral bleaching," which they correctly noted is inconsistent with the global-warming-induced coral bleaching hypothesis. Instead, they noted, "the progression of observable changes that take place during coral bleaching is reminiscent of that of developing microbial biofilms," a point that will later be seen to be of great significance.

With respect to sedimentation, high rates have been conclusively demonstrated to lead to coral bleaching (Wesseling et al., 1999); most historical increases in sedimentation rates are clearly humaninduced. Umar et al. (1998), for example, listed such contributing anthropogenic activities as deforestation, agricultural practices, coastal development, construction, mining, drilling, dredging, and tourism. Nowlis et al. (1997) also discussed "how land development can increase the risk of severe damage to coral reefs by sediment runoff during storms." But it has been difficult to determine just how much these phenomena have varied over the past few centuries.

Knowledge in this area took a quantum leap forward with the publication of a study by McCulloch *et al.* (2003) that provided a 250-year record of sediment transfer to Havannah Reef—a site on the inner Great Barrier Reef of northern Queensland, Australia—by flood plumes from the Burdekin River. According to the authors of that study, sediments suspended in the Burdekin River contain barium (Ba), which is desorbed from the particles that carry it as they enter the ocean, where growing corals incorporate it into their skeletons along with calcium (Ca). Hence, when more sediments are carried to the sea by periodic flooding and more gradual longerterm changes in land use that lead to enhanced soil erosion, the resultant increases in sediment load are recorded in the Ba/Ca ratio of coral skeleton material. Inspired by these facts, McCulloch *et al.* measured Ba/Ca ratios in a 5.3-meter-long coral core from Havannah Reef that covered the period from about 1750 to 1985, as well as in some shorter cores from Havannah Reef and nearby Pandora Reef that extended the proxy sediment record to 1998.

Results of the analysis revealed that prior to the time of European settlement, which began in the Burdekin catchment in 1862, there was "surprisingly little evidence for flood-plume related activity from the coral Ba/Ca ratios." Soon after, however, land clearance and domestic grazing intensified and the soil became more vulnerable to monsoon-raininduced erosion. By 1870, baseline Ba/Ca ratios had risen by 30 percent and "within one to two decades after the arrival of European settlers in northern Queensland, there were already massive impacts on the river catchments that were being transmitted to the waters of the inner Great Barrier Reef." During subsequent periods of flooding, in fact, the transport of suspended sediment to the reef increased by fully five- to ten-fold over what had been characteristic of pre-European settlement times.

In a companion article, Cole (2003) reported that corals from East Africa "tell a similar tale of erosion exacerbated by the imposition of colonial agricultural practices in the early decades of the twentieth century." There, similar coral data from Malindi Reef, Kenya, indicate "a low and stable level of barium before about 1910 which rises dramatically by 1920, with a simultaneous increase in variance," a phenomenon that was also evident in the Australian data.

What are the implications of these observations? Cole concludes that "human activity, in the form of changing land use, has added sedimentation to the list of stresses experienced by reefs." Furthermore, as land-use intensification is a widespread phenomenon, she notes that "many reefs close to continents or large islands are likely to have experienced increased delivery of sediment over the past century," which suggests the stress levels produced by this phenomenon are likely to have increased over the past century as well. In addition, Cole logically concludes that as coastal populations continue to rise, "this phenomenon is likely to expand."

Lastly, a number of poisonous substances are known to have the capacity to induce coral bleaching. Some of them are of human origin, such as herbicides, pesticides, and even excess nutrients that make their way from farmlands to the sea (Simkiss, 1964; Pittock, 1999). Other poisons originate in the sea itself, many the result of metabolic waste products of other creatures (Crossland and Barnes, 1974) and some a by-product of the coral host itself (Yonge, 1968). Each of these toxicants presents the coral community with its own distinct challenge.

Taken together, these findings suggest a number of sources of stress on coral survival and growth that have little or nothing to do with rising CO<sub>2</sub> concentrations or temperatures. It is also clear that human population growth and societal and economic development over the period of the Industrial Revolution have predisposed coral reefs to everincreasing incidences of bleaching and subsequent mortality via a gradual intensification of near-coastal riverine sediment transport rates.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/c/subject\_c.php</u> under the heading Coral Reefs (Bleaching: Causes).

### References

Brown, B.E. 1997. Coral bleaching: Causes and consequences. *Coral Reefs* 16: S129-S138.

Cole, J. 2003. Dishing the dirt on coral reefs. *Nature* **421**: 705-706.

Crossland, C.J. and Barnes, D.J. 1974. The role of metabolic nitrogen in coral calcification. *Marine Biology* **28**: 325-332.

Kushmaro, A., Rosenberg, E., Fine, M. and Loya, Y. 1997. Bleaching of the coral *Oculina patagonica* by *Vibrio* AK-1. *Marine Ecology Progress Series* **147**: 159-165.

Kushmaro, A., Loya, Y., Fine, M. and Rosenberg, E. 1996. Bacterial infection and coral bleaching. *Nature* **380**: 396.

Kushmaro, A., Rosenberg, E., Fine, M., Ben Haim, Y. and Loya, Y. 1998. Effect of temperature on bleaching of the coral *Oculina patagonica* by *Vibrio* AK-1. *Marine Ecology Progress Series* **171**: 131-137.

McCulloch, M., Fallon, S., Wyndham, T., Hendy, E., Lough, J. and Barnes, D. 2003. Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. *Nature* **421**: 727-730.

Meehan, W.J. and Ostrander, G.K. 1997. Coral bleaching: A potential biomarker of environmental stress. *Journal of Toxicology and Environmental Health* **50**: 529-552.

Nowlis, J.S., Roberts, C.M., Smith, A.H. and Siirila, E. 1997. Human-enhanced impacts of a tropical storm on nearshore coral reefs. *Ambio* **26**: 515-521.

Pittock, A.B. 1999. Coral reefs and environmental change: Adaptation to what? *American Zoologist* **39**: 10-29.

Ritchie, K.B. and Smith, G.W. 1998. Type II white-band disease. *Revista De Biologia Tropical* **46**: 199-203.

Simkiss, K. 1964. Phosphates as crystal poisons of calcification. *Biological Review* **39**: 487-505.

Toren, A., Landau, L., Kushmaro, A., Loya, Y. and Rosenberg, E. 1998. Effect of temperature on adhesion of *Vibrio* strain AK-1 to *Oculina patagonica* and on coral bleaching. *Applied and Environmental Microbiology* **64**: 1379-1384.

Umar, M.J., McCook, L.J. and Price, I.R. 1998. Effects of sediment deposition on the seaweed Sargassum on a fringing coral reef. *Coral Reefs* **17**: 169-177.

Wesseling, I., Uychiaoco, A.J., Alino, P.M., Aurin, T. and Vermaat, J.E. 1999. Damage and recovery of four Philippine corals from short-term sediment burial. *Marine Ecology Progress Series* **176**: 11-15.

Yonge, C.M. 1968. Living corals. *Proceedings of the Royal Society of London B* **169**: 329-344.

### 8.3.1.2. Adaptation

Considering the many threats to the health of coral reefs in today's world of extensive socioeconomic and environmental change, how can these incomparable repositories of underwater biodiversity be expected to escape irreversible bleaching and death? In response to this question, Glynn (1996) pointed out that "numerous reef-building coral species have endured three periods of global warming, from the Pliocene optimum (4.3-3.3 million years ago) through the Eemian interglacial (125 thousand years ago) and the mid-Holocene (6000when atmospheric 5000 vears ago).  $CO_2$ concentrations and sea temperatures often exceeded those of today." In fact, Glynn observed that "an increase in sea warming of less than 2°C would result

in a greatly increased diversity of corals in certain high latitude locations."

How does this happen? Living organisms are resilient. Various lifeforms can tolerate temperatures from below freezing to the boiling point of water; others inhabit niches where light intensity varies from complete darkness to full sunlight. One reason for this great versatility is that, given time to adapt, nearly all living organisms can learn to survive in conditions well outside their normal zones of environmental tolerance. As noted by Gates and Edmunds (1999), results of numerous studies indicate that "corals routinely occupy a physically heterogeneous environment," which "suggests they should possess a high degree of biological flexibility." And indeed they do, as evidenced by their successful responses to the different threats that cause coral bleaching, which are examined in the following subsections.

### References

Gates, R.D. and Edmunds, P.J. 1999. The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* **39**: 30-43.

Glynn, P.W. 1996. Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology* **2**: 495-509.

### 8.3.1.2.1. Response to Solar Radiation Stress

One example of adaptation to stress imposed by high solar irradiance comes from studies of corals that exhibit a "zonation" of their symbiont taxa with depth, where symbiont algae that are less tolerant of intense solar radiation grow on corals at greater depths below the ocean surface (Rowan and Knowlton, 1995; Rowan et al., 1997). It has also been demonstrated that zooxanthellae in corals possess a number of light-quenching mechanisms that can be employed to reduce the negative impacts of excess light (Hoegh-Guldberg and Jones, 1999; Ralph et al., 1999). Both the coral host and its symbionts also have the capacity to produce amino acids that act as natural "sunscreens" (Hoegh-Guldberg, 1999); and they can regulate their enzyme activities to enhance internal scavenging systems that remove noxious oxygen radicals produced in coral tissues as a result of high light intensities (Dykens and Shick, 1984; Lesser et al., 1990; Matta and Trench, 1991; Shick et al., 1996).

Another adaptive mechanism to lessen the stress of solar irradiance is coral tissue retraction, according to Brown et al. (1994), who studied the phenomenon in the scleractinian coral Coeloseris mayeri at coral reefs in Phuket, Thailand by examining the retraction and recovery of coral tissues over a tidal cycle. Results of their analysis showed that extreme tissue retraction was observed approximately 85 minutes after initial sub-aerial coral exposure. Tissue retraction, however, did not involve any reduction in chlorophyll concentration or algae symbiont abundance; the tissues expanded over the coral skeletons to pre-retraction conditions following the return of the tide. The adaptive benefits of tissue retraction, according to the authors, "include increased albedo, leading to a reduction in absorbed solar energy of 10%, ... and possible avoidance of photochemical damage or photoinhibition at high solar irradiance."

Another intriguing idea was proposed by Nakamura and van Woesik (2001), who upon evaluating the bleaching of large and small coral colonies along the western coast of Okinawa, Japan during the summers of 1998 and 2001, argued that small coral colonies should survive thermal and light stress more readily than large coral colonies based on mass transfer theory, which suggests that rates of passive diffusion are more rapid for small colonies than for large colonies. Still another reason why large coral colonies suffer more than small colonies during environmental conditions conducive to bleaching is the fact that small Acropora recruits, according to Bena and van Woesik (2004), "contain high concentrations of fluorescent proteins (Papina et al., 2002), which have photoprotective properties (Salih et al., 2000)," and they note that "a high concentration of photoprotective pigments in early life, when planulae are near the surface and as newly settled recruits, may facilitate survival during this phase as well as during stress events involving both high irradiance and thermal anomalies (van Woesik, 2000)."

In addition to the adaptive phenomena described above, the earth appears to possess a natural "heat vent" over the tropics that suppresses the intensity of solar radiation to which corals are exposed whenever dangerously high water temperatures are approached. According to Hoegh-Guldberg (1999), 29.2°C is the threshold water temperature above which significant bleaching can be expected to occur in many tropical corals. However, as Sud *et al.* (1999) have demonstrated, deep atmospheric convection is typically initiated whenever sea surface temperatures (SSTs) reach a value of about 28°C, so that an upper SST on the order of 30°C is rarely exceeded. As SSTs reach 28-29°C, the cloud-base airmass is charged with sufficient moist static energy for the clouds to reach the upper troposphere. At this point, the billowing cloud cover reduces the amount of solar radiation received at the surface of the sea, while cool and dry downdrafts produced by the moist convection tend to promote ocean surface cooling by increasing sensible and latent heat fluxes at the air-sea interface that cause temperatures there to decline. This "thermostat-like control," as Sud et al. describe it, tends "to ventilate the tropical ocean efficiently and help contain the SST between 28-30°C," which is essentially a fluctuating temperature band of  $\pm 1^{\circ}C$ centered on the bleaching threshold temperature of 29.2°C identified by Hoegh-Guldberg.

Some other intriguing observations also point to the existence of a natural phenomenon of this nature. Satheesh and Ramanathan (2000), for example, determined that polluted air from south and southeast Asia absorbs enough solar radiation over the northern Indian Ocean during the dry monsoon season to heat the atmosphere there by 1-3°C per day at solar noon, thereby greatly reducing the intensity of solar radiation received at the surface of the sea. Ackerman et al. (2000), however, calculated that this atmospheric heating would decrease cloud-layer relative humidity and reduce boundary-layer mixing, thereby leading to a 25 percent to 50 percent drop in daytime cloud cover relative to that of an aerosol-free atmosphere, which could well negate the surface cooling effect suggested by the findings of Satheesh and Ramanathan. But in a test of this hypothesis based on data obtained from the Extended Edited Cloud Report Archive, Norris (2001) determined that daytime low-level ocean cloud cover (which tends to cool the water surface) not only did not decrease from the 1950s to 1990s, it actually increased ... in both the Northern and Southern Hemispheres and at essentially all hours of the day.

Commenting on this finding, Norris remarked that "the observed all-hours increase in low-level cloud cover over the time period when soot aerosol has presumably greatly increased argues against a dominant effect of soot solar absorption contributing to cloud 'burn-off'." Hence, he says, "other processes must be compensating," one of which, we suggest, could be the one described by Sud *et al.* 

Another process is the "adaptive infrared iris" phenomenon described by Lindzen *et al.* (2001).

Working with upper-level cloudiness data obtained from the Japanese Geostationary Meteorological Satellite and SST data obtained from the National for Environmental Prediction. Centers the atmospheric scientists found a strong inverse relationship between upper-level cloud area and the mean SST of cloudy regions, such that the area of cirrus cloud coverage (which tends to warm the planet) normalized by a measure of the area of cumulus coverage (which tends to cool the planet) decreased about 22 percent for each 1°C increase in the SST of the cloudy regions.

"Essentially," in the words of the scientists, "the cloudy-moist region appears to act as an infrared adaptive iris that opens up and closes down the regions free of upper-level clouds, which more effectively permit infrared cooling, in such a manner as to resist changes in tropical surface temperatures." So substantial is this phenomenon, Lindzen *et al.* are confident it could "more than cancel all the positive feedbacks in the more sensitive current climate models," which are routinely used to predict the climatic consequences of projected increases in atmospheric CO<sub>2</sub> concentration.

Is there any real-world evidence the natural thermostat discovered by Sud et al. and Lindzen et al. has actually been instrumental in preventing coral bleaching? Mumby et al. (2001) examined long-term meteorological records from the vicinity of the Society Islands, which provide what they call "the first empirical evidence that local patterns of cloud cover may influence the susceptibility of reefs to mass bleaching and subsequent coral mortality during periods of anomalously high SST." With respect to the great El Niño of 1998, Mumby and his colleagues determined that SSTs in the Society Islands sector of French Polynesia were above the 29.2°C bleaching threshold for a longer period of time (two months) than in all prior bleaching years of the historical record. However, mass coral bleaching, which was extensive in certain other areas, was found to be "extremely mild in the Society Islands" and "patchy at a scale of 100s of km." What provided the coral relief from extreme sun and heat? As Mumby and his associates describe it, "exceptionally high cloud cover significantly reduced the number of sun hours during the summer of 1998," much as one would have expected earth's natural thermostat to have done in the face of such anomalously high SSTs. The marine scientists also note that extensive spotty patterns of cloud cover, besides saving most of the coral they studied, "may partly account for spatial patchiness in

bleaching intensity and/or bleaching-induced mortality in other areas."

In conclusion, although the natural thermostat cannot protect all of earth's corals from lifethreatening bleaching during all periods of anomalously high SSTs, it apparently protects enough of them enough of the time to ensure that sufficiently large numbers of corals survive to perpetuate their existence, since living reefs have persisted over the eons in spite of the continuing recurrence of these ever-present environmental threats. And perhaps that is how it has always been, although there are currently a host of unprecedented anthropogenic forces of site-specific origin that could well be weakening the abilities of some species to tolerate the types of thermal and solar stresses they have successfully "weathered" in the past.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/c/bleachrespsolar.php</u>.

### References

Ackerman, A.S., Toon, O.B., Stevens, D.E., Heymsfield, A.J., Ramanathan, V. and Welton, E.J. 2000. Reduction of tropical cloudiness by soot. *Science* **288**: 1042-1047.

Bena, C. and van Woesik, R. 2004. The impact of two bleaching events on the survival of small coral colonies (Okinawa, Japan). *Bulletin of Marine Science* **75**: 115-125.

Brown, B.E., Le Tissier, M.D.A. and Dunne, R.P. 1994. Tissue retraction in the scleractinian coral Coeloseris mayeri, its effect upon coral pigmentation, and preliminary implications for heat balance. *Marine Ecology Progress Series* **105**: 209-218.

Dykens, J.A. and Shick, J.M. 1984. Photobiology of the symbiotic sea anemone *Anthopleura elegantissima*: Defense against photo-dynamic effects, and seasonal photoacclimatization. *Biological Bulletin* **167**: 693-697.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866.

Hoegh-Guldberg, O. and Jones, R. 1999. Photoinhibition and photoprotection in symbiotic dinoflagellates from reefbuilding corals. *Marine Ecology Progress Series* **183**: 73-86.

Lesser, M.P., Stochaj, W.R., Tapley, D.W. and Shick, J.M. 1990. Bleaching in coral reef anthozoans: Effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. Coral Reefs 8: 225-232.

Lindzen, R.S., Chou, M.-D. and Hou, A.Y. 2001. Does the earth have an adaptive infrared iris? *Bulletin of the American Meteorological Society* **82**: 417-432.

Matta, J.L. and Trench, R.K. 1991. The enzymatic response of the symbiotic dinoflagellate *Symbiodinium microadriaticum* (Freudenthal) to growth under varied oxygen tensions. *Symbiosis* **11**: 31-45.

Mumby, P.J., Chisholm, J.R.M., Edwards, A.J., Andrefouet, S. and Jaubert, J. 2001. *Marine Ecology Progress Series* **222**: 209-216.

Nakamura, T. and van Woesik, R. 2001. Differential survival of corals during the 1998 bleaching event is partially explained by water-flow rates and passive diffusion. *Marine Ecology Progress Series* **212**: 301-304.

Norris, J.R. 2001. Has northern Indian Ocean cloud cover changed due to increasing anthropogenic aerosol? *Geophysical Research Letters* **28**: 3271-3274.

Papina, M., Sakihama, Y., Bena, C., van Woesik, R. and Yamasaki, H. 2002. Separation of highly fluorescent proteins by SDS-PAGE in Acroporidae corals. *Comp. Biochem. Phys.* **131**: 767-774.

Ralph, P.J., Gaddemann, R., Larkum, A.W.E. and Schreiber, U. 1999. In situ underwater measurements of photosynthetic activity of coral-reef dwelling endosymbionts. *Marine Ecology Progress Series* **180**: 139-147.

Rowan, R. and Knowlton, N. 1995. Intraspecific diversity and ecological zonation in coral-algal symbiosis. *Proceeding of the National Academy of Sciences, U.S.A.* **92**: 2850-2853.

Rowan, R., Knowlton, N., Baker, A. and Jara, J. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* **388**: 265-269.

Salih, A., Larkum, A., Cox, G., Kuhl, M. and Hoegh-Guldberg, O. 2000. Fluorescent pigments in corals are photoprotective. *Nature* **408**: 850-853.

Satheesh, S.K. and Ramanathan, V. 2000. Large differences in tropical aerosol forcing at the top of the atmosphere and Earth's surface. *Nature* **405**: 60-63.

Shick, J.M., Lesser, M.P. and Jokiel, P.L. 1996. Ultraviolet radiation and coral stress. *Global Change Biology* **2**: 527-545.

Sud, Y.C., Walker, G.K. and Lau, K.-M. 1999. Mechanisms regulating sea-surface temperatures and deep convection in the tropics. *Geophysical Research Letters* **26**: 1019-1022. van Woesik, R. 2000. Modelling processes that generate and maintain coral community diversity. *Biodiversity and Conservation* **9**: 1219-1233.

### 8.3.1.2.2. Response to Temperature Stress

As living entities, corals are not only acted upon by the various elements of their environment, they also react or respond to them. And when changes in environmental factors pose a challenge to their continued existence, they sometimes take major defensive or adaptive actions to ensure their survival. A simple but pertinent example of one form of this phenomenon is thermal adaptation, which feature has been observed by several researchers to operate in corals.

Fang *et al.* (1997), for example, experimented with samples of the coral *Acropora grandis* that were taken from the hot water outlet of a nuclear power plant near Nanwan Bay, Taiwan. In 1988, the year the power plant began full operation, the coral samples were completely bleached within two days of exposure to a temperature of 33°C. Two years later, however, Fang *et al.* report that "samples taken from the same area did not even start bleaching until six days after exposure to 33°C temperatures."

Similar findings have been reported by Middlebrook et al. (2008), who collected multiple upward-growing branch tips of the reef-building coral Acropora aspera from three large colonies at the southern end of Australia's Great Barrier Reef and placed them on racks immersed in running seawater within four 750-liter tanks that were maintained at the mean local ambient temperature (27°C) and exposed to natural reef-flat summer daily light levels. Then, two weeks prior to a simulated bleaching eventwhere water temperature was raised to a value of 34°C for a period of six days—they boosted the water temperature in one of the tanks to 31°C for 48 hours, while in another tank they boosted it to 31°C for 48 hours one week before the simulated bleaching event. In the third tank they had no pre-heating treatment, while in the fourth tank they had no pre-heating nor any simulated bleaching event. And at different points throughout the study, they measured photosystem II xanthophyll efficiency. and chlorophyll а concentrations, and Symbiodinium densities.

Results of the study indicated that the symbionts of the corals that were exposed to the 48-hour prebleaching thermal stress "were found to have more effective photoprotective mechanisms," including

"changes in non-photochemical quenching and xanthophyll cycling," and they further determined that "these differences in photoprotection were correlated with decreased loss of symbionts, with those corals that were not pre-stressed performing significantly worse, losing over 40% of their symbionts and having a greater reduction in photosynthetic efficiency," whereas "pre-stressed coral symbiont densities were unchanged at the end of the bleaching." In light of these findings, Middlebrook *et al.* say their study "conclusively demonstrates that thermal stress events two weeks and one week prior to a bleaching event provide significantly increased thermal tolerance to the coral holobiont, suggesting that short time-scale thermal adaptation can have profound effects on coral bleaching."

Moving out of the laboratory and into the real world of nature, Adjeroud *et al.* (2005) initiated a monitoring program on 13 islands (eight atolls and five high volcanic islands) in four of the five archipelagoes of French Polynesia, with the goal of documenting the effects of natural perturbations on coral assemblages. For the period covered by their report (1992-2002), these reefs were subjected to three major coral bleaching events (1994, 1998, 2002) and three cyclones (1997), while prior to this period, the sites had experienced an additional seven bleaching events and 15 cyclones, as well as several *Acanthaster planci* outbreaks.

Results of the monitoring program revealed that the impacts of the bleaching events were variable among the different study locations. In their 10-year survey, for example, they observed three different temporal trends: "(1) ten sites where coral cover decreased in relation to the occurrence of major disturbances; (2) nine sites where coral cover increased, despite the occurrence of disturbances affecting seven of them; and (3) a site where no significant variation in coral cover was found." In addition, they report that "an interannual survey of reef communities at Tiahura, Moorea, showed that the mortality of coral colonies following a bleaching event was decreasing with successive events, even if the latter have the same intensity (Adjeroud et al., 2002)."

Commenting on their and other researchers' observations, the seven French scientists say the "spatial and temporal variability of the impacts observed at several scales during the present and previous surveys may reflect an acclimation and/or adaptation of local populations," such that "coral

colonies and/or their endosymbiotic zooxanthellae may be phenotypically (acclimation) and possibly genotypically (adaptation) resistant to bleaching events," citing the work of Rowan *et al.* (1997), Hoegh-Guldberg (1999), Kinzie *et al.* (2001) and Coles and Brown (2003) in support of this conclusion.

Other researchers have also confirmed the phenomenon of thermal adaptation in coral reefs. Guzman and Cortes (2007) studied coral reefs of the eastern Pacific Ocean that "suffered unprecedented mass mortality at a regional scale as a consequence of the anomalous sea warming during the 1982-1983 El Niño." At Cocos Island (5°32'N, 87°04'W), in particular, they found in a survey of three representative reefs, which they conducted in 1987, that remaining live coral cover was only 3 percent of what it had been prior to the occurrence of the great El Niño four years earlier (Guzman and Cortes, 1992). Based on this finding and the similar observations of other scientists at other reefs, they predicted that "the recovery of the reefs' framework would take centuries, and recovery of live coral cover, decades." In 2002, therefore, nearly 20 years after the disastrous coral-killing warming, they returned to see just how prescient they might have been after their initial assessment of the El Niño's damage, quantifying "the live coral cover and species composition of five reefs, including the three previously assessed in 1987." The two researchers report that overall mean live coral cover increased nearly five-fold, from 2.99 percent in 1987 to 14.87 percent in 2002, at the three sites studied during both periods, while the mean live coral cover of all five sites studied in 2002 was 22.7 percent. In addition, they found that "most new recruits and adults belonged to the main reef building species from pre-1982 ENSO, Porites lobata, suggesting that a disturbance as outstanding as El Niño was not sufficient to change the role or composition of the dominant species."

With respect to the subject of thermal tolerance, however, the most interesting aspect of the study was the fact that a second major El Niño occurred between the two assessment periods; Guzman and Cortes state that "the 1997-1998 warming event around Cocos Island was more intense than all previous El Niño events," noting that temperature anomalies "above 2°C lasted 4 months in 1997-1998 compared to 1 month in 1982-83." Nevertheless, they report that "the coral communities suffered a lower and more selective mortality in 1997-1998, as was also observed in other areas of the eastern Pacific (Glynn *et al.*, 2001; Cortes and Jimenez, 2003; Zapata and Vargas-Angel, 2003)," which is indicative of some type of thermal adaptation following the 1982-83 El Niño.

One year later in a paper published in *Marine Biology*, Maynard *et al.* (2008) described how they analyzed the bleaching severity of three genera of corals (*Acropora*, *Pocillopora* and *Porites*) via underwater video surveys of five sites in the central section of Australia's Great Barrier Reef in late February and March of 1998 and 2002, while contemporary sea surface temperatures were acquired from satellite-based Advanced Very High Resolution Radiometer data that were calibrated to local shipand drift buoy-obtained measurements, and surface irradiance data were obtained "using an approach modified from that of Pinker and Laszlo (1991)."

With respect to temperature, the four researchers report that "the amount of accumulated thermal stress (as degree heating days) in 2002 was more than double that in 1998 at four of the five sites," and that "average surface irradiance during the 2002 thermal anomaly was 15.6-18.9% higher than during the 1998 anomaly." Nevertheless, they found that "in 2002, bleaching severity was 30-100% lower than predicted from the relationship between severity and thermal stress in 1998, despite higher solar irradiances during the 2002 thermal event." In addition, they found that the "coral genera most susceptible to thermal stress (*Pocillopora* and *Acropora*) showed the greatest increase in tolerance."

In discussing their findings, Maynard *et al.* write that they are "consistent with previous studies documenting an increase in thermal tolerance between bleaching events (1982-1983 vs. 1997-1998) in the Galapagos Islands (Podesta and Glynn, 2001), the Gulf of Chiriqi, the Gulf of Panama (Glynn *et al.*, 2001), and on Costa Rican reefs (Jimenez *et al.*, 2001)," and they say that "Dunne and Brown (2001) found similar results to [theirs] in the Andaman Sea, in that bleaching severity was far reduced in 1998 compared to 1995 despite sea-temperature and light conditions being more conducive to widespread bleaching in 1998."

As for the significance of these and other observations, the Australian scientists say that "the range in bleaching tolerances among corals inhabiting different thermal realms suggests that at least some coral symbioses have the ability to adapt to much higher temperatures than they currently experience in the central Great Barrier Reef," citing the work of Coles and Brown (2003) and Riegl (1999, 2002). In addition, they note that "even within reefs there is a significant variability in bleaching susceptibility for many species (Edmunds, 1994; Marshall and Baird, 2000), suggesting some potential for a shift in thermal tolerance based on selective mortality (Glynn *et al.*, 2001; Jimenez *et al.*, 2001) and local population growth alone." Above and beyond that, however, they say their results additionally suggest "a capacity for acclimatization or adaptation."

In concluding their paper, Maynard *et al.* say "there is emerging evidence of high genetic structure within coral species (Ayre and Hughes, 2004)," which suggests, in their words, that "the capacity for adaptation could be greater than is currently recognized." Indeed, as stated by Skelly *et al.* (2007), "on the basis of the present knowledge of genetic variation in performance traits and species' capacity for evolutionary response, it can be concluded that evolutionary change will often occur concomitantly with changes in climate as well as other environmental changes."

One adaptive mechanism that corals have developed to survive the thermal stress of high water temperature is to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode by one or more varieties of zooxanthellae that are more heat tolerant, a phenomenon we describe in greater detail in the next section of our report. Another mechanism is to produce heat shock proteins that help repair heat-damaged constituents of their bodies (Black et al., 1995; Hayes and King, 1995; Fang et al., 1997). Sharp et al. (1997), for example, demonstrated that sub-tidal specimens of Goniopora djiboutiensis typically have much lower constitutive levels of a 70-kD heat shock protein than do their intertidal con-specifics; and they have shown that corals transplanted from sub-tidal to intertidal locations (where temperature extremes are greater and more common) typically increase their expression of this heat shock protein.

Similar results have been reported by Roberts *et al.* (1997) in field work with *Mytilus californianus*. In addition, Gates and Edmunds (1999) have observed an increase in the 70-kD heat shock protein after six hours of exposure of *Montastraea franksi* to a 2-3°C increase in temperature, which is followed by another heat shock protein increase at the 48-hour point of exposure to elevated water temperature. They state that the first of these protein increases "provides strong evidence that changes in protein turnover during the initial exposure to elevated temperature provides this coral with the biological flexibility to

acclimatize to the elevation in sea water temperature," and that the second increase "indicates another shift in protein turnover perhaps associated with an attempt to acclimatize to the more chronic level of temperature stress."

How resilient are corals in this regard? No one knows for sure, but they've been around a very long time, during which climatic conditions have changed dramatically, from cold to warm and back again, over multiple glacial and interglacial cycles. Thermal adaptation by coral is a biological response that is overlooked or ignored by the IPCC.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/c/bleachresptemp.php</u>.

### References

Adjeroud, M., Augustin, D., Galzin, R. and Salvat, B. 2002. Natural disturbances and interannual variability of coral reef communities on the outer slope of Tiahura (Moorea, French Polynesia): 1991 to 1997. *Marine Ecology Progress Series* **237**: 121-131.

Adjeroud, M., Chancerelle, Y., Schrimm, M., Perez, T., Lecchini, D., Galzin, R. and Salvat, B. 2005. Detecting the effects of natural disturbances on coral assemblages in French Polynesia: A decade survey at multiple scales. *Aquatic Living Resources* **18**: 111-123.

Ayre, D.J. and Hughes, T.P. 2004. Climate change, genotypic diversity and gene flow in reef-building corals. *Ecology Letters* **7**: 273-278.

Black, N.A., Voellmy, R. and Szmant, A.M. 1995. Heat shock protein induction in *Montastrea faveoluta* and *Aiptasia pallida* exposed to elevated temperature. *Biological Bulletin* **188**: 234-240.

Coles, S.L. and Brown, B.E. 2003. Coral bleachingcapacity for acclimatization and adaptation. *Advances in Marine Biology* **46**: 183-223.

Cortes, J. and Jimenez, C. 2003. Corals and coral reefs of the Pacific of Costa Rica: history, research and status. In: Cortes, J. (Ed.) *Latin American Coral Reefs*. Elsevier, Amsterdam, The Netherlands, pp. 361-385.

Dunne, R.P. and Brown, B.E. 2001. The influence of solar radiation on bleaching of shallow water reef corals in the Andaman Sea, 1993-98. *Coral Reefs* **20**: 201-210.

Edmunds, P.J. 1994. Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of

bleaching susceptible clones. *Marine Biology (Berlin)* **121**: 137-142.

Fang, L.-S., Huang, S.-P. and Lin, K.-L. 1997. High temperature induces the synthesis of heat-shock proteins and the elevation of intracellular calcium in the coral *Acropora grandis. Coral Reefs* **16**: 127-131.

Gates, R.D. and Edmunds, P.J. 1999. The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* **39**: 30-43.

Glynn, P.W., Mate, J.L., Baker, A.C. and Calderon, M.O. 2001. Coral bleaching and mortality in Panama and Equador during the 1997-1998 El Niño Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982-1983 event. *Bulletin of Marine Science* **69**: 79-109.

Guzman, H.M. and Cortes, J. 1992. Cocos Island (Pacific of Costa Rica) coral reefs after the 1982-83 El Niño disturbance. *Revista de Biologia Tropical* **40**: 309-324.

Guzman, H.M. and Cortes, J. 2007. Reef recovery 20 years after the 1982-1983 El Niño massive mortality. *Marine Biology* **151**: 401-411.

Hayes, R.L. and King, C.M. 1995. Induction of 70-kD heat shock protein in scleractinian corals by elevated temperature: Significance for coral bleaching. *Molecular Marine Biology and Biotechnology* **4**: 36-42.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866.

Jimenez, C., Cortes, J., Leon, A. and Ruiz, E. 2001. Coral bleaching and mortality associated with the 1997-1998 El Niño in an upwelling environment in the eastern Pacific (Gulf of Papagayo, Costa Rica). *Bulletin of Marine Science* **69**: 151-169.

Kinzie III, R.A., Takayama, M., Santos, S.C. and Coffroth, M.A. 2001. The adaptive bleaching hypothesis: Experimental tests of critical assumptions. *Biological Bulletin* **200**: 51-58.

Marshall, P.A. and Baird, A.H. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* **19**: 155-163.

Maynard, J.A., Anthony, K.R.N., Marshall, P.A. and Masiri, I. 2008. Major bleaching events can lead to increased thermal tolerance in corals. *Marine Biology* (*Berlin*) **155**: 173-182.

Middlebrook, R., Hoegh-Guldberg, O. and Leggat, W. 2008. The effect of thermal history on the susceptibility of reef-building corals to thermal stress. *The Journal of Experimental Biology* **211**: 1050-1056.

Pinker, R.T. and Laszlo, I. 1991. Modeling surface solar irradiance for satellite applications on a global scale. *Journal of Applied Meteorology* **31**: 194-211.

Podesta, G.P. and Glynn, P.W. 2001. The 1997-98 El Niño event in Panama and Galapagos: an update of thermal stress indices relative to coral bleaching. *Bulletin of Marine Science* **69**: 43-59.

Riegl, B. 1999. Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): fauna and community structure in response to recurring mass mortality. *Coral Reefs* **18**: 63-73.

Riegl, B. 2002. Effects of the 1996 and 1998 positive seasurface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). *Marine Biology (Berlin)* **140**: 29-40.

Roberts, D.A., Hofman, G.E. and Somero, G.N. 1997. Heat-shock protein expression in *Mytilus californianus*: Acclimatization (seasonal and tidal height comparisons) and acclimation effects. *Biological Bulletin* **192**: 309-320.

Rowan, R., Knowlton, N., Baker, A. and Jara, J. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* **388**: 265-269.

Sharp, V.A., Brown, B.E. and Miller, D. 1997. Heat shock protein (hsp 70) expression in the tropical reef coral *Goniopora djiboutiensis. Journal of Thermal Biology* **22**: 11-19.

Skelly, D.K., Joseph, L.N., Possingham, H.P., Freidenburg, L.K., Farrugia, T.J., Kinnison, M.T. and Hendry, A.P. 2007. Evolutionary responses to climate change. *Conservation Biology* **21**: 1353-1355.

Zapata, F.A. and Vargas-Angel, B. 2003. Corals and coral reefs of the Pacific coast of Columbia. In: Cortes, J. (Ed.) *Latin American Coral Reefs*. Elsevier, Amsterdam, The Netherlands, pp. 419-447.

### 8.3.1.2.3. Symbiont Shuffling

Although once considered to be members of the single species *Symbiodinium microadriacticum*, the zooxanthellae that reside within membrane-bound vacuoles in the cells of host corals are highly diverse, comprising perhaps hundreds of species, of which several are typically found in each species of coral (Trench, 1979; Rowan and Powers, 1991; Rowan *et al.*, 1997). One way coral respond to stress is to replace the zooxanthellae expelled by the coral host during a stress-induced bleaching episode with one or more varieties of zooxanthellae that are more tolerant of that particular stress.

Rowan et al. (1997) have suggested that this phenomenon occurs in many of the most successful Caribbean corals that act as hosts to dynamic multispecies communities of symbionts, and that "coral communities may adjust to climate change by recombining their existing host and symbiont genetic diversities," thereby reducing the amount of damage that might subsequently be expected from another occurrence of anomalously high temperatures. Buddemeier and Fautin (1993) suggested coral bleaching is an adaptive strategy for "shuffling" symbiont genotypes to create associations better adapted to new environmental conditions. Kinzie (1999) suggested coral bleaching "might not be simply a breakdown of a stable relationship that serves as a symptom of degenerating environmental conditions," but it "may be part of a mutualistic relationship on a larger temporal scale, wherein the identity of algal symbionts changes in response to a changing environment."

This process of replacing less-stress-tolerant symbionts by more-stress-tolerant symbionts is also supported by the investigations of Rowan and Knowlton (1995) and Gates and Edmunds (1999). The strategy seems to be working, for as Glynn (1996) has observed, "despite recent incidences of severe coral reef bleaching and mortality, no species extinctions have yet been documented."

These observations accord well with the experimental findings of Fagoonee et al. (1999), who suggest that coral bleaching events "may be frequent and part of the expected cycle." Gates and Edmunds (1999) additionally report that "several of the prerequisites required to support this hypothesis have now been met," and after describing them in some detail, they conclude "there is no doubt that the existence of multiple Symbiodinium clades, each potentially exhibiting a different physiological optima, provide corals with the opportunity to attain an expanded range of physiological flexibility which will ultimately be reflected in their response to environmental challenge." In fact, this phenomenon may provide the explanation for the paradox posed by Pandolfi (1999); i.e., that "a large percentage of living coral reefs have been degraded, yet there are no known extinctions of any modern coral reef species." Surely, this result is exactly what would be expected if periods of stress lead to the acquisition of morestress-resistant zooxanthellae by coral hosts.

In spite of this early raft of compelling evidence for the phenomenon, Hoegh-Guldberg (1999) challenged the symbiont shuffling hypothesis on the basis that the stress-induced replacement of lessstress-tolerant varieties of zooxanthellae by morestress-tolerant varieties "has never been observed." Although true at the time it was written, a subsequent series of studies has produced the long-sought proof that transforms the hypothesis into fact.

Baker (2001) conducted an experiment in which he transplanted corals of different combinations of host and algal symbiont from shallow (2-4 m) to deep (20-23 m) depths and vice versa. After eight weeks nearly half of the corals transplanted from deep to shallow depths had experienced partial or severe bleaching, whereas none of the corals transplanted from shallow to deep depths bleached. After one year, however, and despite even more bleaching at shallow depths, upward transplants showed no mortality, but nearly 20 percent of downward transplants had died. Why?

The symbiont shuffling hypothesis explains it this way. The corals that were transplanted upwards were presumed to have adjusted their algal symbiont distributions, via bleaching, to favor more-tolerant species, whereas the corals transplanted downward were assumed to not have done so, since they did not bleach. Baker suggested that these findings "support the view that coral bleaching can promote rapid response to environmental change by facilitating change compensatory in algal symbiont communities." Without bleaching, he continued, "suboptimal host-symbiont combinations persist, leading eventually to significant host mortality." Consequently, Baker proposed that coral bleaching may "ultimately help reef corals to survive." And it may also explain why reefs, though depicted by the IPCC as environmentally fragile, have survived the large environmental changes experienced throughout geologic time.

One year later Adjeroud *et al.* (2002) provided additional evidence for the veracity of the symbiont shuffling hypothesis as a result of their assessment of the interannual variability of coral cover on the outer slope of the Tiahura sector of Moorea Island, French Polynesia, between 1991 and 1997, which focused on the impacts of bleaching events caused by thermal stress when sea surface temperatures rose above 29.2°C. Soon after the start of their study, they observed a severe decline in coral cover following a bleaching event that began in March 1991, which was followed by another bleaching event in March 1994. However, they report that the latter bleaching event "did not have an important impact on coral cover," even though "the proportion of bleached colonies ... and the order of susceptibility of coral genera were similar in 1991 and 1994 (Gleason, 1993; Hoegh-Guldberg and Salvat, 1995)." They report that between 1991 and 1992 total coral cover dropped from 51.0 percent to 24.2 percent, but that "coral cover did not decrease between 1994 and 1995."

In discussing these observations, Adjeroud et al. write that a "possible explanation of the low mortality following the bleaching event in 1994 is that most of the colonies in place in 1994 were those that survived the 1991 event or were young recruits derived from those colonies," noting that "one may assume that these coral colonies and/or their endosymbiotic zooxanthellae were phenotypically and possibly genotypically resistant to bleaching events," which is exactly what the symbiont shuffling hypothesis would predict. They further state that "this result demonstrates the importance of understanding the ecological history of reefs (i.e., the chronology of disturbances) in interpreting the specific impacts of a particular disturbance."

In the same year, Brown et al. (2002) published the results of an even longer 17-year study of coral reef flats at Ko Phuket, Thailand, in which they assessed coral reef changes in response to elevated water temperatures in 1991, 1995, 1997, and 1998. As they describe it. "many corals bleached during elevated sea temperatures in May 1991 and 1995, but no bleaching was recorded in 1997." In addition, they report that "in May 1998 very limited bleaching occurred although sea temperatures were higher than previous events in 1991 and 1995 (Dunne and Brown, 2001)." What is more, when bleaching did take place, they say "it led only to partial mortality in coral colonies, with most corals recovering their color within 3-5 months of initial paling," once again providing real-world evidence for what is predicted by the symbiont shuffling hypothesis.

The following year, Riegl (2003) reviewed what is known about the responses of real-world coral reefs to high-temperature-induced bleaching, focusing primarily on the Arabian Gulf, which experienced high-frequency recurrences of temperature-related bleaching in 1996, 1998, and 2002. In response to these high-temperature events, Riegl notes that *Acropora*, which during the 1996 and 1998 events always bleached first and suffered heaviest mortality, bleached less than all other corals in 2002 at Sir Abu Nuair (an offshore island of the United Arab Emirates) and actually recovered along the coast of Dubai between Jebel Ali and Ras Hasyan. As a result, Riegl states that "the unexpected resistance of Sir Abu Nuair *Acropora* to bleaching in 2002 might indicate support for the hypothesis of Baker (2001) and Baker *et al.* (2002) that the symbiont communities on recovering reefs of the future might indeed be more resistant to subsequent bleaching," and that "the Arabian Gulf perhaps provides us with some aspects which might be described as a 'glimpse into the future,' with ... hopes for at least some level of coral/zooxanthellae adaptation."

In a contemporaneous paper, Kumaraguru et al. (2003) reported the results of a study wherein they assessed the degree of damage inflicted upon a number of coral reefs within Palk Bay (located on the southeast coast of India just north of the Gulf of Mannar) by a major warming event that produced monthly mean sea surface temperatures of 29.8 to 32.1°C from April through June 2002, after which they assessed the degree of recovery of the reefs. They determined that "a minimum of at least 50% and a maximum of 60% bleaching were noticed among the six different sites monitored." However, as they continue, "the corals started to recover quickly in August 2002 and as much as 52% recovery could be noticed." By comparison, they note that "recovery of corals after the 1998 bleaching phenomenon in the Gulf of Mannar was very slow, taking as much as one year to achieve similar recovery," i.e., to achieve what was experienced in one month in 2002. Consequently, in words descriptive of the concept of symbiont shuffling, the Indian scientists say "the process of natural selection is in operation, with the growth of new coral colonies, and any disturbance in the system is only temporary." Consequently, as they conclude in the final sentence of their paper, "the corals will resurge under the sea."

Writing in Nature, Rowan (2004) described how he measured the photosynthetic responses of two zooxanthellae genotypes or clades-Symbiodinium C Symbiodinium D-to increasing and water temperature, finding that the photosynthetic prowess of the former decreased at higher temperatures while that of the latter increased. He then noted that "adaptation to higher temperature in Symbiodinium D can explain why Pocillopora spp. hosting them resist warm-water bleaching whereas corals hosting Symbiodinium C do not," and that "it can also explain why Pocillopora spp. living in frequently warm habitats host only Symbiodinium D, and, perhaps, why those living in cooler habitats predominantly host Symbiodinium C," concluding that these observations "indicate that symbiosis recombination may be one mechanism by which corals adapt, in part, to global warming."

Baker *et al.* (2004) "undertook molecular surveys of *Symbiodinium* in shallow scleractinian corals from five locations in the Indo-Pacific that had been differently affected by the 1997-98 El Niño-Southern Oscillation (ENSO) bleaching event." Along the coasts of Panama, they surveyed ecologically dominant corals in the genus *Pocillopora* before, during, and after ENSO bleaching, finding that "colonies containing *Symbiodinium* in clade D were already common (43%) in 1995 and were unaffected by bleaching in 1997, while colonies containing clade C bleached severely." Even more importantly, they found that "by 2001, colonies containing clade D had become dominant (63%) on these reefs."

After describing similar observations in the Persian (Arabian) Gulf and the western Indian Ocean along the coast of Kenya, Baker *et al.* summarized their results by stating they indicate that "corals containing thermally tolerant *Symbiodinium* in clade D are more abundant on reefs after episodes of severe bleaching and mortality, and that surviving coral symbioses on these reefs more closely resemble those found in high-temperature environments," where clade D predominates. They concluded their paper by noting that the symbiont changes they observed "are a common feature of severe bleaching and mortality events," and by predicting that "these adaptive shifts will increase the resistance of these recovering reefs to future bleaching."

Lewis and Coffroth (2004) described a controlled experiment in which they induced bleaching in a Caribbean octocoral (Briareum sp.) and then exposed it to exogenous Symbiodinium sp. containing rare variants of the chloroplast 23S ribosomal DNA (rDNA) domain V region (cp23S-genotype), after which they documented the symbionts' repopulation of the coral, whose symbiont density had been reduced to less than 1 percent of its original level by the bleaching. Also, in a somewhat analogous study, Little et al. (2004) described how they investigated the acquisition of symbionts by juvenile Acropora tenuis corals growing on tiles they attached to different portions of reef at Nelly Bay, Magnetic Island (an inshore reef in the central section of Australia's Great Barrier Reef).

Lewis and Coffroth wrote that the results of their study show "the repopulation of the symbiont community involved residual populations within *Briareum* sp., as well as symbionts from the surrounding water," noting that "recovery of coralalgal symbioses after a bleaching event is not solely dependent on the Symbiodinium complement initially acquired early in the host's ontogeny," but that "these symbioses also have the flexibility to establish new associations with symbionts from an environmental pool." Similarly, Little et al. reported that "initial uptake of zooxanthellae by juvenile corals during natural infection is nonspecific (a potentially adaptive trait)," and "the association is flexible and characterized by a change in (dominant) zooxanthella strains over time." Lewis and Coffroth concluded that "the ability of octocorals to reestablish symbiont populations from multiple sources provides a mechanism for resilience in the face of environmental change." Little et al. concluded that the "symbiont shuffling" observed by both groups "represents a mechanism for rapid acclimatization of the holobiont to environmental change."

Writing in the journal Marine Ecology Progress Series, Chen et al. (2005) reported their study of the seasonal dynamics of Symbiodinium algal phylotypes via bimonthly sampling over an 18-month period of Acropora palifera coral on a reef flat at Tantzel Bay, Kenting National Park, southern Taiwan, in an attempt to detect real-world symbiont shuffling. Results of the analysis revealed two levels of symbiont shuffling in host corals: (1) between Symbiodinium phylotypes C and D, and (2) among different variants within each phylotype. The most significant changes in symbiont composition occurred at times of significant increases in seawater temperature during late spring/early summer, perhaps as a consequence of enhanced stress experienced at that time, leading Chen et al. to state their work revealed "the first evidence that the symbiont community within coral colonies is dynamic ... involving changes in Symbiodinium phylotypes."

Also in 2005, Van Oppen *et al.* (2005) sampled zooxanthellae from three common species of scleractinian corals at 17 sites along a latitudinal and cross-shelf gradient in the central and southern sections of the Great Barrier Reef some four to five months after the major bleaching event of 2002, recording the health status of each colony at the time of its collection and identifying its zooxanthella genotypes, of which there are eight distinct clades (A-H) with clade D being the most heat-tolerant. Results of the analysis revealed that "there were no simple correlations between symbiont types and either the level of bleaching of individual colonies or indicators of heat stress at individual sites." However, they say "there was a very high post-bleaching abundance of the heat tolerant symbiont type D in one coral population at the most heat-stressed site."

With respect to the post-bleaching abundance of clade D zooxanthellae at the high heat-stress site, the Australian researchers say they suspect it was due to "a proliferation in the absolute abundance of clade D within existing colonies that were previously dominated by clade C zooxanthellae," and that in the four to five months before sampling them, "mixed C-D colonies that had bleached but survived may have shifted (shuffling) from C-dominance to Ddominance, and/or C-dominated colonies may have suffered higher mortality during the 2002 bleaching event" and subsequently been repopulated by a predominance of clade D genotypes.

Working within Australia's Great Barrier Reef system, Berkelmans and van Oppen (2006) investigated the thermal acclimatization potential of Acropora millepora corals to rising temperatures through transplantation and experimental manipulation, finding that the adult corals "are capable of acquiring increased thermal tolerance and that the increased tolerance is a direct result of a change in the symbiont type dominating their tissues from Symbiodinium type C to D." Two years later, working with an expanded group of authors (Jones et al., 2008), the same two researchers reported similar findings following the occurrence of a natural bleaching event.

Prior to the bleaching event, Jones et al. report that "A. millepora at Miall reef associated predominantly with Symbiodinium type C2 (93.5%) and to a much lesser extent with Symbiodinium clade D (3.5%) or mixtures of C2 and D (3.0%)." During the bleaching event, they report "the relative difference in bleaching susceptibility between corals predominated by C2 and D was clearly evident, with the former bleaching white and the latter normally pigmented," while corals harboring a mix of Symbiodinium C2 and D were "mostly pale in appearance." Then, three months after the bleaching event, they observed "a major shift to thermally tolerant type D and C1 symbiont communities ... in the surviving colonies," the latter of which types had not been detected in any of the corals prior to bleaching. They report "this shift resulted partly from a change of symbionts within coral colonies that survived the bleaching event (42%) and partly from selective mortality of the more bleaching-sensitive C2-predominant colonies (37%)." In addition, they report that all of the colonies that harbored low levels of D-type symbionts prior to the bleaching event

survived and changed from clade C2 to D predominance.

In conclusion, Jones et al. say that "as a direct result of the shift in symbiont community, the Miall Island A. millepora population is likely to have become more thermo-tolerant," as they note that "a shift from bleaching-sensitive type C2 to clade D increased the thermal tolerance of this species by 1-1.5°C." They say their results "strongly support the reinterpreted adaptive bleaching hypothesis of Buddemeier et al. (2004), which postulates that a continuum of changing environmental states stimulates the loss of bleaching-sensitive symbionts in favor of symbionts that make the new holobiont more thermally tolerant." They state that their observations "provide the first extensive colonyspecific documentation and quantification of temporal symbiont community change in the field in response to temperature stress, suggesting a population-wide acclimatization to increased water temperature."

In a much larger geographical study, Lien et al. (2007) examined the symbiont diversity in a scleractinian coral, Oulastrea crispata, throughout its entire latitudinal distribution range in the West Pacific, i.e., from tropical peninsular Thailand high-latitudinal (<10°N) to outlying coral communities in Japan (>35°N), convincingly demonstrating in the words of the six scientists who conducted the study, "that phylotype D is the dominant Symbiodinium in scleractinian corals throughout tropical reefs and marginal outlying nonreefal coral communities." In addition, they learned that this particular symbiont clade "favors 'marginal habitats' where other symbionts are poorly suited to the stresses, such as irradiance, temperature fluctuations, sedimentation, etc." Being a major component of the symbiont repertoire of most scleractinian corals in most places, the apparent nearuniversal presence of Symbiodinium phylotype D thus provides, according to Lien et al., "a flexible means for corals to routinely cope [our italics] with environmental heterogeneities and survive the consequences (e.g., recover from coral bleaching)."

Also in 2007, Mieog *et al.* (2007) utilized a newly developed real-time polymerase chain reaction assay, which they say "is able to detect Symbiodinium clades C and D with >100-fold higher sensitivity compared to conventional techniques," to test 82 colonies of four common scleractinian corals (*Acropora millepora, Acropora tenuis, Stylophora pistillata* and *Turbinaria reniformis*) from eleven different locations on Australia's Great Barrier Reef for evidence of the presence of background Symbiodinium clades. Results of the analysis showed that "ninety-three percent of the colonies tested were dominated by clade C and 76% of these had a D background," the latter of which symbionts, in their words, "are amongst the most thermo-tolerant types known to date," being found "on reefs that chronically experience unusually high temperatures or that have recently been impacted by bleaching events, suggesting that temperature stress can favor clade D." Consequently, Mieog et al. concluded that the clade D symbiont backgrounds detected in their study can potentially act as safety-parachutes, "allowing corals to become more thermo-tolerant through symbiont shuffling as seawater temperatures rise due to global warming." As a result, they suggest that symbiont shuffling is likely to play a role in the way "corals cope with global warming conditions," leading to new competitive hierarchies and, ultimately, "the coral community assemblages of the future."

In spite of the hope symbiont shuffling provides—that the world's corals will indeed be able to successfully cope with the possibility of future global warming, be it anthropogenic-induced or natural—some researchers have claimed that few coral symbioses host more than one type of symbiont, which has led some commentators to argue that symbiont shuffling is not an option for most coral species to survive the coming thermal onslaught of global warming. But is this claim correct? Not according to the results of Apprill and Gates (2007).

Working with samples of the widely distributed massive corals *Porites lobata* and *Porites lutea* which they collected from Kaneohe Bay, Hawaii— Apprill and Gates compared the identity and diversity of *Symbiodinium* symbiont types obtained using cloning and sequencing of internal transcribed spacer region 2 (ITS2) with that obtained using the more commonly applied downstream analytical techniques of denaturing gradient gel electrophoresis (DGGE).

Results of the analysis revealed "a total of 11 ITS2 types in *Porites lobata* and 17 in *Porites lutea* with individual colonies hosting from one to six and three to eight ITS2 types for *P. lobata* and *P. lutea*, respectively." In addition, the two authors report that "of the clones examined, 93% of the *P. lobata* and 83% of the *P. lutea* sequences are not listed in GenBank," noting that they resolved "sixfold to eightfold greater diversity per coral species than previously reported."

In a "perspective" that accompanied Apprill and Gates' important paper, van Oppen (2007) wrote that
"the current perception of coral-inhabiting symbiont diversity at nuclear ribosomal DNA is shown [by Apprill and Gates] to be a significant underestimate of the wide diversity that in fact exists." These findings, in her words, "have potentially far-reaching consequences in terms of our understanding of *Symbiodinium* diversity, host-symbiont specificity and the potential of corals to acclimatize to environmental perturbations through changes in the composition of their algal endosymbiont community," which assessment, it is almost unnecessary to say, suggests a greater than previously believed ability to do just that in response to any further global warming that might occur.

In a contemporaneous study, Baird *et al.* (2007) also discount the argument that symbiont shuffling is not an option for most coral species, because, "as they see it," it is the sub-clade that must be considered within this context, citing studies that indicate "there are both heat tolerant and heat susceptible sub-clades within both clades C and D *Symbiodinium.*" Hence, the more relevant question becomes: How many coral species can host more than one *sub*-clade? The answer, of course, is that most if not all of them likely do; Baird *et al.* note that "biogeographical data suggest that when species need to respond to novel environments, they have the flexibility to do so."

So how and when might such sub-clade changes occur? Although most prior research in this area has been on adult colonies switching symbionts in response to warming-induced bleaching episodes, Baird *et al.* suggest that "change is more likely to occur between generations," for initial coral infection typically occurs in larvae or early juveniles, which are much more flexible than adults. In this regard, for example, they note that "juveniles of *Acropora tenuis* regularly harbor mixed assemblages of symbionts, whereas adults of the species almost invariably host a single clade," and they indicate that larvae of *Fungia scutaria* ingest symbionts from multiple hosts, although they generally harbor but one symbiont as adults.

Because of these facts, the Australian researchers say there is no need for an acute disturbance, such as bleaching, to induce clade or sub-clade change. Instead, if ocean temperatures rise to new heights in the future, they foresee juveniles naturally hosting more heat-tolerant sub-clades and maintaining them into adulthood.

In a further assessment of the size of the symbiont diversity reservoir, especially among juvenile coral species, Pochon *et al.* (2007) collected more than

1,000 soritid specimens over a depth of 40 meters on a single reef at Gun Beach on the island of Guam, Micronesia, throughout the course of an entire year, which they then studied by means of molecular techniques to identify unique *internal transcribed spacer-2* (ITS-2) types of *ribosomal DNA* (rDNA), in a project self-described as "the most targeted and exhaustive sampling effort ever undertaken for any group of *Symbiodinium*-bearing hosts."

Throughout the course of their analysis, Pochon et al. identified 61 unique symbiont types in only three soritid host genera, making the Guam Symbiodinium assemblage the most diverse derived to date from a single reef. In addition, they report that "the majority of mixed genotypes observed during this survey were usually harbored by the smallest hosts." As a result, the authors speculate that "juvenile foraminifera may be better able to switch or shuffle heterogeneous symbiont communities than adults," so that as juveniles grow, "their symbiont communities become 'optimized' for the prevailing environmental conditions," suggesting that this phenomenon "may be a key element in the continued evolutionary success of these protests in coral reef ecosystems worldwide."

In support of the above statement, we additionally cite the work of Mumby (1999), who analyzed the population dynamics of juvenile corals in Belize, both prior to, and after, a massive coral bleaching event in 1998. Although 70 percent to 90 percent of adult coral colonies were severely bleached during the event, only 25 percent of coral recruits exhibited signs of bleaching. What is more, one month after the event, it was concluded that "net bleaching-induced mortality of coral recruits ... was insignificant," demonstrating the ability of juvenile corals to successfully weather such bleaching events.

In light of these several observations, earth's corals will likely be able to successfully cope with the possibility of further increases in water temperatures, be they anthropogenic-induced or natural. Corals have survived such warmth—and worse—many times in the past, including the Medieval Warm Period, Roman Warm Period, and Holocene Optimum, as well as throughout numerous similar periods during a number of prior interglacial periods; there is no reason to believe they cannot do it again, if the need arises.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/c/bleachrespsymb.php</u>.

# References

Adjeroud, M., Augustin, D., Galzin, R. and Salvat, B. 2002. Natural disturbances and interannual variability of coral reef communities on the outer slope of Tiahura (Moorea, French Polynesia): 1991 to 1997. *Marine Ecology Progress Series* **237**: 121-131.

Apprill, A.M. and Gates, R.D. 2007. Recognizing diversity in coral symbiotic dinoflagellate communities. *Molecular Ecology* **16**: 1127-1134.

Baird, A.H., Cumbo, V.R., Leggat, W. and Rodriguez-Lanetty, M. 2007. Fidelity and flexibility in coral symbioses. *Marine Ecology Progress Series* **347**: 307-309.

Baker, A.C. 2001. Reef corals bleach to survive change. *Nature* **411**: 765-766.

Baker, A.C., Starger, C.J., McClanahan, T.R. and Glynn, P.W. 2002. Symbiont communities in reef corals following the 1997-98 El Niño—will recovering reefs be more resistant to a subsequent bleaching event? *Proceedings of the International Society of Reef Studies* (Abstract Volume 10: European Meeting, Cambridge, UK, September).

Baker, A.C., Starger, C.J., McClanahan, T.R. and Glynn, P.W. 2004. Corals' adaptive response to climate change. *Nature* **430**: 741.

Berkelmans, R. and van Oppen, M.J.H. 2006. The role of zooxanthellae in the thermal tolerance of corals: a "nugget of hope" for coral reefs in an era of climate change. *Proceedings of the Royal Society B* **273**: 2305-2312.

Brown, B.E., Clarke, K.R. and Warwick, R.M. 2002. Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. *Marine Biology* **141**: 24-29.

Buddemeier, R.W., Baker, A.C., Fautin, D.G. and Jacobs, J.R. 2004. The adaptive hypothesis of bleaching. In Rosenberg, E. and Loya, Y. (Eds.) *Coral Health and Disease*, Springer, Berlin, Germany, p. 427-444.

Buddemeier, R.W. and Fautin, D.G. 1993. Coral bleaching as an adaptive mechanism. *BioScience* **43**: 320-326.

Chen, C.A., Wang, J.-T., Fang, L.-S. and Yang, Y.W. 2005. Fluctuating algal symbiont communities in *Acropora palifera* (Schleractinia: Acroporidae) from Taiwan. *Marine Ecology Progress Series* **295**: 113-121.

Dunne, R.P. and Brown, B.E. 2001. The influence of solar radiation on bleaching of shallow water reef corals in the Andaman Sea, 1993-98. *Coral Reefs* **20**: 201-210.

Fagoonee, I., Wilson, H.B., Hassell, M.P. and Turner, J.R. 1999. The dynamics of zooxanthellae populations: A long-term study in the field. *Science* **283**: 843-845.

Gates, R.D. and Edmunds, P.J. 1999. The physiological mechanisms of acclimatization in tropical reef corals. *American Zoologist* **39**: 30-43.

Gleason, M.G. 1993. Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. *Coral Reefs* **12**: 193-201.

Glynn, P.W. 1996. Coral reef bleaching: facts, hypotheses and implications. *Global Change Biology* **2**: 495-509.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866.

Hoegh-Guldberg, O. and Salvat, B. 1995. Periodic massbleaching and elevated sea temperatures: bleaching of outer reef slope communities in Moorea, French Polynesia. *Marine Ecology Progress Series* **121**: 181-190.

Jones, A.M., Berkelmans, R., van Oppen, M.J.H., Mieog, J.C. and Sinclair, W. 2008. A community change in the algal endosymbionts of a scleractinian coral following a natural bleaching event: field evidence of acclimatization. *Proceedings of the Royal Society B* **275**: 1359-1365.

Kinzie III, R.A. 1999. Sex, symbiosis and coral reef communities. *American Zoologist* **39**: 80-91.

Kumaraguru, A.K., Jayakumar, K. and Ramakritinan, C.M. 2003. Coral bleaching 2002 in the Palk Bay, southeast coast of India. *Current Science* **85**: 1787-1793.

Lien, Y.-T., Nakano, Y., Plathong, S., Fukami, H., Wang, J.-T. and Chen, C.A. 2007. Occurrence of the putatively heat-tolerant *Symbiodinium* phylotype D in high-latitudinal outlying coral communities. *Coral Reefs* **26**: 35-44.

Lewis, C.L. and Coffroth, M.A. 2004. The acquisition of exogenous algal symbionts by an octocoral after bleaching. *Science* **304**: 1490-1492.

Little, A.F., van Oppen, M.J.H. and Willis, B.L. 2004. Flexibility in algal endosymbioses shapes growth in reef corals. *Science* **304**: 1492-1494.

Mieog, J.C., van Oppen, M.J.H., Cantin, N.E., Stam, W.T. and Olsen, J.L. 2007. Real-time PCR reveals a high incidence of *Symbiodinium* clade D at low levels in four scleractinian corals across the Great Barrier Reef: implications for symbiont shuffling. *Coral Reefs* **26**: 449-457.

Mumby, P.J. 1999. Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Marine Ecology Progress Series* **190**: 27-35.

Pandolfi, J.M. 1999. Response of Pleistocene coral reefs to environmental change over long temporal scales. *American Zoologist* **39**: 113-130. Pochon, X., Garcia-Cuetos, L., Baker, A.C., Castella, E. and Pawlowski, J. 2007. One-year survey of a single Micronesian reef reveals extraordinarily rich diversity of *Symbiodinium* types in soritid foraminifera. *Coral Reefs* **26**: 867-882.

Riegl, B. 2003. Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). *Coral Reefs* **22**: 433-446.

Rowan, R. 2004. Thermal adaptation in reef coral symbionts. *Nature* **430**: 742.

Rowan, R. and Knowlton, N. 1995. Intraspecific diversity and ecological zonation in coral-algal symbiosis. *Proceeding of the National Academy of Sciences, U.S.A.* **92**: 2850-2853.

Rowan, R., Knowlton, N., Baker, A. and Jara, J. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* **388**: 265-269.

Rowan, R. and Powers, D. 1991. Molecular genetic identification of symbiotic dinoflagellates (zooxanthellae). *Marine Ecology Progress Series* **71**: 65-73.

Trench, R.K. 1979. The cell biology of plant-animal symbiosis. *Annual Review of Plant Physiology* **30**: 485-531.

Van Oppen, M.J.H. 2007. Perspective. *Molecular Ecology* **16**: 1125-1126.

Van Oppen, M.J.H., Mahiny, A.J. and Done, T.J. 2005. Geographic distribution of zooxanthella types in three coral species on the Great Barrier Reef sampled after the 2002 bleaching event. *Coral Reefs* **24**: 482-487.

### 8.3.1.2.4. Bacterial Shuffling

One final adaptive bleaching mechanism is discussed by Reshef *et al.*, (2006), who developed a case for what they call the coral probiotic hypothesis, and what we call "bacterial shuffling." This concept, in their words, "posits that a dynamic relationship exists between symbiotic microorganisms and environmental conditions which brings about the selection of the most advantageous coral holobiont."

This concept is analogous to the adaptive bleaching hypothesis of Buddemeier and Fautin (1993), or what was referred to in the preceding section as symbiont shuffling, wherein corals exposed to some type of stress—such as that induced by exposure to unusually high water temperatures or solar irradiance—first lose their dinoflagellate symbionts (bleach) and then regain a new mixture of zooxanthellae that are better suited to the stress conditions. In fact, the two phenomena work in precisely the same way, in one case by the corals rearranging their zooxanthellae populations (symbiont shuffling) and in the other case by the corals rearranging their bacterial populations (bacterial shuffling).

In seeking evidence for their hypothesis, the team of Israeli researchers concentrated their efforts on looking for examples of corals developing resistance to emerging diseases. This approach makes sense, because corals lack an adaptive immune system; i.e., they possess no antibodies (Nair *et al.*, 2005), and they therefore can protect themselves against specific diseases in no other way than to adjust the relative sizes of the diverse bacterial populations associated with their mucus and tissues so as to promote the growth of those types of bacteria that tend to mitigate most effectively against the specific disease that happens to be troubling them.

Reshef et al. begin by describing the discovery that bleaching of Oculina patagonica corals in the Mediterranean Sea was caused by the bacterium Vibrio shiloi, together with the finding that bleaching of Pocillopora damicornis corals in the Indian Ocean and Red Sea was the result of an infection with Vibrio coralliilvticus. But they then report that (1) "during the last two years O. patagonica has developed resistance to the infection by V. shiloi," (2) "V. shiloi can no longer be found on the corals," and (3) "V. shiloi that previously infected corals are unable to infect the existing corals." They say "by some unknown mechanism, the coral is now able to lyse the intracellular V. shiloi and avoid the disease," and because corals lack the ability to produce antibodies and have no adaptive immune system, the only logical conclusion to be drawn from these observations is that bacterial shuffling must be what produced the welcome results.

With respect to the future of earth's corals in the context of global warming, the Israeli scientists note that "Hoegh-Guldberg (1999, 2004) has predicted that coral reefs will have only remnant populations of reef-building corals by the middle of this century," based on "the assumption that corals cannot adapt rapidly enough to the predicted temperatures in order to survive." However, they report that considerable evidence has been collected in support of the adaptive bleaching hypothesis, and they emphasize that the hundreds of different bacterial species associated with corals "give the coral holobiont an enormous genetic potential to adapt rapidly to changing environmental conditions." They say "it is not unreasonable to

predict that under appropriate selection conditions, the change could take place in days or weeks, rather than decades required for classical Darwinian mutation and selection," and that "these rapid changes may allow the coral holobiont to use nutrients more efficiently, prevent colonization by specific pathogens and avoid death during bleaching by providing carbon and energy from photosynthetic prokaryotes," of which they say there is "a metabolically active, diverse pool" in most corals.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> <u>science.org/subject/c/bacterialshuffling.php</u>.

# References

Buddemeier, R.W. and Fautin, D.G. 1993. Coral bleaching as an adaptive mechanism. *BioScience* **43**: 320-326.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866.

Hoegh-Guldberg, O. 2004. Coral reefs in a century of rapid environmental change. *Symbiosis* **37**: 1-31.

Nair, S.V., Del Valle, H., Gross, P.S., Terwilliger, D.P. and Smith, L.C. 2005. Macroarray analysis of coelomocyte gene expression in response to LPS in the sea urchin. Identification of unexpected immune diversity in an invertebrate. *Physiological Genomics* **22**: 33-47.

Reshef, L., Koren, O., Loya, Y., Zilber-Rosenberg, I. and Rosenberg, E. 2006. The coral probiotic hypothesis. *Environmental Microbiology* **8**: 2068-2073.

# 8.3.1.3. Widespread Coral Bleaching

# 8.3.1.3.1. Not Caused by Global Warming

Hoegh-Guldberg (1999) concluded that "coral bleaching is due to warmer than normal temperatures" and that "increased sea temperature is the primary reason for why coral bleaching has occurred with increasing intensity and frequency over the past two decades." As outlined in the preceding sections, there is some evidence that points toward these conclusions, but there is much other evidence that points to alternative possibilities.

Consider, for example, the persistence of coral reefs through geologic time, which provides

substantive evidence that these ecological entities can successfully adapt to a dramatically changing global environment (Veron, 1995). What can their history tell us about bleaching and global warming in our day?

The earliest coral reefs date to the Palaeozoic Era, over 450 million years ago (Hill, 1956). The scleractinian corals, which are the major builders of the reefs of today (Achituv and Dubinsky, 1990), appeared in the mid-Triassic some 240 million years later (Hill, 1956), when the earth was considerably warmer than it is currently (Chadwick-Furman, 1996). Although reef-building ceased for a time following the extinctions at the end of the Triassic, the Scleractinia came back with a vengeance during the Jurassic (Newell, 1971; Veron, 1995); they continued to exhibit great robustness throughout the Cretaceous, even when temperatures were as much as 8-15°C higher (Chadwick-Furman, 1996; Veizer et al., 1999), and atmospheric  $CO_2$  concentrations two to seven times higher (Berner and Kothavala, 2001), than present.

At the end of the Cretaceous, 70 percent of the genera and one-third of the families of scleractinian corals disappeared (Veron, 1995) in the greatest biospheric extinction event in geological history, which may possibly have been caused by a large asteroid impact (Alvarez et al., 1980, 1984). They developed again, however, throughout the Cenozoic, particularly the Oligocene and Miocene (Chadwick-Furman, 1996). Finally, throughout the past two million years of the Pleistocene, they survived at least seventeen glacial-interglacial cycles of dramatic climate change and sea-level fluctuation, successfully adapting, over and over again, to these enormous environmental challenges (Pandolfi, 1999). In the words of Benzie (1999), this evidence suggests that "coral reef communities are relatively resilient, have survived previous global climate change, and appear likely to survive future changes." This conclusion leads us to wonder why corals should be succumbing to global warming now.

To answer such an inquiry we must first address the question of what is "normal" for coral reefs in our day. Is it what they look like now? Or what they looked like 30 years ago? Or 300 years ago? Kinzie (1999) has emphatically stated that "it is clear that the definition of a healthy reef as 'what it looked like when I started diving' is fraught not only with hubris but strong temporal bias." Indeed, as Greenstein *et al.* (1998a) have observed, "it must be demonstrated that the classic reef coral zonation pattern described in the early days of coral reef ecology, and upon which 'healthy' versus 'unhealthy' reefs are determined, are themselves representative of reefs that existed prior to any human influence." Only when this criterion is met will we have, in the words of Greenstein *et al.* (1998b), a good replacement for "the temporally myopic view afforded by monitoring studies that rarely span a scientific career." Clearly, therefore, there should be no argument over the key fact that we need a proper understanding of the past to correctly judge the present if we ever are to foretell the future.

In an attempt to obtain a true picture of pristine coral conditions in the western North Atlantic and Caribbean, Greenstein et al. (1998a, 1998b) conducted systematic censuses of "life assemblages" and "death assemblages" of corals on healthy modern patch reefs and compared the results with similar censuses they conducted on "fossil assemblages" preserved in Pleistocene limestones in close proximity to the modern reefs. The data revealed a recent decline in thickets of Acropora cervicornis, as evidenced by their abundance in the death assemblage, and a concurrent increase in Porites porites, as evidenced by their abundance in the life assemblage. In comparing these results with those obtained from the fossil assemblage, they found that the present Caribbean-wide decline of A. cervicornis is "without historical precedent" and that it is a dramatic departure from "the long-term persistence of this taxon during Pleistocene and Holocene Optimum time," when "intensifying cycles in climate and sea level" recurred throughout a roughly one-million-year time period.

These observations, along with the similar findings of Jackson (1992) and Aronson and Precht (1997), suggest that if little change in coral community structure occurred throughout the Pleistocene-when it was often warmer than it is now (Petit et al., 1999)-the recent die-off of A. cervicornis cannot be due to global warming alone, or even primarily, for this particular coral has clearly weathered several major episodes of global warming and elevated water temperatures in the past with no adverse consequences. Neither can the coral's die-off be due to the CO<sub>2</sub>-induced decrease in seawater calcium carbonate saturation state that might possibly be occurring at the present time (see the section later in this chapter on coral calcification); for the air's CO<sub>2</sub> content has not risen sufficiently to have caused this parameter to decline enough to significantly impact reef coral calcification rates (Gattuso et al., 1998, 1999), as is also demonstrated by the

opportunistic replacement of *A. cervicornis* by *P. porites*. In addition, in their detailed reconstruction of the history of calcification rates in massive *Porites* colonies from Australia's Great Barrier Reef, Lough and Barnes (1997) report that the mid-twentieth century had the second highest coral growth rate of the past 237 years. Hence, although *A. cervicornis* has indeed suffered an extreme decrease in abundance throughout the Caribbean in recent years (Hughes, 1994), its precipitous decline cannot be attributed to either global warming or the direct effects of rising CO<sub>2</sub>.

In light of these data-driven considerations, Greenstein *et al.* (1998a, 1998b) have attributed the increasing coral bleaching of the past two decades to a host of local anthropogenic impacts. This conclusion is accepted in a much wider context as well, as Buddemeier and Smith (1999) have noted that "reviews of the problems facing coral reefs have consistently emphasized that local and regional anthropogenic impacts are a far greater immediate threat to coral reefs than Greenhouse-enhanced climate change."

# References

Achituv, Y., and Dubinsky, Z. 1990. Evolution and zoogeography of coral reefs. Dubinsky, Z. (Ed.) *Ecosystems of the world: Coral reefs*. Elsevier, New York, NY.

Alvarez, L.W., Alvarez, W., Asaro, F. and Michel, H.V. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. *Science* **208**: 1095-1108.

Alvarez, W., Alvarez, L.W., Asaro, F. and Michel, H.V. 1984. The end of the Cretaceous: Sharp boundary or gradual transition? *Science* **223**: 1183-1186.

Aronson, R.B. and Precht, W.F. 1997. Stasis, biological disturbance, and community structure of a Holocene coral reef. *Paleobiology* **23**: 326-346.

Benzie, J.A.H. 1999. Genetic structure of coral reef organisms: Ghosts of dispersal past. *American Zoologist* **39**: 131-145.

Berner, R.A. and Kothavala, Z. 2001. GEOCARB III: A revised model of atmospheric CO<sub>2</sub> over phanerozoic time. *American Journal of Science* **301**: 182-204.

Buddemeier, R.W. and Smith, S.V. 1999. Coral adaptation and acclimatization: A most ingenious paradox. *American Zoologist* **39**: 1-9. Chadwick-Furman, N.E. 1996. Reef coral diversity and global change. *Global Change Biology* **2**: 559-568.

Gattuso, J.-P., Allemand, D. and Frankignoulle, M. 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**: 160-183.

Gattuso, J.-P., Frankignoulle, M., Bourge, I., Romaine, S. and Buddemeier, R.W. 1998. Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change* **18**: 37-46.

Greenstein, B.J., Curran, H.A. and Pandolfi, J.M. 1998a. Shifting ecological baselines and the demise of *Acropora cervicornis* in the western North Atlantic and Caribbean Province: A Pleistocene perspective. *Coral Reefs* **17**: 249-261.

Greenstein, B.J., Harris, L.A. and Curran, H.A. 1998b. Comparison of recent coral life and death assemblages to Pleistocene reef communities: Implications for rapid faunal replacement on recent reefs. *Carbonates & Evaporites* **13**: 23-31.

Hill, D. Rugosa and Moore, R.D. 1956. (Eds.) *Treatise on invertebrate paleontology*, Volume F, Coelenterata. Lawrence, KS: Geological Society of America/University of Kansas Press, pp. 233-323.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866.

Hughes, T.P. 1994. Catastrophes, phase shifts, and largescale degradation of a Caribbean coral reef. *Science* **265**: 1547-1551.

Jackson, J.B.C. 1992. Pleistocene perspectives on coral reef community structure. *American Zoologist* **32**: 719-731.

Kinzie III, R.A. 1999. Sex, symbiosis and coral reef communities. *American Zoologist* **39**: 80-91.

Lough, J.M. and Barnes, D.J. 1997. Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the Great Barrier Reef: A proxy for seawater temperature and a background of variability against which to identify unnatural change. *Journal of Experimental Marine Biology and Ecology* **211**: 29-67.

Newell, N.D. 1971. An outline history of tropical organic reefs. *Novitates* **2465**: 1-37.

Pandolfi, J.M. 1999. Response of Pleistocene coral reefs to environmental change over long temporal scales. *American Zoologist* **39**: 113-130.

Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis, M.,

Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V.Y., Lorius, C., Pepin, L., Ritz, C., Saltzman, E. and Stievenard, M. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**: 429-436.

Veizer, J., Ala, D., Azmy, K., Bruckschen, P., Buhl, D., Bruhn, F., Carden, G.A.F., Diener, A., Ebneth, S., Godderis, Y., Jasper, T., Korte, C., Pawellek, F., Podlaha, O. and Strauss, H. 1999. <sup>87</sup>Sr/<sup>86</sup>Sr,  $\delta^{13}$ C and  $\delta^{18}$ O evolution of Phanerozoic seawater. *Chemical Geology* **161**, 59-88.

Veron, J.E.N. 1995. *Corals in space and time*. Comstock/Cornell, Ithaca, NY.

### 8.3.1.3.2. An Alternative Hypothesis

The preceding considerations clearly indicate global warming cannot be the primary cause of the massive coral bleaching the earth has experienced in recent years. However, the IPCC tenaciously clings to this hypothesis because (1) no significant massive and widespread coral bleaching was reported in the 1970s and (2) the global warming hypothesis can account for this observation. Specifically, Hoegh-Guldberg (1999) has suggested that the reason "why mass bleaching events are not seen prior to 1980" is that "increases in sea temperatures have only become critical since in the 1980s, when El Niño disturbances began to exceed the thermal tolerances of corals and their zooxanthellae" as a result of global warming increasing the background temperature to which El Niño thermal effects are added.

This reasoning assumes no other theory is capable of accounting for the fact that modern mass bleaching events did not begin to occur until 1980. On the basis of this *assumption*, Hoegh-Guldberg (1999) concludes that the global warming hypothesis must be correct, even in light of the many problems associated with it. This assumption, however, is not true, for there are other ways of satisfying this critical criterion that do account for the lack of bleaching episodes before 1980, which we describe below.

The North Atlantic Oscillation (NAO) is responsible for multiannual to decadal variability in Northern Hemispheric climate that is numerically represented by the pressure difference between the Azores high and the Icelandic low (Dugam *et al.*, 1997). It has been documented over the past 350 years in Greenland ice core reconstructions (Appenzeller *et al.*, 1998) and explicitly quantified from 1864 through 1994 via actual pressure records (Hurrell, 1995), which have been updated through 1998 by Uppenbrink (1999).

Plots of these NAO datasets reveal a shift from strong negative index values in the 1950s and 1960s to what Hurrell (1995) describes as "unprecedented strongly positive NAO index values since 1980." This observation is especially important, for during times of high NAO index values, there is a significant reduction in atmospheric moisture transport across southern Europe, the Mediterranean, and north Africa (Hurrell, 1995); and Richardson *et al.* (1999) note that this phenomenon has led to the development of prolonged drought in the Sahel region of Africa since the NAO shift to positive index values in 1980.

One consequence of this drought has been a gradual increase in the dust content of the atmosphere, which in some areas has grown to fivefold what was deemed normal prior to this climatic transition (Richardson et al., 1999). Of particular significance to corals is the fact that this airborne dust carries bacteria, viruses, and fungi that can kill them. Pearce (1999) notes that outbreaks of a number of coral diseases "have coincided with years when the dust load in the atmosphere was highest." In 1983, for example-when the NAO index reached its highest value since 1864 (Hurrell, 1995) and the atmosphere was exceptionally dusty-a soil fungus of the Aspergillus genus appeared in the Caribbean, initiating an onslaught of soft coral sea fans that has now destroyed more than 90 percent of them. Pearce (1999) notes there are solid scientific reasons for concluding that "the speed and pattern of the fungus's spread indicates that it could only have arrived on the trade winds from Africa."

In addition to carrying its deadly biological cargo, the positive-NAO-induced airborne dust is rich in iron, which extra supply, in the words of R.T. Barber as quoted by Pearce (1999), "may have spurred the worldwide growth of a variety of invader organisms harmful to coral ecosystems." Such iron-rich dust has the capacity to fertilize algae that compete with zooxanthellae for other scarce nutrients and reef living space. Abram et al. (2003), for example, reported that a massive coral bleaching event that killed close to 100 percent of the coral and fish in the reef ecosystem of the Mentawai Islands (located southwest of Sumatra, Indonesia, in the equatorial eastern Indian Ocean) in 1997-1998 was brought about by an anomalous influx of iron provided by atmospheric fallout from the 1997 Indonesian wildfires, which they describe as being "the worst wildfires in the recorded history of southeast Asia."

The enhanced burden of iron, in turn, spawned a large phytoplankton bloom that likely caused the coral and fish death via asphyxiation. In concluding their paper, Abram *et al.* warn that "widespread tropical wildfire is a recent phenomenon, the magnitude and frequency of which are increasing as population rises and terrestrial biomass continues to be disrupted," and "reefs are likely to become increasingly susceptible to large algal blooms triggered by episodic nutrient enrichment from wildfires," which phenomenon, in their words, "may pose a new threat to coastal marine ecosystems that could escalate into the 21<sup>st</sup> century."

The timeline for the appearance and progression of these several related phenomena matches perfectly with the timeline of the historical buildup of modern coral reef bleaching throughout the 1980s and 1990s. This is not to say, however, that these aggregate phenomena comprise the entire answer to the problem to the exclusion of all other possible causes, even including global warming. We only suggest that they, too, must be seriously considered in attempts to identify the true cause or causes of this development in coral reef history.

Although one can make the case for coral bleaching being caused by global warming, there are too many pieces of evidence that contradict this hypothesis for it to be deemed the sole, or even primary, cause of this modern problem. There is at least one alternative explanation—the unprecedented, strongly positive NAO since 1980—during the past two decades.

### References

Abram, N.J., Gagan, M.K., McCulloch, M.T., Chappell, J. and Hantoro, W.S. 2003. Coral reef death during the 1997 Indian Ocean Dipole linked to Indonesian wildfires. *Science* **301**: 952-955.

Appenzeller, C., Stocker, T.F. and Anklin, M. 1998. North Atlantic Oscillation dynamics recorded in Greenland ice cores. *Science* **282**: 446-449.

Dugam, S.S., Kakade, S.B. and Verma, R.K. 1997. Interannual and long-term variability in the North Atlantic Oscillation and Indian summer monsoon rainfall. *Theoretical and Applied Climatology* **58**: 21-29.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866. Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science* **269**: 676-679.

Pearce, F. 1999. Coral grief: The cause of reef health problems may be blowing in the wind. *New Scientist* **163** (2193): 22.

Richardson, L.L., Porter, J.W. and Barber, R.T. 1999. Status of the health of coral reefs: An update. U.S. Global Change Research Program Seminar Series, <u>http://www.usgcrp.gov</u>.

Uppenbrink, J. 1999. The North Atlantic Oscillation. *Science* **283**: 948-949.

### 8.3.1.4. Sea-level Rise

Many people believe rising sea levels, by gradually reducing the amount of life-sustaining light that reaches their algal symbionts, will decimate earth's corals. This assumption is a major concern often expressed in discussions of reef responses to global climate change (Hopley and Kinsey, 1988). But it is probably not valid, for a number of reasons.

First, the 18- to 59-cm warming-induced sea-level rise that is predicted for the coming century (IPCC, 2007)-which could be greatly exaggerated if predictions of CO<sub>2</sub>-induced global warming are wrong-falls well within the range (2 to 6 mm per year) of typical coral vertical extension rates, which exhibited a modal value of 7 to 8 mm per year during the Holocene and can be more than double that value in certain branching corals (Hopley and Kinsey, 1988; Done, 1999). Second, most coral reefs are known to have successfully responded to the sea-level rises that occurred between 14,000 and 6,000 years agowhich were accompanied by large changes in "CO<sub>2</sub> concentrations. ... rainfall, cloud cover, storms and currents" (Wilkinson, 1996)-and which were more than twice as rapid as what is being predicted for the coming century (Digerfeldt and Hendry, 1987). Third, earth's oceans have undergone-and their coral reefs have survived (Chadwick-Furman, 1996)-at least 17 major cycles of sea-level rise and fall during the Pleistocene, the most recent low phase of which ended 18,000 years ago with a global sea level some 120-135 meters below where it is now (Grigg and Epp, 1989). Fourth, most coral reefs handle increases in sea level-even rapid increases-much better than decreases (White et al., 1998). Yet even if reef vertical growth rates could not keep up with rising sea levels, that would not spell their doom.

One of the important characteristics of essentially all reef cnidarians is their ability to produce freeswimming planulae, spores, or dispersive larval stages. Kinzie (1999) notes that "no matter how quickly sea level might rise, propagules of the species could keep pace and settle at suitable depths each generation," thereby creating what he calls jump-up reefs that "might well contain most of the species present in the original community." Done (1999) notes that "coral communities have a history of tracking their preferred environmental niche which may suggest that as an entity, they will be predisposed to 'adapt' to prospective changes in environment over the next century," citing precedents that clearly demonstrate that "coral communities have historically had a good capacity to track their redistributed preferred physical niches."

It is not at all surprising, therefore, as Kinzie and Buddemeier (1996) recount, that coral reefs have survived many periods of "massive environmental changes" throughout the geologic record. Reefs are survivors, they state, "because they do not simply tolerate environmental changes" but "exhibit an impressive array of acclimations" that allow them to deal with a variety of challenges to their continued existence in any given area. Hence, it is highly unlikely that anticipated increases in sea level would spell the doom of earth's coral reefs.

Strange as it may seem, rising sea levels may have a *positive* effect on earth's coral reefs (Roberts, 1993). Over the past 6,000 years, relatively stable sea levels have limited upward reef growth, resulting in the development of extensive reef flats; as Buddemeier and Smith (1988) and Wilkinson (1996) have noted, the sea-level rises predicted to result from CO<sub>2</sub>-induced global warming should actually be beneficial, permitting increased growth in these growth-restricted areas. In the words of Chadwick-Furman (1996), "many coral reefs have already reached their upward limit of growth at present sea level (Buddemeier, 1992), and may be released from this vertical constraint by a rise in sea level." She also notes that rising sea levels may allow more water to circulate between segregated lagoons and outer reef slopes, which could "increase the exchange of coral propagules between reef habitats and lead to higher coral diversity in inner reef areas." She, too, concludes that "coral reefs are likely to survive predicted rates of global change."

# References

Buddemeier, R.W. 1992. Corals, climate and conservation. Proceedings of the Seventh International Coral Reef Symposium 1: 3-10.

Buddemeier, R.W. and Smith, S.V. 1988. Coral-reef growth in an era of rapidly rising sea-level—predictions and suggestions for long-term research. *Coral Reefs* 7: 51-56.

Chadwick-Furman, N.E. 1996. Reef coral diversity and global change. *Global Change Biology* **2**: 559-568.

Digerfeldt, G. and Hendry, M.D. 1987. An 8000 year Holocene sea-level record from Jamaica: Implications for interpretation of Caribbean reef and coastal history. *Coral Reefs* **5**: 165-170.

Done, T.J. 1999. Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. *American Zoologist* **39**: 66-79.

Grigg, R.W. and Epp, D. 1989. Critical depth for the survival of coral islands: Effects on the Hawaiian Archipelago. *Science* **243**: 638-641.

Hopley, D. and Kinsey, D.W. 1988. The effects of a rapid short-term sea-level rise on the Great Barrier Reef. Pearman, G.I. (Ed.) *Greenhouse: Planning for climate change*. CSIRO Publishing, East Melbourne, Australia, pp. 189-201.

IPCC, 2007-II. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. and Hanson, C.E. (Eds.) Cambridge University Press, Cambridge, UK.

Kinzie III, R.A. 1999. Sex, symbiosis and coral reef communities. *American Zoologist* **39**: 80-91.

Kinzie III, R.A. and Buddemeier, R.W. 1996. Reefs happen. *Global Change Biology* **2**: 479-494.

Roberts, C.M. 1993. Coral reefs: Health, hazards and history. *Trends in Ecology and Evolution* **8**: 425-427.

White, B., Curran, H.A. and Wilson, M.A. 1998. Bahamian coral reefs yield evidence of a brief sea-level lowstand during the last interglacial. *Carbonates & Evaporites* **13**: 10-22.

Wilkinson, C.R. 1996. Global change and coral reefs: Impacts on reefs, economies and human cultures. *Global Change Biology* **2**: 547-558.

# 8.3.2. Direct Threats

In addition to the  $CO_2$ -induced indirect threats postulated to harm the world's coral reefs, as discussed in Section 8.3.1. of this document, the global increase in the atmosphere's  $CO_2$  content has been hypothesized to possess the potential to harm coral reefs directly. By inducing changes in ocean water chemistry that can lead to reductions in the calcium carbonate saturation state of seawater, it has been predicted that elevated levels of atmospheric  $CO_2$  may reduce rates of coral calcification, possibly leading to slower-growing—and, therefore, weaker coral skele-tons, and in some cases even death.

We begin this next section by discussing the important role biology plays in driving the physicalchemical process of coral calcification, followed by a discussion of several real-world observations that depict increasing rates of coral calcification in the face of rising temperatures and atmospheric  $CO_2$  concentrations.

# 8.3.2.1. Ocean Acidification

The rate of deposition of calcium carbonate on coral reefs, or coral calcification rate, is controlled at the cellular level by the saturation state of calcium carbonate in seawater. Oceanic surface waters have likely been saturated or supersaturated in this regard—providing a good environment for coral reef growth—since early Precambrian times (Holland, 1984). Currently, however, as the air's CO<sub>2</sub> content rises in response to anthropogenic CO<sub>2</sub> emissions, more carbon dioxide dissolves in the surface waters of the world's oceans, and the pH values of the planet's oceanic waters are, or should be, gradually dropping, leading to a reduction in the calcium carbonate saturation state of seawater.

This phenomenon has been theorized to be leading to a corresponding reduction in coral calcification rates (Smith and Buddemeier, 1992; Buddemeier, 1994; Buddemeier and Fautin, 1996a,b; Holligan and Robertson, 1996; Gattuso *et al.*, 1998; Buddemeier and Smith, 1999; IPCC, 2007-I, 2007-II; De'ath *et al.*, 2009), which reduction has been hypothesized to be rendering corals more susceptible to a number of other environmental stresses, including "sea-level rise, extreme temperatures, human damage (from mining, dredging, fishing and tourism), and changes in salinity and pollutant concentrations (nutrients, pesticides, herbicides and particulates), and in ocean currents, ENSO, and storm damage" (Pittock, 1999). Kleypas *et al.* (1999), for example, have calculated that calcification rates of tropical corals should already have declined by 6 percent to 11 percent or more since 1880, as a result of the concomitant increase in atmospheric  $CO_2$  concentration, and they predict that the reductions could reach 17 percent to 35 percent by 2100. Likewise, Langdon *et al.* (2000) calculated a decrease in coral calcification rate of up to 40 percent between 1880 and 2065.

The ocean chemistry aspect of this theory is rather straightforward, but it certainly is not as solid as some commentators make it out to be. In evaluating global seawater impacts of modelpredicted global warming and direct seawater chemical consequences of a doubling of the air's CO<sub>2</sub> content, Loaiciga (2006) used a mass-balance approach to "estimate the change in average seawater salinity caused by the melting of terrestrial ice and permanent snow in a warming earth." He applied "a chemical equilibrium model for the concentration of carbonate species in seawater open to the atmosphere" in order to "estimate the effect of changes in atmospheric CO<sub>2</sub> on the acidity of seawater." Assuming that the rise in the planet's mean surface air temperature continues unabated, and that it eventually causes the melting of all terrestrial ice and permanent snow, Loaiciga calculated that "the average seawater salinity would be lowered not more than 0.61% from its current 35%." He also reports that across the range of seawater temperature considered ( $0^{\circ}$  to  $30^{\circ}$ C), "a doubling of CO<sub>2</sub> from 380 ppm to 760 ppm increases the seawater acidity [lowers its pH] approximately 0.19 pH units." He thus concludes that "on a global scale and over the time scales considered (hundreds of years), there would not be accentuated changes in either seawater salinity or acidity from the rising concentration of atmospheric CO<sub>2</sub>."

Furthermore, with more  $CO_2$  in the air, additional weathering of terrestrial carbonates is likely to occur, which would increase delivery of  $Ca^{2+}$  to the oceans and partly compensate for the  $CO_2$ -induced decrease in oceanic calcium carbonate saturation state (Riding, 1996). And as with all phenomena involving living organisms, the introduction of *life* into the ocean acidification picture greatly complicates things. Considerations of a suite of interrelated biological phenomena, for example, also make it much more difficult to draw such sweeping negative conclusions as are currently being discussed. Indeed, as shown in the next section, they even suggest that the rising  $CO_2$  content of earth's atmosphere may be a positive phenomenon, enhancing the growth rates of coral reefs and helping them to better withstand the many environmental stresses that truly are inimical to their well-being.

### References

Buddemeier, R.W. 1994. Symbiosis, calcification, and environmental interactions. *Bulletin Institut Oceanographique*, Monaco, no. special **13**, pp. 119-131.

Buddemeier, R.W. and Fautin, D.G. 1996a. Saturation state and the evolution and biogeography of symbiotic calcification. *Bulletin Institut Oceanographique*, Monaco, no. special **14**, pp. 23-32.

Buddemeier, R.W. and Fautin, D.G. 1996b . Global CO<sub>2</sub> and evolution among the Scleractinia. *Bulletin Institut Oceanographique*, Monaco, no. special **14**, pp. 33-38.

Buddemeier, R.W. and Smith, S.V. 1999. Coral adaptation and acclimatization: A most ingenious paradox. *American Zoologist* **39**: 1-9.

De'ath, G., Lough, J.M. and Fabricius, K.E. 2009. Declining coral calcification on the Great Barrier Reef. *Science* **323**: 116-119.

Gattuso, J.-P., Frankignoulle, M., Bourge, I., Romaine, S. and Buddemeier, R.W. 1998. Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change* **18**: 37-46.

Holland, H.D. 1984. *The chemical evolution of the atmosphere and oceans*. Princeton University Press, Princeton, NJ.

Holligan, P.M. and Robertson, J.E. 1996. Significance of ocean carbonate budgets for the global carbon cycle. *Global Change Biology* **2**: 85-95.

IPCC, 2007-I. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller. (Eds.) Cambridge University Press, Cambridge, UK.

IPCC, 2007-II. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. and Hanson, C.E. (Eds.) Cambridge University Press, Cambridge, UK. Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J-P., Langdon, C. and Opdyke, B.N. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**: 118-120.

Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., Goddard, J., Marubini, F., Aceves, H., Barnett, H. and Atkinson, M.J. 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* **14**: 639-654.

Loaiciga, H.A. 2006. Modern-age buildup of  $CO_2$  and its effects on seawater acidity and salinity. *Geophysical Research Letters* **33**: 10.1029/2006 GL026305.

Pittock, A.B. 1999. Coral reefs and environmental change: Adaptation to what? *American Zoologist* **39**: 10-29.

Riding, R. 1996. Long-term change in marine CaCO<sub>3</sub> precipitation. *Mem. Soc. Geol. Fr.* **169**: 157-166.

Smith, S.V. and Buddemeier, R.W. 1992. Global change and coral reef ecosystems. *Annual Review of Ecological Systems* 23: 89-118.

### 8.3.2.1.1. Role of Biology

Over half a century ago, Kawaguti and Sakumoto (1948) illustrated the important role played by photosynthesis in the construction of coral reefs. They analyzed numerous datasets recorded in several publications, demonstrating that coral earlier calcification rates are considerably higher in the daylight (when photosynthesis by coral symbionts occurs) than they are in the dark (when the symbionts lose carbon via respiration). A number of more modern studies have also demonstrated that symbiont photosynthesis enhances coral calcification (Barnes and Chalker, 1990; Yamashiro, 1995); and they have further demonstrated that long-term reef calcification rates generally rise in direct proportion to increases in rates of reef primary production (Frankignoulle et al., 1996; Gattuso et al., 1996, 1999). The work of Muscatine (1990) suggests that "the photosynthetic activity of zooxanthellae is the chief source of energy expensive for the energetically process of calcification" (Hoegh-Guldberg, 1999). Consequently, if an anthropogenic-induced increase in the transfer of  $CO_2$  from the atmosphere to the world's oceans, i.e., hydrospheric CO<sub>2</sub> enrichment, were to lead to increases in coral symbiont photosynthesis—as atmospheric CO<sub>2</sub> enrichment does for essentially all terrestrial plants (Kimball, 1983; Idso, 1992)-it is likely that increases in coral calcification rates would occur as well.

There are several reasons for expecting a positive coral calcification response to CO<sub>2</sub>-enhanced symbiont photosynthesis. One of the first mechanisms to come to mind is the opposite of the phenomenon that has been proffered as a cause of future declines in coral calcification rates. This reverse phenomenon is the decrease in extracellular CO<sub>2</sub> partial pressure in coral tissues that is driven by the drawdown of aqueous  $CO_2$  caused by the photosynthetic process. With CO<sub>2</sub> being removed from the water in intimate contact with the coral host via its fixation by photosynthesis (which CO<sub>2</sub> drawdown is of greater significance to the coral than the increase in the CO<sub>2</sub> content of the surrounding bulk water that is affected by the ongoing rise in the air's  $CO_2$  content), the pH and calcium carbonate saturation state of the water immediately surrounding the coral host should rise (Goreau, 1959), enhancing the coral's calcification rate (Gattuso et al., 1999). If hydrospheric CO<sub>2</sub> enrichment stimulates zooxanthellae photosynthesis to the same degree that atmospheric CO<sub>2</sub> enrichment stimulates photosynthesis in terrestrial plants, i.e., by 30 percent to 50 percent for a 300 ppm increase in CO<sub>2</sub> concentration (Kimball, 1983; Idso 1992, Idso and Idso, 1994), this phenomenon alone would more than compensate for the drop in the calcium carbonate saturation state of the bulk-water of the world's oceans produced by the ongoing rise in the air's  $CO_2$ content, which Gattuso et al. (1999) have calculated could lead to a 15 percent reduction in coral calcification rate for a doubling of the pre-industrial atmospheric CO<sub>2</sub> concentration.

Another reason why coral calcification may proceed at a higher rate in the presence of CO<sub>2</sub>stimulated symbiont photosynthesis is that, while growing more robustly, the zooxanthellae may take up more of the metabolic waste products of the coral host, which, if present in too great quantities, can prove detrimental to the health of the host, as well as the health of the entire coral plant-animal assemblage (Yonge, 1968; Crossland and Barnes, 1974). There are also a number of other substances that are known directly interfere with calcium carbonate to precipitation; they too can be actively removed from the water by coral symbionts in much the same way that symbionts remove host waste products (Simkiss, 1964). More importantly, perhaps, a greater amount of symbiont-produced photosynthates may provide more fuel for the active transport processes involved in coral calcification (Chalker and Taylor, 1975), as well as more raw materials for the synthesis of the coral organic matrix (Wainwright, 1963; Muscatine, 1967; Battey and Patton, 1984). Finally, the photosynthetic process helps to maintain a healthy aerobic or oxic environment for the optimal growth of the coral animals (Rinkevich and Loya, 1984; Rands *et al.*, 1992); greater CO<sub>2</sub>-induced rates of symbiont photosynthesis would enhance this important "environmental protection activity."

Such observations invoke a number of questions. With ever more  $CO_2$  going into the air, driving ever more  $CO_2$  into the oceans, might we not logically expect to see increasingly greater rates of coral symbiont photosynthesis, due to the photosynthesisstimulating effect of hydrospheric  $CO_2$  enrichment? Would not this phenomenon, in turn, increasingly enhance all of the many positive photosyntheticdependent phenomena we have described and thereby increase coral calcification rates? And might it not increase these rates well beyond the point of overpowering the modest negative effect of the purely chemical consequences of elevated dissolved  $CO_2$  on ocean pH and calcium carbonate saturation state?

The answers to these several questions are probably all "yes," but arriving at these conclusions is not as simple as it sounds. For one thing, although many types of marine plant life do indeed respond to hydrospheric CO<sub>2</sub> enrichment (Raven et al., 1985) including seagrasses (Zimmerman et al., 1997). certain diatoms (Riebesell et al., 1993; Chen and Gao, 2004; Sobrino et al., 2008), macroalgae (Borowitzka and Larkum, 1976; Gao et al., 1993), and microalgae or phytoplankton (Raven, 1991; Nimer and Merrett, 1993)—the photosynthesis of many marine autotrophs is normally not considered to be carbonlimited, because of the large supply of bicarbonate in the world's oceans (Raven, 1997). However, as Gattuso et al. (1999) explain, this situation is true only for autotrophs that possess an effective carbonconcentrating mechanism; it is believed that many coral symbionts are of this type (Burris et al., 1983; Al-Moghrabi et al., 1996: Goiran et al., 1996).

Nevertheless, in yet another positive twist to this complex story, Gattuso *et al.* (1999) report that coral zooxanthellae are able to change their mechanism of carbon supply in response to various environmental stimuli. Furthermore, Beardall *et al.* (1998) suggest that an increased concentration of dissolved  $CO_2$ , together with an increase in the rate of  $CO_2$ generation by bicarbonate dehydration in host cells, may favor a transition to the diffusional mode of carbon supply, which *is* sensitive to hydrospheric  $CO_2$ concentration. Consequently, if such a change in mode of carbon supply were to occur—prompted, perhaps, by hydrospheric  $CO_2$  enrichment itself—this shift in  $CO_2$  fixation strategy would indeed allow the several biological mechanisms we have described to operate to enhance reef calcification rates in response to a rise in the air's  $CO_2$  content.

In one final example that demonstrates the importance of biology in driving the physicalchemical process of coral calcification, Muscatine *et al.* (2005) note that the "photosynthetic activity of zooxanthellae is the chief source of energy for the energetically expensive process of calcification," and that long-term reef calcification rates have generally been observed to rise in direct proportion to increases in rates of reef primary production, which they say may well be *enhanced* by increases in the air's  $CO_2$  concentration.

Muscatine et al. begin the report of their investigation of the subject by stating much the same thing, i.e., that endosymbiotic algae "release products of photosynthesis to animal cells ... and augment the rate of skeletal calcification." Then, noting that the "natural abundance of stable isotopes ( $\delta^{13}$ C and  $\delta^{15}$ N) has answered paleobiological and modern questions about the effect of photosymbiosis on sources of carbon and oxygen in coral skeletal calcium carbonate," they go on to investigate the natural abundance of these isotopes in another coral skeletal compartment-the skeletal organic matrix (OM)-in 17 species of modern scleractinian corals, after which they compare the results for symbiotic and nonsymbiotic forms to determine the role played by algae in OM development.

Why is this study an important scientific undertaking? It is because, in the words of Muscatine *et al.*, "the scleractinian coral skeleton is a two-phase composite structure consisting of fiber-like crystals of aragonitic calcium carbonate intimately associated with an intrinsic OM," and although the OM generally comprises less than 0.1 percent of the total weight of the coral skeleton, it is, in their words, "believed to initiate nucleation of calcium carbonate and provide a framework for crystallographic orientation and species-specific architecture." In fact, they say inhibition of OM synthesis "brings coral calcification to a halt."

So what did Muscatine *et al.* learn from their experiments? They say their "most striking observation is the significant difference in mean OM  $\delta^{15}N$  between symbiotic and nonsymbiotic corals," which makes OM  $\delta^{15}N$  an important proxy for photosymbiosis. As an example of its usefulness, they applied the technique to a fossil coral (*Pachythecalis*  *major*) from the Triassic (which prevailed some 240 million years ago), finding that the ancient coral was indeed photosymbiotic. Even more importantly, however, they conclude in the final sentence of their paper that "it now seems that symbiotic algae may control calcification by both modification of physico-chemical parameters within the coral polyps (Gautret *et al.*, 1997; Cuif *et al.*, 1999) and augmenting the synthesis of OM (Allemand *et al.*, 1998)."

Although lacking the research to absolutely identify the "what" and definitively describe the "how" of the hypothesis of hydrospheric CO<sub>2</sub> enhancement of coral calcification, it is clear that something of the nature described above can indeed act to overcome the negative effect of the high-CO<sub>2</sub>induced decrease in calcium carbonate saturation state on coral calcification rate. It has been clearly demonstrated, for example, that corals can grow quite well in aquariums containing water of very high dissolved CO<sub>2</sub> concentration (Atkinson et al., 1995); and Carlson (1999) has stated that the fact that corals often thrive in such water "seems to contradict conclusions ... that high CO<sub>2</sub> may inhibit calcification." There are numerous other examples of such phenomena in the real world of nature, which we examine next.

# References

Al-Moghrabi, S., Goiran, C., Allemand, D., Speziale, N. and Jaubert, J. 1996. Inorganic carbon uptake for photosynthesis by the symbiotic coral-dinoflagelate association. 2. Mechanisms for bicarbonate uptake. *Journal of Experimental Marine Biology and Ecology* **199**: 227-248.

Allemand, D., Tambutte, E., Girard, J.-P. and Jaubert, J. 1998. Organic matrix synthesis in the scleractinian coral *stylophora pistillata*: role in biomineralization and potential target of the organotin tributyltin. *Journal of Experimental Biology* **201**: 2001-2009.

Atkinson, M.J., Carlson, B.A. and Crow, G.L. 1995. Coral growth in high-nutrient, low-pH seawater: A case study of corals cultured at the Waikiki Aquarium, Honolulu, Hawaii. *Coral Reefs* 14: 215-223.

Barnes, D.J. and Chalker, B.E. 1990. *Calcification and photosynthesis in reef-building corals and algae*. Dubinsky, Z. (Ed). Elsevier, Amsterdam, The Netherlands, pp. 109-131.

Battey, J.F. and Patton, J.S. 1984. A reevaluation of the role of glycerol in carbon translocation in zooxanthellae-coelenterate symbiosis. *Marine Biology* **79**: 27-38.

Beardall, J., Beer, S. and Raven, J.A. 1998. Biodiversity of marine plants in an era of climate change: Some predictions based on physiological performance. *Bot. Mar.* **41**: 113-123.

Borowitzka, M.A. and Larkum, W.D. 1976. Calcification in the green alga Halimeda. III. The sources of inorganic carbon for photosynthesis and calcification and a model of the mechanisms of calcification. *Journal of Experimental Botany* **27**: 879-893.

Burris, J.E., Porter, J.W. and Laing, W.A. 1983. Effects of carbon dioxide concentration on coral photosynthesis. *Marine Biology* **75**: 113-116.

Carlson, B.A. 1999. Organism responses to rapid change: What aquaria tell us about nature. *American Zoologist* **39**: 44-55.

Chalker, B.E. and Taylor, D.L. 1975. Light-enhanced calcification and the role of oxidative phosphorylation in calcification of the coral *Acropora cervicornis*. *Proceedings of the Royal Society of London B* **190**: 323-331.

Chen, X. and Gao, K. 2004. Characterization of diurnal photosynthetic rhythms in the marine diatom Skeletonema costatum grown in synchronous culture under ambient and elevated CO<sub>2</sub>. *Functional Plant Biology* **31**: 399-404.

Crossland, C.J. and Barnes, D.J. 1974. The role of metabolic nitrogen in coral calcification. *Marine Biology* **28**: 325-332.

Cuif, J.-P., Dauphin, Y., Freiwald, A., Gautret, P. and Zibrowius, H. 1999. Biochemical markers of zooxanthellae symbiosis in soluble matrices of skeleton of 24 *Scleractinia* species. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **123**: 269-278.

Frankignoulle, M., Gattuso, J.-P., Biondo, R., Bourge, I., Copin-Montegut, G. and Pichon, M. 1996. Carbon fluxes in coral reefs. II. Eulerian study of inorganic carbon dynamics and measurement of air-sea CO<sub>2</sub> exchanges. *Marine Ecology Progress Series* **145**: 123-132.

Gao, K., Aruga, Y., Asada, K. and Kiyohara, M. 1993. Influence of enhanced  $CO_2$  on growth and photosynthesis of the red algae *Gracilaria* sp. and *G chilensis*. *Journal of Applied Phycology* **5**: 563-571.

Gattuso, J.-P., Allemand, D. and Frankignoulle, M. 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**: 160-183.

Gattuso, J.-P., Pichon, M., Delesalle, B., Canon, C. and Frankignoulle, M. 1996. Carbon fluxes in coral reefs. I. Lagrangian measurement of community metabolism and resulting air-sea CO<sub>2</sub> disequilibrium. *Marine Ecology Progress Series* **145**: 109-121.

Gautret, P., Cuif, J.-P. and Freiwald, A. 1997. Composition of soluble mineralizing matrices in zooxanthellate and nonzooxanthellate scleractinian corals: Biochemical assessment of photosynthetic metabolism through the study of a skeletal feature. *Facies* **36**: 189-194.

Goiran, C., Al-Moghrabi, S., Allemand, D. and Jaubert, J. 1996. Inorganic carbon uptake for photosynthesis by the symbiotic coral/dinoflagellate association. 1. Photosynthetic performances of symbionts and dependence on sea water bicarbonate. *Journal of Experimental Marine Biology and Ecology* **199**: 207-225.

Goreau, T.F. 1959. The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. *Biological Bulletin* **116**: 59-75.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**: 839-866.

Idso, K.E. 1992. Plant responses to rising levels of atmospheric carbon dioxide: A compilation and analysis of the results of a decade of international research into the direct biological effects of atmospheric  $CO_2$  enrichment. Office of Climatology, Arizona State University, Tempe, AZ.

Idso, K.E. and Idso, S.B. 1994. Plant responses to atmospheric  $CO_2$  enrichment in the face of environmental constraints: A review of the past 10 years' research. *Agricultural and Forest Meteorology* **69**: 153-203.

Kawaguti, S. and Sakumoto, D. 1948. The effects of light on the calcium deposition of corals. *Bulletin of the Oceanographic Institute of Taiwan* 4: 65-70.

Kimball, B.A. 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**: 779-788.

Muscatine, L. 1967. Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. *Science* **156**: 516-519.

Muscatine, L. 1990. The role of symbiotic algae in carbon and energy flux in reef corals. *Coral Reefs* **25**: 1-29.

Muscatine, L., Goiran, C., Land, L., Jaubert, J., Cuif, J.-P. and Allemand, D. 2005. Stable isotopes ( $\delta^{13}$ C and  $\delta^{15}$ N) of organic matrix from coral skeleton. *Proceedings of the National Academy of Sciences USA* **102**: 1525-1530.

Nimer, N.A. and Merrett, M.J. 1993. Calcification rate in *Emiliania huxleyi* Lohmann in response to light, nitrate and availability of inorganic carbon. *New Phytologist* **123**: 673-677.

Rands, M.L., Douglas, A.E., Loughman, B.C. and Ratcliffe, R.G. 1992. Avoidance of hypoxia in a cnidarian symbiosis by algal photosynthetic oxygen. *Biological Bulletin* **182**: 159-162.

Raven, J.A. 1991. Physiology of inorganic C acquisition and implications for resource use efficiency by marine phytoplankton: Relation to increased  $CO_2$  and temperature. *Plant, Cell and Environment* **14**: 779-794.

Raven, J.A. 1997. Inorganic carbon acquisition by marine autotrophs. *Advances in Botanical Research* **27**: 85-209.

Raven, J.A., Osborne, B.A. and Johnston, A.M. 1985. Uptake of  $CO_2$  by aquatic vegetation. *Plant, Cell and Environment* **8**: 417-425.

Riebesell, U., Wolf-Gladrow, D.A. and Smetacek, V. 1993. Carbon dioxide limitation of marine phytoplankton growth rates. *Nature* **361**: 249-251.

Rinkevich, B. and Loya, Y. 1984. Does light enhance calcification in hermatypic corals? *Marine Biology* **80**: 1-6.

Simkiss, K. 1964. Phosphates as crystal poisons of calcification. *Biological Review* **39**: 487-505.

Sobrino, C., Ward, M.L. and Neale, P.J. 2008. Acclimation to elevated carbon dioxide and ultraviolet radiation in the diatom Thalassiosira pseudonana: Effects on growth, photosynthesis, and spectral sensitivity of photoinhibition. *Limnology and Oceanography* **53**: 494-505.

Wainwright, S.A. 1963. Skeletal organization in the coral *Pocillopora damicornis. Quarterly Journal of Microscopic Science* **104**: 164-183.

Yamashiro, H. 1995. The effects of HEBP, an inhibitor of mineral deposition, upon photosynthesis and calcification in the scleractinian coral, *Stylophora pistillata. Journal of Experimental Marine Biology and Ecology* **191**: 57-63.

Yonge, C.M. 1968. Living corals. *Proceedings of the Royal Society of London B* 169: 329-344.

Zimmerman, R.C., Kohrs, D.G., Steller, D.L. and Alberte, R.S. 1997. Impacts of CO<sub>2</sub> enrichment on productivity and light requirements of eelgrass. *Plant Physiology* **115**: 599-607.

### 8.3.2.1.2. Coral Calcification

Many people have predicted that rates of coral calcification, as well as the photosynthetic rates of their symbiotic algae, will dramatically decline in response to what they typically refer to as an acidification of the world's oceans, as the atmosphere's  $CO_2$  concentration continues to rise in

the years, decades, and centuries to come. As ever more pertinent evidence accumulates, however, the true story appears to be just the opposite.

Herfort *et al.* (2008) note that an increase in atmospheric  $CO_2$  will cause an increase in the abundance of  $HCO_3^-$  (bicarbonate) ions and dissolved  $CO_2$ , and they also report that several studies on marine plants have observed "increased photosynthesis with higher than ambient DIC [dissolved inorganic carbon] concentrations," citing the works of Gao *et al.* (1993), Weis (1993), Beer and Rehnberg (1997), Marubini and Thake (1998), Mercado *et al.* (2001, 2003), Herfort *et al.* (2002), and Zou *et al.* (2003).

To further explore this subject, and to see what it might imply for coral calcification, the three researchers employed a wide range of bicarbonate concentrations "to monitor the kinetics of bicarbonate use in both photosynthesis and calcification in two reef-building corals, *Porites porites* and *Acropora* sp." This work revealed that additions of  $HCO_3^-$  to synthetic seawater continued to increase the calcification rate of *Porites porites* until the bicarbonate concentration exceeded three times that of seawater, while photosynthetic rates of the coral's symbiotic algae were stimulated by  $HCO_3^-$  addition until they became saturated at twice the normal  $HCO_3^-$  concentration of seawater.

Similar experiments conducted on Indo-Pacific *Acropora* sp. showed that calcification and photosynthetic rates in these corals were enhanced to an even greater extent, with calcification continuing to increase above a quadrupling of the  $HCO_3^-$  concentration and photosynthesis saturating at triple the concentration of seawater. In addition, they monitored calcification rates of the *Acropora* sp. in the dark, and, in their words, "although these were lower than in the light for a given  $HCO_3^-$  concentration, they still increased dramatically with  $HCO_3^-$  addition, showing that calcification in this coral is light stimulated but not light dependent."

In discussing the significance of their findings, Herfort et al. suggest that "hermatypic corals incubated in the light achieve high rates of calcification by the synergistic action of photosynthesis," which, as they have shown, is enhanced by elevated concentrations of HCO<sub>3</sub><sup>-</sup> ions that come courtesy of the ongoing rise in the air's CO<sub>2</sub> content. As for the real-world implications of their work, the three researchers note that over the next century the predicted increase in atmospheric CO<sub>2</sub> concentration "will result in about a 15% increase in oceanic HCO<sub>3</sub>," and they say that this development "could stimulate photosynthesis and calcification in a wide variety of hermatypic corals," a conclusion that stands in stark contrast to the contention of the IPCC.

In another study, Pelejero et al. (2005) developed a reconstruction of seawater pH spanning the period 1708-1988, based on the boron isotopic composition  $(\delta^{11}B)$  of a long-lived massive coral (*Porites*) from Flinders Reef in the western Coral Sea of the southwestern Pacific. Results indicated that "there [was] no notable trend toward lower  $\delta^{11}$ B values" over the 300-year period investigated. Instead, they say that "the dominant feature of the coral  $\delta^{11}B$  record is a clear interdecadal oscillation of pH, with  $\delta^{11}B$ values ranging between 23 and 25 per mil (7.9 and 8.2 pH units)," which "is synchronous with the Interdecadal Pacific Oscillation." Furthermore, they calculated changes in aragonite saturation state from the Flinders pH record that varied between ~3 and 4.5, which values encompass "the lower and upper limits of aragonite saturation state within which corals can survive." Despite this fact, they report that "skeletal extension and calcification rates for the Flinders Reef coral fall within the normal range for Porites and are not correlated with aragonite saturation state or pH."

Thus, contrary to claims that historical anthropogenic  $CO_2$  emissions have already resulted in a significant decline in ocean water pH and aragonite saturation state, Pelejero *et al.*'s 300-year record of these parameters (which, in their words, began "well before the start of the Industrial Revolution") provides no evidence of such a decline. What is more, and also contrary to what one would expect from claims of how sensitive coral calcification rate is to changes in pH and aragonite saturation state, they found that huge cyclical changes in these parameters had essentially no detectable effect on either coral calcification or skeletal extension rates.

Moving a little backward in time, in a study of historical calcification rates determined from coral cores retrieved from 35 sites on the Great Barrier Reef, Lough and Barnes (1997) observed a statistically significant correlation between coral calcification rate and local water temperature, such that a 1°C increase in mean annual water temperature increased mean annual coral calcification rate by about 3.5 percent. Nevertheless, they report there were "declines in calcification in *Porites* on the Great Barrier Reef over recent decades." They are quick to point out, however, that their data depict several extended periods of time when coral growth rates were either above or below the long-term mean, cautioning that "it would be unwise to rely on shortterm values (say averages over less than 30 years) to assess mean conditions."

As an example of this fact, they report that "a decline in calcification equivalent to the recent decline occurred earlier this century and much greater declines occurred in the 18th and 19th centuries," long before anthropogenic CO<sub>2</sub> emissions made much of an impact on the air's CO<sub>2</sub> concentration. Over the entire expanse of their dataset, Lough and Barnes say "the 20th century has witnessed the second highest period of above average calcification in the past 237 years," which is not exactly what one would expect in light of (1) how dangerous high water temperatures are often said to be for corals, (2) the claim that earth is currently warmer than it has been at any other time during the entire past millennium, and (3) the fact that the air's CO<sub>2</sub> content is currently much higher than it has been for far longer than a mere thousand years.

Similar findings were reported by Bessat and Buigues (2001), who derived a history of coral calcification rates from a core extracted from a massive *Porites* coral head on the French Polynesian island of Moorea that covered the period 1801-1990. They performed this work, they say, because "recent coral-growth models highlight the enhanced greenhouse effect on the decrease of calcification rate," and rather than relying on theoretical calculations, they wanted to work with real-world data, stating that the records preserved in ancient corals "may provide information about long-term variability in the performance of coral reefs, allowing unnatural changes to be distinguished from natural variability."

Bessat and Buigues found that a 1°C increase in water temperature *increased* coral calcification rates at the site they studied by 4.5 percent. Then, they found that "instead of a 6-14% decline in calcification over the past 100 years computed by the Kleypas group, the calcification has increased, in accordance with [the results of] Australian scientists Lough and Barnes." They also observed patterns of "jumps or stages" in the record, which were characterized by an increase in the annual rate of calcification, particularly at the beginning of the past century "and in a more marked way around 1940, 1960 and 1976," stating once again that their results "do not confirm those predicted by the Kleypas *et al.* (1999) model."

Another major blow to the Kleypas *et al.* model was provided by the work of Lough and Barnes

(2000), who assembled and analyzed the calcification characteristics of 245 similar-sized massive colonies of *Porites* corals obtained from 29 reef sites located along the length, and across the breadth, of Australia's Great Barrier Reef (GBR), which data spanned a latitudinal range of approximately 9° and an annual average sea surface temperature (SST) range of 25-27°C. To these data they added other published data from the Hawaiian Archipelago (Grigg, 1981, 1997) and Phuket, Thailand (Scoffin *et al.*, 1992), thereby extending the latitudinal range of the expanded dataset to 20° and the annual average SST range to 23-29°C.

This analysis revealed that the GBR calcification data were linearly related to the average annual SST data, such that "a 1°C rise in average annual SST increased average annual calcification by 0.39 g cm<sup>-2</sup> year<sup>-1</sup>." Results were much the same for the extended dataset; Lough and Barnes report that "the regression equation [calcification = 0.33(SST)—7.07] explained 83.6% of the variance in average annual calcification (F = 213.59, p less than 0.00)," noting that "this equation provides for a change in calcification rate of 0.33 g cm<sup>-2</sup> year<sup>-1</sup> for each 1°C change in average annual SST."

With respect to the significance of their findings, Lough and Barnes say they "allow assessment of possible impacts of global climate change on coral reef ecosystems," and between the two 50-year periods 1880-1929 and 1930-1979, they calculate a calcification increase of 0.06 g cm<sup>-2</sup> year<sup>-1</sup>, noting that "this increase of ~4% in calcification rate conflicts with the estimated decrease in coral calcification rate of 6-14% over the same time period suggested by Kleypas et al. (1999) as a response to changes in ocean chemistry." Even more stunning is their observation that between the two 20-year periods 1903-1922 and 1979-1998, "the SST-associated increase in calcification is estimated to be less than 5% in the northern GBR.  $\sim 12\%$  in the central GBR. ~20% in the southern GBR and to increase dramatically (up to  $\sim$ 50%) to the south of the GBR."

In light of these real-world observations, and in stark contrast to the doom-and-gloom prognostications of the IPCC, Lough and Barnes conclude that coral calcification rates "may have already significantly increased along the GBR in response to global climate change."

But in *Nature*, Caldeira and Wickett (2003) kept the catastrophe ball rolling. Based on a geochemical model, an ocean general-circulation model, an IPCC  $CO_2$  emissions scenario for the twenty-first century, and a logistic function for the burning of earth's posttwenty-first century fossil-fuel reserves, they calculated the maximum level to which the air's  $CO_2$ concentration might rise, the point in time when that might happen, and the related decline that might be expected to occur in ocean-surface pH. These calculations indicated that earth's atmospheric  $CO_2$ concentration could approach 2,000 ppm around the year 2300, leading to an ocean-surface pH reduction of 0.7 units, a change described by Caldeira and Wickett as being much more rapid and considerably greater "than any experienced in the past 300 million years," which, of course, proves deadly for earth's corals in their scenario.

The following year, similar concerns were aroused by a report prepared for the Pew Center on Global Climate Change, a group advocating immediate action on global warming. In that document, Buddemeier et al. (2004) claimed the projected increase in the air's CO<sub>2</sub> content and the simulated decline in ocean-surface pH would dramatically decrease coral calcification rates, which they predicted would lead to "a slow-down or reversal of reef-building and the potential loss of reef structures." Even Buddemeier et al. (2004), however, were forced to admit that "calcification rates of large heads of the massive coral Porites increased rather than decreased over the latter half of the 20th century," further noting that "temperature and calcification rates are correlated, and these corals have so far responded more to increases in water temperature (growing faster through increased metabolism and the increased photosynthetic rates of their zooxanthellae) than to decreases in carbonate ion concentration."

The most recent claims of impending coral doom derive from the 2009 Science study of De'ath et al. (2009), who examined coral calcification rates on the Great Barrier Reef over the past 400 years. Results of their analysis indicate that there was a 14 percent decline in Porites calcification rate between 1990 and 2005, which observation the authors claim "is unprecedented in at least the past 400 years." As one might expect, the media's coverage of these findings included some ominous declarations. The headline of a BBC News report, for example, proclaimed "coral reef growth is slowest ever," while a Sky News headline read "Barrier Reef coral growth 'will stop'." ABC News went so far as to state when it might stop, concluding their report by quoting the research paper's senior author as saying "coral growth could hit zero by 2050."

How correct are such claims? Beginning with the first media claim that "coral reef growth is slowest ever," it can't possibly be right. The scleractinian corals, which are the major builders of the reefs of today, have been around some 200 million years, during most of which time the atmosphere's CO<sub>2</sub> concentration was greater and its temperature was higher than today, which should immediately raise a red flag about the proffered cause of the recent decline in reef growth.

In regard to the recent decline in calcification being unprecedented in the past 400 years, this is a good example of cherry-picking a time frame to make a sensational claim. All one needs to do is follow the published De'ath *et al.* calcification history back in time a mere 33 years more, from 1605 to 1572, to see the coral calcification rate during that earlier time was approximately 23 percent lower than what it was at its twentieth century peak, and the air's  $CO_2$ concentration was more than 100 ppm less than what it is today.

Another way of looking at De'ath et al.'s data is to realize that from 1572 to the twentieth century peak, Porites calcification rates on the Great Barrier Reef rose by about 29 percent as atmospheric CO<sub>2</sub> concentration and air temperature rose concurrently, after which calcification rates declined, but by a smaller 14 percent. Why would anyone believe that the recent calcification decline implies that Porites coral growth "will stop," and that the end will come "by 2050"? They believe it because certain scientists (such as James Hansen) and politicians (such as Al Gore) imply much the same thing, as even De'ath et al. do. But when scientists feel compelled to be as correct and as true to their data as possible, such as when writing in Science, the three researchers from the Australian Institute of Marine Science clearly state that "the causes for the Great Barrier Reef-wide decline in coral calcification of massive Porites remain unknown." And when the causes of the recent decline in coral calcification rate are admitted to be unknown, it seems foolish indeed to predict, not only that the decline will continue, but that it will lead all the way to the demise of the studied coral, and especially at a specified future date, which, we might add, De'ath et al. appropriately do not do in their Science paper.

A second good reason for not believing that the ongoing rise in the air's  $CO_2$  content will lead to reduced oceanic pH and, therefore, lower calcification rates in the world's coral reefs, is that the same phenomenon that powers the twin processes of coral

calcification and phytoplanktonic growth (photosynthesis) tends to increase the pH of marine waters (Gnaiger *et al.*, 1978; Santhanam *et al.*, 1994; Brussaard *et al.*, 1996; Lindholm and Nummelin, 1999; Macedo *et al.*, 2001; Hansen, 2002). This phenomenon has been shown to have the ability to dramatically increase the pH of marine bays, lagoons, and tidal pools (Gnaiger *et al.*, 1978; Macedo *et al.*, 2001; Hansen, 2002) as well as to significantly enhance the surface water pH of areas as large as the North Sea (Brussaard *et al.*, 1996).

In one recent example, Middelboe and Hansen (2007) studied the pH of a wave-exposed boulder reef in Aalsgaarde on the northern coast of Zealand, Denmark, and a sheltered shallow-water area in Kildebakkerne in the estuary Roskilde Fjord, Denmark, reporting that, in line with what one would expect if photosynthesis tends to increase surfacewater pH, (1) "daytime pH was significantly higher in spring, summer and autumn than in winter at both study sites," often reaching values of 9 or more during peak summer growth periods vs. 8 or less in winter, (2) "diurnal measurements at the most exposed site showed significantly higher pH during the day than during the night," reaching values that sometimes exceeded 9 during daylight hours but that typically dipped below 8 at night, and (3) that "diurnal variations were largest in the shallow water and decreased with increasing water depth."

In addition to their own findings, Middelboe and Hansen cite those of Pearson *et al.* (1998), who found that pH averaged about 9 during the summer in populations of *Fucus vesiculosus* in the Baltic Sea; Menendez *et al.* (2001), who found that maximum pH was 9 to 9.5 in dense floating macroalgae in a brackish coastal lagoon in the Ebro River Delta; and Bjork *et al.* (2004), who found pH values as high as 9.8 to 10.1 in isolated rock pools in Sweden. Noting that "pH in the sea is usually considered to be stable at around 8 to 8.2," the two Danish researchers thus concluded that "pH is higher in natural shallow-water habitats than previously thought."

With each succeeding year, the physical evidence against the  $CO_2$ -reduced calcification theory continues to grow ever more compelling, while support for the positive view promoted here continues to accumulate. Working in the laboratory, for example, Reynaud *et al.* (2004) grew nubbins of the branching zooxanthellate scleractinian coral *Acropora verweyi* in aquariums maintained at 20°, 25°, and 29°C, while weighing them once a week over a period of four weeks. This exercise revealed that coral calcification rates increased in nearly perfect linear fashion with increasing water temperature, yielding values of 0.06 percent, 0.22 percent, and 0.35 percent per day at 20°, 25°, and 29°C, respectively. These data reveal an approximate 480 percent increase in calcification rate in response to a 9°C increase in water temperature and a 160 percent increase in response to a 3°C increase in temperature, the latter of which temperature increases is somewhere in the low to midrange of global warming that the IPCC claims will result from a 300 ppm increase in the air's CO<sub>2</sub> concentration. This positive temperature effect outweighs the negative effect of rising CO<sub>2</sub> concentrations on coral calcification via ocean acidification.

Carricart-Ganivet (2004) developed relationships between coral calcification rate and annual average SST based on data collected from colonies of the reefbuilding coral Montastraea annularis at 12 localities in the Gulf of Mexico and the Caribbean Sea, finding that calcification rate in the Gulf of Mexico increased  $0.55 \text{ g cm}^{-2} \text{ year}^{-1}$  for each 1°C increase, while in the Caribbean Sea it increased 0.58 g cm<sup>-2</sup> year<sup>-1</sup> for each  $1^{\circ}$ C increase. Pooling these data with those of M. annularis and M. faveolata growing to a depth of 10 m at Carrie Bow Cay, Belize, those from reefs at St. Croix in the US Virgin Islands, and those of M. faveolata growing to a depth of 10 m at Curacao, Antilles, Carricart-Ganivet reports he obtained a mean increase in calcification rate of  $\sim 0.5$  g cm<sup>-2</sup> year<sup>-1</sup> for each 1°C increase in annual average SST, which is even greater than what was found by Lough and Barnes for *Porites* corals.

In another important study, McNeil et al. (2004) used a coupled atmosphere-ice-ocean carbon cycle model to calculate annual mean SST increases within the world's current coral reef habitat from 1995 to 2100 for increases in the air's CO<sub>2</sub> concentration specified by the IPCC's IS92a scenario, after which concomitant changes in coral reef calcification rates were estimated by combining the output of the climate model with empirical relationships between coral calcification rate and (1) aragonite saturation state (the negative  $CO_2$  effect) and (2) annual SST (the positive temperature effect). Their choice for the first of these two relationships was that derived by Langdon et al. (2000), which leads to an even greater reduction in calcification than was predicted in the study of Kleypas et al. Their choice for the second relationship was that derived by Lough and Barnes (2000), which leads to an increase in calcification that is only half as large as that derived by Carricart-

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Ganivet (2004). As a result, it can be appreciated that the net result of the two phenomena was doubly weighted in favor of reduced coral calcification. Nevertheless, McNeil et al. found that the increase in coral reef calcification associated with ocean warming outweighed the decrease associated with the CO<sub>2</sub>-induced decrease in aragonite saturate state. They calculated that coral calcification in 2100 would be 35 percent higher than what it was in preindustrial times at the very least. And they found that the area of coral reef habitat expands in association with the projected ocean warming.

Finally, in a study devoted to corals that involves a much longer period of time than all of the others we have discussed, Crabbe et al. (2006) determined the original growth rates of long-dead Quaternary corals found in limestone deposits on islands in the Wakatobi Marine National Park of Indonesia, after which they compared them to the growth rates of present-day corals of the same genera living in the same area. This work revealed that the Quaternary corals grew "in a comparable environment to modern reefs"-except, of course, for the air's CO<sub>2</sub> concentration, which is currently higher than it has been at any other time throughout the Quaternary, which spans the past 1.8 million years. Most interestingly, therefore, their measurements indicated that the radial growth rates of the modern corals were 31 percent greater than those of their ancient predecessors in the case of Porites species, and 34 percent greater in the case of *Favites* species.

To these papers we could add many others (Clausen and Roth, 1975; Coles and Jokiel, 1977; Kajiwara *et al.*, 1995; Nie *et al.*, 1997; Reynaud-Vaganay *et al.*, 1999; Reynaud *et al.*, 2007) that also depict increasing rates of coral calcification in the face of rising temperatures and atmospheric  $CO_2$  concentrations. Clearly, the net impact of twentieth century increases in atmospheric  $CO_2$  and temperature has not been anywhere near as catastrophically disruptive to earth's corals as the IPCC suggests it should have been. Quite to the contrary, the temperature and  $CO_2$  increases appear to not have been hurtful at all, and in fact appear to have been helpful.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> science.org/subject/c/calcification.php.

#### References

Beer, S. and Rehnberg, J. 1997. The acquisition of inorganic carbon by the sea grass *Zostera marina*. *Aquatic Botany* **56**: 277-283.

Bessat, F. and Buigues, D. 2001. Two centuries of variation in coral growth in a massive *Porites* colony from Moorea (French Polynesia): a response of oceanatmosphere variability from south central Pacific. *Palaeogeography, Palaeoclimatology, Palaeoecology* **175**: 381-392.

Bjork, M., Axelsson, L. and Beer, S. 2004. Why is Ulva intestinalis the only macroalga inhabiting isolated rockpools along the Swedish Atlantic coast? *Marine Ecology Progress Series* **284**: 109-116.

Brussaard, C.P.D., Gast, G.J., van Duyl, F.C. and Riegman, R. 1996. Impact of phytoplankton bloom magnitude on a pelagic microbial food web. *Marine Ecology Progress Series* 144: 211-221.

Buddemeier, R.W., Kleypas, J.A. and Aronson, R.B. 2004. Coral Reefs & Global Climate Change: Potential Contributions of Climate Change to Stresses on Coral Reef Ecosystems. The Pew Center on Global Climate Change, Arlington, VA, USA.

Caldeira, K. and Wickett, M.E. 2003. Anthropogenic carbon and ocean pH. *Nature* **425**: 365.

Carricart-Ganivet, J.P. 2004. Sea surface temperature and the growth of the West Atlantic reef-building coral *Montastraea annularis. Journal of Experimental Marine Biology and Ecology* **302**: 249-260.

Clausen, C.D. and Roth, A.A. 1975. Effect of temperature and temperature adaptation on calcification rate in the hematypic *Pocillopora damicornis*. *Marine Biology* **33**: 93-100.

Coles, S.L. and Jokiel, P.L. 1977. Effects of temperature on photosynthesis and respiration in hermatypic corals. *Marine Biology* **43**: 209-216.

Crabbe, M.J.C., Wilson, M.E.J. and Smith, D.J. 2006. Quaternary corals from reefs in the Wakatobi Marine National Park, SE Sulawesi, Indonesia, show similar growth rates to modern corals from the same area. *Journal of Quaternary Science* **21**: 803-809.

De'ath, G., Lough, J.M. and Fabricius, K.E. 2009. Declining coral calcification on the Great Barrier Reef. *Science* **323**: 116-119.

Gao, K., Aruga, Y., Asada, K., Ishihara, T., Akano, T. and Kiyohara, M. 1993. Calcification in the articulated coralline alga *Corallina pilulifera*, with special reference to the effect of elevated  $CO_2$  concentration. *Marine Biology* **117**: 129-132.

Gnaiger, E., Gluth, G. and Weiser, W. 1978. pH fluctuations in an intertidal beach in Bermuda. *Limnology and Oceanography* **23**: 851-857.

Grigg, R.W. 1981. Coral reef development at high latitudes in Hawaii. In: *Proceedings of the Fourth International Coral Reef Symposium*, Manila, Vol. 1: 687-693.

Grigg, R.W. 1997. Paleoceanography of coral reefs in the Hawaiian-Emperor Chain—revisited. *Coral Reefs* **16**: S33-S38.

Hansen, P.J. 2002. The effect of high pH on the growth and survival of marine phytoplankton: implications for species succession. *Aquatic Microbiology and Ecology* **28**: 279-288.

Herfort, L., Thake, B. and Roberts, J. 2002. Acquisition and use of bicarbonate by *Emiliania huxleyi*. New *Phytologist* **156**: 427–36.

Herfort, L., Thake, B. and Taubner, I. 2008. Bicarbonate stimulation of calcification and photosynthesis in two hermatypic corals. *Journal of Phycology* **44**: 91-98.

Kajiwara, K., Nagai, A. and Ueno, S. 1995. Examination of the effect of temperature, light intensity and zooxanthellae concentration on calcification and photosynthesis of scleractinian coral *Acropora pulchra*. J. School Mar. Sci. Technol. **40**: 95-103.

Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J-P., Langdon, C. and Opdyke, B.N. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* **284**: 118-120.

Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., Goddard, J., Marubini, F., Aceves, H., Barnett, H. and Atkinson, M.J. 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* **14**: 639-654.

Lindholm, T. and Nummelin, C. 1999. Red tide of the dinoflagellate *Heterocapsa triquetra* (Dinophyta) in a ferry-mixed coastal inlet. *Hydrobiologia* **393**: 245-251.

Lough, J.M. and Barnes, D.J. 1997. Several centuries of variation in skeletal extension, density and calcification in massive *Porites* colonies from the Great Barrier Reef: A proxy for seawater temperature and a background of variability against which to identify unnatural change. *Journal of Experimental and Marine Biology and Ecology* **211**: 29-67.

Lough, J.B. and Barnes, D.J. 2000. Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology* **245**: 225-243.

Macedo, M.F., Duarte, P., Mendes, P. and Ferreira, G. 2001. Annual variation of environmental variables, phytoplankton species composition and photosynthetic

parameters in a coastal lagoon. *Journal of Plankton Research* **23**: 719-732.

Marubini, F. and Thake, B. 1998. Coral calcification and photosynthesis: evidence for carbon limitation. In: *International Society for Reef Studies (ISRS), European Meeting*, Perpignan, September 1-4, 1998, p. 119.

McNeil, B.I., Matear, R.J. and Barnes, D.J. 2004. Coral reef calcification and climate change: The effect of ocean warming. *Geophysical Research Letters* **31**: 10.1029/2004GL021541.

Menendez, M., Martinez, M. and Comin, F.A. 2001. A comparative study of the effect of pH and inorganic carbon resources on the photosynthesis of three floating macroalgae species of a Mediterranean coastal lagoon. *Journal of Experimental Marine Biology and Ecology* **256**: 123-136.

Mercado, J.M., Niell, F.X. and Gil-Rodriguez, M.C. 2001. Photosynthesis might be limited by light, not inorganic carbon availability, in three intertidal Gelidiales species. *New Phytologist* **149**: 431-439.

Mercado, J.M., Niell, F.X., Silva, J. and Santos, R. 2003. Use of light and inorganic carbon acquisition by two morphotypes of *Zostera noltii* Hornem. *Journal of Experimental Marine Biology and Ecology* **297**: 71-84.

Middelboe, A.L. and Hansen, P.J. 2007. High pH in shallow-water macroalgal habitats. *Marine Ecology Progress Series* **338**: 107-117.

Nie, B., Chen, T., Liang, M., Wang, Y., Zhong, J. and Zhu, Y. 1997. Relationship between coral growth rate and sea surface temperature in the northern part of South China Sea. *Sci. China Ser. D* **40**: 173-182.

Pearson, G.A., Serrao, E.A. and Brawley, S.H. 1998. Control of gamete release in fucoid algae: sensing hydrodynamic conditions via carbon acquisition. *Ecology* **79**: 1725-1739.

Pelejero, C., Calvo, E., McCulloch, M.T., Marshall, J.F., Gagan, M.K., Lough, J.M. and Opdyke, B.N. 2005. Preindustrial to modern interdecadal variability in coral reef pH. *Science* **309**: 2204-2207.

Reynaud, S., Ferrier-Pages, C., Boisson, F., Allemand, D. and Fairbanks, R.G. 2004. Effect of light and temperature on calcification and strontium uptake in the scleractinian coral *Acropora verweyi*. *Marine Ecology Progress Series* **279**: 105-112.

Reynaud, S., Ferrier-Pages, C., Meibom, A., Mostefaoui, S., Mortlock, R., Fairbanks, R. and Allemand, D. 2007. Light and temperature effects on Sr/Ca and Mg/Ca ratios in the scleractinian coral *Acropora* sp. *Geochimica et Cosmochimica Acta* **71**: 354-362.

Reynaud-Vaganay, S., Gattuso, J.P., Cuif, J.P., Jaubert, J. and Juillet-Leclerc, A. 1999. A novel culture technique for scleractinian corals: Application to investigate changes in skeletal  $\delta^{18}$ O as a function of temperature. *Marine Ecology Progress Series* **180**: 121-130.

Santhanam, R., Srinivasan, A., Ramadhas, V. and Devaraj, M. 1994. Impact of *Trichodesmium* bloom on the plankton and productivity in the Tuticorin bay, southeast coast of India. *Indian Journal of Marine Science* **23**: 27-30.

Scoffin, T.P., Tudhope, A.W., Brown, B.E., Chansang, H. and Cheeney, R.F. 1992. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand. *Coral Reefs* **11**: 1-11.

Weis, V.M. 1993. Effect of dissolved inorganic carbon concentration on the photosynthesis of the symbiotic sea anemone *Aiptasia pulchella* Carlgren: role of carbonic anhydrase. *Journal of Experimental Marine Biology and Ecology* **174**: 209-225.

Zou, D.H., Gao, K.S. and Xia, J.R. 2003. Photosynthetic utilization of inorganic carbon in the economic brown alga, *Hizikia fusiforme* (Sargassaceae) from the South China Sea. *Journal of Phycology* **39**: 1095-1100.

### 8.3.2.1.3. Other Marine Organisms

In a paper recently published in Limnology and Oceanography, Richardson and Gibbons (2008) sav there has been a drop of 0.1 pH unit in the global ocean since the start of the Industrial Revolution, and that "such acidification of the ocean may make calcification more difficult for calcareous organisms," resulting in the "opening [of] ecological space for non-calcifying species." In line with this thinking, they report that Attrill et al. (2007) have argued that "jellyfish may take advantage of the vacant niches made available by the negative effects of acidification on calcifying plankton," causing jellyfish to become more abundant, and they note that the latter researchers provided some evidence for this effect in the west-central North Sea over the period 1971-1995. Hence, they undertook a study to see if Attrill et al.'s findings (which were claimed to be the first of their kind) could be replicated on a much larger scale.

Working with data from a larger portion of the North Sea, as well as throughout most of the much vaster Northeast Atlantic Ocean, Richardson and Gibbons used coelenterate (jellyfish) records from the Continuous Plankton Recorder (CPR) and pH data from the International Council for the Exploration of the Sea (ICES) for the period 1946-2003 to explore the possibility of a relationship between jellyfish abundance and acidic ocean conditions. This work revealed that there were, as they describe it, "no significant relationships between jellyfish abundance and acidic conditions in any of the regions investigated."

In harmony with their findings, the two researchers note that "no observed declines in the abundance of calcifiers with lowering pH have yet been reported." In addition, they write that the "larvae of sea urchins form skeletal parts comprising magnesium-bearing calcite, which is 30 times more soluble than calcite without magnesium," and, therefore, that "lower ocean pH should drastically inhibit the formation of these soluble calcite precursors." Yet they report that "there is no observable negative effect of pH." In fact, they say that echinoderm larvae in the North Sea have actually exhibited "a 10-fold increase [our italics] in recent times," which they say has been "linked predominantly to warming (Kirby et al., 2007)." Likewise, they further note that even in the most recent IPCC report, "there was no empirical evidence reported for the effect of acidification on marine biological systems (Rosenzweig et al., 2007)." In light of this body of real-world evidence, Richardson and Gibbons conclude (rather generously, we think) that "the role of pH in structuring zooplankton communities in the North Sea and further afield at present is tenuous."

In another study, Vogt *et al.* (2008) examined the effects of atmospheric  $CO_2$  enrichment on various marine microorganisms in nine marine mesocosms in a fjord adjacent to the Large-Scale Facilities of the Biological Station of the University of Bergen in Espegrend, Norway. Three of the mesocosms were maintained at ambient levels of  $CO_2$  (~375 ppm), three were maintained at levels expected to prevail at the end of the current century (760 ppm or 2x  $CO_2$ ), and three were maintained at levels predicted for the middle of the next century (1,150 ppm or 3x  $CO_2$ ), while measurements of numerous ecosystem parameters were made over a period of 24 days.

Results of the analysis showed no significant phytoplankton species shifts between treatments, and that "the ecosystem composition, bacterial and phytoplankton abundances and productivity, grazing rates and total grazer abundance and reproduction were not significantly affected by  $CO_2$  induced effects," citing in support of this statement the work of Riebesell *et al.* (2007), Riebesell *et al.* (2008), Egge *et al.* (2007), Paulino *et al.* (2007), Larsen *et al.*  (2007), Suffrian *et al.* (2008), and Carotenuto *et al.* (2007). With respect to their many findings, the eight researchers say their observations suggest that "the system under study was surprisingly resilient to abrupt and large pH changes."

Expanding the subject of CO<sub>2</sub> effects on other marine organisms, Gutowska et al. (2008) studied the cephalopod mollusk Sepia officinalis and found that it "is capable of not only maintaining calcification, but also growth rates and metabolism when exposed to elevated partial pressures of carbon dioxide." Over a six-week test period, for example, they found that "juvenile S. officinalis maintained calcification under ~4000 and ~6000 ppm  $CO_2$ , and grew at the same rate with the same gross growth efficiency as did control animals," gaining approximately 4 percent body mass daily and increasing the mass of their calcified cuttlebone by more than 500 percent. These findings thus led them to specifically conclude that "active cephalopods possess a certain level of pre-adaptation to long-term increments in carbon dioxide levels," and to generally conclude that our "understanding of the mechanistic processes that limit calcification must improve before we can begin to predict what effects future ocean acidification will have on calcifying marine invertebrates."

In another study, Berge et al. (2006) continuously supplied five 5-liter aquariums with low-food-content sea water that was extracted from the top meter of the Oslofjord outside the Marine Research Station Norway, Solbergstrand in while  $CO_2$ was continuously added to the waters of the aquaria so as to maintain them at five different pH values (means of 8.1, 7.6, 7.4, 7.1, and 6.7) for a period of 44 days. Prior to the start of the study, blue mussels (Mytilus edulis) of two different size classes (mean lengths of either 11 or 21 mm) were collected from the outer part of the Oslofjord, and 50 of each size class were introduced into each aquarium, where they were examined almost daily for any deaths that may have occurred, after which shell lengths at either the time of death or at the end of the study were determined and compared to lengths measured at the start of the study. Simultaneously, water temperature rose slowly from 16° to 19°C during the initial 23 days of the experiment, but then declined slightly to day 31, after which it rose rapidly to attain a maximum value of 24°C on day 39.

A lack of mortality during the first 23 days of the study showed, in the words of the researchers, that "the increased concentration of  $CO_2$  in the water and the correspondingly reduced pH had no acute effects

on the mussels." Thereafter, however, some mortality was observed in the highest  $CO_2$  (lowest pH) treatment from day 23 to day 37, after which deaths could also be observed in some of the other treatments, which mortality Berge *et al.* attributed to the rapid increase in water temperature that occurred between days 31 and 39.

With respect to growth, the Norwegian researchers report that "mean increments of shell length were much lower for the two largest  $CO_2$  additions compared to the values in the controls, while for the two smallest doses the growth [was] about the same as in the control, or in one case even higher (small shells at pH = 7.6)," such that there were "no significant differences between the three aquaria within the pH range 7.4-8.1."

Berge et al. say their results "indicate that future reductions in pH caused by increased concentrations of anthropogenic  $CO_2$  in the sea may have an impact on blue mussels," but that "comparison of estimates of future pH reduction in the sea (Caldeira and Wickett, 2003) and the observed threshold for negative effects on growth of blue mussels [which they determined to lie somewhere between a pH of 7.4 and 7.1] do however indicate that this will probably not happen in this century." Indeed, Caldeira and Wickett's calculation of the maximum level to which the air's CO<sub>2</sub> concentration might rise yields a value that approaches 2,000 ppm around the year 2300, representing a surface oceanic pH reduction of 0.7 units, which drops the pH only to the upper limit of the "threshold for negative effects on growth of blue mussels" found by Berge et al., i.e., 7.4. Consequently, blue mussels will likely never be bothered by the tendency for atmospheric  $CO_2$ enrichment to lower oceanic pH values.

In a study of a very different creature, Langer et al. (2006) conducted batch-culture experiments on two coccolithophores, Calcidiscus leptoporus and Coccolithus pelagicus, in which they observed a "deterioration of coccolith production above as well as below present-day  $CO_2$  concentrations in C. leptoporus," and a "lack of a CO<sub>2</sub> sensitivity of calcification in C. pelagicus" over an atmospheric CO<sub>2</sub> concentration range of 98-915 ppm. Both of these observations, in their words, "refute the notion of a linear relationship of calcification with the carbonate ion concentration and carbonate saturation state." In an apparent negative finding, however, particularly in the case of C. leptoporus, Langer et al. observed that although their experiments revealed that "at 360 ppm CO<sub>2</sub> most coccoliths show normal

morphology," at both "higher and lower CO<sub>2</sub> concentrations the proportion of coccoliths showing incomplete growth and malformation increases notably."

To determine if such deleterious responses might also have occurred in the real world at different times in the past, the researchers studied coccolith morphologies in six sediment cores obtained along a range of latitudes in the Atlantic Ocean. This work revealed that changes in coccolith morphology similar to those "occurring in response to the abrupt  $CO_2$ perturbation applied in experimental treatments are *not* [our italics] mirrored in the sedimentary record." This finding indicates, as they suggest, that "in the natural environment *C. leptoporus* has adjusted to the 80-ppm  $CO_2$  and 180-ppm  $CO_2$  difference between present [and] preindustrial and glacial times, respectively."

In further discussing these observations, Langer et al. say "it is reasonable to assume that C. leptoporus has adapted its calcification mechanism to the change in carbonate chemistry having occurred since the last glacial maximum," suggesting as a possible explanation for this phenomenon that "the population is genetically diverse, containing strains with diverse physiological and genetic traits, as already demonstrated for E. huxlevi (Brand, 1981, 1982, 1984; Conte et al., 1998; Medlin et al., 1996; Paasche, 2002; Stolte et al., 2000)." They also state that this adaptive ability "is not likely to be confined to C. leptoporus but can be assumed to play a role in other coccolithophore species as well," which leads them to conclude that such populations "may be able to evolve so that the optimal CO<sub>2</sub> level for calcification of the species tracks the environmental value." With respect to the future, therefore, Langer et al. end on a strongly positive note, stating that "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO<sub>2</sub> ocean."

Focusing on another coccolithophore species, Riebesell (2004) notes that "a moderate increase in CO<sub>2</sub> facilitates photosynthetic carbon fixation of some phytoplankton groups," "the including coccolithophorids Emiliania huxlevi and Gephyrocapsa oceanica." Hence, in a major challenge to the claim that atmospheric CO<sub>2</sub> enrichment will definitely harm such marine organisms, Riebesell suggests that "CO2-sensitive taxa, such as the calcifying coccolithophorids, should therefore *benefit more* [our italics] from the present increase in atmospheric CO<sub>2</sub> compared to the non-calcifying diatoms."

In support of this suggestion, Riebesell describes the results of some CO<sub>2</sub> perturbation experiments conducted south of Bergen, Norway, where nine 11m<sup>3</sup> enclosures moored to a floating raft were aerated with CO<sub>2</sub>-depleted, normal and CO<sub>2</sub>-enriched air to achieve CO<sub>2</sub> levels of 190, 370, and 710 ppm, simulating glacial, present-day, and predicted conditions for the end of the century, respectively. In the course of the study, a bloom consisting of a mixed phytoplankton community developed, and, in "significantly Riebesell's words. higher net community production was observed under elevated CO<sub>2</sub> levels during the build-up of the bloom." He further reports that "CO2-related differences in continued primary production after nutrient exhaustion. leading to higher production of transparent exopolymer particles under high CO<sub>2</sub> conditions," something that has also been observed by Engel (2002) in a natural plankton assemblage and by Heemann (2002) in monospecific cultures of both diatoms and coccolithophores.

Another important finding of this experiment was that the community that developed under the high  $CO_2$  conditions expected for the end of this century was dominated by Emiliania huxlevi. Consequently, Riebesell finds even more reason to believe that "coccolithophores may benefit from the present increase in atmospheric CO2 and related changes in seawater carbonate chemistry," in contrast to the many negative predictions that have been made about rising atmospheric CO<sub>2</sub> concentrations in this regard. Finally, in further commentary on the topic, Riebesell states that "increasing CO<sub>2</sub> availability may improve the overall resource utilization of E. huxlevi and possibly of other fast-growing coccolithophore species," concluding that "if this provides an ecological advantage for coccolithophores, rising atmospheric CO<sub>2</sub> could potentially increase the contribution of calcifying phytoplankton to overall primary production." In fact, noting that "a moderate increase in CO<sub>2</sub> facilitates photosynthetic carbon fixation of some phytoplankton groups," including "the coccolithophorids *Emiliania huxleyi* and Gephyrocapsa oceanica," Riebesell suggests that "CO<sub>2</sub>-sensitive taxa, such as the calcifying coccolithophorids, should therefore benefit more [our italics] from the present increase in atmospheric CO<sub>2</sub> compared to the non-calcifying diatoms."

Support of Riebesell's findings was recently provided by an international team of 13 researchers

(Iglesias-Rodriguez *et al.*, 2008), who bubbled air of a number of different atmospheric  $CO_2$  concentrations through culture media containing the phytoplanktonic coccolithophore species *Emiliania hyxleyi*, while determining the amounts of particulate organic and inorganic carbon they produced. In addition, they determined the real-world change in average coccolithophore mass over the past 220 years in the subpolar North Atlantic Ocean, based on data obtained from a sediment core, over which period of time the atmosphere's  $CO_2$  concentration rose by approximately 90 ppm and the earth emerged from the frigid depths of the Little Ice Age to experience the supposedly unprecedented high temperatures of the Current Warm Period.

Results of their analysis revealed an approximate doubling of both particulate organic and inorganic carbon between the culture media in equilibrium with air of today's  $CO_2$  concentration and the culture media in equilibrium with air of 750 ppm  $CO_2$ . In addition, they say the field evidence they obtained from the deep-ocean sediment core they studied "is consistent with these laboratory conclusions," and that it indicates that "over the past 220 years there has been a 40% increase in average coccolith mass."

Focusing more on the future, a third independent team of seven scientists (Feng et al., 2008) studied Emiliania huxleyi coccoliths that they isolated from the Sargasso Sea, and which they grew in semicontinuous culture media at low and high light intensities, low and high temperatures (20 and 24°C), and low and high CO<sub>2</sub> concentrations (375 and 750 ppm). This work revealed that in the low-light environment, the maximum photosynthetic rate was lowest in the low-temperature, low-CO<sub>2</sub> or ambient treatment, but was increased by 55 percent by elevated temperature alone and by 95 percent by elevated CO<sub>2</sub> alone, while in the high-temperature, high-CO<sub>2</sub> or greenhouse treatment it was increased by 150 percent relative to the ambient treatment. Likewise, in the high-light environment, there were maximum photosynthetic rate increases of 58 percent, 67 percent, and 92 percent for the elevated temperature alone, elevated CO<sub>2</sub> alone, and greenhouse treatments, respectively. Consequent-ly, the researchers concluded that "future trends of CO<sub>2</sub> enrichment, sea-surface warming and exposure to higher mean irradiances from intensified stratification will have a large influence on the growth of Emiliania huxlevi."

Clearly, claims of impending marine species extinctions due to ocean acidification are not

supported by real-world evidence—they are refuted by it.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2</u> science.org/subject/c/calcificationother.php.

### References

Attrill, M.J., Wright, J. and Edwards, M. 2007. Climaterelated increases in jellyfish frequency suggest a more gelatinous future for the North Sea. *Limnology and Oceanography* **52**: 480-485.

Berge, J.A., Bjerkeng, B., Pettersen, O., Schaanning, M.T. and Oxnevad, S. 2006. Effects of increased sea water concentrations of  $CO_2$  on growth of the bivalve *Mytilus edulis* L. *Chemosphere* **62**: 681-687.

Brand, L.E. 1981. Genetic variability in reproduction rates in marine phytoplankton populations. *Evolution* **38**: 1117-1127.

Brand, L.E. 1982. Genetic variability and spatial patterns of genetic differentiation in the reproductive rates of the marine coccolithophores *Emiliania huxleyi* and *Gephyrocapsa oceanica*. *Limnology and Oceanography* **27**: 236-245.

Brand, L.E. 1984. The salinity tolerance of forty-six marine phytoplankton isolates. *Estuarine and Coastal Shelf Science* **18**: 543-556.

Caldeira, K. and Wickett, M.E. 2003. Anthropogenic carbon and ocean pH. *Nature* **425**: 365.

Carotenuto, Y., Putzeys, S., Simonelli, P., Paulino, A., Meyerhofer, M., Suffrian, K., Antia, A. and Nejstgaard, J.C. 2007. Copepod feeding and reproduction in relation to phytoplankton development during the PeECE III mesocosm experiment. *Biogeosciences Discussions* **4**: 3913-3936.

Conte, M., Thompson, A., Lesley, D. and Harris, R.P. 1998. Genetic and physiological influences on the alkenone/alkenonate versus growth temperature relationship in *Emiliania huxleyi* and *Gephyrocapsa oceanica*. *Geochimica et Cosmochimica Acta* **62**: 51-68.

Egge, J., Thingstad, F., Engel, A., Bellerby, R.G.J. and Riebesell, U. 2007. Primary production at elevated nutrient and  $pCO_2$  levels. *Biogeosciences Discussions* **4**: 4385-4410.

Engel, A. 2002. Direct relationship between  $CO_2$  uptake and transparent exopolymer particles production in natural phytoplankton. *Journal of Plankton Research* **24**: 49-53. Feng, Y., Warner, M.E., Zhang, Y., Sun, J., Fu, F.-X., Rose, J.M. and Hutchins, A. 2008. Interactive effects of increased pCO<sub>2</sub>, temperature and irradiance on the marine coccolithophore *Emiliania huxleyi* (Prymnesiophyceae). *European Journal of Phycology* **43**: 87-98.

Gutowska, M.A., Pörtner, H.O. and Melzner, F. 2008. Growth and calcification in the cephalopod *Sepia officinalis* under elevated seawater pCO<sub>2</sub>. *Marine Ecology Progress Series* **373**: 303-309.

Heemann, C. 2002. *Phytoplanktonexsudation in Abhangigkeit der Meerwasserkarbonatchemie*. Diplom. Thesis, ICBM, University of Oldenburg, Germany.

Iglesias-Rodriguez, M.D., Halloran, P.R., Rickaby, R.E.M., Hall, I.R., Colmenero-Hidalgo, E., Gittins, J.R., Green, D.R.H., Tyrrell, T., Gibbs, S.J., von Dassow, P., Rehm, E., Armbrust, E.V. and Boessenkool, K.P. 2008. Phytoplankton calcification in a high-CO<sub>2</sub> world. *Science* **320**: 336-340.

Kirby, R.R., Beaugrand, G., Lindley, J.A., Richardson, A.J., Edwards, M. and Reid, P.C. 2007. Climate effects and benthic-pelagic coupling in the North Sea. *Marine Ecology Progress Series* **330**: 31-38.

Langer, G. and Geisen, M., Baumann, K.-H., Klas, J., Riebesell, U., Thoms, S. and Young, J.R. 2006. Speciesspecific responses of calcifying algae to changing seawater carbonate chemistry. *Geochemistry, Geophysics, Geosystems* 7: 10.1029/2005GC001227.

Larsen, J.B., Larsen, A., Thyrhaug, R., Bratbak, G. and Sandaa R.-A. 2007. Marine viral populations detected during a nutrient induced phytoplankton bloom at elevated pCO<sub>2</sub> levels. *Biogeosciences Discussions* **4**: 3961-3985.

Medlin, L.K., Barker, G.L.A., Green, J.C., Hayes, D.E., Marie, D., Wreiden, S. and Vaulot, D. 1996. Genetic characterization of *Emiliania huxleyi* (Haptophyta). *Journal of Marine Systems* **9**: 13-32.

Paasche, E. 2002. A review of the coccolithophorid *Emiliania huxleyi* ((Prymnesiophyceae), with particular reference to growth, coccolith formation, and calcification-photosynthesis interactions. *Phycologia* **40**: 503-529.

Paulino, A.I., Egge, J.K. and Larsen, A. 2007. Effects of increased atmospheric  $CO_2$  on small and intermediate sized osmotrophs during a nutrient induced phytoplankton bloom. *Biogeosciences Discussions* **4**: 4173-4195.

Riebesell, U. 2004. Effects of CO<sub>2</sub> enrichment on marine phytoplankton. *Journal of Oceanography* **60**: 719-729.

Riebesell, U., Bellerby, R.G.J., Grossart, H.-P. and Thingstad, F. 2008. Mesocosm CO<sub>2</sub> perturbation studies: from organism to community level. *Biogeosciences Discussions* **5**: 641-659. Riebesell, U., Schulz, K., Bellerby, R., Botros, M., Fritsche, P., Meyerhofer, M., Neill, C., Nondal, G., Oschlies, A., Wohlers, J. and Zollner, E. 2007. Enhanced biological carbon consumption in a high  $CO_2$  ocean. *Nature* **450**: 10.1038/nature06267.

Richardson, A.J. and Gibbons, M.J. 2008. Are jellyfish increasing in response to ocean acidification? *Limnology and Oceanography* **53**: 2040-2045.

Rosenzweig, C. *et al.* 2007. Assessment of observed changes and responses in natural and managed systems. In Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J. and Hanson, C.E. (Eds.) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK, pp. 79-131.

Stolte, W., Kraay, G.W., Noordeloos, A.A.M. and Riegman, R. 2000. Genetic and physiological variation in pigment composition of *Emiliania huxleyi* (Prymnesiophyceae) and the potential use of its pigment ratios as a quantitative physiological marker. *Journal of Phycology* **96**: 529-589.

Suffrian, K., Simonelli, P., Nejstgaard, J.C., Putzeys, S., Carotenuto, Y. and Antia, A.N. 2008. Microzooplankton grazing and phytoplankton growth in marine mesocosms with increased  $CO_2$  levels. *Biogeosciences Discussions* **5**: 411-433.

Vogt, M., Steinke, M., Turner, S., Paulino, A., Meyerhofer, M., Riebesell, U., LeQuere, C. and Liss, P. 2008. Dynamics of dimethylsulphoniopropionate and dimethylsulphide under different  $CO_2$  concentrations during a mesocosm experiment. *Biogeosciences* **5**: 407-419.

# 8.4. Polar Bears

According to the IPCC, global warming is "inducing declining survival rates, smaller size, and cannibalism among polar bears (Amstrup *et al.*, 2006; Regehr *et al.*, 2006)" (IPCC, 2007-II, p. 88). "Reproductive success in polar bears," the IPCC also claims, "has declined, resulting in a drop in body condition, which in turn is due to melting Arctic Sea ice. Without ice, polar bears cannot hunt seals, their favourite prey (Derocher *et al.*, 2004)" (p. 103). Later in the same report, the IPCC claims to have "very high confidence" that "substantial loss of sea ice will reduce habitat for dependent species (e.g., polar bears)" (p. 213).

As was the case with coral reefs, the IPCC's claims and predictions are based on computer models and untested theories rather than real-world data. They are at odds with much of what is known about sea ice, polar bear populations and behaviors, and the natural ability of wildlife to adapt to climate change.

In this section we review the evidence and conclude polar bears are not endangered by global warming, whether it is caused by human activity or any other causes. Since our findings once again contradict those of the IPCC, we summarize them here:

- There is little or no evidence of global warminginduced reduction in the extent or thickness of Arctic sea ice in the second-half of the twentieth century, particularly during those seasons when polar bears rely on it to reach their favorite food supply (seals), despite what the IPCC calls the "unprecedented warming" of the past century.
- Polar bears have survived changes in climate that exceed those that occurred during the twentieth century or are forecast by the IPCC's computer models.
- Temperatures in Greenland and other Arctic areas exhibit considerable variability described by one group of scientists as "a long term cooling and shorter warming periods."
- Most populations of polar bears are growing, not shrinking, and the biggest influence on polar bear populations is not temperature but hunting by humans, which historically has taken too large a toll on polar bear populations.
- Forecasts of dwindling polar bear populations assume trends in sea ice and temperature that are counterfactual, rely on computer climate models that are known to be unreliable, and violate most of the principles of scientific forecasting.

# References

Amstrup, S.C, Stirling, I., Smith, T.S., Perham, C., and Thiemann, G.W. 2006. Recent observations of intraspecific predation and cannibalism among polar bears in the southern Beaufort Sea. *Polar Biology* **29**: 997-1002.

Derocher A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* **44:** 163-176.

IPCC. 2007-II. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and Hanson, C.E. (Eds.) Cambridge University Press, Cambridge, UK.

Regehr, E.V., Amstrup, S.C., and Stirling, I. 2006. Polar bear population status in the Southern Beaufort Sea. U.S. Geological Survey Open-File Report 2006-1337.

### 8.4.1. Arctic Sea Ice

Global warming is thought to endanger polar bears (*Ursus maritimus*) by melting sea ice. According to Derocher *et al.* (2004), "it is unlikely that polar bears will survive as a species if the sea ice disappears completely as has been predicted by some." (We note that even the IPCC's computer models do not predict the "disappearance" of all sea ice, so this widely cited warning is essentially meaningless.) Amstrup *et al.* (2007) say "Our modeling suggests that realization of the sea ice future which is currently projected, would mean loss of  $\approx 2/3$  of the world's current polar bear population by mid-century."

These dire predictions are based entirely on computer simulations of the effects of warming temperatures on the extent of sea ice in the Arctic region. One way to test the reliability of those simulations is to see what effect the warming of the twentieth century had on the extent and thickness of sea ice. If the warming of the twentieth century hasn't produced trends toward less sea ice extent and thickness, why should we believe computer models that claim future warming would have a different effect? This section summarizes а more comprehensive analysis of Arctic sea ice that appeared in Chapter 4 of this report.

### References

Amstrup, S.C., Marcot, B.G., and Douglas, D.C. 2007. Forecasting the rangewide status of polar bears at selected times in the 21st century. USGS Alaska Science Center, Anchorage, Administrative Report. Derocher A.E., Lunn, N.J., and Stirling, I. 2004. Polar bears in a warming climate. *Integrative and Comparative Biology* **44**: 163-176.

#### 8.4.1.1. Extent

The popular media is filled with reports about the disappearance of sea ice at the North Pole and the possibility of an ice-free summer in the region. The IPCC also focuses on summer (August and September) minimum Arctic sea ice extent (see Figures 4.8, 4.9, and 4.10 on pp. 351-352 of IPCC, 2007-I) and downplays evidence showing relatively little change in sea ice extent at other times of the year (e.g., Figure 4.10 shows relatively stable March sea ice extent but it receives no comment in the text).

Summer sea ice losses are part of an eons-long natural cycle to which polar bears have adapted in order to survive. Polar bears are able to fast for more than four months at a time while fully awake and mobile, without hibernating as other bears do (Watts and Hansen, 1987; Ramsay and Stirling, 1988; Ramsay and Hobson, 1991; Lennox and Goodship, 2008). During their winter feeding season, polar bears rely on sea ice to reach ringed seals (Phoca hispida) and in some regions bearded seals (Erignathus barbatus), their main sources of food (Derocher et al., 2002; Stirling and Øritsland, 1995). Therefore, the measure of sea ice extent that is most relevant to the survival of polar bears is not summer minimums but multi-year. According to numerous studies described below, multi-vear sea ice extent is growing in some parts of the Arctic and declining in others, sometimes changing sign over the course of a single year or two, making it difficult to discern an overall trend. The data show low-frequency oscillations that are not what one would predict based on the greenhouse warming theory and gradually increasing atmospheric CO<sub>2</sub> concentrations.

Johannessen *et al.* (1999) analyzed Arctic sea ice extent over the period 1978-1998 and found it to have decreased by about 14 percent. This finding led them to suggest that "the balance of evidence," as small as it then was, indicates "an ice cover in transition," and that "if this apparent transformation continues, it may lead to a markedly different ice regime in the Arctic," as also was suggested by Vinnikov *et al.* (1999). However, the plots of sea ice area presented by Johannessen *et al.* reveal that essentially all of the drop occurred abruptly over a single period of not more than three years (1987/88-1990/91) and possibly only one year (1989/90-1990/91). Furthermore, it appears from their data that from 1990/91 onward, sea ice area in the Arctic may have *increased*.

More recently, Kwok (2004) estimated the coverage of Arctic multi-year sea ice at the beginning of each year of the study was 3774 x 10<sup>3</sup> km<sup>2</sup> in 2000, 3896 x 10<sup>3</sup> km<sup>2</sup> in 2001, 4475 x 10<sup>3</sup> km<sup>2</sup> in 2002, and 4122 x  $10^3$  km<sup>2</sup> in 2003, representing an *increase* in sea ice coverage of 9 percent over a third of a decade. Belchansky et al. (2004) report that from 1988 to 2001, total January multi-year ice area declined at a mean rate of 1.4 percent per year. They note, however, that in the autumn of 1996 "a large multiyear ice recruitment of over  $10^6$  km<sup>2</sup> fully replenished the previous 8-year decline in total area." They add that the replenishment "was followed by an accelerated and compensatory decline during the subsequent 4 years." In addition, they learned that 75 percent of the interannual variation in January multiyear sea area "was explained by linear regression on two atmospheric parameters: the previous winter's Arctic Oscillation index as a proxy to melt duration and the previous year's average sea level pressure gradient across the Fram Strait as a proxy to annual ice export."

Belchansky *et al.* conclude that their 14-year analysis of multi-year ice dynamics is "insufficient to project long-term trends." They also conclude it is insufficient to reveal "whether recent declines in multiyear ice area and thickness are indicators of anthropogenic exacerbations to positive feedbacks that will lead the Arctic to an unprecedented future of reduced ice cover, or whether they are simply ephemeral expressions of natural low frequency oscillations."

Heide-Jorgensen and Laidre (2004) examined changes in the fraction of open-water found within various pack-ice microhabitats of Foxe Basin, Hudson Bay, Hudson Strait, Baffin Bay-Davis Strait, northern Baffin Bay, and Lancaster Sound over a 23-year interval (1979-2001)using remotelv sensed microwave measurements of sea-ice extent, after which the trends they documented were "related to relative importance of the each wintering microhabitat for eight marine indicator species and potential impacts on winter success and survival were examined." Foxe Basin, Hudson Bay, and Hudson Strait showed small increasing trends in the fraction of open water, with the upward trends at all microhabitats studied ranging from 0.2 to 0.7 percent per decade. In Baffin Bay-Davis Straight and northern Baffin Bay, on the other hand, the open-water trend

was downward, and at a mean rate for all open-water microhabitats studied of fully 1 percent per decade, while the trend in all Lancaster Sound open-water microhabitats was also downward, in this case at a mean rate of 0.6 percent per decade.

Heide-Jorgensen and Laidre report that "increasing trends in sea ice coverage in Baffin Bay and Davis Strait (resulting in declining open-water) were as high as 7.5 percent per decade between 1979-1999 (Parkinson et al., 1999; Deser et al., 2000; Parkinson, 2000a,b; Parkinson and Cavalieri, 2002) and comparable significant increases have been detected back to 1953 (Stern and Heide-Jorgensen, 2003)." They additionally note that "similar trends in sea ice have also been detected locally along the West Greenland coast, with slightly lower increases of 2.8 percent per decade (Stern and Heide-Jorgensen, 2003)."

Grumet et al. (2001) warned that recent trends in Arctic sea ice cover "can be viewed out of context because their brevity does not account for interdecadal variability, nor are the records sufficiently long to clearly establish a climate trend." In an effort to overcome this "short-sightedness," they developed a 1,000-year record of spring sea ice conditions in the Arctic region of Baffin Bay based on sea-salt records from an ice core obtained from the Penny Ice Cap on Baffin Island. They determined that after a period of reduced sea ice during the eleventh through fourteenth centuries, enhanced sea ice conditions prevailed during the following 600 years. For the final (twentieth) century of this period, they report that "despite warmer temperatures during the turn of the century, sea-ice conditions in the Baffin Bay/Labrador Sea region, at least during the last 50 years, are within 'Little Ice Age' variability," suggesting that sea ice extent there has not vet emerged from the range of conditions characteristic of the Little Ice Age.

In an adjacent sector of the Arctic, this latter period of time also was studied by Comiso *et al.* (2001), who used satellite imagery to analyze and quantify a number of attributes of the Odden ice tongue—a winter ice-cover phenomenon that occurs in the Greenland Sea with a length of about 1,300 km and an aerial coverage of as much as 330,000 square kilometers—over the period 1979-1998. By utilizing surface air temperature data from Jan Mayen Island, which is located within the region of study, Comiso and colleagues were able to infer the behavior of this phenomenon over the past 75 years. Trend analyses revealed that the ice tongue has exhibited no statistically significant change in any of the parameters studied over the past 20 years; but the proxy reconstruction of the Odden ice tongue for the past 75 years revealed the ice phenomenon to have been "a relatively smaller feature several decades ago," due to the warmer temperatures that prevailed at that time.

In another study of Arctic climate variability, Omstedt and Chen (2001) obtained a proxy record of the annual maximum extent of sea ice in the region of the Baltic Sea over the period 1720-1997. In analyzing this record, they found that a significant decline in sea ice occurred around 1877. In addition, they reported finding greater variability in sea ice extent in the colder 1720-1877 period than in the warmer 1878-1997 period, suggesting that air temperatures are not the main force at work in determining sea ice extent.

Jevrejeva (2001) reconstructed an even longer record of sea ice duration (and, therefore, extent) in the Baltic Sea region by examining historical data for the observed time of ice break-up between 1529 and 1990 in the northern port of Riga, Latvia. The long date-of-ice-break-up time series was best described by a fifth-order polynomial, which identified four distinct periods of climatic transition: (1) 1530-1640, warming with a tendency toward earlier ice break-up of nine days/century, (2) 1640-1770, cooling with a tendency toward later ice break-up of five days/century, (3) 1770-1920, warming with a tendency toward earlier ice break-up of 15 days/century, and (4) 1920-1990, cooling with a tendency toward later ice break-up of 12 days/century.

On the other hand, in a study of the Nordic Seas (the Greenland, Iceland, Norwegian, Barents, and Western Kara Seas), Vinje (2001) determined that "the extent of ice in the Nordic Seas measured in April has decreased by 33% over the past 135 years." He notes, however, that "nearly half of this reduction is observed over the period 1860-1900," during a period, we note, when the atmosphere's CO<sub>2</sub> concentration rose by only 7 ppm, whereas the second half of the sea-ice decline occurred over a period of time when the air's CO<sub>2</sub> concentration rose by more than 70 ppm. If the historical rise in the air's CO<sub>2</sub> content has been responsible for the historical decrease in sea-ice extent, its impact over the last century has declined to less than a tenth of what its impact was over the preceding four decades. This in turn suggests that the increase in the air's CO<sub>2</sub> content

over the past 135 years has likely had nothing to do with the concomitant decline in sea-ice cover.

In a similar study of the Kara, Laptev, East Siberian, and Chuckchi Seas, based on newly available long-term Russian observations, Polyakov *et al.* (2002) found "smaller than expected" trends in sea ice cover that, in their words, "do not support the hypothesized polar amplification of global warming." Likewise, in a study published the following year, Polyakov *et al.* (2003) report that "over the entire Siberian marginal-ice zone the century-long trend is only -0.5% per decade," while "in the Kara, Laptev, East Siberian, and Chukchi Seas the ice extent trends are not large either: -1.1%, -0.4%, +0.3%, and -1.0% per decade, respectively." Moreover, they say "these trends, except for the Chukchi Sea, are not statistically significant."

Divine and Dick (2006) used historical April through August ice observations made in the Nordic Seas—comprised of the Iceland, Greenland. Norwegian, and Barents Seas, extending from 30°W to 70°E-to construct time series of ice-edge position anomalies spanning the period 1750-2002, which they analyzed for evidence of long-term trend and oscillatory behavior. The authors report that "evidence was found of oscillations in ice cover with periods of about 60 to 80 years and 20 to 30 years. superimposed on a continuous negative trend," which observations are indicative of a "persistent ice retreat since the second half of the 19th century" that began well before anthropogenic CO<sub>2</sub> emissions could have had much effect on earth's climate.

Noting that the last cold period observed in the Arctic occurred at the end of the 1960s, the two Norwegian researchers say their results suggest that "the Arctic ice pack is now at the periodical apogee of the low-frequency variability," and that "this could explain the strong negative trend in ice extent during the last decades as a possible superposition of natural low frequency variability and greenhouse gas induced warming of the last decades." However, as they immediately caution, "a similar shrinkage of ice cover was observed in the 1920s-1930s, during the previous warm phase of the low frequency oscillation, when any anthropogenic influence is believed to have still been negligible." They suggest, therefore, "that during decades to come ... the retreat of ice cover may change to an expansion."

The oscillatory behavior observed in so many of the sea ice studies suggests, in the words of Parkinson (2000b), "the possibility of close connections between the sea ice cover and major oscillatory patterns in the atmosphere and oceans," including connections with: "(1) the North Atlantic Oscillation (e.g., Hurrell and van Loon, 1997; Johannessen et al., 1999; Kwok and Rothrock, 1999; Deser et al., 2000; Kwok, 2000; Vinje, 2001) and the spatially broader Arctic Oscillation (e.g., Deser et al., 2000; Wang and Ikeda. 2000); (2) the Arctic Ocean Oscillation (Polyakov et al., 1999; Proshutinsky et al., 1999); (3) a 'see-saw' in winter temperatures between Greenland and northern Europe (Rogers and van Loon, 1979); and (4) an interdecadal Arctic climate cycle (Mysak et al., 1990; Mysak and Power, 1992)." The likelihood that Arctic sea ice trends are the product of such natural oscillations, Parkinson continues, "provides a strong rationale for considerable caution when extrapolating into the future the widely reported decreases in the Arctic ice cover over the past few decades or when attributing the decreases primarily to global warming."

The latest observations on Greenland's outlet glaciers, reported in January 2009 by a writer for *Science* who attended a December 2008 meeting of the American Geophysical Union, amply confirm Parkinson's conclusion. They show the acceleration of melting that had occurred between 2003-2005 had "come to an end" and "nearly everywhere around southeast Greenland, outlet glacier flows have returned to the levels of 2000" (Anonymous, 2009). The article quotes a team of researchers led by glacial modeler Faezeh Nick of Durham University in the United Kingdom as saying "our results imply that the recent rates of mass loss in Greenland's outlet glaciers are transient and should not be extrapolated into the future" (Ibid.)

In conclusion, there is little or no evidence of a consistent, global warming-induced reduction in the extent of Arctic sea ice, especially during those seasons when polar bears rely on it to reach their favorite food supply (seals), despite what the IPCC calls the "unprecedented warming" of the past century. This is a key finding that undermines the claim that global warming would have a harmful effect on polar bears in the future.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2science.org/</u><u>subject/s/seaicearctic.php</u>.

### References

Anonymous. 2009. Galloping glaciers of Greenland have reined themselves in. *Science*. **323**: 458.

Belchansky, G.I., Douglas, D.C., Alpatsky, I.V. and Platonov, N.G. 2004. Spatial and temporal multiyear sea ice distributions in the Arctic: A neural network analysis of SSM/I data, 1988-2001. *Journal of Geophysical Research* **109**: 10.1029/2004JC002388.

Comiso, J.C., Wadhams, P., Pedersen, L.T. and Gersten, R.A. 2001. Seasonal and interannual variability of the Odden ice tongue and a study of environmental effects. *Journal of Geophysical Research* **106**: 9093-9116.

Derocher, A.E., Wiig, Ø., and Andersen, M. 2002. Diet composition of polar bears in Svalbard and the western Barents Sea. *Polar Biology* **25**: 448-452.

Deser, C., Walsh, J. and Timlin, M.S. 2000. Arctic sea ice variability in the context of recent atmospheric circulation trends. *Journal of Climate* **13**: 617-633.

Divine, D.V. and Dick, C. 2006. Historical variability of sea ice edge position in the Nordic Seas. *Journal of Geophysical Research* **111**: 10.1029/2004JC002851.

Grumet, N.S., Wake, C.P., Mayewski, P.A., Zielinski, G.A., Whitlow, S.L., Koerner, R.M., Fisher, D.A. and Woollett, J.M. 2001. Variability of sea-ice extent in Baffin Bay over the last millennium. *Climatic Change* **49**: 129-145.

Heide-Jorgensen, M.P. and Laidre, K.L. 2004. Declining extent of open-water refugia for top predators in Baffin Bay and adjacent waters. *Ambio* **33**: 487-494.

Hurrell, J.W. and van Loon, H. 1997. Decadal variations in climate associated with the North Atlantic Oscillation. *Climatic Change* **36**: 301-326.

IPCC 2007-I. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (Eds.) Cambridge University Press, Cambridge, United Kingdom and New York, NY.

Jevrejeva, S. 2001. Severity of winter seasons in the northern Baltic Sea between 1529 and 1990: reconstruction and analysis. *Climate Research* **17**: 55-62.

Johannessen, O.M., Shalina, E.V. and Miles, M.W. 1999. Satellite evidence for an Arctic sea ice cover in transformation. *Science* **286**: 1937-1939.

Kwok, R. 2000. Recent changes in Arctic Ocean sea ice motion associated with the North Atlantic Oscillation. *Geophysical Research Letters* **27**: 775-778.

Kwok, R. 2004. Annual cycles of multiyear sea ice coverage of the Arctic Ocean: 1999-2003. *Journal of Geophysical Research* **109**: 10.1029/2003JC002238.

Kwok, R. and Rothrock, D.A. 1999. Variability of Fram Strait ice flux and North Atlantic Oscillation. *Journal of Geophysical Research* **104**: 5177-5189.

Lennox. A.R. and Goodship, A.E. 2008. Polar bears (*Ursus maritimus*), the most evolutionary advanced hibernators, avoid significant bone loss during hibernation. *Comparative Biochemistry and Physiology Part A* **149**: 203-208.

Mysak, L.A., Manak, D.K. and Marsden, R.F. 1990. Seaice anomalies observed in the Greenland and Labrador Seas during 1901-1984 and their relation to an interdecadal Arctic climate cycle. *Climate Dynamics* **5**: 111-133.

Mysak, L.A. and Power, S.B. 1992. Sea-ice anomalies in the western Arctic and Greenland-Iceland Sea and their relation to an interdecadal climate cycle. *Climatological Bulletin/Bulletin Climatologique* **26**: 147-176.

Omstedt, A. and Chen, D. 2001. Influence of atmospheric circulation on the maximum ice extent in the Baltic Sea. *Journal of Geophysical Research* **106**: 4493-4500.

Parkinson, C.L. 2000a. Variability of Arctic sea ice: the view from space, and 18-year record. *Arctic* **53**: 341-358.

Parkinson, C.L. 2000b. Recent trend reversals in Arctic sea ice extents: possible connections to the North Atlantic Oscillation. *Polar Geography* **24**: 1-12.

Parkinson, C.L. and Cavalieri, D.J. 2002. A 21-year record of Arctic sea-ice extents and their regional, seasonal and monthly variability and trends. *Annals of Glaciology* **34**: 441-446.

Parkinson, C.L., Cavalieri, D.J., Gloersen, P., Zwally, H.J. and Comiso, J.C. 1999. Arctic sea ice extents, areas, and trends, 1978-1996. *Journal of Geophysical Research* **104**: 20,837-20,856.

Polyakov, I.V., Proshutinsky, A.Y. and Johnson, M.A. 1999. Seasonal cycles in two regimes of Arctic climate. *Journal of Geophysical Research* **104**: 25,761-25,788.

Polyakov, I.V., Alekseev, G.V., Bekryaev, R.V., Bhatt, U., Colony, R.L., Johnson, M.A., Karklin, V.P., Makshtas, A.P., Walsh, D. and Yulin, A.V. 2002. Observationally based assessment of polar amplification of global warming. *Geophysical Research Letters* **29**: 10.1029/2001GL011111.

Polyakov, I.V., Alekseev, G.V., Bekryaev, R.V., Bhatt, U.S., Colony, R., Johnson, M.A., Karklin, V.P., Walsh, D. and Yulin, A.V. 2003. Long-term ice variability in Arctic marginal seas. *Journal of Climate* **16**: 2078-2085.

Proshutinsky, A.Y., Polyakov, I.V. and Johnson, M.A. 1999. Climate states and variability of Arctic ice and water dynamics during 1946-1997. *Polar Research* **18**: 135-142.

Ramsay, M.A. and Hobson, K.A. 1991. Polar bears make little use of terrestrial food webs: Evidence from stable-carbon isotope analysis. *Oecologia* **86**:598-600.

Ramsay, M.A. and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology* (London) **214**:601-634.

Rogers, J.C. and van Loon, H. 1979. The seesaw in winter temperatures between Greenland and Northern Europe. Part II: Some oceanic and atmospheric effects in middle and high latitudes. *Monthly Weather Review* **107**: 509-519.

Stern, H.L. and Heide-Jorgensen, M.P. 2003. Trends and variability of sea ice in Baffin Bay and Davis Strait. *Polar Research* 22: 11-18.

Stirling, I. and Øritsland, N.A. 1995. Relationships between estimates of ringed seal and polar bear populations in the Canadian Arctic. *Canadian Journal of Fisheries and Aquatic Science* **52**:2594-2612.

Vinje, T. 2001. Anomalies and trends of sea ice extent and atmospheric circulation in the Nordic Seas during the period 1864-1998. *Journal of Climate* 14: 255-267.

Vinnikov, K.Y., Robock, A., Stouffer, R.J., Walsh, J.E., Parkinson, C.L., Cavalieri, D.J., Mitchell, J.F.B., Garrett, D. and Zakharov, V.R. 1999. Global warming and Northern Hemisphere sea ice extent. *Science* **286**: 1934-1937.

Wang, J. and Ikeda, M. 2000. Arctic Oscillation and Arctic Sea-Ice Oscillation. *Geophysical Research Letters* 27: 1287-1290.

Watts, P.D. and Hansen, S.E. 1987. Cyclic starvation as a reproductive strategy in the polar bear. *Symposium of the Zoological Society of London* **57**:306-318.

#### 8.4.1.2. Thickness

In addition to its extent, the thickness of Arctic sea ice is of concern since it must support the weight of hunting polar bears. Male polar bears can weigh up to 800 kg (1,764 pounds) (DeMaster and Stirling, 1981), and there is anecdotal evidence of bears larger than this (Dowsley, 2005). Thick sea ice can negatively affect populations of marine mammals by reducing the size and number of airholes, thereby suffocating some species of whales and seals and reducing the number of hunting areas for polar bears (Stirling, 2002; Laidre *et al.*, 2008; Harington, 2008). Trends in the thickness of sea ice might also be precursors of changes in sea ice extent.

Based on analyses of submarine sonar data, Rothrock *et al.* (1999) suggested that Arctic sea ice in the mid 1990s had thinned by about 42 percent of the average 1958-1977 thickness. The IPCC reports this finding but also reports that other more recent studies found "the reduction in ice thickness was not gradual, but occurred abruptly before 1991." and acknowledges that "ice thickness varies considerably from year to year at a given location and so the rather sparse temporal sampling provided by submarine data makes inferences regarding long term change difficult" (IPCC 2007, p. 353). Johannessen et al. (1999), for example, found that essentially all of the drop occurred rather abruptly over a single period of not more than three years (1987/88-1990/91) and possibly only one year (1989/90-1990/91).

Two years after Johannessen et al., Winsor (2001) analyzed a more comprehensive set of Arctic sea-ice data obtained from six submarine cruises conducted between 1991 and 1997 that had covered the central Arctic Basin from 76°N to 90°N, as well as two areas that had been particularly densely sampled, one centered at the North Pole (>87°N) and one in the central part of the Beaufort Sea (centered at approximately 76°N, 145°W). The transect data across the entire Arctic Basin revealed that the mean Arctic sea-ice thickness had remained "almost constant" over the period of study. Data from the North Pole also showed little variability, and a linear regression of the data revealed a "slight increasing trend for the whole period." As for the Beaufort Sea region, annual variability in sea ice thickness was greater than at the North Pole but once again, in Winsor's words, "no significant trend" in mean seaice thickness was found. Combining the North Pole results with the results of an earlier study, Winsor concluded that "mean ice thickness has remained on a near-constant level around the North Pole from 1986 to 1997."

The following year, Holloway and Sou (2002) explored "how observations, theory, and modeling work together to clarify perceived changes to Arctic sea ice," incorporating data from "the atmosphere, rivers, and ocean along with dynamics expressed in an ocean-ice-snow model." On the basis of a number of different data-fed model runs, they found that for the last half of the past century, "no linear trend [in Arctic sea ice volume] over 50 years is appropriate," noting their results indicated "increasing volume to the mid-1960s, decadal variability without significant trend from the mid-1960s to the mid-1980s, then a loss of volume from the mid-1980s to the mid-1990s." The net effect of this behavior, in their words, was that "the volume estimated in 2000 is close to the

volume estimated in 1950." They suggest that the initial inferred rapid thinning of Arctic sea ice was, as they put it, "unlikely," due to problems arising from under-sampling. They also report that "varying winds that readily redistribute Arctic ice create a recurring pattern whereby ice shifts between the central Arctic and peripheral regions, especially in the Canadian sector," and that the "timing and tracks of the submarine surveys missed this dominant mode of variability."

In the same year, Polyakov et al. (2002) employed newly available long-term Russian landfast-ice data obtained from the Kara, Laptev, East Siberian, and Chuckchi Seas to investigate trends and variability in the Arctic environment poleward of 62°N. This study revealed that fast-ice thickness trends in the different seas were "relatively small, positive or negative in sign at different locations, and not statistically significant at the 95% level." A year later, these results were reconfirmed by Polyakov et al. (2003), who reported that the available fast-ice records "do not show a significant trend," while noting that "in the Kara and Chukchi Seas trends are positive, and in the Laptev and East Siberian Seas trends are negative," but stating that "these trends are not statistically significant at the 95% confidence level "

Laxon et al. (2003) used an eight-year time series (1993-2001) of Arctic sea-ice thickness data derived from measurements of ice freeboard made by radar altimeters carried aboard ERS-1 and 2 satellites to determine the mean thickness and variability of Arctic sea ice between latitudes 65°N and 81.5°N, which region covers the entire circumference of the Arctic Ocean, including the Beaufort, Chukchi, East Siberian, Kara, Laptev, Barents, and Greenland Seas. These real-world observations (1) revealed "an interannual variability in ice thickness at higher frequency, and of greater amplitude, than simulated by regional Arctic models," (2) undermined "the conclusion from numerical models that changes in ice thickness occur on much longer timescales than changes in ice extent," and (3) showed that "sea ice mass can change by up to 16% within one year," which finding "contrasts with the concept of a slowly dwindling ice pack, produced by greenhouse warming." Laxon et al. concluded that "errors are present in current simulations of Arctic sea ice," stating in their closing sentence that "until models properly reproduce the observed high-frequency, and thermodynamically driven, variability in sea ice

thickness, simulations of both recent, and future, changes in Arctic ice cover will be open to question."

In a paper on landfast ice in Canada's Hudson Bay, Gagnon and Gough (2006) cite nine different studies of sea-ice cover, duration, and thickness in the Northern Hemisphere, noting that the Hudson Bay region "has been omitted from those studies with the exception of Parkinson et al. (1999)." For 13 stations located on the shores of Hudson Bay (seven) and surrounding nearby lakes (six), Gagnon and Gough then analyzed long-term weekly measurements of ice thickness and associated weather conditions that began and ended, in the mean, in 1963 and 1993, respectively. The study revealed that a "statistically significant thickening of the ice cover over time was detected on the western side of Hudson Bay, while a slight thinning lacking statistical significance was observed on the eastern side." This asymmetry, in their words, was "related to the variability of air temperature, snow depth, and the dates of ice freezeup and break-up," with "increasing maximum ice thickness at a number of stations" being "correlated to earlier freeze-up due to negative temperature trends in autumn," and with high snow accumulation being associated with low ice thickness, "because the snow cover insulates the ice surface, reducing heat conduction and thereby ice growth." Noting that their findings "are in contrast to the projections from general circulation models, and to the reduction in sea-ice extent and thickness observed in other regions of the Arctic," Gagnon and Gough say "this contradiction must be addressed in regional climate change impact assessments."

Finally, the relationship between sea ice thickness and polar bear survival is not so simple that any reduction in the one leads to a reduction in the other. As mentioned previously, research has found that expanding sea ice extent and thickness can negatively affect populations of marine mammals, including polar bears (Stirling, 2002; Laidre et al., 2008; Harington, 2008). Laidre and Heide-Jergensen (2005) report that "cetacean occurrence is generally negatively correlated with dense or complete ice cover due to the need to breathe at the surface," and that "lacking the ability to break holes in the ice," narwhals are vulnerable to reductions in the amount of open water available to them, as has been demonstrated by ice entrapment events "where hundreds of narwhals died during rapid sea ice formation caused by sudden cold periods (Siegastad and Heide-Jorgensen, 1994; Heide-Jorgensen et al., 2002). Such events were becoming ever more likely

as temperatures continued to decline and sea ice cover and variability increased." They concluded that "with the evidence of changes in sea ice conditions that could impact foraging, prey availability, and of utmost importance, access to the surface to breathe, it is unclear how narwhal sub-populations will fare in light of changes in the high Arctic."

While the negative effects of too much or too thick ice are well known and documented, the evidence is less clear that thinner ice is a major impediment to hunting by polar bears. The bears are known to hunt on new ice that is less than 30 cm (about 1 foot) thick and to use first-year ice that is greater than 120 cm (about 4 feet) thick for overwintering and denning (Ferguson et al., 1997; Ferguson et al., 2000). For context, consider that firstyear ice in March 2008 was about 160 cm (about 5 feet) thick (NSIDC 2008). Polar bears also are able to migrate to other areas in response to changes in sea ice, as they have been observed to do in response to competition for food. contact with human development, and other environmental impacts (Messier et al., 2001; Dyke et al., 2007).

These observations suggest there has not been a steady or continuing thinning of Arctic sea ice that can be attributed to  $CO_2$ -induced global warming. Rather, and as was the case with changes in the extent of Arctic sea ice, changes in sea ice thickness appear to be a consequence of changes in ice dynamics caused by periodic climate oscillations having nothing to do with changes in the air's  $CO_2$  content. Consequently, there is once again no evidence that polar bears are endangered by global warming, whether it results from human activities or other causes.

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2science.org/</u><u>subject/s/seaicearcticthick.php</u>.

### References

DeMaster, D.P. and Stirling, I. 1981. Ursus maritimus. Polar bear. Mammalian Species 145:1-7.

Dowsley, M. 2005. Inuit knowledge regarding climate change and the Baffin Bay polar bear population. Government of Nunavut, Department of Environment, Final Wildlife Report 1, Iqaluit, Nunavut.

Dyck, M.G., Soon, W., Baydack, R.K., Legates, D.R., Baliunas, S., Ball, T.F., and Hancock, L.O. 2007. Polar bears of western Hudson Bay and climate change: Are warming spring air temperatures the "ultimate" survival control factor? *Ecological Complexity* **4**: 73-84.

Ferguson, S.H., Taylor, M.K., and Messier, F. 1997. Space use by polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. *Canadian Journal of Zoology* **75**: 1585-1594.

Ferguson, S.H., Taylor, M.K., and Messier, F. 2000. Influence of sea ice dynamics on habitat selection by polar bears. *Ecology* **81**: 761-772.

Gagnon, A.S. and Gough, W.A. 2006. East-west asymmetry in long-term trends of landfast ice thickness in the Hudson Bay region, Canada. *Climate Research* **32**: 177-186.

Harington, C.R. 2008. The evolution of Arctic marine mammals. *Ecological Applications* **18** (Suppl.): S23-S40.

Heide-Jorgensen, M.P., Richard, P., Ramsay, M. and Akeeagok, S. 2002. In: *Three Recent Ice Entrapments of Arctic Cetaceans in West Greenland and the Eastern Canadian High Arctic.* Volume 4, NAMMCO Scientific Publications. 143-148.

Holloway, G. and Sou, T. 2002. Has Arctic sea ice rapidly thinned? *Journal of Climate* **15**: 1691-1701.

IPCC. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (Eds.) Cambridge University Press, Cambridge, United Kingdom and New York, NY.

Johannessen, O.M., Shalina, E.V. and Miles, M.W. 1999. Satellite evidence for an Arctic sea ice cover in transformation. *Science* **286**: 1937-1939.

Kwok, R. 2000. Recent changes in Arctic Ocean sea ice motion associated with the North Atlantic Oscillation. *Geophysical Research Letters* **27**: 775-778.

Laxon, S., Peacock, N. and Smith, D. 2003. High interannual variability of sea ice thickness in the Arctic region. *Nature* **425**: 947-950.

Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.P., and Ferguson, S.H. 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecological Applications* 18(2, Suppl.): S97-S125.

Laidre, K.L. and Heide-Jorgensen, M.P. 2005. Arctic sea ice trends and narwhal vulnerability. *Biological Conservation* **121**: 509-517.

Messier, F., Taylor, M.K., Plante, A. and Romito, T. 2001. Atlas of polar bear movements in Nunavut, Northwest Territories, and neighboring areas. Nunavut Wildlife Service and University of Saskatchewan, Saskatoon, SK.

NSIDC 2008. A different pattern of sea ice retreat. (National Snow and Ice Data Center). Web site, last accessed July 17, 2008. <u>http://nsidc.org/arcticsea icenews/index.html</u>

Parkinson, C.L., Cavalieri, D.J., Gloersen, P., Zwally, J., and Comiso, J.C. 1999. Arctic sea ice extent, areas, and trends, 1978-1996. *Journal of Geophysical Research* **104**: 20,837-20,856.

Polyakov, I.V., Alekseev, G.V., Bekryaev, R.V., Bhatt, U., Colony, R.L., Johnson, M.A., Karklin, V.P., Makshtas, A.P., Walsh, D. and Yulin, A.V. 2002. Observationally based assessment of polar amplification of global warming. *Geophysical Research Letters* **29**: 10.1029/2001GL011111.

Polyakov, I.V., Alekseev, G.V., Bekryaev, R.V., Bhatt, U.S., Colony, R., Johnson, M.A., Karklin, V.P., Walsh, D. and Yulin, A.V. 2003. Long-term ice variability in Arctic marginal seas. *Journal of Climate* **16**: 2078-2085.

Rothrock, D.A., Yu, Y. and Maykut, G.A. 1999. Thinning of the Arctic sea ice cover. *Geophysics Research Letters* **26**: 3469-3472.

Siegstad, H. and Heide-Jorgensen, M.P. 1994. Ice entrapments of narwhals (*Monodon monoceros*) and white whales (*Delphinapterus leucas*) in Greenland. *Meddeleser om Gronland Bioscience* **39**: 151-160.

Stirling, I. 2002. Polar bears and seals in the eastern Beaufort Sea and Amundsen Gulf: a synthesis of population trends and ecological relationships over three decades. *Arctic* **55** (Suppl. 1): 59-76.

Winsor, P. 2001. Arctic sea ice thickness remained constant during the 1990s. *Geophysical Research Letters* **28**: 1039-1041.

# 8.4.2. Temperatures

Polar bears evolved from brown bears (*Ursus arctos*) sometime in the last 400,000 years and probably no more than 200,000 years ago (Amnason *et al.*, 1995; Davis *et al.*, 2008; Harington, 2008). This means they have survived whatever changes in the Arctic climate took place over the course of many millennia, including two major warming periods over the last 11,000 years, the Early Holocene Climatic Optimum and the Medieval Warm Period.

In this section we review evidence of these warm periods first in Greenland and then in the rest of the Arctic. Then we look at more recent temperature trends in Greenland and the rest of the Arctic and find considerable variability, recently described by one group of scientists as "a long term cooling and shorter warming periods" (Chylek *et al.*, 2006). These topics are addressed in greater detail in Chapter 3 of this report.

### References

Arnason, U., Bodin, K., Gullberg, A., Ledje, C., and Mouchaty, S. 1995. A molecular view of pinniped relationships with particular emphasis on the true seals. *Journal of Molecular Evolution* **40**: 78-85.

Chylek, P., Dubey, M.K, and Lesins, G. 2006. Greenland warming of 1920-1930 and 1995-2005. *Geophysical Research Letters* **33**: L11707.

Davis, C.S., Stirling, I., Strobeck, C., and Coltman, D.W. 2008. Population structure of ice-breeding seals. *Molecular Ecology* **17**: 3078-3094.

Harington, C.R. 2008. The evolution of Arctic marine mammals. *Ecological Applications* **18** (Suppl.): S23-S40.

### 8.4.2.1. Prehistoric Greenland

Dahl-Jensen et al. (1998) used data from two ice sheet boreholes to reconstruct the temperature history of Greenland over the past 50,000 years. Their analysis indicated that temperatures on the Greenland Ice Sheet during the Last Glacial Maximum (about 25,000 years ago) were  $23 \pm 2$  °C colder than at present. After the termination of the glacial period, however, temperatures increased steadily to a value that was 2.5°C warmer than at present, during the Climatic Optimum of 4,000 to 7,000 years ago. The Medieval Warm Period and Little Ice Age were also evident in the borehole data, with temperatures 1°C warmer and 0.5-0.7°C cooler than at present, respectively. Then, after the Little Ice Age, the scientists report "temperatures reached a maximum around 1930 AD" and that "temperatures have decreased during the last decades."

In another study of Greenland climate, Bard (2002) describes glacial-period millennial-scale episodes of dramatic warming called Dansgaard-Oeschger events (with temperature increases "of more than 10°C"), which are evident in Greenland ice core records, as well as episodes of "drastic cooling" called Heinrich events (with temperature drops "of up to about 5°C"), which are evident in sea surface temperature records derived from the study of North

Atlantic deep-sea sediment cores. In the Greenland record, according to Bard, the progression of these events is such that "the temperature warms abruptly to reach a maximum and then slowly decreases for a few centuries before reaching a threshold, after which it drops back to the cold values that prevailed before the warm event."

Wagner and Melles (2001) retrieved a sediment core from a lake on an island situated just off Liverpool Land on the east coast of Greenland. Analyzing it for a number of properties related to the past presence of seabirds there, they obtained a 10,000-year record that tells us much about the region's climatic history. Key to the study were certain biogeochemical data that reflected variations in seabird breeding colonies in the catchment area of the lake. These data revealed high levels of the various parameters measured by Wagner and Melles between about 1,100 and 700 years before present (BP) that were indicative of the summer presence of significant numbers of seabirds during that "medieval warm period," as they describe it, which had been preceded by a several-hundred-year period of little to no inferred bird presence. Then, after the Medieval Warm Period, the data suggested another absence of birds during what they refer to as "a subsequent Little Ice Age," which they note was "the coldest period since the early Holocene in East Greenland." Their data also showed signs of a "resettlement of seabirds during the last 100 years, indicated by an increase of organic matter in the lake sediment and confirmed by bird observations." However, values of the most recent data were not as great as those obtained from the earlier Medieval Warm Period; and temperatures derived from two Greenland ice cores led to the same conclusion: It was warmer at various times between 1,100 to 700 years BP than it was over the twentieth century.

Kaplan *et al.* (2002) also worked with data obtained from a small lake, this one in southern Greenland, analyzing sediment physical-chemical properties, including magnetic susceptibility, density, water content, and biogenic silica and organic matter concentrations. They discovered that "the interval from 6000 to 3000 cal yr BP was marked by warmth and stability." Thereafter, however, the climate cooled "until its culmination during the Little Ice Age," but from 1,300-900 years BP, there was a partial amelioration of climate (the Medieval Warm Period) that was associated with an approximate 1.5°C rise in temperature.

Following another brief warming between AD 1500 and 1750, the second and more severe portion of the Little Ice Age occurred, which was in turn followed by "naturally initiated post-Little Ice Age warming since AD 1850, which is recorded throughout the Arctic." They report that Viking "colonization around the northwestern North Atlantic occurred during peak Medieval Warm Period conditions that ended in southern Greenland by AD 1100," noting that Norse movements around the region thereafter "occurred at perhaps the worst time in the last 10,000 years, in terms of the overall stability of the environment for sustained plant and animal husbandry."

These many studies of the temperature history of Greenland depict long-term oscillatory cooling ever since the Climatic Optimum of the mid-Holocene, when it was perhaps 2.5°C warmer than it is now, within which cooling trend is included the Medieval Warm Period, when it was about 1°C warmer than it is currently, and the Little Ice Age, when it was 0.5 to 0.7°C cooler than now, after which temperatures rebounded to a new maximum in the 1930s and 1940s, only to fall steadily thereafter.

Polar bears obviously survived these large-scale and often sudden climate changes in Greenland, otherwise none would be found living in Greenland today. This does not mean the population of polar bears remained constant throughout this period; more likely they flourished in some periods and declined in numbers in others. But changes in climate did not lead to their extinction. This history begs the question: Why would temperature changes that are predicted to be of the same scale or less than those that occurred naturally, before there was any human impact on climate, be expected to cause the extinction of polar bears, when early natural cycles did not?

Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2science.org/</u><u>subject/g/greenland.php</u>.

### References

Bard, E. 2002. Climate shock: Abrupt changes over millennial time scales. *Physics Today* **55**: 32-38.

Dahl-Jensen, D., Mosegaard, K., Gundestrup, N., Clow, G.D., Johnsen, S.J., Hansen, A.W., and Balling, N. 1998. Past temperatures directly from the Greenland Ice Sheet. *Science* **282**: 268-271.

Kaplan, M.R., Wolfe, A.P., and Miller, G.H. 2002. Holocene environmental variability in southern Greenland inferred from lake sediments. *Quaternary Research* **58**: 149-159.

Wagner, B. and Melles, M. 2001. A Holocene seabird record from Raffles So sediments, East Greenland, in response to climatic and oceanic changes. *Boreas* **30**: 228-239.

# 8.4.2.2. Rest of the Prehistoric Arctic

Polar bears faced similar temperature changes in the rest of the Arctic region. Naurzbaev and Vaganov (2000) developed a 2,200-year temperature history using tree-ring data obtained from 118 trees near the upper-timberline in Siberia for the period 212 BC to AD 1996, as well as a similar history covering the period of the Holocene Climatic Optimum (3300 to 2600 BC). They reported that several warm and cool periods prevailed for several multi-century periods throughout the last two millennia: a cool period in the first two centuries AD, a warm period from AD 200 to 600, cooling again from 600 to 800 AD, followed by the Medieval Warm Period from about AD 850 to 1150, the cooling of the Little Ice Age from AD 1200 though 1800, followed by the recovery warming of the twentieth century. In regard to this latter temperature rise, however, the two scientists say it was "not extraordinary" and that "the warming at the border of the first and second millennia [AD 1000] was longer in time and similar in amplitude." In addition, their reconstructed temperatures for the Holocene Climatic Optimum revealed there was an even warmer period about 5,000 years ago, when temperatures averaged 3.3°C more than they did over the past two millennia.

Moore et al. (2001) analyzed sediment cores extracted from Donard Lake, Baffin Island, Canada (~66.25°N, 62°W) to produce a 1,240-year record of mean summer temperature for this region that averaged 2.9°C over the period AD 750-1990. Within this period there were several anomalously warm decades with temperatures that were as high as 4°C around AD 1000 and 1100, while at the beginning of the thirteenth century Donard Lake witnessed what they called "one of the largest climatic transitions in a millennium." as over "average summer temperatures rose rapidly by nearly 2°C from AD 1195-1220, ending in the warmest decade in the record," with temperatures near 4.5°C. This latter temperature rise was then followed by a period of extended warmth that lasted until an abrupt cooling

event occurred around AD 1375, resulting in the following decade being one of the coldest in the record and signaling the onset of the Little Ice Age on Baffin Island, which lasted 400 years. At the modern end of the record, a gradual warming trend occurred over the period 1800-1900, followed by a dramatic cooling event that brought temperatures back to levels characteristic of the Little Ice Age, which chilliness lasted until about 1950. Thereafter, temperatures rose once more throughout the 1950s and 1960s, whereupon they trended downwards toward cooler conditions to the end of the record in 1990.

Gedalof and Smith (2001) compiled a transect of six tree ring-width chronologies from stands of mountain hemlock growing near the treeline that extends from southern Oregon to the Kenai Peninsula, Alaska. Over the period of their study (AD 1599-1983), they determined that "much of the preinstrumental record in the Pacific Northwest region of North America [was] characterized by alternating regimes of relatively warmer and cooler SST [sea surface temperature] in the North Pacific, punctuated by abrupt shifts in the mean background state," which were found to be "relatively common occurrences." They concluded, "regime shifts in the North Pacific have occurred 11 times since 1650." A significant aspect of these findings is the fact that the abrupt 1976-77 shift in this Pacific Decadal Oscillation, as it is generally called, is what was responsible for the vast majority of the past half-century's warming in Alaska, which some commentators wrongly point to as evidence of CO<sub>2</sub>-induced global warming.

Kasper and Allard (2001) examined soil deformations caused by ice wedges (a widespread and abundant form of ground ice in permafrost regions that can grow during colder periods and deform and crack the soil). Working near Salluit, northern Quebéc (approx. 62°N, 75.75°W), they found evidence of ice wedge activity prior to AD 140, reflecting cold climatic conditions. Between AD 140 and 1030, however, this activity decreased, reflective of warmer conditions. Then, from AD 1030 to 1500, conditions cooled; and from 1500 to 1900 ice wedge activity was at its peak, when the Little Ice Age ruled, suggesting this climatic interval exhibited the coldest conditions of the past 4,000 years. Thereafter, a warmer period prevailed, from about 1900 to 1946, which was followed by a return to cold conditions during the last five decades of the twentieth century, during which time more than 90 percent of the ice wedges studied reactivated and grew by 20-30 cm, in harmony with a
reported temperature decline of 1.1°C observed at the meteorological station in Salluit.

Naurzbaev et al. (2002) developed a 2,427-year proxy temperature history for the part of the Taimyr Peninsula, northern Russia, lying between 70°30' and 72°28' North latitude, based on a study of ring-widths of living and preserved larch trees, noting that it has been shown that "the main driver of tree-ring variability at the polar timber-line [where they worked] is temperature (Vaganov et al., 1996; Briffa et al., 1998; Schweingruber and Briffa, 1996)." This work revealed that "the warmest periods over the last two millennia in this region were clearly in the third [Roman Warm Period], tenth to twelfth [Medieval Warm Period] and during the twentieth [Current Warm Period] centuries." With respect to the second of these three periods, they emphasize that "the warmth of the two centuries AD 1058-1157 and 950-1049 attests to the reality of relative mediaeval warmth in this region." Their data also reveal three other important pieces of information: (1) the Roman and Medieval Warm Periods were both warmer than the Current Warm Period has been to date, (2) the beginning of the end of the Little Ice Age was somewhere in the vicinity of 1830, and (3) the Current Warm Period peaked somewhere in the vicinity of 1940.

These studies demonstrate that polar bears throughout the Arctic region experienced periods of warming and cooling in the past that exceed the variability observed in the twentieth century and likely to occur in the twenty-first century. Additional information on this topic, including reviews of newer publications as they become available, can be found at <u>http://www.co2science.org/subject/a/arctictemp trends.php</u>.

### References

Briffa, K.R., Schweingruber, F.H., Jones, P.D., Osborn, T.J., Shiyatov, S.G. and Vaganov, E.A. 1998. Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* **391**: 678-682.

Gedalof, Z. and Smith, D.J. 2001. Interdecadal climate variability and regime-scale shifts in Pacific North America. *Geophysical Research Letters* **28**: 1515-1518.

Kasper, J.N. and Allard, M. 2001. Late-Holocene climatic changes as detected by the growth and decay of ice wedges on the southern shore of Hudson Strait, northern Québec, Canada. *The Holocene* **11**: 563-577.

Moore, J.J., Hughen, K.A., Miller, G.H. and Overpeck, J.T. 2001. Little Ice Age recorded in summer temperature reconstruction from varved sediments of Donard Lake, Baffin Island, Canada. *Journal of Paleolimnology* **25**: 503-517.

Naurzbaev, M.M. and Vaganov, E.A. 2000. Variation of early summer and annual temperature in east Taymir and Putoran (Siberia) over the last two millennia inferred from tree rings. *Journal of Geophysical Research* **105**: 7317-7326.

Naurzbaev, M.M., Vaganov, E.A., Sidorova, O.V. and Schweingruber, F.H. 2002. Summer temperatures in eastern Taimyr inferred from a 2427-year late-Holocene tree-ring chronology and earlier floating series. *The Holocene* **12**: 727-736.

Schweingruber, F.H. and Briffa, K.R. 1996. Tree-ring density network and climate reconstruction. In: Jones, P.D., Bradley, R.S. and Jouzel, J. (Eds.) *Climatic Variations and Forcing Mechanisms of the Last 2000 Years*, NATO ASI Series 141. 43-66. Springer-Verlag, Berlin, Germany.

Vaganov, E.A., Shiyatov, S.G. and Mazepa, V.S. 1996. Dendroclimatic Study in Ural-Siberian Subarctic. Nauka, Novosibirsk, Russia.

## 8.4.2.3. Twentieth Century

The IPCC theorizes that warming temperatures in the twentieth century have had a harmful effect on polar bears, but it overlooks evidence that temperatures in Greenland and the rest of the Arctic region peaked in the 1930s. We review that research in this section.

Starting in Greenland, Hanna and Cappelen (2003) determined the air temperature history of coastal southern Greenland from 1958-2001, based on data from eight Danish Meteorological Institute stations in coastal and near-coastal southern Greenland, as well as the concomitant sea surface temperature (SST) history of the Labrador Sea off southwest Greenland, based on three previously published and subsequently extended SST datasets (Parker et al., 1995; Rayner et al., 1996; Kalnay et al., 1996). The coastal temperature data showed a cooling of 1.29°C over the period of study, while two of the three SST databases also depicted cooling: by 0.44°C in one case and by 0.80°C in the other. Both the land-based air temperature and SST series followed similar patterns and were strongly correlated, but with no obvious lead/lag either way. In addition, it was determined that the cooling was "significantly inversely correlated with an increased phase of the North Atlantic Oscillation (NAO) over

the past few decades." The two researchers say this "NAO-temperature link doesn't explain what caused the observed cooling in coastal southern Greenland but it does lend it credibility."

Several other studies also have reported latetwentieth century cooling on Greenland. Based on mean monthly temperatures of 37 Arctic and seven sub-Arctic stations, as well as temperature anomalies of 30 grid-boxes from the updated dataset of Jones, for example, Przybylak (2000) found that "the level of temperature in Greenland in the last 10-20 years is similar to that observed in the 19th century." Likewise, in a study that utilized satellite imagery of the Odden ice tongue (a winter ice cover that occurs in the Greenland Sea with a length of about 1,300 km and an aerial coverage of as much as 330,000 square kilometers) plus surface air temperature data from adjacent Jan Mayen Island, Comiso et al. (2001) determined that the ice phenomenon was "a relatively smaller feature several decades ago," due to the warmer temperatures that were prevalent at that time. In addition, they report that observational evidence from Jan Mayen Island indicates temperatures there cooled at a rate of  $0.15 \pm 0.03$  °C per decade during the past 75 years.

Taurisano et al. (2004) examined the temperature history of the Nuuk ford during the last century. where their analyses of all pertinent regional data led them to conclude that "at all stations in the Nuuk fjord, both the annual mean and the average temperature of the three summer months (June, July and August) exhibit a pattern in agreement with the trends observed at other stations in south and west Greenland (Humlum 1999; Hanna and Cappelen, 2003)." As they describe it, the temperature data "show that a warming trend occurred in the Nuuk fjord during the first 50 years of the 1900s, followed by a cooling over the second part of the century, when the average annual temperatures decreased by approximately 1.5°C." Coincident with this cooling trend there was also what they describe as "a remarkable increase in the number of snowfall days (+59 days)." What is more, they report that "not only did the cooling affect the winter months, as suggested by Hannna and Cappelen (2002), but also the summer mean," noting that "the summer cooling is rather important information for glaciological studies, due to the ablation-temperature relations."

In a study of three coastal stations in southern and central Greenland that possess almost uninterrupted temperature records between 1950 and 2000, Chylek *et al.* (2004) discovered that "summer temperatures,

which are most relevant to Greenland ice sheet melting rates, do not show any persistent increase during the last fifty years." In fact, working with the two stations with the longest records (both over a century in length), they determined that coastal Greenland's peak temperatures occurred between 1930 and 1940, and that the subsequent decrease in temperature was so substantial and sustained that current coastal temperatures "are about 1°C below their 1940 values." Furthermore, they note that "at the summit of the Greenland ice sheet the summer average temperature has decreased at the rate of 2.2°C per decade since the beginning of the measurements in 1987." Hence, as with the Arctic as a whole, it would appear that Greenland has not experienced any net warming over the most dramatic period of atmospheric CO<sub>2</sub> increase on record. In fact, it has cooled during this period.

At the start of the twentieth century, however, Greenland was warming, as it emerged, along with the rest of the world, from the depths of the Little Ice Age. Between 1920 and 1930, when the atmosphere's CO<sub>2</sub> concentration rose by a mere 3 to 4 ppm, there was a phenomenal warming at all five coastal locations for which contemporary temperature records are available. In the words of Chylek *et al.*, "average annual temperature rose between 2 and 4°C [and by as much as 6°C in the winter] in less than ten years." And this warming, as they note, "is also seen in the <sup>18</sup>O/<sup>16</sup>O record of the Summit ice core (Steig *et al.*, 1994; Stuiver *et al.*, 1995; White *et al.*, 1997)."

In commenting on this dramatic temperature rise, which they call the "great Greenland warming of the 1920s," Chylek *et al.* conclude that "since there was no significant increase in the atmospheric greenhouse gas concentration during that time, the Greenland warming of the 1920s demonstrates that a large and rapid temperature increase can occur over Greenland, and perhaps in other regions of the Arctic, due to internal climate variability such as the NAM/NAO [Northern Annular Mode/North Atlantic Oscillation], without a significant anthropogenic influence." These facts led them to speculate that "the NAO may play a crucial role in determining local Greenland climate during the 21st century, resulting in a local climate that may defy the global climate change."

Two years later, Chylek and another team of researchers compared average summer temperatures recorded at Ammassalik, on Greenland's southeast coast, and Godthab Nuuk on the island's southwestern coast, for the period 1905 to 2005 (Chylek *et al.*, 2006). They found "the 1955 to 2005 averages of the summer temperatures and the temperatures of the warmest month at both Godthab Nuuk and Ammassalik are significantly lower than the corresponding averages for the previous 50 years (1905-1955). The summers at both the southwestern and the southeastern coast of Greenland were significantly colder within the 1955-2005 period compared to the 1905-1955."

Chylek *et al.* also compared temperatures for the 10-year periods of 1920-1930 and 1995-2005. They found the average summer temperature for 2003 in Ammassalik was a record high since 1895, but "the years 2004 and 2005 were closer to normal being well below temperatures reached in the 1930s and 1940s." Similarly, the record from Godthab Nuuk showed that while temperatures there "were also increasing during the 1995-2005 period, they stayed generally below the values typical for the 1920-1940 period." The authors conclude that "reports of Greenland temperature changes are .... diverse suggesting a long term cooling and shorter warming periods."

Moving to the rest of the Arctic region, Overpeck *et al.* (1997) combined paleoclimatic records obtained from lake and marine sediments, trees, and glaciers to develop a 400-year history of circum-Arctic surface air temperature. From this record they determined that the most dramatic warming of the last four centuries of the past millennium  $(1.5^{\circ}C)$  occurred between 1840 and 1955. Then, from 1955 to the end of the record (about 1990), the mean circum-Arctic air temperature declined by  $0.4^{\circ}C$ .

Zeeberg and Forman (2001) analyzed twentieth century changes in glacier terminus positions on north Novaya Zemlya, a Russian island located between the Barents and Kara Seas in the Arctic Ocean, providing in the process a quantitative assessment of the effects of temperature and precipitation on glacial mass balance. This work revealed a significant and accelerated post-Little Ice Age glacial retreat in the first and second decades of the twentieth century; but by 1952, the region's glaciers had experienced between 75 to 100 percent of their net twentieth century retreat. During the next 50 years, the recession of more than half of the glaciers stopped, and many tidewater glaciers actually began to advance. These glacial stabilizations and advances were attributed by the two scientists to observed increases in precipitation and/or decreases in temperature. In the four decades since 1961, for example, weather stations at Novava Zemlva show summer temperatures to have been 0.3° to 0.5°C colder than they were over the prior 40 years, while winter temperatures were 2.3° to 2.8°C colder than they were over the prior 40-year period. Such observations, in Zeeberg and Forman's words, are "counter to warming of the Eurasian Arctic predicted for the twenty-first century by climate models, particularly for the winter season."

Comiso et al. (2000) utilized satellite imagery to analyze and quantify a number of attributes of the Odden ice tongue, including its average concentration, maximum area, and maximum extent over the period 1979-1998. They used surface air temperature data from Jan Mayen Island, located within the region of study, to infer the behavior of the phenomenon over the past 75 years. The Odden ice tongue was found to vary in size, shape, and length of occurrence during the 20-year period, displaying a fair amount of interannual variability. Quantitatively, trend analyses revealed that the ice tongue had exhibited no statistically significant change in any of the parameters studied over the short 20-year period. However, a proxy reconstruction of the Odden ice tongue for the past 75 years revealed the ice phenomenon to have been "a relatively smaller feature several decades ago," due to the significantly warmer temperatures that prevailed at that time. The fact that the Odden ice tongue has persisted, virtually unchanged in the mean during the past 20 years, is in direct contrast with predictions of rapid and increasing warmth in earth's polar regions as a result of CO<sub>2</sub>-induced global warming. This observation, along with the observational evidence from Jan Mayen Island that temperatures there actually cooled at a rate of  $0.15 \pm 0.03$  °C per decade during the past 75 years, bolsters the view that there has been little to no warming in this part of the Arctic, as well as most of its other parts, over the past seven decades.

Przybylak (2002) conducted a detailed analysis of intraseasonal and interannual variability in maximum, minimum, and average air temperature and diurnal air temperature range for the entire Arctic-as delineated by Treshnikov (1985)-for the period 1951-1990, based on data from 10 stations "representing the majority of the climatic regions in the Arctic." This work indicated that trends in both the intraseasonal and interannual variability of the temperatures studied did not show any significant changes, leading Przybylak to conclude that "this aspect of climate change, as well as trends in average seasonal and annual values of temperature investigated earlier (Przybylak, 1997, 2000), proves that, in the Arctic in the period 1951-90, no tangible manifestations of the greenhouse effect can be identified."

Isaksson et al. (2003) retrieved two ice cores (one from Lomonosovfonna and one from Austfonna) far above the Arctic Circle in Svalbard, Norway, after which the 12 cooperating scientists from Norway, Finland, Sweden, Canada, Japan, Estonia, and the Netherlands used  $\delta^{18}$ O data to reconstruct a 600-year temperature history of the region. As would be expected—in light of the earth's transition from the Little Ice Age to the Current Warm Period-the international group of scientists reported that "the  $\delta^{18}$ O data from both Lomonosovfonna and Austfonna ice cores suggest that the twentieth century was the warmest during at least the past 600 years." However, the warmest decade of the twentieth century was centered on approximately 1930, while the instrumental temperature record at Longyearbyen also shows the decade of the 1930s to have been the warmest. In addition, the authors remark, "as on Svalbard, the 1930s were the warmest decade in the Trondheim record." Consequently, there was no net warming over the last seven decades of the twentieth century in the parts of Norway cited in this study.

In the same year, Polyakov et al. (2003) derived a surface air temperature history that stretched from 1875 to 2000, based on measurements carried out at 75 land stations and a number of drifting buoys located poleward of 62°N latitude. From 1875 to about 1917, the team of eight U.S. and Russian scientists found the surface air temperature of the huge northern region rose hardly at all; but then it climbed 1.7°C in just 20 years to reach a peak in 1937 that was not eclipsed over the remainder of the record. During this 20-year period of rapidly rising air temperature, the atmosphere's CO<sub>2</sub> concentration rose by a mere 8 ppm. But then, over the next six decades, when the air's CO<sub>2</sub> concentration rose by approximately 55 ppm, or nearly seven times more than it did throughout the 20-year period of dramatic warming that preceded it, the surface air temperature of the region poleward of 62°N experienced no net warming and, in fact, may have cooled.

Laidre and Heide-Jorgensen (2005), using a combination of long-term satellite tracking data, climate data, and remotely sensed sea ice concentrations to detect localized habitat trends of narwhals—a species of whale that polar bears are known to hunt—in Baffin Bay between Greenland and Canada, home to the largest narwhal population in the world. They found "since 1970, the climate in West Greenland has cooled, reflected in both oceanographic and biological conditions (Hanna and Cappelen, 2003)," with the result that "Baffin Bay

and Davis Strait display strong significant increasing trends in ice concentrations and extent, as high as 7.5 percent per decade between 1979 and 1996, with comparable increases detected back to 1953 (Parkinson *et al.*, 1999; Deser *et al.*, 2000; Parkinson, 2000a,b; Parkinson and Cavalieri, 2002; Stern and Heide-Jorgensen, 2003)."

Groisman et al. (2006) reported using "a new Global Synoptic Data Network consisting of 2100 stations within the boundaries of the former Soviet Union created jointly by the [U.S.] National Climatic Center and Russian Institute Data for Hydrometeorological Information ... to assess the climatology of snow cover, frozen and unfrozen ground reports, and their temporal variability for the period from 1936 to 2004." They determined that "during the past 69 years (1936-2004 period), an increase in duration of the period with snow on the ground over Russia and the Russian polar region north of the Arctic circle has been documented by 5 days or 3% and 12 days or 5%, respectively," and they note this result "is in agreement with other findings." In commenting on this development, plus the similar findings of others, the five researchers say "changes in snow cover extent during the 1936-2004 period cannot be linked with 'warming' (particularly with the Arctic warming)." Why? Because, as they continue, "in this particular period the Arctic warming was absent."

Karlén (2005), focusing on Svalbard Lufthavn (located at 78°N latitude), which he later shows to be representative of much of the Arctic, reports that "the Svalbard mean annual temperature increased rapidly from the 1910s to the late 1930s," that "the temperature thereafter became lower, and a minimum was reached around 1970," and that "Svalbard thereafter became warmer, but the mean temperature in the late 1990s was still slightly cooler than it was in the late 1930s," indicative of a cooling trend of 0.11°C per decade over the last 70 years of the twentieth century.

In support of his contention that cooling was truly the norm in the Arctic over this period, Karlén goes on to say (1) "the observed warming during the 1930s is supported by data from several stations along the Arctic coasts and on islands in the Arctic, e.g. *Nordklim* data from Bjornoya and Jan Mayen in the north Atlantic, Vardo and Tromso in northern Norway, Sodankylae and Karasjoki in northern Finland, and Stykkisholmur in Iceland," and (2) "there is also [similar] data from other reports; e.g. Godthaab, Jakobshavn, and Egedesmindde in Greenland, Ostrov Dikson on the north coast of Siberia, Salehard in inland Siberia, and Nome in western Alaska." All of these stations, to quote him further, "indicate the same pattern of changes in annual mean temperature: a warm 1930s, a cooling until around 1970, and thereafter a warming, although the temperature remains slightly below the level of the late 1930s." In addition, he says "many stations with records starting later than the 1930s also indicate cooling, e.g. Vize in the Arctic Sea north of the Siberian coast and Frobisher Bay and Clyde on Baffin Island." Finally, Karlén reports that the 250-year temperature record of Stockholm "shows that the fluctuations of the 1900s are not unique," and that "changes of the same magnitude as in the 1900s occurred between 1770 and 1800, and distinct but smaller fluctuations occurred around 1825."

Karlén notes that "during the 50 years in which the atmospheric concentration of  $CO_2$  has increased considerably, the temperature has decreased," which leads him to conclude that "the Arctic temperature data do not support the models predicting that there will be a critical future warming of the climate because of an increased concentration of  $CO_2$  in the atmosphere." And this is especially important, in Karlén's words, because the model-based prediction "is that changes will be strongest and first noticeable in the Arctic."

All these studies suggest that concern over the effect of the "unprecedented warming" of the twentieth century on polar bears has overlooked a key fact: In the areas where polar bears actually live, there has not been a consistent or unprecedent warming trend in the past 50 years. Consequently, changing temperatures cannot be blamed for changes in polar bear populations, the subject of the next section.

### References

Chylek, P., Box, J.E. and Lesins, G. 2004. Global warming and the Greenland ice sheet. *Climatic Change* **63**: 201-221.

Chylek, P., Dubey, M.K, and Lesins, G. 2006. Greenland warming of 1920-1930 and 1995-2005. *Geophysical Research Letters* **33**: L11707.

Comiso, J.C., Wadhams, P., Pedersen, L.T. and Gersten, R.A. 2001. Seasonal and interannual variability of the Odden ice tongue and a study of environmental effects. *Journal of Geophysical Research* **106**: 9093-9116. Deser, C., Walsh, J.E. and Timlin, M.S. 2000. Arctic sea ice variability in the context of recent atmospheric circulation trends. *Journal of Climatology* **13**: 617-633.

Groisman, P.Ya., Knight, R.W., Razuvaev, V.N., Bulygina, O.N. and Karl, T.R. 2006. State of the ground: Climatology and changes during the past 69 years over northern Eurasia for a rarely used measure of snow cover and frozen land. *Journal of Climate* **19**: 4933-4955.

Hanna, E. and Cappelen, J. 2002. Recent climate of Southern Greenland. *Weather* **57**: 320-328.

Hanna, E. and Cappelen, J. 2003. Recent cooling in coastal southern Greenland and relation with the North Atlantic Oscillation. *Geophysical Research Letters* **30**: 10.1029/2002GL015797.

Humlum, O. 1999. Late-Holocene climate in central West Greenland: meteorological data and rock-glacier isotope evidence. *The Holocene* **9**: 581-594.

Isaksson, E., Hermanson, M., Hicks, S., Igarashi, M., Kamiyama, K., Moore, J., Motoyama, H., Muir, D., Pohjola, V., Vaikmae, R., van de Wal, R.S.W. and Watanabe, O. 2003. Ice cores from Svalbard—useful archives of past climate and pollution history. *Physics and Chemistry of the Earth* **28**: 1217-1228.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R. and Joseph, D. 1996. The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society* **77**: 437-471.

Karlén, W. 2005. Recent global warming: An artifact of a too-short temperature record? *Ambio* **34**: 263-264.

Laidre, K.L. and Heide-Jorgensen, M.P. 2005. Arctic sea ice trends and narwhal vulnerability. *Biological Conservation* **121**: 509-517.

Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, J., Retelle, M., Smith, S., Wolfe, A. and Zielinski, G. 1997. Arctic environmental change of the last four centuries. *Science* **278**: 1251-1256.

Parker, D.E., Folland, C.K. and Jackson, M. 1995. Marine surface temperature: Observed variations and data requirements. *Climatic Change* **31**: 559-600.

Parkinson, C.L. 2000a. Variability of Arctic sea ice: the view from space, and 18-year record. *Arctic* **53**: 341-358.

Parkinson, C.L. 2000b. Recent trend reversals in Arctic Sea ice extents: possible connections to the North Atlantic oscillation. *Polar Geography* **24**: 1-12.

Parkinson, C.L. and Cavalieri, D.J. 2002. A 21-year record of Arctic sea-ice extents and their regional, seasonal and monthly variability and trends. *Annals of Glaciology* **34**: 441-446.

Parkinson, C., Cavalieri, D., Gloersen, D., Zwally, J. and Comiso, J. 1999. Arctic sea ice extents, areas, and trends, 1978-1996. *Journal of Geophysical Research* **104**: 20,837-20,856.

Polyakov, I.V., Bekryaev, R.V., Alekseev, G.V., Bhatt, U.S., Colony, R.L., Johnson, M.A., Maskshtas, A.P. and Walsh, D. 2003. Variability and trends of air temperature and pressure in the maritime Arctic, 1875-2000. *Journal of Climate* **16**: 2067-2077.

Przybylak, R. 1997. Spatial and temporal changes in extreme air temperatures in the Arctic over the period 1951-1990. *International Journal of Climatology* **17**: 615-634.

Przybylak, R. 2000. Temporal and spatial variation of surface air temperature over the period of instrumental observations in the Arctic. *International Journal of Climatology* **20**: 587-614.

Przybylak, R. 2002. Changes in seasonal and annual high-frequency air temperature variability in the Arctic from 1951-1990. *International Journal of Climatology* **22**: 1017-1032.

Rayner, N.A., Horton, E.B., Parker, D.E., Folland, C.K. and Hackett, R.B. 1996. Version 2.2 of the global sea-ice and sea surface temperature data set, 1903-1994. *Climate Research Technical Note* 74, Hadley Centre, U.K. Meteorological Office, Bracknell, Berkshire, UK.

Stern, H.L. and Heide-Jorgensen, M.P. 2003. Trends and variability of sea ice in Baffin Bay and Davis Strait, 1953-2001. *Polar Research* **22**: 11-18.

Steig, E.J., Grootes, P.M. and Stuiver, M. 1994. Seasonal precipitation timing and ice core records. *Science* **266**: 1885-1886.

Stuiver, M., Grootes, P.M. and Braziunas, T.F. 1995. The GISP2  $\delta^{18}$ O climate record of the past 16,500 years and the role of the sun, ocean, and volcanoes. *Quaternary Research* **44**: 341-354.

Taurisano, A., Boggild, C.E. and Karlsen, H.G. 2004. A century of climate variability and climate gradients from coast to ice sheet in West Greenland. *Geografiska Annaler* **86A**: 217-224.

Treshnikov, A.F. (Ed.) 1985. *Atlas Arktiki*. Glavnoye Upravlenye Geodeziy i Kartografiy, Moskva.

White, J.W.C., Barlow, L.K., Fisher, D., Grootes, P.M., Jouzel, J., Johnsen, S.J., Stuiver, M. and Clausen, H.B. 1997. The climate signal in the stable isotopes of snow from Summit, Greenland: Results of comparisons with modern climate observations. *Journal of Geophysical Research* **102**: 26,425-26,439.

Zeeberg, J. and Forman, S.L. 2001. Changes in glacier extent on north Novaya Zemlya in the twentieth century. *Holocene* **11**: 161-175.

# 8.4.3. Population

The world's polar bear populations live in the wild only in the Northern Hemisphere on land and sea ice in the area surrounding the North Pole. Polar bears tend to stay in, or return to, local areas (Taylor and Lee, 1995; Bethke et al., 1996; Taylor et al., 2001), although some migration is known to occur (Messier et al., 2001; Amstrup et al., 2004). Their range expands and contracts with the accretion and contraction of sea ice with the seasons, with bears moving south during the winter as sea ice advances (Amstrup et al., 2000). In some areas (e.g., Hudson Bay, Foxe Basin, Baffin Bay, and James Bay) polar bears move from sea ice to land for several months during the summer open-water season (Ferguson et al., 1997; Lunn et al., 1997; Taylor et al., 2001, 2005).

The total polar bear population is unknown, since its numbers in the huge central Arctic Basin have never been counted (Aars et al., 2006), although polar bears have been reported there (Van Meurs and Splettstoesser, 2003). A common estimate is of approximately 23,000, with a range of 17,600 to 28,500 (Aars et al., 2006). There is even less certainty regarding the number of polar bears in the 1950s and 1960s, with most estimates around 5,000 to 10,000. Virtually all scientists agree that polar bear populations have grown since the 1970s. For example, Derocher has said "after the signing of the International Agreement on Polar Bears in the 1970s, harvests were controlled and the numbers increased. There is no argument from anyone on this point" (Derocher, 2009).

Even though polar bear populations grew during the second half of the twentieth century, a time when the IPCC claims there was a rapid increase in global temperatures and loss of sea ice, Derocher and others say this population growth is evidence of the effects of hunting bans and quotas and does not contradict their claim that warming temperatures and melting sea ice have hurt polar bear populations. They point, with apparent merit, to negative demographic impacts on polar bear populations identified in the Southern Beaufort Sea and in Western Hudson Bay, and possible adverse nutritional impacts in the Northern Beaufort Sea and Southern Hudson Bay, due to changes in local sea ice conditions. But this is not evidence that global warming threatens polar bears with extinction. If anthropogenic global warming were a real threat to polar bears, its effects should be observable throughout the Current Warming Period, not just the last few years, and the warming would have to affect more than only a small number of subpopulations, as appears to have been the case (see discussion below). The modified argument-that global warming only in recent years is negatively affecting some subpopulations of polar bears but not others-is not what is being reported in daily newspapers or even what the IPCC claims. The realworld long-term trends in polar bear populations contradict what would be expected if the theory of anthropogenic global warming were true.

The polar bear population is divided into 19 subpopulations for management purposes. According to the IUCN Polar Bear Specialist Group, five subpopulations are declining, five are stable, two are increasing, and seven have insufficient data on which to base a decision. (Aars *et al.*, 2006). Significantly, four of the five subpopulations listed as declining are at risk due to hunting, not reduced sea ice (Aars *et al.*, 2006). This is hardly a picture of a species in steep decline, or even in decline at all. It certainly does not provide an empirical basis for predictions of imminent extinction.

Hunting historically has been the greatest threat to polar bear populations. The arrival of snowmobiles, helicopters, and high-powered rifles led to "harvest" levels that were not sustainable (Taylor *et al.*, 2002; Taylor *et al.*, 2006; Taylor *et al.*, 2008). Hunting was largely unregulated until passage of the 1974 International Agreement for the Conservation of Polar Bears and Their Habitat. Greenland didn't institute a quota for polar bear hunting until 2006 (Polar Bear Technical Committee, 2006). Annual kills for most populations now have been substantially reduced, but it will take at least 20 years for populations to recover.

The range of polar bears is affected by changes in climate but not in a linear fashion with temperature or the extent or thickness of sea ice. As explained previously, sea ice extent and thickness are only indirectly related to polar bear populations. Only two subpopulations—the Western Hudson Bay (WH) and Southern Beaufort Sea (SB) populations—probably have declined due to climate change effects (Ferguson *et al.*, 2005; Regehr *et al.*, 2006, 2007a,b; Rode *et al.*, 2007; Hunter *et al.*, 2007), and even one of these (WH) is disputed (Dyck *et al.*, 2007).

Taylor and Dowsley (2008) summarized recent population surveys as follows:

Of six polar bear populations recently evaluated during the climate warming period, two populations appear to have been reduced (WH, SB), 2 populations appear to have remained constant (SH, NB), and one population appears to have increased (DS), and one was abundant but the information was not sufficient to estimate trend (BS). Seven other populations (VM, LS, NW, BB, KB, MC, GB) surveyed during the period of climate warming had vital rates sufficient to sustain substantial rates of harvest [i.e., hunting] at the time they were studied. Information from a Foxe Basin (FB) population survey was sufficient to document that the population had remained abundant although it had been harvested at a relatively high rate, although the survival and recruitment estimates necessary to determine trend were not available. The biological information on the remaining four populations (CS, LS, KS, EG) and the few bears that may inhabit the Arctic Basin is insufficient to suggest anything about current numbers or trend.

Taylor and Dowsley go on to say "the increase to current high numbers of polar bears in the Davis Strait has occurred during the current warming period, and has occurred with declining sea ice conditions that are sometimes less than 40% coverage at winter maximum (Stirling and Parkinson, 2006). Clearly the DS bears do manage to hunt successfully in unconsolidated pack ice." They comment, as do Dyck *et al.* (2007), that polar bears have been observed to successfully hunt seals in tidal flats along shores during ice-free periods.

"Considered together," Taylor and Dowsley conclude, "these demographic data do not suggest that polar bears as a species are headed for extinction in the next three generations (45 years) or the foreseeable future. The demographic data do support increased monitoring, and augmenting periodic population surveys with ecological and behavioral studies." They also observe that "to date, no population has been expatriated due to climate change effects, so the effect of decreased densities, alternative food sources, or behavioral adaptation to less ice on population persistence is not known."

The fact that polar bear populations are not declining should come as no surprise once it is

understood that sea ice is not receding (at least not in all areas inhabited by polar bears or during their feeding season) or getting thinner, and that temperatures in the circumpolar region in recent years have not been unusually warm. Polar bears are adapted to the extremes of warming and cooling that can and do occur. Polar bears will move out of affected areas and return when conditions improve and when the sea ice is neither too thick nor too ephemeral. Transition will stress some populations and if warming continues for whatever reason, some populations may be expatriated. However, polar bears as a species are not in danger of depletion, let alone extinction.

# References

Aars J., Lunn N.J., and Derocher, A.E. (Eds). 2006. Polar Bears: Proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 20-24 June 2005, Seattle, Washington, USA. Occasional Paper of the IUCN Species Survival Commission. Gland (Switzerland) and Cambridge (UK).

Amstrup, S.C., Durner, G., Stirling, I., Lunn, N.J., and Messier, F. 2000. Movements and distribution of polar bears in the Beaufort Sea. *Canadian Journal of Zoology* **78**: 948-966.

Amstrup, S.C., McDonald, T.L. and Durner, G.M. 2004. Using satellite radio telemetry data to delineate and manage wildlife populations. *Wildlife Society Bulletin* **32**: 661-679.

Bethke, R., Taylor, M.K., Amstrup, S. and Messier, F. 1996. Population delineation of polar bears using satellite collar data. *Ecological Applications* **6**: 311-317.

Derocher, A. 2009. Ask the experts: Are polar bear populations increasing? Polar Bears International. Web site, last accessed April 30, 2009. <u>http://www.polarbears international.org/ask-the-experts/ population/</u>

Dyck, M.G., Soon, W., Baydack, R.K., Legates, D.R., Baliunas, S., Ball, T.F., and Hancock, L.O. 2007. Polar bears of western Hudson Bay and climate change: Are warming spring air temperatures the 'ultimate' survival control factor? *Ecological Complexity* **4**: 73-84.

Ferguson, S.H., Taylor, M.K. and Messier, F. 1997. Space use by polar bears in and around Auyuittuq National Park, Northwest Territories, during the ice-free period. *Canadian Journal of Zoology* **75**: 1585-1594.

Ferguson, S.H., Stirling, I. and P. McLoughlin. 2005. Climate change and ringed seal (Phoca hispida) recruitment in western Hudson Bay. *Marine Mammal Science* **21**: 121-135. Hunter, C.M., Caswell, H., Runge, M.C., Amstrup, S.C., Regehr, E.V. and Stirling, I. 2007. Polar bears in the southern Beaufort Sea II: Demography and population growth in relation to sea ice conditions. USGS Alaska Science Center, Anchorage, Administrative Report.

Lunn, N.J., Stirling, I., and Nowicki, S.N. 1997. Distribution and abundance of ringed (Phoca hispida) and bearded seals (Erignathus barbatus) in western Hudson Bay. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 914-921.

Messier, F., Taylor, M.K., Plante, A. and Romito, T. 2001. Atlas of polar bear movements in Nunavut, Northwest Territories, and neighboring areas. Nunavut Wildlife Service and University of Saskatchewan, Saskatoon, SK.

Polar Bear Technical Committee. 2006. Minutes of the 2006 Federal/Provincial/Territorial Polar Bear Technical Committee Meeting, St. John's, Newfoundland and Labrador, 6-8 February 2006. Canadian Wildlife Service, Edmonton, AB.

Regehr, E.V., Amstrup, S.C. and Stirling, I. 2006. Polar bear population status in the Southern Beaufort Sea. U.S. Geological Survey Open-File Report 2006-1337.

Regehr, E.V., Lunn, N.J., Amstrup, S.C., and Stirling, I. 2007a. Survival and population size of polar bears in western Hudson Bay in relation to earlier sea ice breakup. *Journal of Wildlife Management* **71**: 2673-2683.

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C., and Stirling, I. 2007b. Polar bears in the southern Beaufort Sea I: survival and breeding in relation to sea ice conditions, 2001-2006. Administrative Report, U.S. Department of the Interior- U.S. Geological Survey, Reston, VA.

Rode, K.D., Amstrup, S.C., and Regehr, E.V. 2007. Polar bears in the southern Beaufort Sea III: stature, mass, and cub recruitment in relationship to time and sea ice extent between 1982 and 2006. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Stirling, I. and Parkinson, C.L. 2006. Possible effects of climate warming on selected populations of polar bears (Ursus maritimus) in the Canadian Arctic. *Arctic* **59**: 261-275.

Taylor, M.K. and Lee, L.J. 1995. Distribution and abundance of Canadian polar bear populations: a management perspective. *Arctic* **48**: 147–154.

Taylor, M.K., Akeeagok, S., Andriashek, D., Barbour, W., Born, E.W., Calvert, W., Cluff, H.D., Ferguson, S., Laake, J., Rosing-Asvid, A., Stirling, I. and Messier, F. 2001. Delineating Canadian and Greenland polar bear (Ursus maritimus) populations by cluster analysis of movements. *Can. J. Zool.***79:** 690–709. Taylor, M.K., Laake, J., Cluff, H.D., Ramsay, M. and Messier, F. 2002. Managing the risk of harvest for the Viscount Melville Sound polar bear population. *Ursus* **13**: 185-202.

Taylor, M.K., Laake, J., McLoughlin, P.D., Born, E.W., Cluff, H.D., Ferguson, S.H., Rosing-Asvid, A., Schweinsburg, R., and Messier, F. 2005. Demography and viability of a hunted population of polar bear. *Arctic* **58**: 203–214.

Taylor, M.K., Laake, J.L., McLoughlin, P.D., Cluff, H.D., and Messier, F. 2006. Demographic parameters and harvest-explicit population viability analysis for polar bears in M'Clintock Channel, Nunavut. *Journal of Wildlife Management* **70**: 1667–1673.

Taylor, M.K., Laake, J., McLoughlin, P.D., Cluff, H.D., Born, E.W., Rosing-Asvid, A., and Messier, F. 2008. Population parameters and harvest risks for polar bears (Ursus maritimus) in Kane Basin, Nunavut and Greenland. *Polar Biology* **31** (4): 491-499.

Taylor, M., and Dowsley, M. 2008. Demographic and ecological perspectives on the status of polar bears. Science & Public Policy Institute, Washington D.C.

Van Meurs, R. and Splettstoesser, J.F. 2003. Farthest North Polar Bear (Letter to the Editor). *Arctic* **56**:309.

# 8.4.4. Forecasts

Since most polar bear subpopulations are either growing or stable, and since there is little evidence that global warming is causing a loss of sea ice that is affecting most polar bear populations, the IPCC is left only with computer models that predict future declines in polar bear populations. In this section we ask whether those predictions are reliable. The reliability of computer climate models is addressed in greater detail in Chapter 1 of this report.

Green and Armstrong (2007) make the important point that forecasting is a practice and a discipline that is separate from physics, biology, geology, and the other sciences that are often applied to the question of climate change. Physicists, biologists, and other scientists often do not know how to make accurate forecasts, and consequently their predictions of the future are no more reliable than those made by nonexperts (Tetlock, 2005; Ascher, 1978). It is telling that Green and Armstrong's search of the IPCC Working Group I report (2007) "found no references ... to the primary sources of information on forecasting methods" and "the forecasting procedures that were described [in sufficient detail to be evaluated] violated 72 principles. Many of the violations were, by themselves, critical." In other words, the forecasts contained in the IPCC report are unscientific regardless of the scientific qualifications of the report's many contributors.

Scientists working in fields characterized by complexity and uncertainty are apt to confuse the output of models-which are nothing more than a statement of how the modeler believes a part of the world works-with real-world trends and forecasts (Bryson, 1993). Computer climate models certainly fall into this class, and they have been severely criticized for their failure to replicate real-world phenomena by many scientists, including Balling (2005),Christy (2005),Frauenfeld (2005),Posmentier and Soon (2005), and Pilkey and Pilkey-Jarvis (2007). Many of these writers observe that computer models can be "tweaked" to reconstruct climate histories after the fact, but this provides no assurance that the new model will do a better job forecasting future climates. Individual climate models often have widely differing assumptions about basic climate mechanisms but are then "tweaked" to produce similar forecasts. This is nothing at all like how real scientific forecasting is done.

Turning to predictions of the possible extinction of polar bears due to anthropogenic global warming. in response to calls to list polar bears as a threatened species under the U.S. Endangered Species Act, the U.S. Geological Survey commissioned nine administrative reports to forecast future polar bear populations. The reports eventually produced were Amstrup et al. (2007), Bergen et al. (2007), DeWeaver (2007), Durner et al. (2007), Hunter et al. (2007), Obbard et al. (2007), Regehr et al. (2007), Rode et al. (2007), and Stirling et al. (2007). Two of those studies—Anstrup et al. (2007) and Hunter et al. (2007), thought to give the strongest support for listing polar bears as endangered-were subsequently analyzed by J. Scott Armstrong, Kesten C. Green, and Willie Soon (2008) experts on forecasting at the Wharton School at the University of Pennsylvania and Monash University in Victoria, Australia, and an astrophysicist at the Harvard-Smithsonian Center for Astrophysics in Cambridge. Massachusetts. respectively. The three researchers gave the two studies failing grades for the following reasons:

• Both studies assumed things that are untrue or unknown, such as that "global warming will occur and will reduce the amount of summer sea ice" and "polar bears will not adapt; thus, they will obtain less food than they do now by hunting from the sea ice platform."

- Amstrup *et al.* (2007) "definitely contravened 41 principles and apparently contravened an additional 32 principles," referring to scientific forecasting principles established by the Forecasting Principles Project and set forth in a book titled *Principles of Forecasting* (Armstrong, 2001). "Of the 116 relevant principles, we could find evidence that [Amstrup *et al.* (2007)] properly applied only 17 (14.7 percent)."
- Hunter *et al.* (2007) "clearly contravened 61 principles and probably contravened an additional 19 principles ... the authors properly applied only 10 (9.5 percent) of the 105 relevant principles."

Among the many errors they identified in Amstrup *et al.* (2007) were (1) relying on a single polar bear expert, (2) choosing an extreme forecast rather than a conservative one despite the presence of complex interactions and instability, and (3) failure to include all important variables. Mistakes made by Hunter *et al.* (2007) included (1) heavy reliance on five years of data with unknown measurement errors, (2) failure to include newly available data, (3) failure to give other researchers access to their data, and (4) failure to list possible outcomes and their likelihoods. According to Armstrong, Green, and Soon, the failure of these forecasters to adhere to the principles of scientific forecasting makes their forecasts "of no value to decisionmakers."

More generally, forecasts of the possible extinction of polar bears fail to explain how a decline in population (or some subpopulations) necessarily raises the prospect of species extinction. For example, the IUCN/SSC Polar Bear Specialists Group forecast that climate change might reduce polar bear stocks by as much as 30 percent over the next three generations. Such a reduction, should it occur (and we have given ample reasons to doubt it would), would be unfortunate, but it is not extinction and would not necessarily lead to extinction. It suggests the number of polar bears would decline from approximately 24,000 to approximately 17,000. For the sake of comparison, the National Wildlife Federation supports removing grizzly bears in Yellowstone Park USA from the endangered species list even though that population is estimated to be only 600 (Taylor and Dowsley, 2007).

As Crockford (2008) explains, "even if substantial declines in polar bears and their prey do occur because of anthropogenic global warming ... this does not doom them to extinction: Many species have recovered from far more dramatic declines in population than predicted by even the most pessimistic scenarios conceived of by climate models, including humpback whales (Dalton, 2008), gray whales (Reeves *et al.*, 2002), northern fur seals (Reeves *et al.*, 2002), Atlantic cod (Bigg *et al.*, 2008), and sea otters (Doroff *et al.*, 2003; Estes, 1990), among others. Contrary to common biological assumption, small populations often retain sufficient genetic variation for significant recovery (e.g. Aguilar *et al.*, 2004; Kaeuffer *et al.*, 2007)."

Dyck *et al.* (2008) also point out that the climate models used by the forecasters predict a complete disappearance of sea ice over the central Arctic only for the late summer (September), and sea ice at Hudson Bay during the late winter or early spring is not predicted to completely disappear by the end of this century, even under extreme scenarios. They cite Gagnon and Gough (2005b, p. 291) who concluded that "Hudson Bay is expected to remain completely ice covered in those five models by the end of this century for at least part of the year."

Tavlor and Dowsley (2008) report "the majority (60%) of the IPCC models project ice cover in all seasons for the next 40-50 years throughout much of the North American continental shelf where most polar bears reside (Alley et al., 2007; Serreze et al., 2007). The IPCC climate model forecasts for ice reductions in fall, winter, and spring are substantially less than for the summer open water season (Serreze et al., 2007)." This is significant because, as we previously reported, polar bears can fast for four months during the summer when the lack of ice reduces their access to seals (Watts and Hansen, 1987; Ramsay and Stirling, 1988; Ramsay and Hobson, 1991). So even the computer models that predict melting ice, which we've criticized as inherently unreliable and unsuited to forecasting, do not forecast a condition that would make it impossible for polar bears to survive.

Taylor and Dowsley also point out that most forecasts of declining polar bear populations assume a simple linear function between population and habitat availability, an argument similar to the discredited "survival envelopes" theory discussed earlier in this chapter. But the fact that polar bears in most subpopulations are being harvested (hunted) in significant numbers means their populations are not at ecological carrying capacity, which means habitat availability is not the constraining factor affecting population. Populations in some areas (e.g., Viscount Melville Sound, M'Clintock Channel, and Kane Basin) are currently depleted due to over-hunting, so it should be obvious that polar bears there are not constrained by lack of habitat. "There is no evidence that polar bears are at carrying capacity for any population," write Taylor and Dowsley, "and there is no evidence to support any mechanism/s of density dependent population regulation for polar bears."

In conclusion, forecasts of dwindling polar bear populations assume trends in sea ice and temperature that are counterfactual, rely on computer climate models that are known to be unreliable, and violate most of the principles of scientific forecasting. In light of other evidence presented in this section showing no long-term trends toward less sea ice or rising temperatures in the Arctic, plus evidence of rising polar bear populations and their adaptability to climate change and other environmental stresses, we find there is no basis for concern that climate change will ever cause the extinction of polar bears.

## References

Aars, J., Lunn, N.J., and Derocher, A.E. (Eds.) 2006. Polar Bears: Proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, 20-24 June 2005, Seattle, Washington, USA. Occasional Paper of the IUCN Species Survival Commission 32. Gland (Switzerland) and Cambridge (UK).

Aguilar, A., Roemer, G., Debenham, S., Binns, M., Garcelon, D., and Wayne, R.K. 2004. High MHC diversity maintained by balancing selection in an otherwise genetically monomorphic mammal. *Proceedings of the National Academy of Sciences USA* **101**: 3490-3494.

Alley, R., Berntsen, T., Bindoff, N.L., Chen, Z., Chidthaisong, A., Friedlingstein, P., Gregory, J., Hegerl, G., Heimann, M., Hewitson, B., Hoskins, B., Joos, F., Jouzel, J., Kattsov, V., Lohmann, U., Manning, M., Matsuno, T., Molina, M., Nicholls, N., Overpeck, J., Qin, D., Raga, G., Ramaswamy, V., Ren, J., Rusticucci, M., Solomon, S., Somerville, R., Stocker, T.F., Stott, P., Stouffer, R.J., Whetton, P., Wood, R.A., and Wratt, D. 2007. *Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* IPCC Secretariat, Geneva Switzerland.

Amstrup, S.C., Marcot, B.G., and Douglas, D.C. 2007. Forecasting the rangewide status of polar bears at selected times in the 21st century. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Armstrong, J.S. 2001. *Principles of Forecasting – A Handbook for Researchers and Practitioners*. Kluwer Academic Publishers, Norwell, MA.

Armstrong, J.S., Green, K.C., and Soon, W. 2008. Polar bear population forecasts: a public-policy forecasting audit. *Interfaces* **38** (5): 382-405.

Ascher, W. 1978. Forecasting: An Appraisal for Policy Makers and Planners. Johns Hopkins University Press. Baltimore, MD.

Balling, R.C. 2005. Observational surface temperature records versus model predictions. In Michaels, P.J. (Ed.) *Shattered Consensus: The True State of Global Warming.* Rowman & Littlefield. Lanham, MD. pp. 50-71.

Bergen, S., Durner, G.M., Douglas, D.C. and Amstrup, S.C. 2007. Predicting movements of female polar bears between summer sea ice foraging habitats and terrestrial denning habitats of Alaska in the 21st century: Proposed methodology and pilot assessment. Administrative Report, USGS Alaska Science Center, Anchorage, AK.

Bigg, G.R., Cunningham, C.W., Ottersen, G., Pogson, G.H., Wadley, M.R., and Williamson, P. 2008. Ice-age survival of Atlantic cod: agreement between palaeoecology models and genetics. *Proceedings of the Royal Society B* **275**: 163-172.

Bryson, R.A. 1993. Environment, environmentalists, and global change: A skeptic's evaluation. *New Literary History* **24**: 783-795.

Christy, J. 2005. Temperature changes in the bulk atmosphere: beyond the IPCC. In Michaels, P.J. (Ed.) *Shattered Consensus: The True State of Global Warming.* Rowman & Littlefield. Lanham, MD. pp. 72-105.

Crockford, S. 2008. Some things we know—and don't know—about polar bears. Science and Public Policy Institute, Washington, DC.

Dalton, R. 2008. Whales are on the rise. Nature 453: 433.

DeWeaver, E. 2007. Uncertainty in climate model projections of arctic sea ice decline: An evaluation relevant to polar bears. USGS Alaska Science Center, Anchorage, Administrative Report.

Doroff, A.M., Estes, J.A., Tinker, M.T., Burn, D.M., and Evans, T.J. 2003. Sea otter population declines in the Aleutian Archipelago. *Journal of Mammalogy* **84**: 55-64.

Durner, G.M., Douglas, D.C., Nielson, R.M., Amstrup, S.C., and McDonald, T.L. 2007. Predicting the future distribution of polar bears in the polar basin from resource selection functions applied to 21<sup>st</sup> century general

circulation model projections of sea ice. USGS Alaska Science Center, Anchorage, Administrative Report.

Dyck, M.G., Soon, W., Baydack, R.K., Legates, D.R., Baliunas, S., Ball, T.F., and Hancock, L.O. 2007. Polar bears of western Hudson Bay and climate change: Are warming spring air temperatures the "ultimate" survival control factor? *Ecological Complexity* **4**:73-84.

Estes, J.A. 1990. Growth and equilibrium in sea otter populations. *Journal of Animal Ecology* **59**: 385-401.

Frauenfeld, O.W. 2005. Predictive skill of the El Nino-Southern Oscillation and related atmospheric teleconnections. In Michaels, P.J. (Ed.) *Shattered Consensus: The True State of Global Warming*. Rowman & Littlefield. Lanham, MD. pp. 149-182.

Gagnon, A.S., Gough, W.A., 2005b. Climate change scenarios for the Hudson Bay region: an intermodel comparison. *Climate Change* **69**: 269–297.

Green, K.C. and Armstrong, J.S. 2007. Global warming: forecasts by scientists versus scientific forecasts. Energy *Environ.* **18**: 997–1021.

Hunter, C.M., Caswell, H., Runge, M.C., Amstrup, S.C., Regehr, E.V. and Stirling, I. 2007. Polar bears in the southern Beaufort Sea II: Demography and population growth in relation to sea ice conditions. USGS Alaska Science Center, Anchorage, Administrative Report.

Kaeuffer, R., Coltman, D.W., Chapius, J.-L., Pontier, D., and Réale, D. 2007. Unexpected heterozygosity in an island mouflon population founded by a single pair of individuals. *Proceedings of the Royal Society B* **274**: 527-533.

Obbard, M.E., McDonald, T.L., Howe, E.J., Regehr, E.V. and Richardson, E.S. 2007. Trends in abundance and survival for polar bears from Southern Hudson Bay, Canada, 1984–2005. Administrative Report, USGS Alaska Science Center, Anchorage, AK.

Pilkey, O.H. and Pilkey-Jarvis, L. 2007. Useless Arithmetic. Columbia University Press, New York.

Posmentier, E.S. and Soon, W. 2005. Limitations of computer predictions of the effects of carbon dioxide on global temperature. In Michaels, P.J. (Ed.) *Shattered Consensus: The True State of Global Warming*. Rowman & Littlefield. Lanham, MD. pp. 241-281.

Ramsay, M.A. and Hobson, K.A. 1991. Polar bears make little use of terrestrial food webs: Evidence from stable-carbon isotope analysis. *Oecologia* **86**:598-600.

Ramsay, M.A. and Stirling, I. 1988. Reproductive biology and ecology of female polar bears (Ursus maritimus). *Journal of Zoology* (London) **214**: 601-634.

Reeves, R.R, Stewart, B.S., Clapham, P.J. and Powell, J.A. 2002. *National Audobon Society's Guide to Marine Mammals of the World*. Alfred A. Knopf.

Regehr, E.V., Hunter, C.M., Caswell, H., Amstrup, S.C. and Stirling, I. 2007. Polar bears in the southern Beaufort Sea I: survival and breeding in relation to sea ice conditions, 2001-2006. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Rode, K.D., Amstrup, S.C. and Regehr, E.V. 2007. Polar bears in the southern Beaufort Sea III: stature, mass, and cub recruitment in relationship to time and sea ice extent between 1982 and 2006. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Serreze, M.C., Holland, M.M. and Stroeve, J. 2007. Perspectives on the Arctic's shrinking sea-ice cover. *Science* **315** (5818): 1533-1536.

Stirling, I., McDonald, T.L., Richardson, E.S. and Regehr, E.V. 2007. Polar bear population status in the Northern Beaufort Sea. Administrative Report, U.S. Department of the Interior-U.S. Geological Survey, Reston, VA.

Taylor, M.E., and Dowsley, M. 2008. Demographic and ecological perspectives on the status of polar bears. Science and Public Policy Institute, Washington, DC.

Tetlock, P.E. 2005. *Expert Political Judgment—How Good Is It? How Can We Know?* Princeton University Press, Princeton, NJ.

Watts, P.D., and Hansen, S.E., 1987. Cyclic starvation as reproductive strategy in the polar bear. *Symp. Zool. Soc.Lond.* **57**: 305–318.