Symbiosis
https://doi.org/10.1007/s13199-021-00817-w

Robert Kent Trench (1940–2021): a life devoted to symbiotic mutualisms and seeking nature's truth

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Received: 18 August 2021 / Accepted: 12 October 2021

Keywords Dinoflagellate · Endosymbiosis · Kleptoplasty · Minority scientist · Photophysiology · Specificity

> "It ain't necessarily so"
>
> – A favored mantra recited by R. K. Trench in the context of "received truth," or established beliefs; and the title of his unfinished autobiography.

Professor Robert (Bob) Kent Trench's research career brought together multiple disciplines in the study of mutualistic symbioses that are crucial to understanding the physiology, ecology, and co-evolution of metazoan and protist associations, many of which are beneficial to the Earth's biosphere. Through the development and use of complementary techniques, he pioneered important discoveries about metabolically coupled interactions between "plants" and animals. Having grown up in Belize (formerly British Honduras), his journey in academia started at the University College of the West Indies (UCWI) on the island nation of Jamaica, then proceeded to the University of California, Los Angeles (USA); Oxford University (UK); and Yale University (Connecticut, USA). He was a longtime faculty member in the Department of Ecology, Evolution and Marine Biology at the University of California, Santa Barbara (Figs. 1a–f). Over the course of his life (August 3 1940–April 27 2021), he recognized that many things presented as fact were often accumulated dogma. His direct application of the scientific method ultimately helped to change these misconceptions. By deconstructing established 'beliefs,' he greatly improved our understanding of several mutualistic symbioses, and many of his insights and hypotheses published decades ago remain at the forefront of intense investigation to this day.

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1 Contributions to science

Bob's contributions to the biological sciences were manifold (Fig. 2). He is most noted for his seminal work on the diversity, physiology, and ecology of photosynthetic endosymbionts found in reef-building corals and giant clams. He also made significant contributions to the study of sea slugs that steal chloroplasts from the seaweeds upon which they graze. As 'acquired' organelles, Bob showed how these plastids continued to photosynthesize and deliver important nutrients to the animal. As a contemporary of the late Lynn Margulis (Fig. 1c), he also advanced our understanding of unicellular flagellates that possess cyanobacterial endosymbionts, a mutually obligate relationship on the spectrum close to accomplishing complete organelle evolution. Below are brief descriptions of some of his contributions to these fields of study.

1.1 Animal-dinoflagellate mutualisms

Reef-building corals that are wholly dependent on photosynthetic micro-algae—single-celled dinoflagellates—construct an ecosystem vital to the Earth's biosphere. Bob introduced a fresh perspective about the relationship between host and symbiont, which changed how we view these mutualisms. As research intensified in the 1970s and 1980s, the

Published online: 10 January 2022

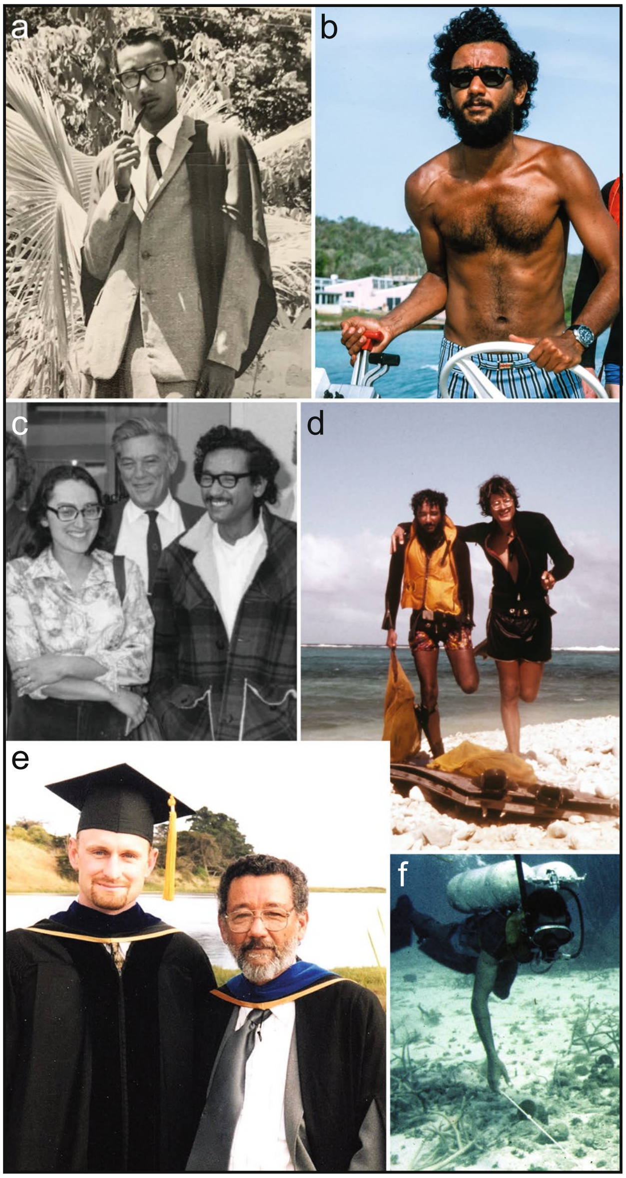

Fig. 1 **a** (1965) Robert Kent Trench's graduation photo from the College of the West Indies, Jamaica. **b** (1974) Assistant Professor, fieldwork at Discovery Bay Jamaica. **c** (1975) Associate Professor at UCSB with visitors, Lynn Margulis (U. Mass) and Elso Barghoorn (Harvard). **d** (1974) With Jim Porter (Yale) on Enewetak Atoll to study coral photo-inhibition by cyanide and DCMU. **e** (2000) Graduation at UCSB with his last graduate student, Todd C. LaJeunesse. **f** (~1964) Undergraduate research conducting ecological transects at Pear Tree Bottom site in Jamaica with double air tanks characteristic for the early days of SCUBA.

prevailing view was that the host entirely controlled the symbiont. However, Bob recognized that this one-dimensional view masked the true nature of the mutualism and stressed that the symbiont's attributes were critical to the establishment and maintenance of the relationship.

Bob entered science at a time when funding was plentiful and research directions were strongly influenced by thought-provoking questions and unrestrained curiosities. For decades, he and his students enjoyed a degree of intellectual solitude. This suited Bob's demeanor as he rarely pursued or needed fame. He sought to understand the biology of coral endosymbionts long before episodes of severe thermal stress, and mass coral mortality from 'coral bleaching' made them extremely popular research topics.

While it was known since the late 1800s that these animals harbored high densities of unicellular algae (Brandt 1881; Geddes 1882) that contributed to the corals' growth and metabolism (Gardiner 1931), their quantitative importance to the animal remained unappreciated until about the late 1950s to early 1960s. Applying radioactive ^{14}C allowed investigators, including Bob's Ph.D. advisor Leonard (Len) Muscatine, to make the first measurements of carbon translocation from the symbiont to the animal (Muscatine and Hand 1958). As one of Len's first graduate students, Bob focused his dissertation research on the transfer rates and total amounts of photosynthetically fixed carbon translocated to the animal (e.g., Trench 1971a, b, 1974). Interestingly, he noted that symbionts isolated from different hosts did not produce the same photosynthetic products (Trench 1971b); and foreshadowed the concept that not all symbionts were functionally the same. It was from this and the work of others that calculations were made regarding the contribution by zooxanthellae to animal respiration (i.e., CZAR, Muscatine 1990). These collective observations provided further empirical evidence that the symbiont was critical to the animal's physiology, growth, and general well-being.

Bob became convinced that studying the dinoflagellate partner in isolation would provide insight into its function as a symbiont. Work with cultured isolates and infection experiments testing host-symbiont specificity and selectivity influenced his insights about partner sorting among these intimate relationships (Schoenberg and Trench 1980c; Colley and Trench 1983; Fitt and Trench 1983). As an assistant professor at Yale in the early 1970s, Bob's research direction was mentored and inspired by the venerable Luigi Provasoli. Luigi had developed growth media for culturing phytoplankton that McLaughlin and Zahl (1959) used to first culture zooxanthellae. Bob would build on this progress and that of Freudenthal (1962) by isolating numerous cell cultures sourced from various hosts. He and his graduate student, Dave Schoenberg, employed a breadth of biochemical, genetic, morphological, and physiological analyses to show that cultured isolates were fundamentally different when grown under the same nutrient, light, and temperature conditions (Schoenberg and Trench 1980a,b,c). Karyotype studies demonstrated that the genus *Symbiodinium* sensu lato comprised more than one species (Blank and Trench 1985; Trench and Blank 1987).

Bob guided the first detailed research that comprehensively examined differences in the photophysiological

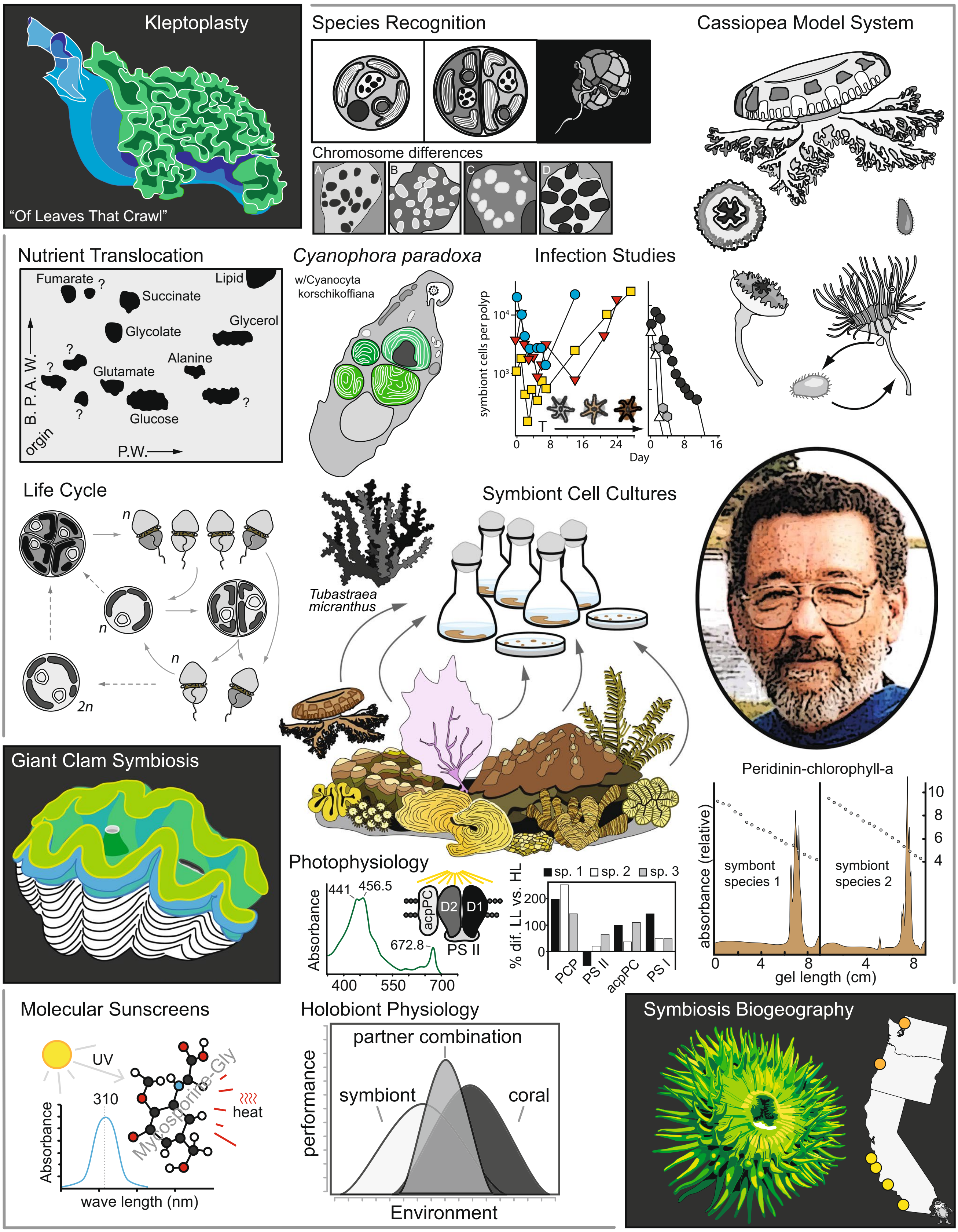

Fig. 2 Research highlights and discoveries of Bob Trench in collaboration with his mentors, graduate students, post-doctoral scholars, and colleagues

capacities of different symbiont species and contributed to the characterization of the photosynthetic apparatus of dinoflagellates (Iglesias-Prieto et al. 1993). In doing so, it became clear that different species possessed distinct photophysiological adaptations, including the production of different peridinin-chlorophyll-*a* proteins, marked changes in chlorophyll-protein compositions under low and high irradiances, and expression of mycosporine-like amino acids and changes in morphology in response to exposure to UV radiation (Fig. 2; Chang and Trench 1982; Banaszak and Trench 1995a, b; Iglesias-Prieto and Trench 1997a; Banaszak et al. 2000). His lab also first showed that these symbionts were sensitive to temperature stress (Iglesias-Prieto et al. 1992).

This identification of physiological differences among symbiont species established the functional significance of symbiont diversity to the biology and ecology of reef-building corals. With his doctoral student, Roberto Iglesias-Prieto, they developed the concept of how coral physiological responses to environmental pressures are determined, in part, by particular host-symbiont combinations (i.e., the holobiont; Iglesias-Prieto and Trench 1997b). Identifying such functional differences explained, in large part, how reef corals with broad biogeographic distributions could occupy a range of depths and habitats (Rowan and Knowlton 1995; Finney et al. 2010; Hoadley et al. 2019) and laid the foundation for the proliferation of 'remediation' and 'resilience' research projects that are so prevalent in the restoration of coral communities now threatened by bleaching and other factors.

Bob's approach to experimental research was always laboratory focused. His students used *Aiptasia* and *Cassiopea* as experimental systems to study host-symbiont compatibility under controlled conditions. This helped to characterize the cellular processes of host inoculation and symbiont proliferation while revealing patterns of host-symbiont specificity (Schoenberg and Trench 1980c; Colley and Trench 1983; Fitt and Trench 1983).

Bob and his students conducted field research at various places in the Pacific (e.g., Palau, Hawaii, and Eniwetok Atoll) and in the Caribbean (e.g. Jamaica, Mexico). The biggest federal grant he ever received was from USAID to study the importance of symbiosis between dinoflagellates and the giant clams (*Tridacna*) in Palau. This work showed how early infections and establishment of symbiont populations greatly increased survivorship of larval clams, thereby enhancing their successful aquaculture (Fitt et al. 1984; Fisher et al. 1985).

Despite his production of numerous important papers, Bob felt at times that his contributions required validation by others who re-discovered them. Near to his retirement, he lamented that his papers with Rudolf Blank demonstrating that the 'zooxanthellae' of cnidarian hosts constituted more than one species had limited impact. However, most of Bob's contributions have endured scientific scrutiny and his original insights remain the basis of ongoing investigations. Indeed, only in recent years has a large international research community, employing the newest technologies, begun to measurably advance our basic understanding of the biodiversity, physiology, ecology, and evolution of symbiotic dinoflagellates and their host relationships. For example, the application of DNA-based symbiont identification advanced Bob's insight regarding high host-symbiont fidelity. This was exhibited by numerous host taxa over large spatial and evidently long temporal scales, encompassing different ocean basins, over durations of millions of years (e.g. LaJeunesse and Trench 2000; LaJeunesse et al. 2014; Turnham et al. 2021). Environmental factors (mainly light and temperature) and a symbiont's physiological attributes determine the distribution of specific partner pairings for corals that exhibit symbiont flexibility (e.g. Rowan and Knowlton 1995). The recognition that various partner combinations exhibited ecological and geographic zonation was explained by the initial discoveries made in Bob's laboratory showing symbiodiniacean dinoflagellates displayed broad physiological differences.

1.2 Kleptoplasty by gastropod molluscs – "of leaves that crawl"

Bob's first, and one of his favorite, research papers was published on the topic of photosynthetic animals in the journal *Nature* in 1969 while Bob was a post-doctoral scholar at Oxford (Trench 1969). Contrary to the dogma that dismissed the importance of algal chloroplasts in sea slugs, his exciting and innovative research demonstrated that these chloroplasts remained functional after being engulfed by animal digestive cells lining hollow pockets (cerata) of sacoglossan sea slugs (Gastropoda; Mollusca). In this and subsequent papers, he described how green seaweed chloroplasts continued to photosynthesize and persist for long periods of time as 'captive' intracellular organelles. The translocation of carbon from chloroplasts to animal cells provided additional and reliable nutrients that benefited these "solar-powered" animals. For this body of work, he was awarded the prestigious Miescher-Ishida Prize for outstanding contributions to the field of endocytobiology.

1.3 Model system for chloroplast evolution

> "Within the context of the serial endosymbiosis hypothesis of the origin of eukaryotic cell organelles, the line separating a semiautonomous endosymbiont

from a semiautonomous organelle might be vanishingly thin." –Trench et al. 1978.

Further highlighting his varied interests in symbiotic systems, Bob also focused research on the mutualism between single-celled flagellates (*Cyanophora paradoxa*) and photosynthetic bacteria (*Cyanocyta korshikoffiana*). Like the relationship between sea slugs and chloroplasts, this flagellate internalizes a specific species of cyanobacteria upon which it relies, thereby consuming the organic molecules produced by photosynthesis. While both partners are separate biological entities, they are mutually obligate, and therefore, an ideal system to study the evolution of chloroplasts and other organelles (Trench et al. 1978; Burnap and Trench 1989a,b,c).

2 Major influencers in Bob's Life

Bob was a college undergraduate returning *On the Origin of Species* to the library when he 'discovered' another of Charles Darwin's books, *The Structure and Distribution of Coral Reefs*. While the written text of *Origins* was not to his liking, the revelations he gained from the more 'accessible' *Coral Reefs*, inspired Bob to study marine biology and corals. Beyond the writings of Darwin, Bob had several influential mentors who were critical to his growth as a scientist. Not long after arriving in Jamaica in 1961 with a scholarship to attend the University College of the West Indies, he joined the research group of the famed coral reef biologist Thomas F. Goreau (Tom). As a father figure, Tom's mentorship had a profound impact on Bob's life and future career. Bob would learn coral biology and many laboratory skills as well as how to conduct underwater research using SCUBA. Tom was one of the first biologists to develop and use this technology for marine research. Tom would test Bob's resolve by challenging him with menial tasks, such as cleaning rotting tissues from specimen coral colonies to be archived at the marine laboratory at Discovery Bay. During one memorable instance, while laboring to push a skiff across the reef flat at low tide in the midday heat, sweating and exhausted, Tom turned to young Bob and exclaimed, "This [the profession of marine biology] is a hell of a way to earn a living!" Years later, upon retelling of this exchange to his graduate advisor at UCLA, the quick-witted Len Muscatine wryly responded, "It sure beats working!" This was a favorite story of Bob's, and he would burst out laughing each time he retold it. Indeed, his boisterous laugh was a charming attribute that would reverberate through halls at UCSB; you always knew when he was present at parties or smaller gatherings no matter where he was or how big the room.

Len Muscatine was perhaps Bob's most consequential mentor (Hoegh-Guldberg et al. 2007). Under Len's tutelage, Bob developed his focused and multi-faceted approach to gathering evidence. Like his advisor, he sought to answer relevant questions using the methods and techniques available. Through his experiences at UCLA, he developed his attention to fact gathering, critical thinking, and scholarship, so by the time he arrived at Oxford, he was an independent and detail-oriented investigator.

3 Philosophies on the human endeavor of science

Bob was passionate about understanding biological phenomena based on good evidence. Papers making broad claims with little evidence frustrated him. Moreover, he rarely hesitated to confront inconsistencies in people's logic. This he did without the intent of malice. Recognizing the truth of things was ultimately more important to Bob than protecting a person's feelings. Notably, he rarely let scientific disagreements interfere with his personal relationships. He remained genuinely amicable with fellow investigators because he separated the person from their scientific work.

Bob was particularly sensitive to the misuse of *acquired authority*. As he defined it, certain individuals leveraged their prestige to discount, or question, the research of other investigators without using evidence. One example involved how new discoveries about the symbioses between dinoflagellates and giant clams were initially suppressed in favor of the untested ideas of a more *prominent* scientist (e.g. Norton et al. 1992). Ultimately, the true nature of these symbioses prevailed many decades later after additional scientific scrutiny (Norton et al. 1992; Farmer et al. 2001).

Bob was often critical of those who learned the newest technology and then sought questions to answer by using it. Like his Ph.D. advisor (who frequently asked his students, "What is the question?"; Hoegh-Guldberg et al. 2007), Bob also approached science by first formulating questions that would improve biological understanding and then seek out and employ the technological and methodological approaches to best answer them. A major concern of his was that too many people followed technology rather than advancing hypotheses and testing them. He increasingly saw that many younger investigators trying to solve "big-picture" questions without trying to gain an in-depth understanding of the organisms involved.

Bob's first manuscript was initially rejected for publication by the journal *Science*. The journal *Nature* accepted his findings for publication ironically on the same day that a *Science* editor invited him to resubmit the manuscript. He regrettably informed *Science* that it had been accepted by another *prestigious* journal. The whole experience of rejection by *Science* and then acceptance by *Nature*, to the displeasure of the editors at *Science*, motivated his criticisms of how hype and fads often distracted from the advance of research and how arbitrary a process can be in determining what science constitutes an important and newsworthy contribution. Nevertheless, over the course of his career, Bob published often in high-profile journals, including *Nature* and *Science*, as well as the *Proceedings of the Royal Society of London* and the *Proceedings of the National Academy of Sciences,* and wrote many substantive review articles (e.g. Trench 1975, 1979, 1993).

Bob respected the power of words especially when conveying ideas and concepts through writing. He was weary of their misuse and was careful to choose words that avoided confusion. This strict obsession meant that each sentence was evaluated meticulously and the dictionary often consulted when preparing a manuscript; and why his scientific papers remain among the clearest and most precisely written.

4 On being a mentor

When mentoring graduate students, Bob had a remarkable ability to let people find themselves. Bob recognized that a big part of the scientific process required plenty of time devoted to exploration and failure before things were *worked out*, and, only then, capitalizing on any breakthroughs gained during this process. However, his relaxed approach of intentionally not assigning explicit research projects was tough on young, inexperienced, graduate students. Nevertheless, Bob's minimal guidance meant that his students were free to do what they found to be of interest to them. Moreover, the rite-of-passage in formulating their own course of research created self-reliant and well-rounded scientists. Bob felt that he had succeeded as a mentor when his students, beyond focusing on specific questions, placed greater emphasis on understanding general phenomena.

5 As an instructor

Bob taught a highly regarded course on the biology and geology of coral reefs while he was a professor at UCSB. Many undergraduates took this experience to become marine biologists, including some that continued onto graduate school to study coral physiology and ecology, in depth. He also was a long time co-instructor in the highly popular Invertebrate Biology course, where his lectures on the Cnidaria were original and outstanding. In smaller group settings, Bob captivated students with guiding questions about the invertebrates they discovered while exploring California's rocky intertidal and mudflat habitats. During these exchanges, Bob sometimes became gleefully nostalgic about times as a youth finding and catching invertebrates on the reefs of Belize. Once formally recognized for his teaching, he was quoted in a news article announcement of the award, "I want to teach them how to learn on their own, so that I become irrelevant."

6 A youth in Central America

Bob was born in Belize (formerly, British Honduras), where his grandmother raised him. He made good use of the freedom of his youth and loved exploring the islands and waters along Belize's barrier reef, often alone. Unlike his peers, he had an interest in school and science, although his support for studying biology was very limited. In Belize at that time, the only important fields were Law and Medicine. No one understood what marine biology was, nor did they appreciate what it involved or its overall importance. His family was relatively affluent by Belizean standards and this supported his attendance of the Jesuit high school in Belize City. He often acknowledged that the quality of education he received from the priests served him well for the rest of his life.

7 Professional life as a multi-racial person

While widely admired for his academic successes, and appreciated for his kindness and wisdom by those who knew him, Bob experienced some negative racial stereotypes. He accepted that his mixed-race background occasionally brought unwanted attention. While returning with a large group of researchers from fieldwork at the Enewetak Atoll, he alone was singled out for inspection. When at UCSB, he was confronted a few times by campus police because he did not "look like he belonged on campus." He did not let these types of experiences define him and was not afraid to talk candidly about racial biases and his responses to them with the hope of instilling a positive influence on his students and peers.

8 Personal interests, activities, and hobbies

Bob was an avid reader of history and especially war history, particularly the American Civil War. He enjoyed ocean fishing and boating, especially when done simultaneously and with little talking. He liked his rum with ice. He curated and beautifully displayed a large collection of coral skeletons obtained mostly during his research in the Pacific. After retirement, he took up woodworking and made rustic furniture and invested time corresponding with many of his former graduate students and professional colleagues, as well as their students. Through this frequent communication, Bob kept himself informed about the newest research discoveries and provided helpful background, insight, and advice to his extended academic family for many years past his retirement.

9 Summary

Bob saw things as they were, not as they seemed to be. He was not afraid to test established ideas, including his own. He valued the truth above all, which is why he loved the scientific process. He was a respected scholar, mentor, father-figure, confidante, and friend. His life's work spurred new and exciting disciplines of symbiosis research. His insights and many research accomplishments provided the necessary foundations for younger researchers to build upon, and his scientific legacy will likely inspire generations to come.

Acknowledgements We posthumously thank Robert K. Trench for his written responses to questions posed to him about his life many years ago. His answers helped to write this paper. The authors also wish to thank Clayton Cook, Eugenia Sampayo, Rob Burnap, Sara LaJeunesse, and Ove Hoegh-Guldberg for their constructive comments to improve this tribute. We also thank Tom J. F. Goreau, Paulette Aguilar (Bob's niece), Roger LaJeunesse, and Bill Sacco (Discovery Bay) for photographs chronicling Bob's life.

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