

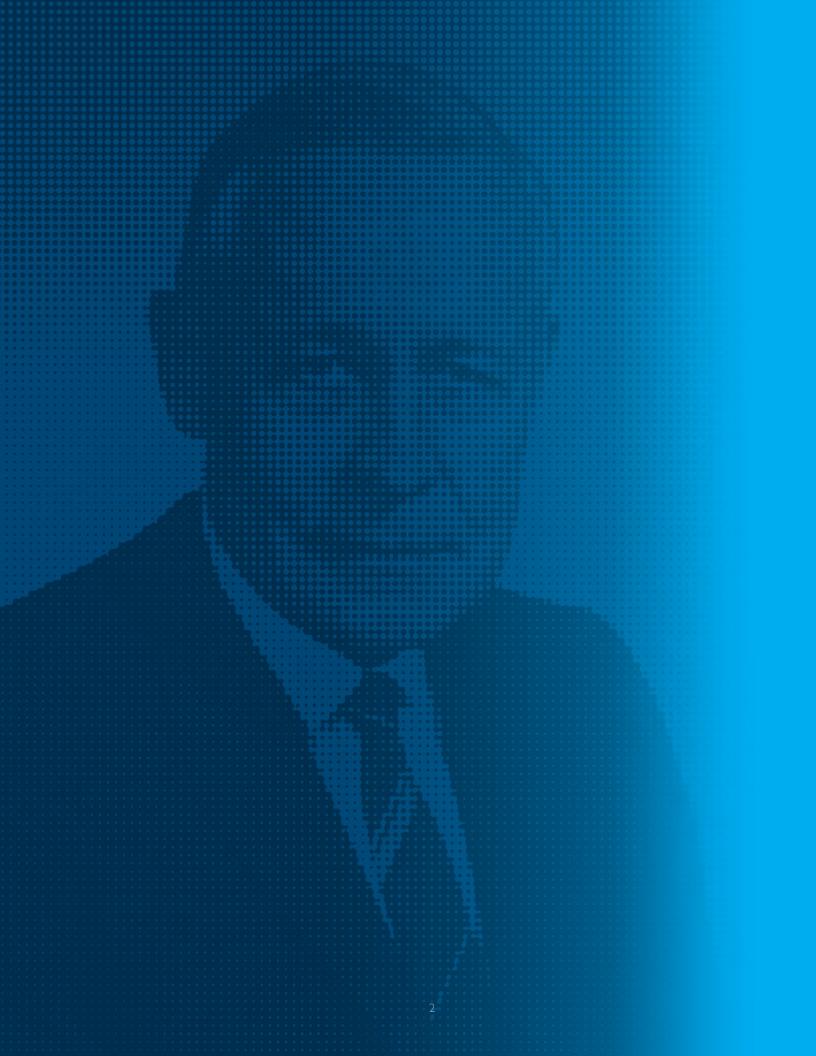
ROGER REVELLE COMMEMORATIVE LECTURE

PRESENTED BY THE NATIONAL ACADEMIES' OCEAN STUDIES BOARD

# Contemporary Challenge

OF THE SEA: Science, society & sustainability





The National Academy of Sciences is a private, non-profit, self-perpetuating society of distinguished scholars engaged in scientific and engineering research, dedicated to the furtherance of science and technology and to their use for the general welfare. Upon the authority of the charter granted to it by the Congress in 1863, the Academy has a mandate that requires it to advise the federal government on scientific and technical matters. Dr. Ralph J. Cicerone is president of the National Academy of Sciences.

The National Academy of Engineering was established in 1964, under the charter of the National Academy of Sciences, as a parallel organization of outstanding engineers. It is autonomous in its administration and in the selection of its members, sharing with the National Academy of Sciences the responsibility for advising the federal government. The National Academy of Engineering also sponsors engineering programs aimed at meeting national needs, encourages education and research, and recognizes the superior achievements of engineers. Dr. C.D. Mote, Jr. is president of the National Academy of Engineering.

The Institute of Medicine was established in 1970 by the National Academy of Sciences to secure the services of eminent members of appropriate professions in the examination of policy matters pertaining to the health of the public. The Institute acts under the responsibility given to the National Academy of Sciences by its congressional charter

to be an adviser to the federal government and, upon its own initiative, to identify issues of medical care, research, and education. Dr. Harvey V. Fineberg is president of the Institute of Medicine.

The National Research Council was organized by the National Academy of Sciences in 1916 to associate the broad community of science and technology with the Academy's purposes of furthering knowledge and advising the federal government. Functioning in accordance with general policies determined by the Academy, the Council has become the principal operating agency of both the National Academy of Sciences and the National Academy of Engineering in providing services to the government, the public, and the scientific and engineering communities. The Council is administered jointly by both Academies and the Institute of Medicine. Dr. Ralph J. Cicerone and Dr. C.D. Mote, Jr. are chair and vice chair, respectively, of the National Research Council.

W W W . N A T I O N A L - A C A D E M I E S . O R G

Board of the National Academies' National Research Council, we would like to welcome you to the Fifteenth Annual Roger Revelle Commemorative Lecture. This lecture was created by the Ocean Studies Board in honor of Dr. Roger Revelle to highlight the important links between the ocean sciences and public policy.

#### **ROGER REVELLE**

For almost half a century, Roger Revelle was a leader in the field of oceanography.

Revelle trained as a geologist at Pomona College and the University of California,

Berkeley. In 1936, he received his Ph.D. in oceanography from the Scripps Institution of Oceanography. As a young naval officer, he helped persuade the Navy to create the Office of Naval Research (ONR) to support basic research in oceanography and was the first head of ONR's geophysics branch. Revelle served for 12 years as the Director of Scripps (1950–1961, 1963–1964), where he built up a fleet of research ships and initiated a decade of expeditions to the deep Pacific that challenged existing geological theory.

Revelle's early work on the carbon cycle suggested that the sea could not absorb all the carbon dioxide released from burning fossil fuels. He organized the first continual measurement of atmospheric carbon dioxide, an effort led by Charles Keeling, resulting in a long-term record that has been essential to cur-

rent research on global climate change. With Hans Suess, he published the seminal paper demonstrating the connection between increasing atmospheric carbon dioxide and burning of fossil fuels. Revelle kept the issue

of increasing carbon dioxide levels before the public and spearheaded efforts to investigate the mechanisms and consequences of climate change. Revelle left Scripps for critical posts as Science Advisor to the Department of the Interior (1961–1963) and as the first Director of the Center for Population Studies at Harvard (1964–1976). Revelle applied his knowledge of geophysics, ocean resources, and population dynamics to the world's most vexing problems: poverty, malnutrition, security, and education.

In 1957, Revelle became a member of the National Academy of Sciences to which he devoted many hours of volunteer service. He served as a member of the Ocean Studies Board, the Board on Atmospheric Sciences and Climate, and many committees. He also chaired a number of influential Academy studies on subjects ranging from the

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environmental effects of radiation to understanding sea-level change.

### SMITHSONIAN'S NATIONAL MUSEUM OF NATURAL HISTORY

The Ocean Studies Board is pleased to have the opportunity to present the Revelle Lecture in cooperation with the Smithsonian National Museum of Natural History through our partnership with the Smithsonian Science Education Center. The museum maintains and preserves the world's most extensive collection of natural history specimens and human artifacts and supports scientific research, educational programs, and exhibitions. The museum is part of the Smithsonian Institution, the world's largest museum and research complex. Dr. Kirk R. Johnson is the director.

The Smithsonian Science Education Center (SSEC) was founded in 1985 by the National Academy of Sciences and the Smithsonian Institution and continues today as a successful unit of the Smithsonian Institution. The mission of the SSEC is to develop STEM literate students from early childhood through the workplace. The SSEC does this through the implementation of a truly systemic approach that engages participants at every level, from students and classroom teachers up through the highest levels of district, state, national and international leadership.

#### **TONIGHT'S LECTURE**

Life on Earth arose as single-celled microorganism: nearly four billion years ago in an ancient ocean. Microorganisms still dominate our planetary environment despite the subsequent evolution of a diverse spectrum of plants and animals. Microbes play a crucial role in maintaining the habitability of Earth.

Tonight Dr. David M. Karl, Professor of Oceanography and Director of the Daniel K. Inouye Center for Microbial Oceanography: Research and Education (C-MORE) at the University of Hawaii, will discuss the growing need to better understand our microbial ocean in the face of a changing planet, which he describes as the contemporary "challenge of the sea." Dr. Karl will be introduced by Dr. Ralph Cicerone, the president of the National Academy of Sciences.

#### **SPONSORSHIP**

The Ocean Studies Board thanks the National Oceanic and Atmospheric Administration, the National Science Foundation, the National Aeronautics and Space Administration, the Office of Naval Research, the U.S. Geological Survey, Scripps Institution of Oceanography, and the Gordon and Betty Moore Foundation. This lecture series would not be possible without their generous support. The Board extends gratitude to the Smithsonian Science Education Center and the Smithsonian Institution for their continued partnership in hosting the lecture at the National Museum of Natural History. A "West Coast Edition" of the lecture will be held at Scripps Institution of Oceanography later this year.

We hope you enjoy tonight's event.

let A. Duce

Robert A. Duce, Chair, Ocean studies board

Susan Roberts,

DIRECTOR, OCEAN STUDIES BOARD

burg / CLAUDIA BENITEZ-NELSON, University of South Carolina, Columbia / JOHN A. ORCUTT, Scripps Institution of Oceanography, LaJolla, CA / STEVEN E. RAMBERG, National Defense University, Washington, DC / MARTIN D. SMITH, Duke University's Nicholas School of the Environment, Durham, NC / DON WALSH, International Maritime Incorporated, Myrtle Point, OR / MARY (MISSY) H. FEELEY (ex-officio), U.S. Delegate to SCOR, ExxonMobil Exploration Company, Houston, TX OSB STAFF MEMBERS SUSAN ROBERTS, Director / CLAUDIA MENGELT, Senior Program Officer / DEBORAH GLICKSON, Senior Program Officer / STACEE KARRAS, Research Associate / PAMELA LEWIS, Administrative Coordinator / PAYTON KULINA, Program Assistant

phy and Director of the Daniel K. Inouye Center for Microbial Oceanography: Research and Education (C-MORE) at the University of Hawaii. He grew up in Buffalo, New York on a polluted Lake Erie which at that time was his 'ocean.' Karl majored in biology at the State University College at Buffalo, and following graduation taught math and science at an inner city vocational high school before starting his career as an oceanographer. He received a M.S. degree from Florida State University in 1974, and a Ph.D. degree from Scripps Institution of Oceanography in 1978—both in Oceanography—before moving to the University of Hawaii as an Assistant Professor of Oceanography that same year.

In spring of 1973, he participated in his first oceanographic research expedition to the Cariaco Basin aboard the *RV Eastward*. Since that time Karl has spent more than 1,000 days conducting research at sea including 23 expeditions to Antarctica. In 1979 Karl participated in the first biology expedition to the recently discovered deep-sea hydrothermal vents at the Galapagos Rift, and he conducted subsequent submersible-assisted vent research at 11° and 21° N on the East Pacific Rise, in the Guaymas Basin and at Loihi Seamount, Hawaii. In 1988 he helped to establish the Hawaii Ocean Time-series (HOT) program that has conducted sustained physical, biogeochemical and microbial measurements and experiments at



Station ALOHA on approximately monthly intervals for the past 25 years. In 2006, he led a team of scientists in the establishment of a new NSF-supported Science and Technology Center at the University of Hawaii. C-MORE conducts collaborative research on marine microorganisms from genomes to biomes, and has a vital training mission to help prepare the next generation of microbial oceanographers. Karl has received numerous awards and honors including the G.

Evelyn Hutchinson Medal from the American Society for Limnology and Oceanography, the Henry Bryant Bigelow Medal from Woods Hole Oceanographic Institution, the Alexander Agassiz Medal from the U.S. National Academy of Sciences and an honorary D.Sc. degree from the University of Chicago. He is a Fellow of the American Geophysical Union and the American Academy of Microbiology, and a member of the U.S. National Academy of Sciences.

RALPH J. CICERONE is President of the National Academy of Sciences and Chair of the National Research Council. His research has focused on atmospheric chemistry, the radiative forcing of climate change due to trace gases, and the sources of atmospheric methane, nitrous oxide, and methyl halide gases. His scientific work has involved him in shaping science and environmental policy nationally and internationally. He is the recipient of numerous awards, including the Bower Award and Prize for Achievement in Science from the Franklin Institute (1999), the Albert Einstein World Award in Science from the World Cultural Council (2004), and the James B. Macelwane Award from the American Geophysical Union (1979). He served as AGU president (1992-1994) and was awarded AGU's 2002 Roger Revelle Medal for outstanding research contributions to the understanding of Earth's atmospheric processes, biogeochemical cycles, and key elements of the climate system. Dr. Cicerone is a member of the National Academy of Sciences, the American Academy of Arts and Sciences, and the American Philosophical Society. He is a foreign member of the Accademia Nazionale dei Lincei, the Russian Academy of Sciences,

the Korean Academy of Science and Technology, Academia Sinica, the Real Academia de Ciencias, and the Royal Society. Dr. Cicerone was educated at the Massachusetts Institute of Technology (BSEE and captain of the baseball team) and the University of Illinois. He began his research career at the University of Michigan. In 1989 he joined the University of California, Irvine, where he was founding chair of the Department of Earth System Science and later Chancellor (1998-2005). Dr. Cicerone has served on the Secretary of Energy's Advisory Committee (2009-2013), and is a trustee of the Carnegie Corporation of New York.





At the influential age of 10 years old...
I knew then that I wanted to be an

# oceanographer

and now, more than 50 years later, I am still pursuing my dream.

#### **ABOUT THE TITLE**

# The Contemporary Challenge of the Sea: Science, society and sustainability

Both the title and the inspiration for my talk derive from Arthur C. Clarke, brilliant author and futurist. In his forward-looking book, The Challenge of the Sea (1960), Clarke told the story of our new underwater frontier and speculated about the tremendous impact it will have on our lives in the future. At the influential age of 10 years old, I was captivated by the great potential for future scientific discovery and motivated by Clarke's challenge of the sea. I knew then that I wanted to be an oceanographer and now, more than 50 years later, I am still pursuing my dream. / Like Clarke, Roger Revelle was also a visionary. His pioneering research on the role of the coupled ocean-atmosphere system on global climate, and the impact of human societies helped to raise awareness of the state of our planet and its vulnerabilities. These inextricably linked themes of science, society and sustainability are among the most urgent contemporary challenges of the sea.

The ocean covers nearly 71% of the surface of our planet yet it is still largely unexplored despite its fundamental roles in global food production and climate regulation. The most expansive ocean regions, termed subtropical gyres (Figure 1), are the largest ecosystems on Earth yet we know little about how they are structured, how they function or how they may respond to stresses imposed on them by human activities. The North Pacific Subtropical Gyre (NPSG) is the largest of these gyres and is isolated from other ocean regions by permanent, clockwise rotating boundary currents. The NPSG is also very old with present boundaries having been established at least 10 million years ago. These conditions of great age and isolation create a habitat that is nutrient starved (e.g., nitrate and phosphate) and relatively devoid of photosynthetic microbes termed phytoplankton, that harvest sunlight and serve as the base of the marine food chain. These regions have been termed 'oceanic deserts' by analogy to the deserts on land. However, due to their vast expanse, regions like the NPSG control global ocean fluxes of carbon and oxygen and therefore sustain planetary habitability. But like many open ocean regions, the NPSG ecosystem is poorly sampled and not well understood.

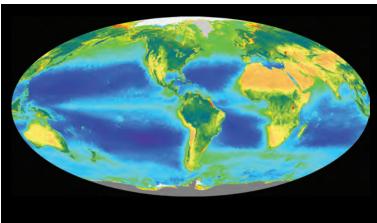


FIGURE 1: Global distribution of terrestrial vegetation and oceanic plant life as determined by satellite detection of chlorophyll showing a range of habitats from forests (e.g., Amazon basin in green) to deserts (e.g., oceanic subtropical gyres in dark blue). Source: NASA/Goddard Space Flight Center and ORBIMAGE.

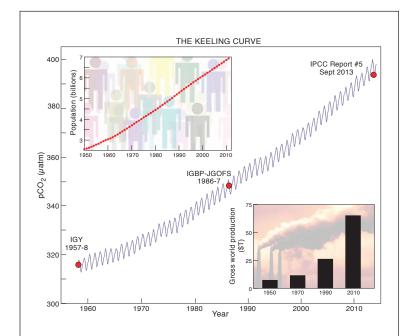


FIGURE 2: The Keeling curve of atmospheric carbon dioxide measured at Mauna Loa, Hawaii from 1958 to the present, along with global human population and global world production increases since David Karl's birth in 1950. Source: Mauna Loa data provided by Dr. Pieter Tans, NOAA/ESRL (www.esrl.noaa.gov/gmd/ccgg/trends/) and Dr. Ralph Keeling, Scripps Institution of Oceanography (scrippsco2.ucsd.edu/).

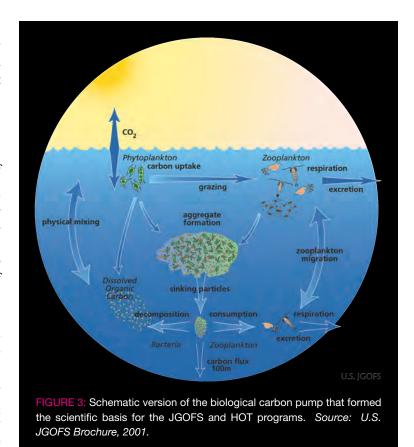
Roger Revelle made pioneering contributions to our understanding of the NPSG. In 1950, he organized and led the Mid-Pacific Expedition, the first of many interdisciplinary research cruises around the Hawaiian Islands. Just as in the retail sales industry, location matters, and Hawaii soon became a major center for mid-Pacific research with the establishment of the Hawaii Institute of Geophysics in 1958, a graduate degree program in Oceanography in 1962 and a School of Ocean and Earth Science and Technology in 1988, all at the University of Hawaii at Manoa (Karl, 2012).

Mauna Loa, Hawaii was also selected as one of the first observatories to track the atmospheric concentrations of carbon dioxide (CO<sub>2</sub>), and again Revelle played a major role in this effort and in the discovery of greenhouse gas-induced global warming. In his 1957 Tellus paper with Hans Suess, Revelle set out to measure the residence time of CO<sub>2</sub> in the atmosphere. Based on the best information available at that time, they concluded that "the average lifetime of a CO, molecule before dissolution into the sea is on order of 10 years" (Revelle and Suess, 1957). Revelle warned that "human beings are now carrying out a largescale geophysical experiment of a kind that could not have happened in the past, nor be reproduced in the future." This experiment, one

of man's doing, was an opportunity to learn more about the coupled ocean-atmosphere system and Revelle set out to do just that during the International Geophysical Year (IGY) 1957-1958.

Revelle and other scientists made a strong case to the U.S. National Committee for IGY of the value of atmospheric CO, measurements to establish a baseline against which one could measure future change. To accomplish this goal, Revelle who was at that time Director of Scripps Institution of Oceanography (SIO) – hired Charles David Keeling, then a post-doctoral fellow at Cal Tech. Initial measurements in 1958 obtained atop Mauna Loa on the island of Hawaii established a baseline CO, concentration of approximately 315 parts per million (ppm). The concentration has risen, year after year, to current levels of ~400 ppm (Figure 2). This well-calibrated, atmospheric time-series is an indelible imprint of humans and an ominous warning of the future state of our planet in a business-as-usual scenario.

The ocean plays a central role in regulating global atmospheric  $CO_2$  concentration. Since the start of the industrial revolution, the ocean has taken up more than 25% of the  $CO_2$  that humans have added to the atmosphere (Sabine et al., 2004). The value of the atmospheric  $CO_2$  measurement program initiated by Revelle and Keeling was strong justification



for the establishment of ocean observatories to improve our understanding of the oceanic carbon cycle. The Joint Global Ocean Flux Study (JGOFS), part of the International Geosphere-Biosphere Programme (IGBP), led to an improved understanding of the ocean, especially the biological carbon pump (Figure 3).

#### DISCOVERIES FROM THE HAWAII OCEAN TIME-SERIES AND STATION ALOHA

The key event that gave rise to JGOFS was a 5-day workshop

in 1984, which was organized to assess the state of knowledge and to plan a decade-long study of the physical, chemical, and biological processes controlling biogeochemical cycling in the ocean, and their interaction with the atmosphere. In describing the situation at that time, especially the uncertainties in the rates of key carbon cycle variables and lack of quantitative understanding of ocean dynamics, Peter Brewer (2003) concluded "It was an interesting mess." But the science moved forward with great alacrity in large part because of visionary leaders who helped to

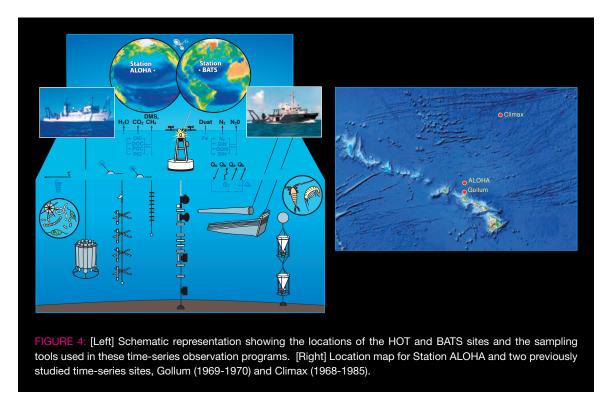
frame the challenges and opportunities into a viable, interdisciplinary research program.

It was forcefully and successfully argued that this knowledge was urgently required because of mankind's rapid and significant influence on the global carbon cycle. JGOFS got off to a great start with the establishment of two open ocean observatories, one in the North Atlantic near Bermuda, the Bermuda Atlantic Time Series (BATS), and the other in the North Pacific near Hawaii, the Hawaii Ocean Timeseries (HOT; Figure 4). Despite the knowledge gained on previous expeditions in both ocean regions, no one could have anticipated the sheer number and

magnitude of scientific discoveries that were about to be made over the next few decades.

The HOT program's deep ocean station, dubbed Station ALOHA (A Long-term Oligotrophic Habitat Assessment), is located at 22°45'N, 158°W, approximately 100 km north of Oahu, Hawaii in the North Pacific Subtropical Gyre. After 25 years of intensive sampling, this site has become one of the most well-studied open-ocean ecosystems, providing a global reference point for tracking the health of the ocean, including the rate of atmospheric CO, absorption and resulting ocean acidification (Dore et al., 2009; Figure 5). Station ALOHA also provides opportunity for investigations of seasonal and interannual diversity and dynamics of microorganisms, for detailed studies of carbon and associated biogenic elements, for hypothesis testing experimentation, and for training the next generation of oceanographers.

Despite chronic nutrient limitation, regions like Station ALOHA can support blooms of phytoplankton, generally during summer months when the water column is well stratified and most depleted of essential inorganic nutrients (Figure 6). These aperiodic and enigmatic phytoplankton blooms consume CO<sub>2</sub> and recharge the upper water column with dissolved organic matter and oxygen (O<sub>3</sub>) that can support post-



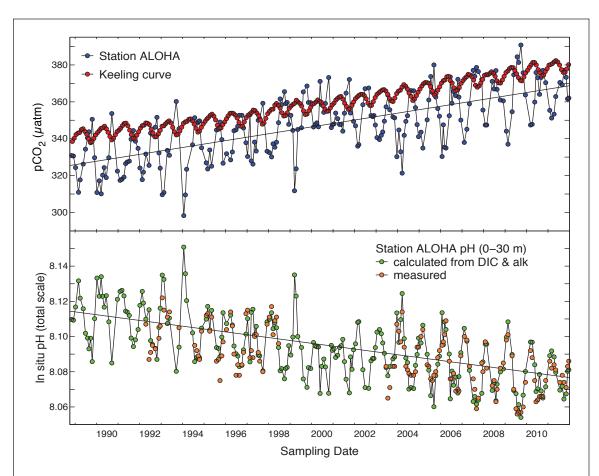


FIGURE 5: Station ALOHA observations from 1988-present along with the Keeling curve, showing an increase in carbon dioxide and acidification of the near surface ocean. Source: Data from Hawaii Ocean Time-series program (http://hahana.soest.hawaii.edu/).

bloom heterotrophic microbial metabolism. More importantly, blooms contribute to the seascape mosaic that is essential for maintaining the genetic diversity of microorganisms in these expansive habitats. These stochastic events of major ecological significance may be short lived (<1 month). To capture these ephemeral events requires a more regular presence than the occasional observations available from oceanographic re-

search cruises.

In recent years, Station ALOHA capabilities have been enhanced by an ocean mooring for meteorological and physical oceanographic observations (WHOTS), deployment of floats with sensors to provide depth profiles of oxygen and nitrate concentrations, deployment of a fleet of Seagliders equipped with sensors to detect a variety of environmental variables, such as chlo-

rophyll, and a fiberoptic cable that provides the capacity for real-time monitoring of transient events. In 2006, the Center for Microbial Oceanography: Research and Education, was established as a complement to the ongoing Station ALOHA observation program (cmore.soest.hawaii.edu).

The new discoveries of microbial diversity and the capacity of microbes to influence the chemistry and food webs of the ocean have led to new paradigms and hypotheses. As described below, these discoveries open the door to what should still be viewed as a major contemporary challenge of the sea for science, society and sustainability.

#### **MICROBES**

#### MICROBES THROUGHOUT EARTH'S HISTORY

Planet Earth has been more than 4.6 billion years in the making. If we view Earth's history as a 24-hr nautical clock (Figure 7), an initial cooling phase, which lasted nearly 500 million years, created the continents and the oceans. Life arose in an ancient ocean more than 3.5 billion years ago, or at 0500 hr (5 a.m.) on our Earth history clock. The first life forms were simple, single-celled microorganisms that evolved in an early ocean that was sulfideand iron-rich, and devoid of oxygen. These conditions persisted for hundreds of millions of years until the process of microbial oxygenic photosynthesis transformed the planet, starting at about 0820 hr (8:20 a.m.). This was one of the most fundamental transitions in the history of our planet, a lasting imprint of the activities of marine microorganisms. Among other consequences, the presence of oxygen enabled the evolution of the first eukaryotes, also single-celled microorganisms, just after 1500 hr (3:00 p.m.). However, it was not until much later, nearly 2100 hr (9:00 p.m.), or 4 billion years after the formation of the Earth, that eukaryotes evolved into larger, more complex life forms and moved onto the land. Despite the diversity of life that has evolved during our planet's history, it began with and still is dominated by microorganisms, and as Arthur C. Clarke noted, "all life came from the sea and most of it is still there." Incredibly, modern man (Homo sapiens sapiens) did not appear on Earth until about 200,000 years

ago, and the period since the start of the industrial revolution represents just a few milliseconds on the 24-hr clock of Earth's history! It is amazing that humans have had such a dramatic influence during this brief time on Earth, including fundamental changes in how our planet operates.

Environmental change, adaptation, and evolution over Earth's history have created a diverse spectrum of plants and animals, including humans, but microorganisms have always dominated the planet and always will. For example, there are more micro-

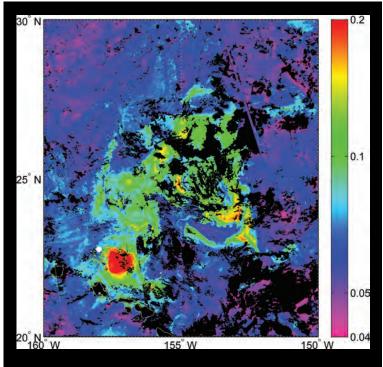


FIGURE 6: The ocean's desert blooms! Satellite-based chlorophyll *a* (mg m<sup>-3</sup>) image of the region north of Hawaii showing a major phytoplankton bloom near Station ALOHA in July 2005. *Image provided by J. Nahorniak* (Oregon State University) using AQUA MODIS L2 ocean color data publicly available from NASA's Ocean Biology Processing Group website.

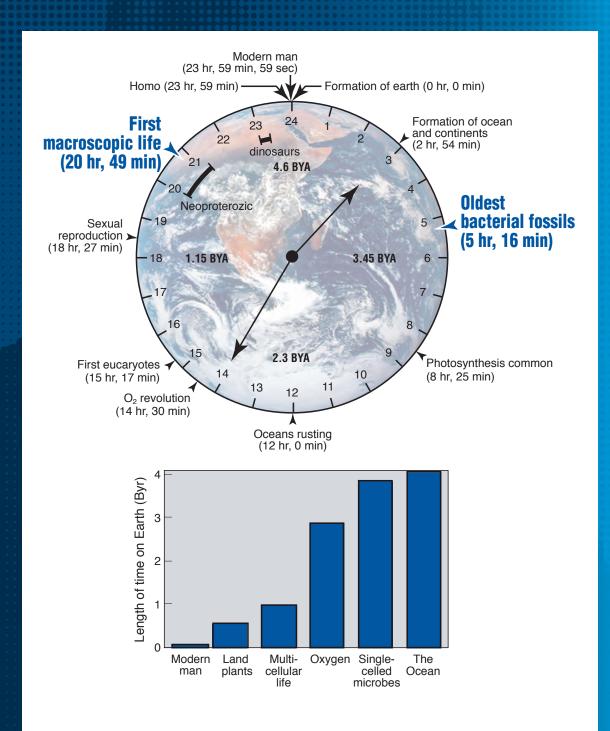


FIGURE 7: The Earth clock showing significant benchmarks in the evolutionary history of life, emphasizing the extended period of time since microorganisms first appeared on our planet.

organisms (bacteria, archaea, protozoa, and viruses) in one liter of seawater (~10 billion) than there are people on Earth (~7 billion). Contemporary marine microbial assemblages are numerically abundant and functionally diverse. Among many vital roles, they contribute nearly one-half of global photosynthesis and thus help to sequester CO<sub>2</sub>, produce O2, and sustain planetary habitability. Recent discoveries of new microorganisms, some with novel solar energy capture and nutrient transformation pathways, are changing our views of how oceanic ecosystems are structured and how they function.

When the Hawaii Ocean Time-series (HOT) began in 1988, momentum was building toward development of detailed understanding of marine microbial assemblages, their impacts on biogeochemical cycles and the sensitivities of microbially-medi-

ated processes to climate change. Because most naturally occurring microorganisms were not in laboratory cultures, detailed taxonomic identities and metabolic characteristics were lacking and interactions among marine microorganisms were largely unexplored. Incredibly, the three major groups of microorganisms that are most abundant at Station ALOHA (Prochlorococcus, the SAR11 clade of alphaproteobacteria, and planktonic archaea) were all discovered after the HOT program began in 1988. There are numerous examples where sampling at Station ALOHA catalyzed major advances in our understanding of the role of these microorganisms, and others, in ocean metabolism, biogeochemistry, and ecology (Table 1). Much of this new understanding, the 2nd Golden Age of Microbiology, arose from advances in molecular biology that led to the marine -omics revolution: genomics, transcriptomics, and proteomics (e.g., Gilbert and Dupont, 2011).

### MICROBES AND METABOLISM

In the simplest analysis, there are three main ingredients for life: energy, electrons, and carbon. While all animals, including humans, use organic matter to satisfy all three requirements, marine microbes have evolved specialized and diversified pathways to optimize growth, and often rely on mixtures of various multiple sources of energy, electrons, and carbon to sustain a hybrid-type of metabolism referred to as mixotrophy (Figure 8). Because the metabolic menu of the sea is so diverse, it promotes a diversification of microbial life leading to a complex interdependent web of metabolic processes.

The process of photosynthe-

TABLE 1: The second "golden age" of microbiology (1988-present)

YEAR	DISCOVERY	DISCOVERER
1988	Prochlorococcus – the most abundant photosynthetic microbe in the sea	Chisholm et al.
1990	SAR-11 clade – the most abundant microbe in the sea	Giovannoni et al.
1992	Planktonic Archaea - the third domain of life (along with bacteria and eukaryotes)	DeLong/Fuhrman
2000	Aerobic anoxygenic phototrophy – a novel, specialized type of solar energy capture	Kolber et al.
2000	Proteorhodopsin phototrophy – a novel, ubiquitous type of solar energy capture	DeLong/Béjà
2001	Picoplanktonic N <sub>2</sub> fixers – a novel component of the oceanic nitrogen cycle	Zehr et al.
2005-2013	Full genome sequences of marine microbes – novel organisms with new genes, new proteins, and new metabolic processes	many

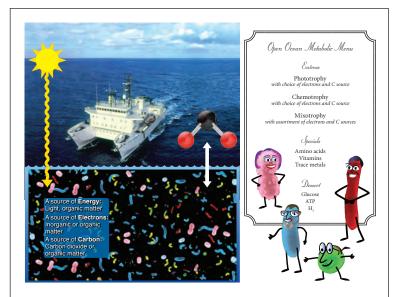


FIGURE 8: A sea of microbes and the diverse metabolic menu that supports them. Shown at right are caricatures of the principal investigators of the C-MORE program (clockwise from upper left: Penny Chisholm, Ed DeLong, Jon Zehr, and Dave Karl).

sis, whereby solar energy is captured by chlorophyll-containing phytoplankton and stored as chemical bond energy in organic molecules, is a fundamental ecological process that ultimately sustains all life in the sea. This well-known process also produces O, and is termed oxygenic phototrophy (OP). Recently, two new pathways of solar energy capture by marine microorganisms have been discovered, and this will likely lead to a quantitative reassessment of ecological energy flow in the sea.

The first of these pathways involves solar energy capture by proteorhodopsin (PR)-containing microorganisms (Béjà et al. 2000). The PR molecule resides in the cell membrane and func-

tions as a light-activated proton pump that produces ATP but does not produce O2. In fact, it appears that most, if not all, PR-containing microbes are net consumers of O<sub>2</sub> and organic matter, and use light energy to supplement their organic carbon-based heterotrophic metabolism. Major roles for PR-phototrophy in the sea appear to be for both growth and for survival, and may vary among different PR-containing microbes. Goméz-Consarnau et al. (2007) were the first to report that light has a positive influence on the cell yield of a PR-containing marine bacterium, when compared to cells grown in darkness. Additionally, PR-phototrophy appears to be a common mechanism for survival under environmental

stress. For example, PR-phototrophy was shown to increase the long-term survival in carbon-limited cultures of marine bacteria. Despite these critical roles in nature, estimation of the rates of solar energy capture by this novel pathway in nature is unknown.

The second unexpected discovery was the widespread occurrence of aerobic anoxygenic phototrophs (AAP) in the tropical Pacific Ocean (Kolber et al. 2000). Like PR-based phototrophy, AAPs use both solar energy and dissolved organic matter, and consume O2 to support their metabolic needs. The genes coding for AAP pigment synthesis appear to be broadly distributed in marine bacteria, but as with PR-based phototrophy their quantitative contribution to the ocean energy budget is unknown.

In the first ever study of gene expression in the sea using state-of-the-art metatranscriptomic analysis, Frias-Lopez et al. (2008) discovered that all three major forms of phototrophic metabolism (e.g., OP, PR, and APP) were among the most highly expressed of all gene clusters at Station ALOHA. This indicates that all three pathways may be significant for solar energy capture and transformation in the open sea.

## ROLE OF MICROBES IN OTHER CHEMICAL CYCLES

In addition to these new path-

ways of solar energy capture, we have also discovered novel pathways for the transformation of carbon, nitrogen, and phosphorus - the primary building blocks of life. Some of these newly discovered metabolic processes result in the formation of nitrous oxide and methane, two gases that along with CO, may contribute to greenhouse warming. It is imperative that we understand the environmental controls on these metabolic pathways to assess their role in a changing ocean. Along with the discovery of novel microorganisms and unexpected metabolic pathways and nutrient transformations, is the interaction between and among microorganisms and multicellular life forms in the sea. Just as we are beginning to learn about the microbes that live beneficially with all of us – the human microbiome – every marine plant and animal is likely to have a unique community of symbiotic microorganisms that it cannot live without. These are just a few examples of the vital importance of our magnificent marine microbes!

## RELEVANCE AND IMPORTANCE TO MODERN SOCIETY

### CHEMICAL NITROGEN FIXATION AND THE MINING OF PHOSPHATES

In addition to alteration of the global carbon cycle through intensive use of fossil fuels, human-kind has also impacted the global nitrogen (N) and phosphorus (P) cycles, essential nutrients for the growth of plants. With the inven-

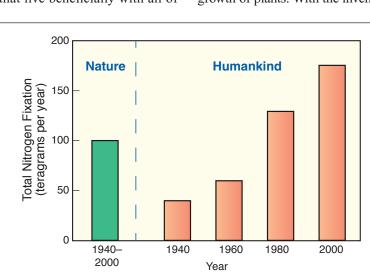


FIGURE 9: Global nitrogen  $(N_2)$  fixation rates by natural microbial communities and by artificial means (Haber-Bosch process) showing a rapid growth in man-made fixed N production over the past 60 years.

tion of ammonia synthesis from nitrogen gas (N<sub>2</sub>) by Fritz Haber in 1908 and subsequent commercialization by Carl Bosch (e.g., the Haber-Bosch process) there was a novel pathway for the production of reactive N from the inexhaustible supply of N, in the atmosphere. By 1980, the rate of industrial N, fixation – mostly for fertilizer manufacturing to enhance soil fertility and increase crop yields – surpassed the pace at which nature had previously provided reactive N to our planet (Figure 9). Likewise, accelerated mining of mineral phosphate – also for fertilizer production – has led to a disruption in the pace and pathways of the pre-industrial P cycle (Figure 10). Because both N and P are essential elements for life, there is great concern for unintended consequences of N and P pollution of coastal and open ocean ecosystems. Human activities, especially increased nutrient loads to rivers and estuaries, set in motion a cascade of events leading to large blooms of phytoplankton, high rates of bacterial respiration, and the death of marine organisms that require O2 to survive (the socalled dead zones; Rabalais et al. 2014). Recent studies have also shown that nitrate concentrations in the surface waters of the North Pacific Ocean located downwind of fast growing economies of northeast Asia have increased significantly since 1970 (Duce et al., 2008; Kim et al., 2011). This enhanced N deposition leads to a

decoupling of the oceanic N and P cycles, changing the diversity and function of microbial assemblages, and thereby affecting other fundamental ecosystem processes. Global surveys indicate that the impact of this man-made, reactive N pollution may have already reached the remote central regions of the North Pacific Ocean.

#### DEPLETION OF TERRESTRIAL PHOSPHATES

A major contemporary challenge

for science, society, and sustainability is the future scarcity of phosphate, which is an absolute requirement for life. In a 1938 address to the U.S. Congress, President Franklin D. Roosevelt stated: "The phosphorus content of our land, following generations of cultivation, has greatly diminished. It needs replenishing. I cannot overemphasize the importance of phosphorus not only to agriculture and soil conservation but also to the physical health and economic security of the people of the nation." This

call to arms helped to fuel the green revolution, including the production of high-yield crops to feed an increasing urbanized society. This revolution was supported by the availability of high grade phosphate fertilizer. More recently society has looked to biofuels (including marine microalgae) as a possible renewable energy source. However, the production of biofuels also requires phosphate, and fertilizer use in biofuel production competes head-on with food security.

In pre-industrialized societ-

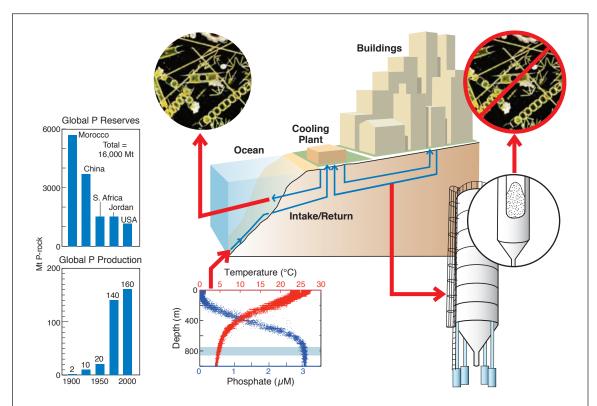


FIGURE 10: Schematic view of a seawater air conditioning system using cold, phosphate (P)-rich seawater as the heat exchange medium, with and without the removal of P prior to waste water discharge. P removal may help to control coastal nutrient pollution and phytoplankton blooms, while at the same time recovering P for reuse in agriculture. Data on left show trends in global P production and major P reserves on land.

ies, phosphate was cycled from farms to humans and other animal consumers back to farms through the application of organic wastes to sustain soil fertility. However, advances in sanitation and public health have removed most organic wastes from the cycle, forcing the developing world to look elsewhere for new sources of phosphate. Since the 1950's, mineral phosphate mined from nonrenewable, land-based deposits has surpassed the global use of all other forms of phosphate for high-yield agriculture (Ashley et al., 2011). To further complicate the present situation, the global reserves of mineral phosphate are very uneven, with just five countries (Morocco, China, U.S., Jordan, and South Africa) controlling nearly all of the known global resource (Figure 10). At current rates of extraction, it has been estimated that the natural resource may be exhausted in 50-100 years, probably before oil and natural gas reserves, leading to the collapse of modern agriculture and biofuel production, global strife, famine, and human suffering.

The impending global phosphate crisis has only recently been discussed among scientists, and is generally unknown to policy makers and society at large. In March 1999, Philip Abelson, distinguished physicist and U.S. National Medal of Science honoree, wrote an editorial in *Science* entitled *A potential phosphate crisis*. In that commentary, Abel-

son called for "further research to avert problems in the long term." More recently, a special volume of Current Opinions in Biotechnology focused on the phosphate crisis including authoritative articles on improvements in fertilizer use in agriculture, genetic modifications to crops and livestock for more efficient use of phosphate in feeds, and phosphate capture and reuse from livestock and human wastes. However, as Jim Elser lamented at the close of his article entitled Phosphorus: a limiting nutrient for humanity (Elser, 2012), "Given the scale and scope of the needed changes in coming decades, concerted efforts in research, technology transfer, and regulatory and institutional innovation should already be well underway. I end this piece by expressing my concern that they are not." A global resolution of the phosphate crisis is a major contemporary challenge for science, society, and sustainability.

### THE OCEAN AS THE SOLUTION?

Can the ocean play a role as a new source of phosphate for humanity? While the ocean, especially depths greater than 1,000 m, contains dissolved phosphate, it is in an extremely dilute form compared to the mineral phosphate reservoirs on land. However, the immense volume of the sea means that total P in the ocean is significant if only there

were a method to access the deep-sea phosphate reservoir and efficiently concentrate it.

In Honolulu, Hawaii, my home town, plans are moving forward to use deep seawater for district cooling and for energy production using an ocean thermal energy conversion (OTEC) system (Figure 10). These novel uses of renewable resources from the sea will replace fossil fuel, and in the case of seawater air conditioning (SWAC), will also conserve fresh water that would otherwise be required for conventional air conditioning cooling towers. However, a potential unintended environmental consequence of both SWAC and OTEC is nutrient pollution, especially phosphate, from discharge of the spent seawater effluent. Based on recent field experiments conducted at scales ranging from 20:1 to 60,000:1 we have determined that the removal of phosphate prior to discharge will eliminate phytoplankton blooms that otherwise occur. Furthermore, we have initiated laboratory-scale testing of several approaches that we believe may lead to an efficient phosphate capture from the waste stream prior to coastal ocean discharge. The recovered phosphate could be sold, with the profits used to sustain basic research efforts. Development of a marine-based, phosphate-capture and reuse process is a major contemporary challenge for science, society, and sustainability.

#### **FINAL REMARKS**

The contemporary challenge of the sea is enormous. There is great urgency to obtain a more comprehensive, mechanistic understanding of marine ecosystems, including the role of microorganisms in solar energy capture and transformation, global C, N and P cycles, and their sensitivities to the impacts of a burgeoning human population, global industrialization, and climate change. I remain bullish on humankind, but believe that our future will require a greater public understanding of the sea around us, and new policy to conserve and sustain our limiting natural resources. I hope that my comments might inspire a reader, young or old, to pursue a career in science or to assist with the creation of new sciencebased public policy. Who knows, that person might become the next Arthur C. Clarke, Ralph

Cicerone, or Roger Revelle.

From my perspective, Roger Revelle's greatest legacy was the integration of science and technology with humanities and social sciences. His vision for a better world has left a lasting impression, but also unfinished business to promote public welfare. In creating a new university in San Diego he realized, long before most others, that science, society, and sustainability were inextricably linked and inseparable in the modern world. In the future, society will become even more reliant on the sea for food and energy security, transportation, and related ecosystem services. In a 1980 lecture at Lawrence Livermore National Laboratory, Revelle lamented the "morass of uncertainties" regarding our understanding of the Earth's climate system. Decisive action is needed now on issues of overpopulation, the development of alternative energy, and improving the public understanding of science.

As William Nierenberg eloquently stated in an obituary following Revelle's death, "The challenges he undertook were the important ones, and they can be classified as insoluble in the sense that they are never ending. What Roger Revelle did was to improve our understanding of them and our ability to deal with them to the greatest extent possible in our times."

Finally, I leave you with a quote, indeed a credence, from Robert F. Kennedy which is one of the most inspiring of my generation. "Some men see things as they are and say 'why?' – I dream things that never were and say 'why not." Roger Revelle was an epic dreamer, but also a person of uncommon vision and significant achievement for science, society, and sustainability in his lifetime – Don't be afraid to dream!

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