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Profile of David M. Karl

From the moment 17-year-old David Karl first glimpsed the ocean from the summit of Cadillac Mountain on Maine's Mount Desert Island, he was captivated by the blue waters surrounding the fog-veiled islands. Since then, he has contributed to some of the world's most pivotal discoveries in oceanography. Karl, who was elected to the National Academy of Sciences (NAS) in 2006 and is now a professor of oceanography at the School of Ocean and Earth Science and Technology at the University of Hawaii, has witnessed iconic moments like the discovery of hydrothermal vents at the Galapagos Rift. His work on 23 research expeditions to Antarctica helped to reveal the unanticipated thriving food web that exists in those frigid waters. He has developed or refined more than 50 analytical methods to probe ocean life and biogeochemistry. Many, like the MAGnesium Induced Co-precipitation (MAGIC) method for measuring phosphate, have been widely adopted. The work that has earned him the most recognition, however, is the Hawaii Ocean Time-series (HOT) program.

Since 1988, HOT program researchers have made monthly measurements of water column biogeochemistry and microbial dynamics at Station ALOHA, a site ~100 km north of Oahu. Their datasets are freely available and have been used by hundreds of researchers worldwide.

The most startling finding to emerge from HOT program data is that climate change is affecting the ocean ecosystem. Data from the HOT program provided the first "bulletproof" evidence that rising atmospheric carbon dioxide (CO_2) from burning fossil fuels is making the ocean more acidic, a finding that was published in PNAS and won the 2009 Cozzarelli Prize (1).

Karl's work has garnered many honors, including the G. Evelyn Hutchinson Medal from the American Society for Limnology and Oceanography in 1998, the A. G. Huntsman Medal from the Bedford Institute of Oceanography in 2001, the Henry Bryant Bigelow Medal in Oceanography from the Woods Hole Oceanographic Institution in 2004, and the David Packard Medal in Oceanography from the Monterey Bay Aquarium Research Institute in 2005. Karl has received fellowships in the American Geophysical Union and the American Academy of Microbiology, and he received an honorary Doctor of Science degree from University of Chicago in 2010. Now, at the University of Hawaii, he directs the Center for Microbial Oceanography: Research and Education (C-MORE), a National Science Foundation (NSF) Science and Technology Center.

Image courtesy of Rowen Tabusa, University of Hawaii.

David M. Karl.

Call of the Sea

David Karl, born May 9, 1950, in Buffalo, New York, was an unlikely candidate for future NAS membership. Although he ranked in the top 5% of his class in school, he did not enjoy learning. "I was the dunce of the academically talented; I spent most of my time outdoors playing sports, mostly baseball." Looking back, Karl says that his involvement in sports was a "life lesson in discipline and team spirit."

Karl's team-building skills would later serve him well in science. Although he lacked passion for schoolwork, he was interested in people and leadership, and he served as class president for his last 3 years of high school (1965–1968), a tumultuous era that he says was "an exciting time to be in student government."

If he was trying to avoid an academic career, however, the odds were against him. His brother and sister were National Merit Scholars, and although his parents were not college-educated—his father was a self-employed soft drink distributor and, later, a mailman, and his mother was a librarian—they expected him to go to college.

Early on, Karl wanted to be a commercial fisherman, a desire sparked by watching documentaries on tuna fishing and strengthened by summer fishing trips on New York's Finger Lakes. Reading piqued his interest in the ocean, however. His mother knew that reading was the ticket to a good education and brought home books about fish anatomy, fisheries science, and even Arthur C. Clarke's *The Challenges of the Sea* (2). "She was trying to get me to set a target a little bit higher than becoming a commercial fisherman," Karl recalls.

Karl's parents gave their children a long leash, encouraging their interest in the hippie movement; Karl's father even helped him pick out a motorcycle when David was 15 years old. They also financed his trek to the 1969 Festival of Music and Art, also known as Woodstock. "It was all about direction without guidance but with plenty of love," he says.

Florida, Not Fish

After the 17-year-old's fateful trip to the summit of Maine's Cadillac Mountain, Karl decided to study biology at the State University College of New York at Buffalo. He graduated in 3½ years, *magna cum laude*. Frustrated with teaching "book classes" like algebra and physical science at an inner-city vocational high school, Karl applied to graduate oceanography programs and was eventually accepted at Florida State University, a program that boasted a seagoing vessel and distinguished faculty.

He intended to study coral reef fishes; however, his advisor, Paul LaRock, studied ocean-dwelling microorganisms and convinced Karl to do the same. LaRock was such a good mentor and teacher that Karl "just fell in love with the subject matter." LaRock stepped beyond academics, exposing him to contemporary research problems and introducing him to other scientists.

Two years later, MS degree in hand, Karl attended Holger Jannasch's summer course on microbial ecology at the Marine Biological Laboratory in Woods Hole, Massachusetts. During the summer of 1974, after several rejected applications in years past, Karl was admitted to a PhD program at The Scripps Institution of Oceanography (SIO) in La Jolla, California. He spent the next 3½ years in the laboratory, in the library, and aboard research vessels at sea. His PhD project earned him the prestigious Eckard Prize in 1979 for best dissertation of the year.

Exotic Cruises

Soon after Karl arrived at SIO, Jannasch invited him to participate in a month-long

This is a Profile of a recently elected member of the National Academy of Sciences to accompany the member's Inaugural Article on page 1842.

expedition to the Black Sea, a poorly studied area that had been off limits to American ships for more than 10 years because of the Cold War. Scientists consider the Black Sea an extreme environment: below 50 m, the oxygen dissipates, and between 200 and 2,500 m, there is none. This expedition provided a peek into a world of "relic communities" that may have existed before the emergence of an oxygen-rich world more than 2 billion years ago. Karl analyzed the distribution of microbial life there using methods he had developed at Florida State University (3).

In 1976, Osmund Holm-Hansen, Karl's coadvisor at SIO, received funding for a bold research program to drill through the ~400-m-thick Ross Ice Shelf in Antarctica and sample the dark ocean beneath it. Just hours before they were set to depart from New Zealand to Antarctica, equipment failure postponed the project for a year. Karl and a colleague went anyway, however, for the sheer adventure and to do whatever contingency science they could muster.

They traveled from McMurdo Sound to the Dry Valley Lakes and to South Pole Station, flying between points in Vietnam War-era helicopters and ski-equipped LC-130 Hercules cargo planes.

Since then, Karl has returned to Antarctica on 22 more expeditions, many of which were made on behalf of the Research on Antarctic Coastal Ecosystem Rates (RACER) and Palmer Long-Term Ecological Research (LTER) programs. Karl and his fellow RACER and LTER program researchers conducted the first "time-series" experiments (4) in a body of water south of 60 °S latitude that had been studied for many years but did not have a formal designation until the US Geographical Board of Names approved Karl's proposal to dub it the "Southern Ocean" in 1999. Later that year, Karl published the first account of microorganisms in the accreted ice of Lake Vostok, an ancient subglacial lake in eastern Antarctica (5).

Image courtesy of David Franzen, copyright 2011.

The C-MORE Hale laboratory.

How Many, How Much?

During the early years of Karl's career, there was little quantitative understanding of the role that microorganisms played in the sea—how many there were and what they did. "We didn't know the very basics of the marine food web," Karl remembers. Application of fluorescent microscopy revealed there were a thousand times more bacteria in a drop of seawater than were present by traditional plate count; which method was more accurate?

In the late 1960s, Holm-Hansen developed a new way of quantifying ocean microbes—by measuring ATP, the common energy currency of life. LaRock and Karl improved the assay at Florida State University and first applied it to marine sediments (6). "I learned early on in my career that if you develop a new assay or if you borrow and adapt an assay from some other field of study, it opens a new window of opportunity," says Karl.

Using this assay, Karl and his colleagues established the distribution and abundance of microbial life in many regions of the global ocean, a delicate balance that arises from production of new biomass from nutrient and energy supply and cell losses resulting from grazing, viral lysis, and death (7). Even today these processes are contemporary research topics in microbial oceanography, the discipline he helped to create during the past decade (8).

Fairyland of Exotic Colors

Just before completing his PhD degree in 1977, Karl was offered a faculty position at the University of Hawaii. The year before, Bob Ballard, John Corliss, and others had discovered communities of giant white tubeworms living around hydrothermal vents in the deep sea of the Galapagos Rift. Jannasch and Karl collaborated on an NSF proposal to test the hypothesis that microbes in the Galapagos Rift might harness energy from the sulfur bubbling up from the molten earth, much like the microbes in the Black Sea. With Karl's first NSF grant under his belt, he headed for the Galapagos Rift hydrothermal vents to study the newest form of life on the planet.

On a return expedition in 1979, Ballard could not find the vents on the first dive, but Karl and fellow researcher James Childress from the University of California, Santa Barbara, landed right on them on the second dive. It took more than 1½ hours for the submarine to sink. "All you see is bioluminescence in the deep sea, and then suddenly you hit the bottom and there's this fairyland of exotic organisms and all the colors… iron-stained basalts, bright yellow sulfur, and blood red *Riftia* plumes, to name a few. It was just incredible. We were literally the first biologists to see the deep-sea hydrothermal vents. This became one of the most important discoveries in the past 100 years in oceanography and revealed how little we actually knew about our planet," Karl says.

Karl and Jannasch showed that microorganisms consumed chemicals spewing from the vents, forming the base of the deep-sea food chain. They published the seminal scientific paper on the nature of the food web at these hydrothermal systems (9). "That was a good start to my academic career," says Karl.

He continued these investigations at hydrothermal vents located at 11 °N and 21 °N on the East Pacific Rise and in the Guaymas Basin. Ten years later, he discovered another hydrothermal system near Hawaii around the emerging island of Loihi (10).

Hot Vents to HOT Program

Karl studied hydrothermal vents for more than a decade and edited a book capturing the scientific results to date (11). Eventually, he turned his focus elsewhere, realizing studies of the hydrothermal vent system would require deep-sea observatories and 50–100 years of research.

Instead, he moved toward the surface, creating the HOT program to establish baselines for various oceanic processes and element cycles (12). During the late 1970s and early 1980s, he began teasing apart the rates of various ocean cycles (i.e., carbon, nitrogen, phosphorus) that Karl says are key to understanding the global models of production, fisheries, and climate change (13–15). His studies revealed that microbes were key players in the carbon cycle and the missing link in the marine food web (16).

In the early 1980s, Karl and other leaders in the field were summoned by the NAS to plan the Global Ocean Flux Study (GOFS), a research prospectus for exploring the ocean's carbon cycle during the next decade.

Over the next few years, Karl pitched ocean time-series measurements as a key component of GOFS, particularly to explore how microbes sustain nutrient cycles and organic production. The timing was fortuitous because Charles David Keeling's atmospheric CO_2 curve had garnered tremendous interest and underscored the value of time-series projects. Using measurements taken at the South Pole and the Mauna Loa observatory since 1958, Keeling had tracked increasing concentrations of atmospheric CO_2. "If he hadn't been making those measurements month after month after month, we would never have been able to understand the role of CO_2 in global climate," Karl says.

To crack the ocean's carbon cycle, Karl needed to generate a time series for plankton and biogeochemistry. The study required a team of scientists and engineers to make repeat measurements, "which, quite frankly, are pretty boring until you get a long time series," says Karl. He notes that it was a risky early career move because the research was not hypothesis-driven; rather, it was driven by a "build it and they will come" mentality. He proposed the HOT program to the NSF in 1987.

The HOT program was one of two proposed GOFS time-series stations, each costing 1 million dollars. The proposals were funded, and the first cruises were launched simultaneously in October 1988. In Hawaii, the biogeochemical and ecological study was complemented by a systematic study of ocean physics and climate led by Karl's colleague in Hawaii, Roger Lukas.

Originally, the HOT program research was entirely ship-based, with scientists going out once a month to make observations and conduct experiments over 5 days. After a few years, they added a mooring, basically a string of instruments from the seabed to the sea surface that took more frequent measurements. In 2007, the HOT program team launched a fleet of autonomous "Seagliders," battery-operated robots capable of data collection and transmission back to shore.

The two ocean time-series programs have each produced 23 years' worth (and counting) of data that are now recognized as being equivalent to the Keeling Curve of the ocean. In 2009, Karl and his colleagues published data from the HOT program in PNAS, proving that the oceans were becoming more acidic because of rising atmospheric CO_2 levels (1).

In his Inaugural Article (17), Karl and his colleagues in the HOT program describe the marine biological carbon pump and its role in deep-sea carbon sequestration. The authors document a large, annually recurrent sedimentation event in late summer at their study site in the Pacific Ocean north of Hawaii. Because oceanographic habitat features vary between years while export is temporally predictable, the authors hypothesize that the regularity of the massive sedimentation event may be controlled by day length, a general phenomena known as photoperiodism. The results underscore how little we know about some of the most fundamental ecological processes on Earth.

Time Series and C-MORE

Today, Karl has taken on an even bigger venture as director of C-MORE, a partnership between the University of Hawaii and collaborators at five US mainland institutions.

Karl describes C-MORE as a "super-HOT program." It is based at the HOT Station ALOHA and complements the HOT program with more variables, including genomics measurements. The goal will be to "understand the dynamics of life in the sea, from the genome to the biome": how the ocean and marine life respond to habitat changes, both natural and human-made. The *pièce de résistance* will be the 6-month manned occupation of Station ALOHA using an 80-ft ex-military ship that Karl plans to reconfigure as a remote laboratory. "It's going to be a one-of-a-kind dataset, a gold mine for knowledge creation and dissemination," says Karl. A new research facility, C-MORE Hale, has recently been constructed on the University of Hawaii campus to support the research mission.

Although Karl is not going on as many research expeditions as he used to, he has logged more than 1,000 days at sea in his career and is adamant that he has not retired, just shifted responsibilities. "I would like to think of my role, especially in the last 5 years, as being a science facilitator and opportunity broker. For my entire scientific career, I have been the beneficiary; it is time to give back," states Karl.

Bijal P. Trivedi, *Freelance Science Writer*

1. Dore JE, Lukas R, Sadler DW, Church MJ, Karl DM (2009) Physical and biogeochemical modulation of ocean acidification in the central North Pacific. *Proc Natl Acad Sci USA* 106:12235–12240.
2. Clarke AC (1966) *The Challenge of the Sea* (Mayflower Books, London).
3. Karl DM (1978) Distribution, abundance and metabolic states of microorganisms in the water column and sediments of the Black Sea. *Limnol Oceanogr* 23:936–949.
4. Karl DM (1993) Microbial processes in the Southern Ocean. *Antarctic Microbiology*, ed Friedmann EI (Wiley, New York), pp 1–63.
5. Karl DM, et al. (1999) Microorganisms in the accreted ice of Lake Vostok, Antarctica. *Science* 286:2144–2147.
6. Karl DM, LaRock PA (1975) Adenosine triphosphate measurements in soil and marine sediments. *J Fish Res Board Can* 32:599–607.
7. Karl DM, Dobbs FC (1998) Molecular approaches to microbial biomass estimation in the sea. *Molecular Approaches to the Study of the Ocean*, ed Cooksey KE (Chapman & Hall, London), pp 29–89.
8. Karl DM (2007) Microbial oceanography: Paradigms, processes and promise. *Nat Rev Microbiol* 5:759–769.
9. Karl DM, Wirsen CO, Jannasch HW (1980) Deep-sea primary production at the Galapagos hydrothermal vents. *Science* 207:1345–1347.
10. Karl DM, McMurtry GM, Malahoff A, Garcia MO (1988) Loihi Seamount, Hawaii: A mid-plate volcano with a distinctive hydrothermal system. *Nature* 335:532–535.
11. Karl DM (1995) Ecology of free-living, hydrothermal vent microbial communities. *The Microbiology of Deep-Sea Hydrothermal Vents*, ed Karl DM (CRC, Boca Raton, FL), pp 35–124.
12. Karl DM, Lukas R (1996) The Hawaii Ocean Time-series (HOT) Program: Background, rationale and field implementation. *Deep-Sea Res* 43:129–156.
13. Karl DM (1999) A sea of change: Biogeochemical variability in the North Pacific subtropical gyre. *Ecosystems (NY)* 2:181–214.
14. Karl D, et al. (2002) Dinitrogen fixation in the world's oceans. *Biogeochemistry* 57/58:47–98.
15. Karl D, et al. (1997) The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* 388:533–538.
16. Karl DM (2000) Aquatic ecology: Phosphorus, the staff of life. *Nature* 406:31–33.
17. Karl DM et al. (2012) Predictable and efficient carbon sequestration in the North Pacific Ocean supported by symbiotic nitrogen fixation. *Proc Natl Acad Sci USA* 109:1842–1849.