A Tribute to Richard W. Eppley
Compiled and Edited by Paul G. Falkowski

INTRODUCTION
By Paul G. Falkowski, Rutgers University
Richard W. Eppley (1931–2023), better known as “Dick,” was a tour de force in biological oceanography. Most of his research life was at Scripps Institution of Oceanography (Scripps), where he studied marine phytoplankton and their roles in biogeochemical processes. Over the course of his career, he influenced many people, not only in science but also as exemplar of integrity and fundamental curiosity about the ocean. His formidable contributions to phytoplankton physiology and biological oceanography were appreciatively reviewed shortly after his retirement (Weiler et al., 1990), and with added perspective after his death (Cullen and Eppley, 2024). What follows are tributes from several of his former students, postdocs, and colleagues.

TRIBUTES
Barney Balch, Bigelow Laboratory for Ocean Sciences
Dick Eppley instilled a passion for science in the people around him, covering the spectrum of research, from highly reductionist lab experiments to whole-ecosystem observations. Dick’s wide-ranging intellect is reflected in his remarkable scientific path, first studying seaweed ion transport, then phytoplankton nutrient transport and assimilation, and then biogeochemistry using ship and satellite remote-sensing studies over entire ocean basins. Little did I know, Dick would inspire a similar spectrum of scientific discovery in my own career.

Dick’s influence began when I was a student in the Food Chain Research Group (FCRG) at Scripps in 1980. He insisted that his students participate in Southern California Bight Study (SCBS) cruises, a systematic, regional time series through which we learned the power of making repeated, fundamental biogeochemical measurements. These cruises provided a critical platform for leveraging our student research. Early on, Dick allowed me to experiment with various algal phenomena in search of the almighty “thesis topic.” Through some trial and error, I came across some surprising results using radio-labeled nutrient analogues that launched my thesis work into short-term nutrient transport kinetics. This work led to a follow-on postdoc on nutrient analogues in Glenn Harrison’s lab at the Bedford Institute of Oceanography, then back to Scripps as a postdoc in Dick’s lab. Dick was emphatic, however, that postdoc positions are critical for expanding one’s scientific horizons beyond the PhD, and this postdoc was to work on the satellite remote sensing of phytoplankton. Dick’s excitement at showing the very first Coastal Zone Color Scanner image of SCB chlorophyll was infectious. This single synoptic image made instant sense of thousands of SCBS observations and led me to expand my scientific focus into the remote sensing of primary production, coccolithophores, and their associated particulate inorganic carbon. In 1998, Dick’s SCBS work motivated me to start a regional time series, the Gulf of Maine North Atlantic Time Series (GNATS) that matches satellite views of the Gulf of Maine with ship measurements to provide fundamental time-series observations of the Gulf’s changing oceanography. GNATS continues to this day. When Dick was cleaning his office pre-retirement, he gifted me, as he said, given my “interest in coccolithophores,” an old Scripps thesis by William Blankley (1971). That thesis inspired an all-new, updated study
of coccolithophore osmotrophy as a survival strategy and completed a full-circle transition back to uptake and growth kinetic studies—yet another example of Dick Eppley’s large spectrum of influence on my career!

Sallie (Penny) W. Chisholm, Massachusetts Institute of Technology

It is not hyperbole to say that I owe my career to Dick Eppley. He took a chance taking me on as a postdoc in 1974. As a woman (there were not many in oceanography in those days) from outside the field (I was a limnologist), with a PhD from a non-top-tier university and an advisor known for his eccentric views, I was not without risk. But Dick looked past it all and gave me a chance. I am certain that the opportunity he gave me was the foundation for all the good fortune that followed in my career.

I remember vividly a few months after I arrived at Scripps when Dick pulled me aside in the hallway and said, “Want to go on a cruise? Talk to Oizzie Holm-Hansen.” I did, and that got me on an R/V Alpha Helix cruise to the Gulf of California. I had never been on the ocean (I am a midwesterner), let alone the extraordinary Gulf of California. What an experience that was. After that, I was a regular on the SCBS cruises and could finally call myself an aspiring oceanographer. (I had learned that, unlike lakes, the ocean does not mix to the bottom!)

Dick was a “hands-off” mentor—always letting me do my thing while quietly guiding me from the sidelines. That gave me the courage and independence to forge ahead after I left Scripps. I remember vividly one time when he stopped by my office soon after I had arrived and handed me a big data set from the SCBS cruises and said, “Here is some interesting data. Write a paper about it.” I was new to oceanography and had no idea how to think about it. I plotted everything against everything trying to see how a story could emerge. It didn’t. I did not have the insight to see it. I was just too green. After much agonizing, I finally had to tell him I had come up short. I could not find the story. I handed him all the graphs of the data I had carefully put together and, in no time, he could see patterns that told a story. He wrote the paper and very generously made me a co-author. I learned so much by watching him see things in data that others could not see. It seemed to just “pop” for him. And I always felt supported by him, even when I felt I failed to deliver.

Speaking of support, after I interviewed at MIT, Dick told me that the search committee asked him to compare the top candidates—I among them (thank you Title IX!). He said he refused to do so and told them to hire all of us. That was the way he was. Always supporting young scientists and never pitting them against each other.

I remember toward the end of my stay at Scripps, when I was about to leave for MIT, Dick called me to his office to chat about what he should write about for his next grant proposal. He had two things in mind and wanted my opinion. (I was stunned that he valued my opinion! A confidence boost for me.) One of his ideas was to try to figure out what the “wee chlorophyll-containing things that go through filters” were. I remember his words so clearly. I did not weigh in but just engaged about the pros and cons of the two directions. He ultimately picked the “wee things.” At least a decade later, it became clear that among them was Prochlorococcus. He was always WAY ahead of his time.1

John Cullen, Dalhousie University

Bearded, long-haired, and wearing patched blue jeans, I visited Dick Eppley at the FCRG to talk about my offer from Scripps to begin PhD studies under his supervision in 1975. A lifelong Northern Californian steeped in the counter-culture of UC Santa Cruz, I preferred utopian Corvallis (Oregon State University) or comfortable Seattle (University of Washington) to the sociopolitical badlands of San Diego. So, with cringeworthy arrogance rooted in stunning ignorance, I told Dick that coming to San Diego was my third choice, and I asked him to “twist my arm.” Rather than throwing me out on my ear as I richly deserved, he kept calm, pulled out Parsons and Takahashi’s Biological Oceanographic Processes, and flipped through the references, pointing out one after another: “That one was done over there (the office of an FCRG scientist), that one over there, those from down there…” Then, “Oh! This one was from Oregon State!”

It was classic Eppley: rather than making pronouncements about how good he and his colleagues were, he let the data make the case. It was also a sign of his patience, generosity, and tolerance. He would give you a chance to make mistakes, learn, and grow.

Dick Eppley was a great teacher, but—with the exception of his pronouncement that I would finish in five years just like Jim McCarthy did—I don’t remember him ever telling me what to do. Instead, he would talk about how things were done, using sheaves of yellow graph paper to illustrate analyses and regularly sending me to the library to read up on what was already known. Meeting with Dick in his office as he was formulating questions, analyzing data, and writing his own papers was particularly instructive; I could see how the entire process worked when conducted by a master. We talked often and went through a lot of graph paper; there is no other way that I could have learned so much during my five years at Scripps.

Years after I completed my degree, the profundity of Dick’s influence began to dawn on me. As a supervisor, I continually referred to Eppley when discussing best practices in science and more generally, the right thing to do when trying to navigate a career in oceanography.

Some of the lessons we can learn from Dick Eppley’s example:

• Work on significant problems.
• Do your homework first. Find out what is already known, then formulate hypotheses.

1 In 2011, President Barack Obama presented Penny Chisholm with the National Medal of Science, chiefly for her work on understanding Prochlorococcus.
• Don’t grandstand. Let your presentation and discussion of the data tell the story.
• Acknowledge uncertainties in your assumptions and interpretations and explain their implications.
• Always present your work in historical context.

The final point is especially important. In Dick’s own words, “you have an obligation to say what others have found—it is the only intellectually honest way to do it.”

In the world before time, when there were no cell phones, laptop computers, or internet, I read physical papers every week in the library at the University of British Columbia, where I was a graduate student in zoology studying comparative animal physiology. I devoured the papers by Dick Eppley. They were not only articulate but, to me, aspirational. The papers I consumed were about competition among phytoplankton, based on their ability to acquire inorganic nutrients, especially fixed nitrogen. The papers were always well written, and the science was, to me, the “cutting edge” of biological oceanography.

My thesis focused on nitrogen metabolism in phytoplankton and its role in the global cycles of biologically relevant elements. Because of Dick’s influence, I have worked to this day on nitrogen as a limiting nutrient in the world ocean.

I became a student of F.J.R. (“Max”) Taylor and embarked on a career that was truly inspired by Dick. Indeed, in winter of 1975, Max paid for me to visit Scripps—by bus. After enduring a snowstorm in the mountains, I arrived at the Greyhound station in San Diego at 2 a.m., and, as per Dick’s previous letter, I dropped 10 cents into a payphone and called him from the station. He answered and picked me up in about 30 minutes. I spent a week with him and Jean in their house, learning not only how to be a scientist but also how to enjoy life, through ballroom dancing, the outdoors, and music (Dick played the piano very well).

Over the next two decades, I would become a scientist at Brookhaven National Laboratory (BNL), which was originally funded by the Atomic Energy Commission (AEC), and later, by the Department of Energy. The FCRG at Scripps was also similarly funded. The concept was that there should be “four corners” of oceanography: the Pacific Northwest, the Pacific Southwest, the Atlantic Northeast, and the Atlantic Southeast. Indeed, for about a decade, that was the case with (hold onto your seat) about 25 million dollars for the program.

During that period, I learned that BNL could make $\text{^{15}N}$, a radioactive isotope of N with a half-life of 10 minutes. Together with my colleague Doug Capone, then at Stony Brook University, and a new postdoc, Jon Zehr, we analyzed the pathway for the incorporation of ammonium into amino acids in a marine diatom. That publication didn’t change the world, but it did lead to many other publications that have.

In the end, Dick was a scientist who wanted to understand mechanisms in biology that made phytoplankton what they are, the “grass” of the sea. Long before “omics,” he taught me how to learn and understand basic processes. I have followed that advice to my great advantage.

Paul Falkowski, Rutgers University

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I brought a strong background in biochemistry and physics to my graduate work, but after a few weeks in a laboratory specializing in mosquitoes, where I had to hang shaved guinea pigs upside down in a cage for food for the insects, I came to be more interested in plants, especially phytoplankton. Why? I liked the idea of going on ships to do research. I still do.

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Glenn Harrison, Bedford Institute of Oceanography

I became aware of Dick Eppley’s research on phytoplankton nitrogen metabolism in the early 1970s while I was working on my doctoral research in a North Carolina estuary. I was particularly interested in his nitrate reductase (NR) assay and its application to natural water samples (Eppley et al., 1969). I adapted his technique for our waters, and my experiments worked well enough that I managed to get an article published in Limnology and Oceanography, fortuitously about the time I was preparing to defend my thesis and looking for a postdoctoral position. Soon after, I sent a copy of the paper to Dick and indicated my interest in doing further work on NR with the leader in the field and learning about the new tools for studying the nitrogen cycle in the open ocean, specifically, stable isotope ($\text{^{15}N}$) tracers. It was a long shot, because my previous work had been mostly in estuarine waters, and I had only one short “blue water” cruise under my belt. I didn’t even have an oceanography degree (my PhD was in zoology because, at that time, North Carolina State University did not offer a marine science/oceanography degree program). Within a few weeks, however, Dick sent me a very encouraging letter that included an offer for a two-year postdoctoral position to work on laboratory and field projects at Scripps. This I considered an opportunity of a lifetime. The two years working with Dick turned into almost three: I not only expanded my work on nitrogen enzymes in the lab but also got my real sea legs within months of my arrival at Scripps, on the last of the North Pacific Gyre cruises where I learned $\text{^{15}N}$ tracer methodology. Subsequently, I participated in a number of the SCBS cruises and the Controlled Ecosystem Pollution Experiment (CEPEX) program and its sister program in Loch Ewe, Scotland.

When I left Scripps in late 1976, I was armed with the theoretical and methodological foundation that set the trajectory for my oceanography career for the next 36 years. Over that time, I have had the privilege of working with leaders in the field on landmark multidisciplinary programs (e.g., PRPOOS, VERTEX, JGOFS), most of these through my continuing connections with Dick. I have also been fortunate to study phytoplankton
nitrogen dynamics in the subtropical, temperate, and polar open ocean waters of both the Atlantic and the Pacific in addition to numerous inshore studies on both coasts. My mission throughout most all these studies was to follow Dick's lead and contribute in some small way to our understanding of the role of "new" and "regenerated" primary production in defining the structure and function of marine ecosystems.

As a working scientist, Dick was a natural leader who had great rapport with colleagues and (especially) his students. He had an exceptionally creative mind, yet he could simplify complex concepts with ease. He was a relaxed, confident communicator. Despite the pressures of his many academic/administrative responsibilities, Dick was the most "cool/calm/collected" person in my experience. On a personal basis, Dick was the kindest, most altruistic person I have had the privilege to know. From the first time I met him until our last visit, Dick (and Jean) always treated me as family, and for that I will be eternally grateful.

David Karl, University of Hawai‘i

I met Dick Eppley in fall 1974 when I started my PhD studies at Scripps. I was one of several new students in the FCRG, a consortium of scholars created by John Strickland in 1963 to improve our understanding of microbial ecology and biogeochemistry. Over the next few years, I received hands-on training from Dick aboard R/V Ellen B. Scripps on several SCBS cruises—I was living my dream. Shortly after I left Scripps for a new job at the University of Hawai‘i, I had another opportunity to work with Dick when he organized and led the PRPOOS project. The success of PRPOOS and the new knowledge gained helped to formulate the much larger Global Ocean Flux Study (GOFS). Dick was a member of the planning committee for the first GOFS workshop in September 1984 where he delivered one of the keynote presentations, "Relationships between primary production and ocean chlorophyll determined by satellites." Dick was later elected to the GOFS Executive Committee and helped to create a research framework for the next decade. This is where we crossed paths again. As one of the intellectual leaders of GOFS, Dick was a strong proponent of time-series investigations. He was especially supportive of the plan to create a new ocean observatory in the oligotrophic North Pacific Subtropical Gyre, where he and others from the FCRG had conducted pioneering research during the early 1970s (e.g., Eppley et al., 1973). In October 1988, the Hawaii Ocean Time-series (HOT) project deployed its first cruise, HOT-1, and in December 2023 the field team completed HOT-348 in the ongoing project. Over the years, especially during the first decade of the HOT project, Dick and I exchanged many emails, letters, and manuscripts about the emergent HOT scientific results and our common research interests. Dick was always generous with his time and sage advice, and this helped to build the program that we enjoy today. Throughout my career, I always considered Dick an academic mentor, even though his signature was not on my formal PhD dissertation. The collective guidance that he provided helped many early career scientists, and I was very fortunate to have known Dick Eppley. His legacy will live on through his many major contributions to oceanography. May he rest in peace.

Edward Laws, Louisiana State University

There is an old adage among physical oceanographers that there are two problems with data: one is that we do not have enough, and the other is that we have too many. These same problems arise in biological oceanography, and one of Dick's great strengths as a scientist was his ability to deal with data problems. First, he could deal with large numbers of data. His 1972 paper on temperature and phytoplankton growth in the sea is a good example. Where others might have seen a cloud of numbers, Dick saw a pattern, and he quantified that pattern by drawing a curve through what he perceived to be the envelope to the data. That curve became known as the Eppley curve, and it has stimulated numerous theoretical, laboratory, and field studies ever since. Then there is the problem of not enough data, or perhaps better stated, not enough of the right kind of data. Dick's reading of the literature told him that there was a serious inconsistency in the reported growth rates of phytoplankton in the ocean, and he organized a workshop and headed up a multi-investigator study funded by the National Science Foundation (NSF) to collect the kind of data that would hopefully resolve the growth rate issue. That study, PRPOOS, revealed that phytoplankton in the oligotrophic ocean were growing rapidly even though their biomass was low. The implication was that much phytoplankton growth in oligotrophic waters was supported by recycled nutrients, and the now classic paper by Eppley and Peterson (1979) anticipated that discovery. Dick realized early in his career that continuous culture systems (i.e., chemostats) allowed independent control of biomass (via the concentration of the limiting nutrient in the reservoir) and growth rate (via the dilution rate of the growth chamber). He then set out to explore the relationships between nutrient concentrations, phytoplankton growth rate, and phytoplankton composition (i.e., to get the right kinds of data). Those chemostat studies led to the realization that phytoplankton could grow rapidly at concentrations of limiting nutrients that were bordering on or below the limit of detection by methods then available and that a more informative indicator of the degree of nutrient limitation might be the carbon-to-nitrogen ratio in the cells. The latter discovery stimulated the concept of relative growth rate and provided a hitherto unrecognized significance to the Redfield ratio.

Patricia Matrai, Bigelow Laboratory for Ocean Sciences

By the time I arrived at Scripps, Dick Eppley had had a bunch of PhD students and postdocs, of whom I was the last full-time graduate student. I had just finished an MS degree on dinoflagellate biogeography in the North Pacific that convinced me that I was more interested in biogeochemical rates than on cell counts. I had watched Dick in seminars, read his papers, and interacted
with his students, so I requested an appointment with him to ask if he would take me as a PhD student. I told him I had already accepted a research assistantship in another lab so he wouldn’t have to support me financially. He listened. After what seemed a long pause, he agreed to be my PhD advisor as long as I finished my research assistantship as soon as possible because it was his policy to support his own students. Wow—he sure did, including travel to conferences, analytical trainings, a new instrument for my samples, unlimited supplies, etc. His generosity extended beyond finances, to challenge and open one’s mind. As I searched for a thesis topic, he gave me a recently published paper in *Limnology and Oceanography* by Andy Andreae and others showing vertical profiles of a gas that resembled profiles of chlorophyll *a*, which Dick was somewhat dubious, somewhat curious about. Researching the background of that paper for similar data (I didn’t find any) and for the phytoplankton physiology behind such gaseous production led to papers on oxygenated organic sulfur and dimethyl sulfide production by phytoplankton, assisted by Jean Eppley who also helped filter many samples (that’s another story!). These papers, and the gained expertise, launched me into a life-long career in studying air-sea exchange processes—to Dick’s great amusement (e.g., gassy, bubbles, stinky, bipolar—because of my Arctic and Antarctic fieldwork). Here again, Dick’s example in “giving back” to the communities that supported his research (e.g., ASLO, JGOFS, NSF committees) encouraged my long-term participation in similar organizations that provided an invaluable and international professional network, just as Dick had told me they would.

I followed his advice in many other aspects, from life-work balance as he looked back ("Paty, don’t do weekend meetings") to financial investments for retirement ("invest green when you can" ca. 1990) to retiring when I was ready to do so.

**John F. Marra, City University of New York**

I was a second-year graduate student in the Department of Oceanography at Dalhousie University working on zooplankton with Carl Boyd (following an undergrad zoology major) when Carl assigned student seminars for the spring semester. Having chosen a date in January, I knew that Carl was seeking ideas for using Dal’s Aquatron, a seawater system with a tower tank, a pool tank, and seawater supply to various labs. A bunch of papers Carl gave me to read over the Christmas break included those on the "large-volume plastic sphere" regarding research organized by John Strickland, and papers from Strickland’s "Deep Tank" facility. The bunch also included a paper by Dick Eppley, Jane Rogers, and James McCarthy (Eppley et al., 1969). Though the plastic sphere and deep-tank papers were interesting, what intrigued me most was the Eppley et al. paper, which surveyed phytoplankton species for their *K* values, attempted to explain them ecologically, and differentiated them by combining *K* and cell size. Picking up on that idea, I decided to apply it to the springtime North Atlantic. I presented a simple scheme in my talk, by way of a small chart on the blackboard, where big cells dominate early when there are abundant nutrients, followed by medium- and small-sized cells with lower *K* values (greater affinity) as the season progressed and nutrients became depleted. Gordon Riley was there, sitting near the front. He quickly pointed out that it was *small forms* dominating early on, not large. I didn’t have an answer, and anyway, who was I to say? I was deflated, but I was encouraged when a few other students gathered around the blackboard to ponder the idea. And Eric Mills, a benthic ecologist, said he would now include *K* and its significance in his biological oceanography course. So, although I hadn’t yet met him, Dick Eppley set me on a new path and had a consequential effect on my future in oceanography.

**Donald Redalje, University of Southern Mississippi**

In the late 1970s, finishing up my doctoral work at the University of Hawai’i’s with Ed Laws as my advisor, I was looking for what to do next and applied for an NSF Postdoctoral Fellowship. As part of the fellowship application, I needed to develop a two-year research plan and project description for continuing my studies of phytoplankton specific growth rates and carbon biomass using the labeled chlorophyll technique developed during my dissertation research. I did not get the fellowship, but decided to send the research plan/project description to a few phytoplankton ecologists who I thought might find it interesting, including Dick Eppley. During my graduate studies, I had become interested in his research and how I might be able to progress scientifically working with him. Dick was the only recipient of the materials who responded positively. He offered to use my research plan/project description as the basis for a research proposal to be submitted to NSF Biological Oceanography Program—very good news to me. Sometime later, I heard from Dick that NSF funded the proposal and that my postdoctoral position would begin in September 1980. Incidentally, the proposal also funded graduate assistantships for two of Dick’s incoming graduate students—Barney Balch and Jim Nelson.

Over the course of the time I spent in Dick’s lab group, I tried my best to soak up as much knowledge from him and others in the Scripps community as I could. This was also the time during which Dick was developing plans for the large multi-investigator PROOPS project. I am very grateful that Dick included me in that project so that I could continue my collaboration with Ed Laws as well as many other of the leading researchers in the field of plankton rate processes. The time I spent working in Dick’s lab and during the subsequent PROOPS program years gave me the opportunity to expand my scientific network of oceanographic colleagues that continues to this day. I am thankful for the opportunities that came my way due to the time I spent learning from Dick Eppley, both during the postdoc and throughout the rest of my career.

Many may not know this, but Dick was an excellent glass blower. When I got to Scripps and wanted to begin setting up two
I was contemplating my next steps. Out of the blue, I received an invitation to do postdoctoral research with Dick. The iconic geochemist Bob Garrels, whom I knew from time spent in Bermuda, had suggested to Dick that I would be a good candidate for his laboratory. After I arrived in La Jolla, Dick went off for a year as a rotator at the AEC, and I was given the honor of supervising his laboratory during that period. It was an easy task because his lab group was outstanding—I guided and also learned from them. Although Dick was in Washington, DC, he had significant contact with me and gave much advice. By the time he returned, I had truly become a member of the FCRG, a rare collection of great scientists who were also interesting people. I feel that I learned much from Dick about humility and generosity to students and fellow scientists. After 40 years of research and teaching and now retired, as I look back on my career, I recognize the tremendous influence that Dick had on the way I carried out my career at the University of Delaware.

REFERENCES

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