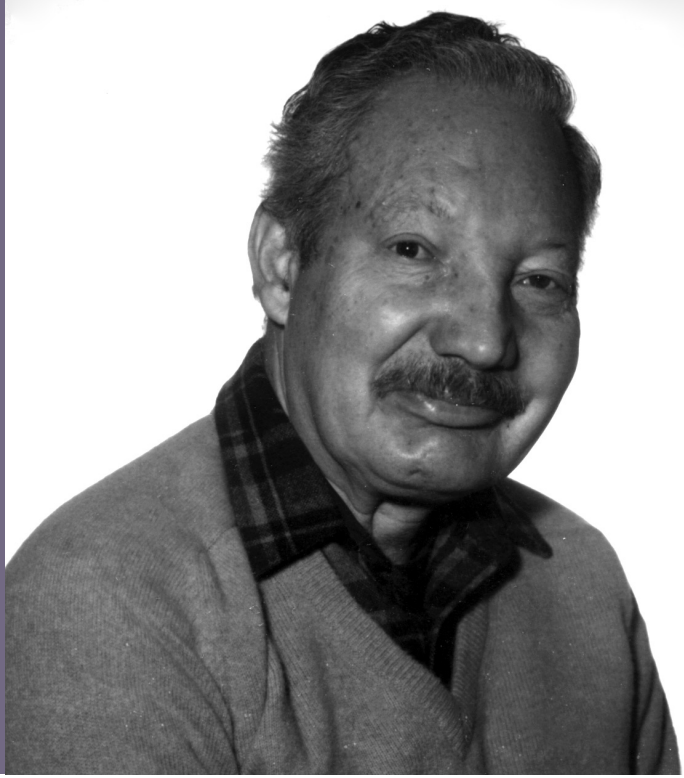
Howard L. Sanders

1921–2001

BIOGRAPHICAL *Memoirs*



A Biographical Memoir by
Richard C. Brusca
and Isabelle P. Williams

NATIONAL ACADEMY OF SCIENCES

HOWARD LAWRENCE **SANDERS**

March 17, 1921–February 8, 2001

Elected to the NAS, 1983

Photography by Woods Hole Oceanographic Institution

By Richard C. Brusca and Isabelle P. Williams

This biography of pioneer marine ecologist Howard Sanders is long overdue, but it was important to compile, and we are honored to have been invited by the National Academy of Sciences to write it. Sanders was a unique individual and a forward-looking scientist. He was a trail-blazer in evolutionary ecology, deep-sea ecology, and oil spill ecology—three very different fields. But his scientific enthusiasm didn't stop there. While still a graduate student, he discovered an entirely new class of Crustacea that led to decades of debate on crustacean evolution and also led him to a career in crustacean systematics. And in the late 1960s, he began what became a long-term research program, with John Allen at the University of London, on protobranch bivalves that lasted until 1996, when he published his last paper. Howard Sanders effortlessly excelled in multiple fields of science while simultaneously being a loving and devoted husband and father, raising two sons, tending his garden and smokehouse, taking friends to his favorite fishing hole off Woods Hole, mentoring graduate students and newly minted Ph.D.s, serving on numerous national science advisory committees, and teaching classes at top universities, all the while acquiring a reputation for his modest, almost self-deprecating ways. Needless to say, he was also a highly focused and hard-working individual.

In a 1969 interview for the Woods Hole Oceanographic Institution (WHOI) house magazine, *Woods Hole Notes*, Sanders adamantly proclaimed, "Mankind is rapidly, maybe even irreversibly, 'progressing' toward a world environment which won't support life." He later stated, "I see irrefutable evidence of the gradual destruction of the planet's environment." If this statement had been made by a young graduate student at the time it would be unremarkable. But Sanders was a soft-spoken, normally reserved, 48-year-old scientist whose hallmark was credibility. He went on in the interview to state, "If scientists, particularly biologists, remain silent or cloistered, vital environmental decisions

continue to be made, but by people who can't possibly comprehend the consequences of their actions." Strong words for man with a reputation of being quiet and docile. But Rachel Carson's *Silent Spring* had been published just a few years prior, and the environmental movement had begun, first on university campuses and then spreading far and wide. Certainly, it's safe to surmise that Sanders had read the book and was paying attention to the new "movement."

In his lab at WHOI, Sanders hosted a stream of visitors, all of whom he treated with the greatest courtesy and kindness. Curiously, however, Sanders' own CV is sparse, including just the bare-bones essentials. It lists no lab guests, no graduate students or postdocs, no grants, none of his research trips (not even the more than a dozen dives on the submersible research vessel *Alvin* that he participated in), and no conferences attended. The thing about Sanders is that he was an unpretentious man, someone whose mind was always on the next scientific question and not on trying to impress anyone. This is not to say he wasn't typically in command of the situation, but he was a leader by example and stature, not because of need or position.

Over his career Sanders authored/co-authored sixty-eight scientific publications of high, original scientific merit. He served on numerous national and international research committees, as well as on the editorial boards of several major scientific journals (such as the *Journal of Marine Research* and *Limnology and Oceanography*). He was elected a Fellow of the American Association for the Advancement of Science (AAAS), and in 1983 was elected to the National Academy of Sciences. He taught classes at the Marine Biological Laboratory (MBL) in Woods Hole, as an associate in invertebrate zoology at Harvard University, and as an adjunct professor at the State University of New York (SUNY) at Stony Brook (now Stony Brook University). He also taught a summer course at the University of Washington's Friday Harbor Laboratory and at the University of Southern California's Catalina Island Marine Laboratory. From 1975 to 1986, he was a *Correspondent du Museum National d'Histoire Naturelle*.

Howard Sanders was a beloved gentleman, and he left a great many devoted friends and colleagues who have only fond memories of him. He gave generously of his time (and his benthic samples) to aspiring young students, and he mentored many scientists early in their career, receiving no particular credit for this beyond his own satisfaction and their appreciation and lasting memory. He was Howie to his friends, who remember him not only as a creative and relentless researcher but as an enthusiastic and skilled fisherman whose smoked fish left a legacy nearly as memorable (though not as wide) as his scientific legacy.

1. Howard Sanders, off to war, ca. 1942. (Photo courtesy of Mark Sanders.)

Beginnings and Family Life

Howard Sanders was born on March 17, 1921, in Newark, New Jersey, to Isaac Sandusky and Marion Rosenfeld Sandusky. Isaac owned a lumber business in Newark. The legal name change from "Sandusky" to "Sanders" took place sometime in the 1930s, after Isaac had passed away. Howard attended school there, graduating from high school in 1940. A thyroid condition kept him nearly bedridden for the year after he graduated and eventually resulted in a thyroidectomy. His higher education was delayed by service in the Army Signal Corps in World War II, from 1942–1945 (Figure 1). Initially stationed in England, after D-Day his unit was deployed to the Continent, accompanying other troops as they slowly made their way to Germany. Sanders' children have noted that this experience, which included the Battle of the Bulge, had a profound effect on him. And when he and Lillian first married (Figure 2), he declared that he never wanted to eat spam or ever go camping again. Robert Sanders recalls his mother saying that early in their marriage, Howard frequently would wake her up in the middle of the night from his cries of terror in his dreams. He also had a lifelong antipathy toward high-ranking military officers. After the war, Sanders would make up for lost time by moving quickly through his undergraduate and graduate years.

2. Newlyweds Howard Sanders and Lillian Selchen Sanders, ca. 1940. (Photo courtesy of Mark Sanders.)

After a brief enrollment at Rutgers University in 1946, Sanders matriculated at the University of British Columbia (UBC) in Vancouver, first as a forestry major (on the GI bill) but later switching to zoology. He completed his bachelor of arts degree in zoology in less than four years, in 1949. During his undergraduate years, he also worked as a fisheries aide for the Fish and Wildlife Department in 1948—first in Bristol Bay, Alaska, (tagging salmon and doing stream surveys) and then in Pensacola, Florida (conducting chemical analyses of seawater and growth studies of oysters, and initiating a faunal survey of invertebrates and fish of Pensacola Bay). It was in Vancouver

that Howard and Lillian Selchen would meet, fall in love, and begin their lifetime partnership.

Sanders' wife Lillian was born in Winnipeg, Canada, and grew up speaking Yiddish, learning English upon starting school at age six. She graduated from the University of Saskatchewan with a bachelor's degree in nursing and worked for more than four years as a public health nurse in Hamden, Connecticut. She met Howard when she was working as a nurse in Vancouver, British Columbia; the two were in the same bowling league. In 1949, Howard and Lillian married in Gulfport, Mississippi, and then he jumped straight into a master's program at the University of Rhode Island (URI), where he was in the very first class in URI's new master's degree program in oceanography. He studied under Donald Zinn, who in turn had studied under legendary British ecologist G. Evelyn Hutchinson of Yale University. Sanders' thesis was titled *The Herring of Block Island Sound*. His precocious scientific nature led to an informal appointment at WHOI during his graduate studies, from October 1949 to June 1951, where he was given the agreeable title of "Casual Research Assistant."

Sanders completed his degree at warp speed in 1951 and then matriculated into Yale University's Ph.D. program, quickly attaching himself to Hutchinson, who had just been elected to the National Academy of Sciences and in 1952 would be named Sterling Professor in Zoology, Yale's highest academic rank. Gordon Riley, who himself had been one of Hutchinson's graduate students, would be Sanders' thesis advisor of record, but Hutchinson became a more influential mentor. Sanders was fortunate in studying under Zinn and Riley, both direct students of Hutchinson, thus making Sanders the intellectual grandson of Hutchinson twice over.[1]

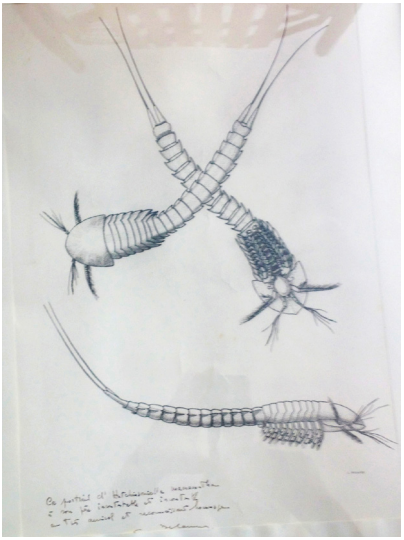
Hutchinson is frequently referred to as the "Father of Modern Ecology." Two of his most famous graduate students, Larry Slobodkin and Howard Odum, had just graduated and fledged to their own careers. Sanders would be strongly affected by Hutchinson's scientific approach, which was to think broadly, in interdisciplinary terms, and in the context of biological communities, rather than focusing on individual species. Thanks to Hutchinson, European attitudes towards ecology had entered the United States and then gradually taken on a life of their own. Prior to Hutchinson's arrival, ecology in the United States focused largely on natural history, and systems approaches were rarely mentioned. Hutchinson considered issues like species extinction, resource management, and the social anthropology of endangered cultures decades before they were attracting attention as crises. He had raised the idea of climate change thirty years before the

problem became popular, teaching his students as early as 1947 that the increase in atmospheric carbon dioxide would lead to global temperature increases. As Slobodkin put it, "Hutchinson and his graduate students intellectualized American ecology by forcing its practitioners to confront all of the processes that maintain to change ecological systems, whether these processes were biological, physical or geological."[2] Building on Charles Elton's idea of an ecological niche,[3] Hutchinson famously redefined it as "a highly abstract multi-dimensional hyperspace in which the organism's needs and properties were defined as dimensions." Hutchinson recognized the tight link between biological and physical processes and that they formed systems that followed well known mechanical principles. Of course, this led to the development of the field of systems ecology by Howard Odum.[4] Hutchinson would be awarded the National Medal of Science posthumously, in 1991.

The Hutchinsonian world that Howard Sanders found himself in would imprint deeply upon his thinking about biology. Under Hutchinson's guidance, Sanders developed a thesis project to study ocean bottom life in Long Island Sound that would quickly set his mark as a forward-thinking marine benthic ecologist. He was not just interested in knowing what species lived on the seafloor, but what the structure of a biotic community was in terms of diversity and relationships to sediments of different sorts. Following his Ph.D. research, Sanders studied benthic communities in Buzzards Bay and would publish four innovative, benchmark papers about the distribution of marine benthic suspension feeders and deposit feeders.[5,6,7,8] Those papers would become highly influential to the pioneering work of other benthic ecologists, such as Don Rhoads and Dave Young, who worked on the effects of deposit feeders on sediment structure and near-surface water column properties, and also the pioneering work of Bob Berner on the role of borrowing and oxidative-reductive reactions in muddy sediments, especially with regard to sulfide interactions. Although Long Island Sound and Buzzards Bay are both shallow, with average depths of just 70 and 20 meters, respectively, Sanders was, without realizing it, putting himself on a track to "modernize" deep-sea biology with the sampling techniques and protocols he developed. In the process of pursuing his Ph.D. work, he also became one of the first biologists to study species diversity patterns in estuarine environments.

One of his Ph.D. findings also led him to become a carcinologist. Sorting through his sediment samples one day, he came upon a type of most unusual crustacean. It was just a few millimeters long, blind, and had a uniquely unspecialized and homonomously segmented body. All of the specimens were female and rather resembled fairy shrimps, which had long been regarded as primitive crustaceans. He and Hutchinson realized

that he had discovered a totally new kind of crustacean, and what appeared to be an extremely primitive form. Hutchinson advised Sanders to put his thesis work on hold to describe and publish on the animal (Figure 3). This led to the second single-authored paper in his career, in the *Proceedings of the National Academy of Sciences U.S.A.*, in which he named the new subclass Cephalocarida, new family Hutchinsoniellidae, and new genus *Hutchinsoniella* (the family and genus names being in honor of his advisor).[9] (His first paper was also single-authored, on the herring of Block Island Sound found along the southern coast of Fisher's Island, New York, Connecticut and Rhode Island.) Today, Cephalocarida is considered a class in the large crustacean superclass Altocrustacea.



3. Drawing of *Hutchinsoniella macracantha* by the renowned French zoologist Claude Delamare-Debouteville, drawn as a gift for Howard Sanders. The inscription reads, "This portrait of *Hutchinsoniella macracantha* to its unquestionable and unquestioned father, in friendly and grateful homage." Translation by Philippe Bouchet. (Photo courtesy of Robert Sanders.)

As it turned out, 1955 would be a pivotal year for Sanders. He was awarded his Ph.D. (at the age of 34), his son Robert was born, his discovery of Cephalocarida made national news, and he was offered a position at WHOI. The January 27, 1955, issue of the *New York Times* published an article on Sanders' discovery of a new subclass of Crustacea, featuring a photo of him with a photo of *Hutchinsoniella macracantha*, describing it as "a tiny missing link" among the Crustacea.

Shortly after Sanders received his degree, WHOI Associate Director Alfred Redfield appointed him to the staff as a research associate in marine biology working for senior oceanographer Bostwick (Buck) Ketchum. Ketchum wanted to expand his own work into intertidal benthic ecology, especially in the Cape Cod area, so Sanders was the perfect choice as an assistant. Sanders went on to be promoted to associate scientist in 1963 and senior scientist in 1965. He worked at WHOI for his entire career and was given the title Senior Scientist Emeritus when he retired in 1986.

When Sanders first joined the faculty at WHOI, the family lived in a home they rented on Woods Hole Road, about two miles north of the village of Woods Hole. With the impending birth of their second son, Mark, in 1958, they bought a home at nearby 7

4. Howard Sanders family at home, ca. early 1980s. (Photo courtesy of Mark Sanders.)

Oyster Pond Road, and that is the house where Bob and Mark grew up (Figure 4). The house was just a few minutes' walk from Quissett Harbor in one direction, and a 15-minute walk to Vineyard Sound in the other direction. A path behind their house led to an extensive trail system in the Falmouth area.

At home, around the dining room table, Sanders would update the family on the most exciting events in his work. He was perhaps most passionate about his deep-sea research, but as his oil-spill research grew, this also became a spirited part of his professional life.

Sanders worked hard, typically working in the evenings after dinner until around 8 o'clock, when he would come downstairs for a tea break with the family. This usually included Earl Grey tea, cheese, and crackers (saltines). His children remember his excitement about new deep-sea discoveries and especially his work with *Alvin*.

After the move to Falmouth, Lillian became actively involved in town affairs, including working for the Visiting Nurse Association. In 1972, she began working at Mary Mavor Batik, the Woods Hole store of artist and close friend Mary Mavor, wife of James Mavor, a WHOI engineer who helped design the *Alvin*. Lillian eventually came to manage the store, and in 1980 the shop's name was changed to From Far Corners. In 1986, Lillian bought the store, running it until 1992. She undertook many buying trips around the world for the store, visiting China, Thailand, Nepal, Senegal, Peru, and Eastern Europe, among others. Through all this, Lillian also provided tremendous support in taking charge of family management and household maintenance, allowing her husband to pursue his science.

On a New York buying trip in 1990 she suffered a serious stroke, and for several weeks afterward it looked as if she would never be able to walk again. But being a determined woman, she eventually went from walker to cane and became mobile again. As Howard's Alzheimer's disease progressed and her own ongoing mobility regressed, she was still determined to keep him at home at all costs. As his dementia progressed and his speech shut down, the last topic he held on to was a memory of the summer he spent working in Alaska in 1948 for the Fish and Wildlife Department as an undergraduate student. Howard and Lillian lived in the same house that their children grew up in until Howard

entered an assisted care facility. Thereafter, Lillian visited him daily and attended to his needs until his death in 2001, and not long after that Lillian went into residential care herself.

Deep-Sea Ecology

During the late nineteenth century, several nations launched expeditions focused on deep-sea biology. For example, the British *Challenger* expedition (1872–1876), sampling at depths up to 5,176 meters, had proven that the deep-sea was not devoid of life, as many had believed. In the United States, Alexander Agassiz used the U.S. Coast Survey steamer *Blake* from 1877 into the 1880s, then the U.S. Fish Commission steamer *Albatross* from 1891 to 1900 and again in 1904–1905, to investigate the deep sea.[10,11] Agassiz, who was trained as a mining engineer and financially underwrote much of his deep-sea work, introduced new techniques such as wire rope for trawling.[12] Around the turn of the nineteenth century, Prince Albert I of Monaco funded deep-sea research from his yachts, notably the *Princesse-Alice II*, trawling to depths of 6,035 meters off the Cape Verde Islands in the Atlantic. Other European nations also undertook deep-sea explorations, including the first Danish *Galathea* expedition of 1845–1847,[13] and the German *Valdivia* expedition of 1898-1899. However, after publication of the last *Challenger* Report in 1895, deep-sea biology seemed to largely fall out of favor in the scientific world.

After World War II, deep-sea exploration began a gradual but persistent renewal. Stimulating this resurgence were the high-profile round-the-world expeditions of the Swedish *Albatross* (1947–1948)[14,15,16] and the second Danish *Galathea* expedition (1950–1952).[17,18,19] WHOI's director, Paul Fye, was intrigued by the idea of deep-sea research and also saw the potential for significant government funding. He developed a new vision for the institution that would focus keenly on offshore ecology, including benthic ecology. His strong encouragement of the research staff to move in that direction understandably disgruntled a number of researchers, who had little interest in "moving offshore" with their research. Some even left WHOI over what came to be called "the palace revolt." According to colleague Bob Hessler, Sanders was told to either move into blue-water ecology or find another job.[20] Many years later, Eric Mills was told by Buck Ketchum that it was he who had told Sanders to move into deep-sea biology.[21] Sanders, with his equable personality, chose to stay at WHOI. Although Sanders initially appeared to be unhappy with such redirection, he was also intrigued by the idea of adapting his shallow-water sampling protocols to the deep sea.[22] He believed he could adopt the same kinds of protocols and sampling devices used in his successful studies in Long Island

Sound and more recently in Buzzards Bay, to address similar questions of ecological biogeography in much deeper waters. He began with the audacious idea of a benthic sampling transect from Martha's Vineyard, an island offshore from Woods Hole, to Bermuda that became known as the Gay Head-Bermuda Transect.[23] Gay Head is named after a cliff on the southwest corner of Martha's Vineyard composed of bands of colorful sediments.

The first "shakedown" cruise of the Gay Head-Bermuda Transect was on WHOI's original research vessel, the ketch *Atlantis*, from May 20–25, 1961. On that first cruise were Sanders and his new assistant Robert Hessler. Hessler had just obtained his Ph.D. at the University of Chicago under paleontologist Marvin Weller and was recommended to Sanders by Ralph Johnson, also a University of Chicago professor. Johnson, a close colleague of Sanders, introduced Bob to Howard, who was looking for someone to help with the study of *Hutchinsoniella*, and Bob, whose Ph.D. involved a study of trilobites, was hired.

Soon thereafter, in tandem with work on cephalocarids, deep-sea benthic collecting cruises began. The initial device they used was an anchor dredge for collecting large samples; and it was deployed successfully during the first 11 cruises (1960–1963). But it became clear that a new sampling device was needed to collect the larger surface-dwelling organisms. The most important of these for Sanders' collections was the epibenthic sled. It was designed by Hessler and incorporated new ideas with features gleaned from a number of earlier designs, and with contributions by George Hampson and Rudolf Scheltema.[24] This device would go on to become standard equipment for sampling soft-bottom deep-sea benthic habitats for a number of years. Indeed, it was adopted by the French for their first deep-sea program led by Lucien Laubier, probably in 1972 for the BIOGAS 1 cruise on their ship *Jean Charcot*, and used until the late 1980s, when sampling by box core became the norm. During all that time, the French designated samples taken with the epibenthic sled as DS for *Drague Sanders*.[25] It would be the key instrument (along with fine-mesh screens of 0.42 mm used to retain small animals for preservation and identification) that revealed the very high diversity of deep-sea benthic fauna.

During the 1960s, Sanders attracted a group of young and enthusiastic students, and they set out to devise new ways to sample deep seafloor sediments. Until the twentieth century, most of what we knew about life at great depths was based on the nineteenth century studies previously mentioned. The British *Challenger* Expedition (1872–1876)

5. Left-to-right: Rudy Schelteema, George Hampson, Howard Sanders, unidentified crew member. Anchor dredge with sediment aboard the *Atlantis*, 1961. (Photo courtesy WHOI.)

under the scientific direction of C. Wyville Thompson had been the first to disprove the long-standing idea that the deep sea must be a barren wasteland, bereft of life because of the lack of sunlight. But that early and haphazard research had still suggested that species diversity in the deep sea was very low. Sanders' deep-sea program would turn those ideas on their head. Earlier work had been greatly biased and hindered by the relatively primitive sampling gear used and an inability to sample small benthic infaunal organisms. With Sanders' new sampling devices, tested and refined during his extraordinary Gay Head-Bermuda Transect expeditions, the group began exploring the abyssal plains of the Atlantic Ocean, documenting that they are not species poor at all, but are some of the most biologically diverse habitats in the sea (Figures 5 and 6). Sanders and his colleagues would go on to document unexpectedly high deep-sea species diversity, mostly of small invertebrates living in soft sediments; in some areas, diversities were found to be as high as those recorded in diverse terrestrial habitats such as tropical rain forests.

6. Howard Sanders and science crew aboard the *Knorr* during the February 1972 Guiana Basin expedition. Left-to-right: Fred Grassle (standing), George Hampson (seated), John Allen (seated), Steve Page (seated behind Allen and Sanders), Howard Sanders (seated and dining), Cpt. Emerson Hiller (standing), Bob Morse (standing). (Photo by Isabelle Williams.)

Sanders developed the rarefaction method of comparing samples from a wide range of benthic environments. This involved plotting the cumulative number of species at different sample sizes, the asymptote of this graphic then being used to characterize diversity gradients ranging from estuaries to the deep sea. First proposed verbally at a conference in 1961,[26] Sanders

later published a graph comparing plots from one shallow water station and one abyssal station in a 1965 article.[27] Three years later, he published an article summarizing data gathered from many more samples from a wide variety of sediment types and various regions of the world.[28]

The Gay Head-Bermuda Transect cruises organized by Sanders become legendary for their thorough survey of the deep sea. Sanders usually acted as chief scientist on those cruises, but on occasion others did (for example, Rudy Scheltema, Buck Ketchum, Bob Hessler, and Fred Grassle). Sanders' deep-sea collecting expeditions were made largely on WHOI ships, but he acquired samples for his work from other cruises as well. For example, his longtime research partner and friend John Allen sent him samples from the British *RRS Discovery* 1968 expedition to the Canary Basin, as well as from the 1967 *Sarsia* cruise to the Bay of Biscay (led by Alan and Eve Southward).

Of the thirty research cruises that yielded samples for Sanders' studies, six were on the *Atlantis** (1961–1962), eleven were on the *Atlantis* II (1963-1971), and six were on the *Chain.*** Other ships used included the *Panulirus, Knorr, Oceanus, Sarsia, A. E. Verrill*, and *Discovery*. Sanders participated in at least seventeen of those cruises, thirteen times as chief scientist (1960–1976). Samples came from depths up to 5,000 meters and deeper and included the continental shelf, slope, and rise, the abyssal plain of the Bermuda Rise, and the deeps beneath the Sargasso Sea. Bob Hessler had joined WHOI and Sanders' group in 1960, and he was deeply involved in this project, which produced many papers on crustaceans, annelids, brachiopods, molluscs, and other taxa, as well as ecological studies. Hessler participated on about a dozen of the Gay Head-Bermuda cruises. Sanders and his team would analyze invertebrate distributions by depth, latitude, and sediment types. Sanders would also analyze patterns of diversity on latitudinal and depth gradients, and he became one of the first people to measure productivity in the deep sea. In 1969, this work spurred Sanders to develop the stability-time hypothesis to explain how diversity reflects evolutionary processes over millennial time spans and enormous landscape scales.

* The *Atlantis*, a 143 ft sailboat with an auxiliary diesel engine, was WHOI's first and main research vessel from 1931 to 1964. In 1966 she was sold to Argentina, who made her a research vessel of the National Science and Technology Center (renamed *El Austral*), and she is now a research vessel of the Argentine Naval Prefecture (renamed Dr. Bernardo A. Houssay). Having sailed over 1.3 million miles to date, she is one of the oldest serving oceanographic vessels in the world.

** The *Chain* was one of the 19 Navy diver-class rescue and salvage ships built in 1943 or 1944, but decommissioned in 1946 and reclassified as an oceanographic research vessel in 1958; she was scrapped in 1979.

The high diversity of the deep sea, which is largely uniform in its landscape, begged explanation. Sanders' stability-time hypothesis postulated that the stable conditions of the deep sea and the great age of the abyssal environment enabled competition and niche differentiation to go to completion, resulting in the presence of a high number of species finely partitioned under seemingly uniform conditions.[29-33] The hypothesis stated that young (or stressed) environments would have lower species diversity than old (and stable) environments. Competitive interactions (competitive niche diversification) over long time periods in stable environments, according to Sanders, leads to the evolution of many specialized species with narrow niches.[34,35,36,37] Although the stability-time hypothesis was an important idea that stimulated twenty years of research and studies that tested and critiqued the idea, it was quickly contested.[38,39] Larry Abele and Keith Walters reanalyzed Sanders' original data in 1979 and concluded the hypothesis to be tautological and untestable.[40] In 1983, David Thistle tested the hypothesis in the San Diego Trough using the benthic copepod fauna and found it did not hold up.[41] Paul Dayton and Bob Hessler concluded in 1972 that "high species diversity in the deep sea is more a result of continued biological disturbance than of highly specialized competitive niche diversification [in an undisturbed environment]."[42] The "disturbance vs. stability" argument would generate hundreds of research papers over many years. Thus is science served and advances.

Sanders was not an experimentalist, or perhaps we should say he relied on "natural experiments." This descriptive approach went against the grain of the emerging field of experimental ecology, in which the more intransigent advocates insisted that without controls and manipulation it cannot be called a "true experiment." But, of course, Sanders was doing his natural experiments across time scales of millennia and space scales of thousands of kilometers of seafloor—not amenable to controls and manipulations. Jeff Levinton remembers one summer when Sanders taught a course at Friday Harbor Laboratory and socialized with the pioneering experimental marine ecologist Bob Paine. Despite the possibility, Levinton recalls, "there were no fireworks or criticisms from Bob as I recall. They got along very well. But then again, we were all celebrating Nixon's resignation." But, in fact, the fundamental and field-changing successes of Sanders' research (and the research of many other ecologists) done outside the framework of experimental biology *sensu stricto* showed the great value of conducting natural, or descriptive field experiments, especially across landscape and long time scales. Nevertheless, many narrowly focused experimental ecologists still needlessly continue to devalue such an approach.

WHOI had a long history of innovative deep-water marine research even before Howard Sanders arrived. In the mid-1930s, Maurice Ewing, a young physicist on the faculty at Lehigh University, came to WHOI to use its new deep-sea research ship *Atlantis*. During the summers of 1937, 1938, and 1939, Ewing and his colleagues, including his graduate student Allyn Vine, launched novel experiments using explosions to generate sound waves to probe the structure of the sea floor. In the process, they made profound and fundamental discoveries about seawater properties and how sound propagates through the ocean. In 1940, on the eve of war, WHOI Director Columbus O'Donnell Iselin wrote a letter to the government setting forth "some suggestions as to how the personnel and equipment of his laboratory can be better utilized for the national defense." In 1940, with war raging in Europe, Ewing's group began year-round National Defense Research Council-sponsored operations at WHOI with antisubmarine activities as the major focus. Soon after, geophysicist and engineer Allyn Vine began incorporating this newly gained knowledge. He built instruments (bathythermographs) to measure ocean properties, namely temperature vs. water pressure, and eventually even trained sailors to use them. Vine was a major contributor to the redesign of the bathythermographs that were used on submarines during World War II to detect the ocean thermocline. In 1973, Vine was given an honorary Ph.D. from his alma mater, Lehigh University. Many scientists pursued the marine geophysics research initiated by Ewing (who moved to Columbia University after World War II). Their work culminated in the late 1960s with the unifying theory of plate tectonics and also the recognition that significant oil reservoirs, which make up many of the richest oil fields being exploited today, lay beneath the seafloor.

After the war, Allyn Vine (for whom the *Alvin* is named, in honor of his pioneer work in deep submergence research and technology) would remain at WHOI to spearhead this technology, including the research submersible *Alvin*. Two years after it was commissioned, *Alvin* helped resolve a national emergency by locating a hydrogen bomb that had accidentally fallen into the Mediterranean Sea following a mid-air collision between a bomber and its refueling plane. A decade later, in 1977, *Alvin* was vectored to the first hydrothermal vent community discovered by geologist Bob Ballard's ANGUS (Acoustically Navigated Geological Underwater Survey) camera sled, operated by WHOI, which had captured measurements of a temperature anomaly correlating with photographs of giant clams. On the following day, *Alvin* dove on that site and started its decades-long use by numerous scientists to study seafloor hydrothermal vents all over the world.

In January 1979, Sanders was a participant in the earliest biological expedition to hydrothermal vents in the eastern Pacific Ocean. Photographers from National Geographic and a new RCA underwater color video camera specially designed for use by *Alvin* (and strapped onto its arm) were present during the first expedition to study the vent communities of the Galapagos vents in 1979. Their efforts led to the National Geographic documentary, "Dive to the Edge of Creation." Sanders, Grassle, and Hessler appear in some of the footage taken on the deck of the *Lulu*, *Alvin*'s mother ship. The two trips to the Galapagos vents and another two to those on the East Pacific Rise in 1982 were among a total of eight *Alvin* dives Sanders made to view the biological communities at those exciting sites.

Oil Spill Research

In 1969, the oil barge *Florida* ran aground in Buzzards Bay, off West Falmouth (just up the road from WHOI), spilling 189,000 gallons of oil. The event called to Sanders, and he quickly organized his colleague George Hampson and some students to collect benthic samples of animals, sediments, and seawater (Figure 7). They shared samples with two WHOI geochemists, Max Blumer and Jerry Sass, who had pioneered the use of gas chromatography to detect low levels of organic compounds in such samples. WHOI marsh ecologist John Teal and graduate student Kathy Burns adapted techniques to study the fate and effects of that oil over several years. The goal was to see if they could evaluate the effects of the spill in serious scientific terms. To Sanders, it seemed an important natural experiment that had begun in his own backyard.

7. Howard Sanders sampling at Wild Harbor, 1970s. (Photo courtesy of Mark Sanders.)

Early on, reports on the effect of the oil spills on fauna were mainly descriptive. But the first WHOI technical report on that spill concentrated on the chemist's evaluation of persistence of the pollution eight months after the accident.[43] Until 1972, little information on the long-term effects of the oil was available. This was rectified by the release of a second technical report prepared for the Environmental Protection Agency, the Commonwealth of Massachusetts, and the National Science Foundation.[44] In it, Sanders clearly presented sampling techniques, details about which fauna had been completely analyzed, and the resulting data. He did not include a "conclusion" section but did provide graphed comparisons of living and dead organisms at various oiled

and unoiled stations, discussed data on the large increase in numbers of opportunistic species, and showed that ampeliscid amphipods were more adversely affected by the oil than the polychaetes and bivalves. And yet, this report, along with an undated progress report presented to the Federal Water Quality Association by Sanders (not seen by us), came under a scathing attack in a report by Texas A&M University faculty member J. G. Mackin.[45] Sanders was angry enough to spend what must have been a considerable amount of time writing a detailed rebuttal at the behest of the editor of a short-lived journal, the *New Engineer*.[46] Typical of Sanders' peaceful temperament was that the strongest language he used in his rebuttal was " irritated." The Mackin report, never peer-reviewed and containing numerous glaring errors pointed out by Sanders, was withdrawn, and no copy could be found by us.

The project would go on for ten years, from 1969 to 1979, showing the profound long-term effects of the spill. Sanders' rigorous ecological approach to the spill and its effects set entirely new standards for such work and established a model for assessing the long-term ecological effects of oil spills. From the West Falmouth study, Sanders and his colleagues refuted the prevailing wisdom that oil was gone when it was no longer visible in the water and on beaches. Instead, they showed that oil persisted in marshes and sediments for years and continued to have impacts on ecosystems. Needless to say, this did not sit well with the powerful oil companies, and it led to the WHOI scientists involved in the work coming under vicious attack from the press and by political means. But they stood their ground, published carefully researched peer-reviewed papers and popular articles, and even ended up testifying before Congress.[47,48] On the positive side, several writers were accurate in their reporting on the project's findings. William Wertenbaker wrote a very comprehensive article published in the *New Yorker* magazine in which he explained the details of the spill, the immediate adverse effects on local shellfish, and the sampling efforts that were still ongoing.[49] He interviewed the local shellfish warden, Blumer, Sanders, and even participated in a sampling trip. Before reporting on his interview, Wertenbaker described Sanders as "quiet and soft-spoken, and walks slightly stooped; he has a pink face, pale eyelashes, and a small rust-brown mustache." The article ended by explaining that "the spill showed that some parts of petroleum will dissolve in water—namely, the toxic aromatics—and that petroleum will as readily sink as evaporate." And, as well, "the present study showed that the present means of dealing with an oil spill are ineffective." Wertenbaker went on to describe ideas for refinements in tanker construction that could prevent the occurrence of oil spills, opposition to those ideas as being too expensive, and what would be needed to actually implement the ideas.

A long-time family friend of Williams, Judith Fischer, had met Howard socially in Woods Hole and was a science, energy and environment writer for a large New York metro daily newspaper, and she wrote about the West Falmouth oil spill and its implications for her region of Long Island, New York. She later held a telephone interview with Howard to include his findings on the oil spill in testimony that she had prepared for the county executive of Suffolk County, New York, to give before the U.S. Department of the Interior concerning proposed offshore oil and natural gas exploration on Georges Bank. Sanders' work became an important part of the county executive's testimony. Both the *New York Times* and *Newsday* carried positive editorials about the testimony. She said, "Dr. Sanders was unfailingly polite and patient with me, a non-scientist. He explained his work and answered my questions clearly and understandably. I was privileged to have met him and to have discussed his work with him."

John Farrington, a marine chemist who came to WHOI as a postdoc with Max Blumer just after the spill and collaborated with Teal and others, heralded successive generations of scientists who made WHOI a leader in oil spill research. This included later work on the infamous 1976 *Argo Merchant* oil spill on Georges Bank. The tradition of oil spill research was still thriving on April 20, 2010, when the *Deepwater Horizon* oil rig exploded in the Gulf of Mexico, killing 11 people and causing the largest oil spill in history. Responding to calls from several government agencies, more than 100 WHOI staff—chemists, biologists, physical oceanographers, engineers, and technicians—mobilized a spectrum of equipment and technology to step into the *Deepwater Horizon* fray with scientific expertise.

Crustacean Systematics and Evolution

Sanders' 1955 discovery of cephalocarids shook evolutionary thinking about crustaceans. And as new species and genera of cephalocarids were described, these tiny (2–4 mm long) creatures were found to live almost everywhere in the world's seas. Today there are 12 known species in 5 genera. All are benthic marine detritus feeders, although many seem to have commensal relationships with sedentary polychaetes. Most are associated with sediments covered by a layer of flocculent organic detritus, although some have been found in clean sands. They occur from the intertidal zone to depths of over 1,500 meters throughout the Pacific and Atlantic Oceans and the Mediterranean Sea. Their body is composed of a head, an eight-segmented thorax, and an eleven-segmented limbless abdomen. The thoracic legs are flattened paddles ("phyllopods"), as seen in fairy shrimp and other members of the closely related class Branchiopoda. Both cephalocarids and many branchiopods (e.g., fairy shrimp) are suspension feeders that use their setose

phyllopods to stir up bottom sediments and then form a boxlike "filter press" to capture suspended particles (a mechanism also seen in some malacostracans). Also, in cephalocarids and most branchiopods, the heart is a long tube with many segmental ostia, and the ganglia associated with each body segment remain separate along the ventral nerve cord. The three closely related classes of Cephalocarida, Remipedia, and Branchiopoda are largely anamorphic—the nauplius larva grows by a series of molts that add new segments and appendages gradually as the adult morphology appears.

In morphology-based phylogenies, for many decades, cephalocarids and branchiopods (fairy shrimps, tadpole shrimps, cladocerans, among others) were viewed as the most primitive Crustacea. Then the 1981 discovery by Jill Yager of remipedes, strange vermiform crustaceans first collected from a cave in the Bahamas, gave the carcinological world an even larger turn than had the cephalocarids.[50] The combination of features distinguishing remipedes was puzzling, for they possess characteristics that seemed primitive (such as a long homonomous trunk, double ventral nerve cord, segmental digestive ceca, and cephalic shield) as well as some attributes traditionally recognized as advanced (such as maxillipeds, nonphyllopodous [though flattened] and biramous limbs). They swim about on their backs as a result of metachronal beating of the trunk appendages, similar to anostracan branchiopods. At an annual meeting of the Crustacean Society in Seattle, when Yager first presented her discovery to the scientific community, Bob Hessler got so excited that he jumped up from the audience, walked rapidly onto the stage, and began pointing out the primitive attributes of the creature being shown by a slide projector. Others in the audience chimed in excitedly, everyone realizing the importance (and enigma) of this new creature that Yager was calling a remipede. Bob and Jill would go on to produce a detailed anatomical atlas of remipede skeletomusculture.[51]

The powerful bias for long, multi-segmented crustacean bodies (such as those of cephalocarids, branchiopods, and remipedes) to be *a priori* considered primitive probably has roots in the long-held belief that the multi-segmented annelids and arthropods were sister groups. But alas, as in many other cases of animal phylogeny, molecular biology was destined to overturn those notions. Beginning with the pioneering work of Kathryn Field, Rudy Raff, and colleagues, and consistently supported by molecular analyses since, we now know that annelids belong to the clade Spiralia, whereas arthropods belong to the Ecdysozoa.[52] The segmentation in the two phyla shows no direct ancestral link, despite its developmental similarity. And today, although Cephalocarida, Branchiopoda, and Remipedia are still united (as the clade Allotriocarida), arthropod molecular phylogenetics has turned the tree of Crustacea almost upon its head.[53–57] We now know

that Pancrustacea (Crustacea+Hexapoda) comprises three great clades: Oligostraca (Ostracoda, Mystacocarida, Branchiura, Pentastomida), Multicrustacea (Thecostraca, Copepoda, Malacostraca), and Allotriocarida (Cephalocarida, Branchiopoda, Remipedia, Hexapoda). Hexapoda (insects and their kin) appears to have its ancestry in the clade Allotriocarida, as a sister group to the remipedes (the two forming a clade recognized as Labiocarida).[58] The first branch off the Crustacea tree of life is not the many-segmented Allotriocarida, but the Oligostraca—short-bodied, possibly ostracod-like creatures similar to Cambrian stem and crown group fossil forms.

In addition to the idea that annelids and arthropods were sister groups, early assumptions of long, serially homonomous crustaceans being primitive were also influenced by two scientifically flawed lines of reasoning. First was an underlying naive notion that evolution always moved from "simple" toward more "complex," and the second was a reliance on largely tautological narratives of ur-crustacean body morphology as a starting point (i.e., the hypothetical ancestor approach, wherein a bias for annelid-like bodies suggests cephalocarids, branchiopods, and remipedes were primitive crustaceans). The new view, of Oligostraca being the earliest branching Crustacea, suggests that stem-line forms may have had a short thorax with gonopores on the fourth thoracic somite—nothing at all like cephalocarids, branchiopods, or remipedes.

Academic Influence

To the best of our knowledge, Sanders never served as principal advisor (of record) for any graduate students. This may be because his university appointments were non-tenure-track (courtesy appointments) and university bureaucracy excluded him from that role. He was a member of numerous student thesis committees, however, and clearly played an important role in mentoring a great many graduate students who consider him a primary intellectual influence during their formative years.

In 1968, WHOI Director Paul M. Fye proposed a joint degree-granting program with Harvard University and the Massachusetts Institute of Technology (MIT), even though there were few faculty members at MIT with scholarly interests that overlapped with those at WHOI. Harvard rejected the proposal, perhaps because of ongoing debates at the time between the molecular biologists and ecologists (a debate that resonated at other universities through the 1970s). But MIT signed on, and the first such Ph.D. degree was awarded in 1970. Nevertheless, Sanders got his own courtesy appointment at Harvard and was able to mentor students there anyway, though apparently never serving as a major advisor.

A great many people were mentored by Sanders or influenced by his work, both as graduate students (Lion Gardiner, Eric Mills, Michael Rex, Donald Rhoads, Jacek Sulanowski, Craig Smith) and as emerging young Ph.D.s (Bob Hessler and Fred Grassle). Some of these folks worked in Sanders' lab right after completion of their Ph.D. in positions that would be called postdocs in today's world. Other working visitors to the Sanders lab included Alan and Eve Southward (Plymouth Marine Lab), Claude and Françoise Monniot (Muséum National d'Histoire Naturelle), Alexey Kusnetsov (Shirshov Institute of Oceanology), Ken Grange (New Zealand Institute of Oceanography), Carmela Cuomo (Yale University), Bob Whitlach (University of Connecticut), Kristian Fauchald (University of Southern California), Andrew Carey (Oregon State University), Victor Gallardo (Universidad of Concepción, Chile), and John Gage (Dunstaffnage Marine Lab).

Lion Gardiner *** spent three years in Sanders' lab working on his Ph.D. research for a degree at the University of Rhode Island. Sanders was on Gardiner's Ph.D. committee, which was chaired by Saul Saila and also included Donald Zinn and Mel Carriker. Lion's thesis became a monograph on the deep-sea family Neotanaidae.[59] While working in Sanders' lab, Lion had access to all of the neotanaids from the Gay Head-Bermuda Transect as well as specimens sent to him from museums all over the world. He made detailed descriptions of all twenty-eight species known to him at the time. He described ten new species (eight of which still stand) and two new genera, and he redescribed the remaining eighteen species. He found nine neotanaid species from forty-six of the Gay Head-Bermuda Transect samples, most from greater than 2,000 meters in depth, five of which were new to science. He named one species from the Gay Head-Bermuda Transect after Howard Sanders (*Neotanais sandersi*) and another from more than 5,000 meters depth in the southeast Pacific after Bob Hessler (*Neotanais hessleri*). Between 1966 and 1968, Lion participated in five of Sanders' deep-sea cruises. Lion went on to become a professor at Rutgers University in 1969 and became interested in helping higher education move from a tradition-based to a research-based, theory-guided enterprise. Today he remembers Sanders as the main person who intellectually oversaw his Ph.D. work.

Eric Mills (now Professor Emeritus of History of Science, Dalhousie University) recalls Sanders having a formative influence on his science and his life. They first met in the summer of 1959, after Sanders had invited Eric (sight unseen) to work as a summer

*** Lion Gardiner is a lineal descendant of Lion Gardiner, the original English settler and large landholder on eastern Long Island.

assistant, especially with the field collecting of sediment and animal samples on Barnstable Flats on Cape Cod. That experience would inspire Eric to go on to Yale for a Ph.D., although he undertook a good deal of his graduate research in the Sanders lab. Mills also went to sea on some of Sanders' Gay Head-Bermuda Transect deep-sea cruises. The surprising story of how Eric and Howard met is worth telling. Eric was an undergraduate finishing an honors bachelor's degree at Carleton University, in Ottawa. During his senior year (1958–1959), he took a course on arthropods taught by Herbert H. J. Nesbitt, who assigned to Eric the now famous paper by Sanders titled "The Cephalocarida and Crustacean Phylogeny."[60] Nesbitt liked Eric's essay on the paper so much that he suggested he send it to Sanders at WHOI. Neither Nesbitt nor Eric Mills had ever met Sanders. A few weeks later Eric received a reply from Sanders thanking him for sending his essay and, to everyone's surprise, inviting Eric to spend the summer of 1959 working with him on the Cape Cod benthic project. This style (and good judgment) of Sanders became one of his hallmark features. That summer, Eric worked alongside Sanders, George Hampson, and Esther Goudsmit, and their work would be published with all of them as coauthors.[61] But Sanders' influence on young Eric didn't stop there. Eric had been turned down by Harvard for graduate school and was dealing with some other personal issues. Sanders wisely recommended that he take some time off and then apply to work under Hutchinson at Yale. And early in the fall of 1960, Eric found himself in grad school at Yale, being supervised by G. Evelyn Hutchinson and Gordon Riley. It was then that Sanders offered space in his lab and access to WHOI fellowships for Eric's work. Eric would graduate with his Ph.D. from Yale and take a position at Queen's University in Canada, and for the next four summers he would teach an invertebrate zoology course at the Marine Biological Laboratory in Woods Hole. Eric also joined Sanders on a number of the Gay Head-Bermuda cruises, beginning with the original *Atlantis*, and later on cruises with its successor *Atlantis II*. He remembers Sanders as being "an intellectual force, although in the gentle, unassuming, and almost imperceptible way that was so characteristic of him," and he considers Howard Sanders to have been "more than a great scientist, he was a great person."

Another Ph.D. student mentored by Sanders was Michael Rex, through Harvard University. Rex's other committee members were Ernst Mayr and Kenneth Boss. Sanders was Rex's main supporter, providing the deep-sea specimens he used for his thesis research, and Rex (now at the University of Massachusetts, Boston) remembers Sanders fondly. Rex's 2010 book with Ron Etter, *Deep-Sea Biodiversity: Pattern and Scale*, is dedicated to Howard Sanders and Bob Hessler. Rex and Sanders published a

landmark paper together in 1993 on global scale latitudinal patterns of species diversity in the deep sea.[62] After Sanders' death, Rex worked with George Hampson, John Allen, and Carol Stuart to see that his massive collection of molluscan material, as well as the remaining unsorted sediment samples from his Atlantic Ocean work was deposited in the Museum of Comparative Zoology (MCZ) at Harvard (Figure 8).

8. George Hampson preparing Sanders' remaining sediment samples stored in 3-gallon jugs, prior to transfer to the Museum of Comparative Zoology (Harvard University) in 2002. (Photo courtesy WHOI.)

Although Sanders was not on his committee, Ron Etter (now at the University of Massachusetts, Boston) remembers Sanders' cordiality during a postdoc at WHOI (1989–1991), which led to Sanders giving Etter a collection of bivalves from his many deep-sea expeditions that formed the basis of Etter's work for decades to come.

Donald Rhoads (now Kerner Emeritus Professor of Geology at Yale University) first met Howard Sanders around 1961 or 1962, when Rhoads was a master's degree student at the University of Iowa. He had just received a predoctoral fellowship at WHOI, where he planned to work at the interface of sedimentology, paleoecology, and classical benthic ecology. Howard and others (such as Rudy Scheltema, Hal Turner, and George Hampson) mentored Rhoads at WHOI. Later, as a Ph.D. candidate at the University of Chicago, his mentoring group expanded to include Fred Grassle and Bob Hessler. One of his most important and memorable experiences was working on Sanders' Gay Head-Bermuda Transect project, and Rhoads was on one of Sanders' earliest cruises for that project aboard the ketch *Atlantis* in the early 1960s. Rhoads' Ph.D. thesis built on Sanders' massive Buzzards Bay intertidal study, work that was published from 1958 to 1961. Rhoads' work found that bioturbation is a major factor controlling sediment stability and community tropic structure. Out of this arose the concept of "trophic group amensalism," now recognized as a major ecological process structuring level soft-bottom communities.[63]

John Culliney, recently retired from Hawaii Pacific University, was introduced to Sanders by Ruth Turner. While he was working with her as a postdoc at the MCZ at Harvard,

they set up a lab at the Marine Biological Laboratory (MBL) at Woods Hole in space they rented with Office of Naval Research (ONR) funding. They were mostly engaged in developmental biology and larval ecology of wood-boring bivalves. Ruth wrangled the invitation for John, who was invited to participate on Sanders' research cruise to the Argentine Basin in 1971. He recalls that Ruth thought they might find some pieces of waterlogged wood with new borer fauna on the deep-sea floor off the Rio de la Plata. He remembers being on deck with several people during the cruise before one of the first deep sample runs, when members of the group took turns sketching their favorite, hoped for, deep-sea benthic invertebrate to turn up in the sample on the canvas apron of the anchor dredge. Although his memory is murky, he thinks he tried to draw a *Neopilina*. Sanders appeared, picked up the pen, and proceeded to sketch a neat trilobite, stimulating the procession of additional hastily rendered critters. Along with publications of several papers about bivalve larvae and teredo shipworms with Ruth Turner, Culliney also became an author of several popular Sierra Club books. In his chapter on oceanic oil in *Forests of the Sea*, he states that the efforts of Sanders and Blumer to describe the behavior of oil in the marine environment generated "vituperative personal and professional harassment that seems to emanate from the dominion of big oil." John notes that Sanders was angry at the misrepresentation of his research and particularly worried "over the effect …on congressmen and federal resource managers.…"[64]

Jacek Sulanowski spent two years in Sanders' lab "picking invertebrate samples" for Sanders while finishing up his Ph.D. at the University of Chicago, following the death of his advisor, Ralph Johnson. Jacek's conversations with Sanders about crustacean phylogeny, in the lab and at the Sanders home, sparked an interest that would influence his teaching career in paleontology at Bridgewater State University, where he was hired in 1978. While at WHOI, Jacek also helped Sanders with his oil spill work, including the 1976 *Argo Merchant* grounding on Nantucket Shoals that spilled nearly eight million gallons of heavy fuel oil, and the 1977 grounding of the oil barge *Bouchard #65* on Cleveland Ledge in Buzzards Bay that spilled 100,000 gallons of #2 fuel oil.

Craig Smith, now retired from the University of Hawaii, first worked with Sanders in 1976, as "starry-eyed undergraduate from Michigan State University" (as he puts it) in the summer Student Fellowship Program at WHOI. Sanders sponsored Smith in his lab and took him on his first oceanographic cruise on the new *Oceanus*, sampling the Gay Head-Bermuda Transect. Craig remembers Sanders being so seasick on that cruise that he was "operating only at 20% capacity," yet still having fun and never missing the arrival of a single sample on the ship's deck (mainly epibenthic sled and box core sampling). Seven

years later, Sanders and Fred Grassle sponsored Craig as a WHOI postdoc after he'd completed his Ph.D. with Bob Hessler at Scripps Institution of Oceanography. During this stay in the Sanders lab, Craig undertook research on colonization and successional processes in the intertidal of Barnstable Harbor. Craig remembers Howard Sanders as a role model in the care and effort he put into every aspect of his science and even his careful use of resources (e.g., gathering up half-spent pencils from his lab to use at home). In Craig's words, "Howard served as a model for me throughout my 70+ research expeditions in oceanography. His modesty and appreciation for humanity in all its forms has inspired me throughout my career. The world needs more wonderful people like Howard Sanders."

Bob Hessler and Howard Sanders struck up a long-lasting friendship and research partnership driven by their interests in primitive crustaceans and the deep sea and, perhaps, their similar temperaments. They began working together in 1960, when Hessler joined the scientific staff at WHOI after completing his Ph.D. at the University of Chicago (just a few years ahead of Fred Schram, another notable crustacean biologist who earned his Ph.D. at Chicago). By all appearances, Sanders played a key role in Hessler's appointment at WHOI. It was a perfect marriage: Sanders mentored Hessler in benthic ecology and Hessler taught Sanders crustacean systematics.

The benthic samples from Sanders' Gay-Head Bermuda Transect gave Hessler an immense amount of material to use in his career as a crustacean biologist. The transect showed that the Isopoda were a major contributor to the deep-sea fauna, and Hessler used these data to contribute several taxonomic works on the isopods, choosing the asellote family Desmosomatidae to describe in great detail. Hessler found that of the thirty-nine desmosomatid species collected along the transect, twenty-nine were new to science; in addition, many species were present in numbers large enough to allow a detailed analysis of development, dimorphism, and individual variation.[65] Although Hessler moved to Scripps in 1968, he and Sanders continued to undertake important projects together on deep-sea biology. In fact, Hessler became one of Sanders' most engaged and long-term research partners, and they would publish twenty papers together between 1962 and 1985 that described new species of crustaceans (and even priapulans) and patterns of diversity and faunal zonation in the deep sea based on data from the Gay Head-Bermuda Transect. Their papers described new species of Cephalocarida in the genus *Sandersiella*, a new species in a new genus *Hirsutia* for which they erected the new order Mictacea,[66,67] and added to the descriptions of two species of bathyal *Nebalia* belonging to the Leptostraca.[68] In addition, their detailed anatomical descriptions of the

reproductive system of *Hutchinsoniella macracantha* and larval development of *Lightiella* remain benchmark works fundamental to our understanding of Crustacea.[69,70]

Sanders' children have many fond memories of visits by Bob Hessler and his wife Anita at their home. One of Hessler's Ph.D. students, Scott France, would go on to work on deep-sea biology in the Pacific and describe patterns of deep-water crustaceans and corals, eventually using molecular biology to probe evolutionary questions about deep-sea life. France's first postdoc was with Richard Brusca and included developing monographs on two groups of deep-sea isopods, the genus *Rocinela* and the family Cirolanidae.[71,72]

Rudolf and Amelie Scheltema arrived full-time in Woods Hole in 1960. Rudy had just received his Ph.D. from the University of North Carolina, Chapel Hill, with his dissertation entitled "Effect of the Substratum on the Metamorphosis of the Intertidal Gastropods *Nassarius obsoletus* and *Nassarius vibex*." His lab was next door to Sanders' lab, and they became colleagues and friends with common interests in the biology of marine invertebrates. Rudy immediately joined Sanders on the Gay Head–Bermuda sampling cruises, participating in most of those, often as chief scientist, during the 1960s. His interest turned to the transport of larvae of benthic animals, both those living in shallow water and the depths. Over the years, he collected a huge number of plankton samples from all over the world, and these were examined for larvae present in the plankton. He even invented a name for those benthic larvae that could survive in the plankton for months and still remain competent to settle when the right opportunity arose. He called such larvae "teleplanic" (for "far-wandering"). Rudy was a meticulous and careful author, and when it came time to write to the WHOI administration in support of Sanders' appointment as Scientist Emeritus he wrote a far more thorough letter than those written by other members of the Biology Department. He wrote in descriptive detail of Sanders' contributions to the major biological oceanographic fields of taxonomy, deep-sea biology, and oil spill research (this recommendation is still on file in WHOI's Biology Department).

Amelie, meanwhile, was looking for a project. She had received her bachelor's degree in geology from Bryn Mawr College, had taken graduate courses in geology, and then joined the editorial staff at the University of North Carolina Press while Rudy was in graduate school. By 1969, her sons were in school, and she took the opportunity to take a course in invertebrate zoology taught by Ralph Johnson at the Boston University Marine Program held in Woods Hole. A few years later she joined Howard on his research cruise to the Argentine Basin. At about that time, Howard came to her rescue with

an enormous project. He offered her his entire collection of the molluscs then called Aplacophora for study. She leapt at the chance and by 1990 was one of six world experts on the taxonomy, morphology, and biology of these animals, particularly the Caudofoveata that were very common in the deep-sea samples. Her final tally of new described species was sixty; also, two species and one genus have been named in her honor. In 1992, she received her Ph.D. from the University of Oslo. And this was all due, in no small part, to the initial generosity of Howard Sanders.

Fred and Judy Grassle came to Woods Hole in 1969, Fred as an assistant scientist in Sanders' lab. Fred and his wife Judy, who was from Australia, had gotten their Ph.D.s at Duke University after which Fred had a Fulbright at the University of Queensland in Brisbane, Australia. Because Judy had been in the United States on a student visa that required her to leave for two years at the completion of her studies, Fred arrived at WHOI before her. WHOI petitioned Massachusetts senator Ted Kennedy for help in granting a waiver to allow Judy early entry into the States; the waiver was granted, and Judy was able to enter three months early, arriving in late 1969.

Fred initially worked with Sanders on both the local West Falmouth oil spill and deep-sea ecological questions. By this time, Howard and Fred were using a 0.297-millimeter mesh sieve for screening samples, allowing collection of many smaller invertebrates, including some meiofauna and larvae. This allowed them to find newly settled larvae in some of the later West Falmouth collections as well as ampeliscid "eyeballs" as indicators of dead amphipods that had been killed by the oil. For deep-sea work, Fred led the way for WHOI to begin using the Sandia 0.25 m^2 box corer to obtain excellent undisturbed benthic samples that, in addition, provided accurate densities of the collected animals. Fred also started efforts to experiment on deep-sea fauna in situ. Using *Alvin*, Fred designed and deployed boxes containing defaunated sediment onto the seafloor to be collected after a known period of time. This allowed him to do some recolonization as well as feeding experiments on deep-sea animals. Fred led the first two biological expeditions to the Galapagos hydrothermal vents as chief scientist and became a well-known benthic ecologist. He was granted tenure at WHOI in 1977 and promoted to senior scientist in 1983. Fred left WHOI in 1990 to establish the Institute of Marine and Coastal Sciences at Rutgers University. Fred had several grad students while at WHOI, including Cheryl Ann Hannan, Jeremy Collie, Tracy McClellan, Cindy Van Dover, and Paul Snelgrove, although, at that time, some of the institution's scientists had little or no interest in supervising students. Cindy subsequently qualified and worked as an *Alvin* pilot before moving on to an academic research career.

After arrival in Woods Hole, Judy was given space in H. Burr Steinbach's lab at the MBL where Lucena Barth was very helpful as Judy was writing up her research on box jellies that she had started in Brisbane. However, she soon became very caught up in the West Falmouth oil spill research with a special interest in the capitellid polychaetes. These opportunistic worms had undergone a huge population explosion following the West Falmouth oil spill. These worms, initially thought to be *Capitella capitata*, were collected from the West Falmouth oil-contaminated marsh and cultured in Fred's lab at WHOI. It became apparent that at least six sibling species were present in the samples leading to many questions about genetic differences between and among species. Similar morphologically, these sibling species showed distinct differences in life history and reproduction as well as in terms of genetics. In 1972, the cultures were transferred from Fred's lab to Judy's lab at MBL. Judy, then a scientist at MBL, maintained those cultures at MBL and later at Rutgers University. *Capitella* sp. I, was the provisional name given to the species that has been maintained in culture by multiple scientists for about fifty years, for experiments on a variety of subjects. Finally, a close examination and redescription of the type species of *C. capitata* from Greenland established a baseline, allowing sibling species to be compared, described, and named. Thus, *Capitella* I was formally designated as *C. teleta*.[73]

Sanders also mentored Isabelle (Izzie) Williams, who first began working at WHOI, in the Sanders lab, in 1969, as Lion Gardiner was just finishing up his Ph.D. thesis. Izzie was originally hired to work for both Sanders and Rudy Scheltema because she had experience in paraffin sectioning and preparation of histological slides. The idea was to study the reproduction of seven species of protobranch nuculid bivalves. There were three local species living in shallow water and four species from the deep-sea that were found very commonly in Sanders' benthic samples. She made histological preparations of whole specimens following their identification to species, measurement of shell length, and decalcification of the shell. This allowed examination of the gonads and determination of egg size during different seasons of the year. This might have been the only paper authored by both Sanders and Scheltema, but a very long delay in completion of the manuscript meant that it was not published until eight years after Sanders' death.[74]

Within a few years, Izzie had gone on three research cruises with Sanders. At the conclusion of their research cruise to the Guiana Basin, Izzie, a former spelunker, joined Sanders in visiting Cole's Cave in Barbados. This was four years after Howard (probably along with Bob Hessler) had had the opportunity to explore the famous Bat Cave on Table Mountain, South Africa, to look for cave-dwelling crustaceans. Williams continued working at WHOI, largely with Fred Grassle (on benthic invertebrates) and Rudy

Scheltema (on larval development of benthic animals). Grassle encouraged Williams to learn how to identify tanaid species as they were very common in deep-sea sediments and because he was interested in determining species diversity levels in the deep sea. Scheltema encouraged Williams to take numerous plankton samples, even sending her out as chief scientist on a four-day cruise on the *Gosnold* to look for teleplanic larvae in the Gulf Stream. In 1990, she left WHOI to take up a career in environmental consulting. However, Izzie still remains a guest investigator at WHOI.

Izzie recollects always looking forward to the days and ongoing projects in Howard Sanders' lab, usually working closely with his longtime lab manager, George Hampson. She did a good deal of sorting with the benthic samples, and that provided her with a broad overview of invertebrate taxonomy that built a foundation for her future career work. She also remembers Sanders being a bit absent-minded, such as picking up her Rapidograph pen and carrying it in his shirt pocket for months before it was discovered, or forgetting to renew his driver's license for over a year! Izzie and her husband Sandy enjoyed many dinner parties at the Sanders home in Quissett, Massachusetts, as well as attending the wedding of Bob Sanders that took place at Fenno House on the WHOI campus, where Howard was eager to introduce them to Evelyn Hutchinson. They also enjoyed Howard Sanders' retirement party at the Dome Restaurant (built by students of Buckminster Fuller) in Woods Hole in 1986. During her years working at WHOI, she and her husband became good friends with John Allen and his second wife, Margaret, a friendship that lasted many years and included visits to Millport to spend time with the couple. These visits only stopped after John suffered a debilitating case of shingles. When Amelie Scheltema died, Izzie volunteered to clean out her half of the shared Scheltema lab. This entailed shipping forty-two boxes of specimens (including many type specimens of Aplacophora species) to universities and museums around the world; it was a project that took several years to complete. Meanwhile, Rudy Scheltema, then a WHOI Scientist Emeritus, began suffering from dementia, so Izzie began cleaning out his office as well. Much of Rudy's planktonic collection went to the MCZ at Harvard.

George Hampson graduated from Northeastern University, where he had played football. In 1961, after a stint in the National Guard, he started working at WHOI for Howard Sanders. In the early to mid-1960s, Hampson and the Sanders family would go together once a year to watch the Boston Celtics play basketball in the old Boston Garden arena. The arena was designed by boxing promoter Tex Rickard, who also designed the third iteration of New York's Madison Square Garden (when the Boston arena first opened in 1928 it was called Boston Madison Square Garden).

By 1969, when Isabelle Williams first met him, he had become a highly skilled technician and basically lab manager. He ably instructed a parade of young research assistants on how to process benthic samples, pick animals from the sediments, and categorize them taxonomically. He had helped design the final version of the WHOI epibenthic sled and had used scuba equipment to dive on it in shallow water to ensure that it was collecting sediment as planned. He was crucial in operating heavy sampling equipment at sea and sorely missed during the Argentine Basin cruise, when, after flying as far as Santiago to meet the ship in Montevideo, he had to fly home because of a family emergency.

George tried his hand at being a taxonomist with the publication of a paper that distinguished two populations of *Nucula*, the Atlantic nut clam, found in Buzzards Bay.[75] He described a new species, *N. annulata*, as distinct from *N. proxima*, based on both external and internal features. *N. proxima* was found in shallow sandy sediments, whereas *N. annulata* was common in deeper muddy sediments. R. Tucker Abbott disagreed, however, and sunk *N. annulata* back into *N. proxima* as a junior synonym, a decision followed by Markus Huber and currently by the World Register of Marine Species (WoRMS).[76,77]

George was a gracious host to the many visitors to Sanders' lab. He was always ready to help arrange a collecting trip for Bob Hessler when Bob visited to collect more specimens of the local cephalocarid for study. And during the many summers when John Allen visited the lab to work on Sanders' extensive collection of protobranch bivalves, George made sure that John had lab space, microscopes for his use, and easy access to the collection. George was so well liked by the many taxonomists that he met that he had one genus (a cephalocarid) and eight species (three polychaetes, one bivalve, one bryozoan, one pycnogonid, one isopod, and one copepod) named in his honor. Guests in the Sanders lab remember George as an engaging and pleasant man with a knack for engineering.

George was also very involved in the affairs of the Town of Falmouth and was a planning board member for many years, member of the Association for the Preservation of Cape Cod, recipient of the Falmouth Historical Society Falmouth Heritage Award, a founding member of the Buzzards Bay Coalition, and member of other environmental and local organizations. He loved working with and teaching students. After he retired from WHOI as a research specialist in biology, he continued teaching students and their teachers how to collect and study sediment samples. He was a wonderful field naturalist

and died many years after his retirement in the field searching for cephalocarids, grabbing sediment samples from the Buzzards Bay Coalition's research vessel in New Bedford Harbor.

Other Colleagues

Howard Sanders had so many close friends and colleagues who we wish we could have interviewed for this biography, but most are deceased. Some of them we knew well ourselves, and some, like Bob Hessler inspired our own scientific careers. In addition to Hessler, the list includes John Allen, Jeff Levinton, Paul Mangelsdorf Jr., Eve and Alan Southward, Ruth Turner (a marine biologist and Harvard's first tenured female professor), Larry Slobodkin (an ecologist at Stony Brook University, New York), and John Farrington (who joined WHOI in 1971 and is still there, and who considers Sanders one of his mentors, even though he is a biogeochemist and Sanders was not on his thesis committee).

John A. Allen was another pioneer in deep-sea biology, and he was probably the person Sanders was closest to professionally and spiritually in his later years. Allen graduated from the University of London with a degree in biology in 1950. After graduation, he spent time in Millport at the Scottish Marine Biological Association's laboratory working under R. B. Pike on the fauna of the Clyde Sea area. There he worked on benthic molluscs and swimming decapod crustaceans. But soon after his arrival in Millport, his scientific potential was recognized, and he was invited in 1952 by C. Maurice Yonge to become an assistant lecturer in zoology at the University of Glasgow. There he joined a growing faculty being assembled by Yonge. His appointment there fueled his growing interest in deep-sea benthic molluscs under the tutelage of Yonge. In 1954, Allen was appointed to a lectureship at the Dove Marine Laboratory, a facility of King's College (later the University of Newcastle). With Yonge's encouragement, he applied for and was awarded the first Royal Society John Murray studentship, allowing him to visit laboratories on France, the West Indies, the Bahamas, and the United States. During this period, he began what would become a series of visits to Scripps Institution of Oceanography, the University of Washington, and WHOI (1965, 1966, 1969, 1972). The work abroad cemented what became a lifelong career working on the functional morphology and adaptive radiation of deep-sea bivalves. He participated in many deep-sea cruises and became the first British marine biologist to investigate the fauna of the Philippine Trench. It was during his visits to WHOI that Allen got Sanders excited about deep-sea bivalves, leading to a friendship and research partnership that would last for over thirty years and lead to co-authored papers on deep-sea bivalves (mostly protobranchs) that

span the years 1966–1996. The driving force of their work was documenting adaptations to life in the deep sea. This work was fundamental in the development of the Sanders time-stability hypothesis. Allen would go on to take a professorship at his alma mater, the University of London, and then to appointments at the Universities of Glasgow and Newcastle. In 1968 he was elected as a Fellow of the Royal Society of Edinburgh and in 2009 as a Fellow of the Royal Society of Biology. John Allen and his second wife, Margaret, became close friends of the Sanders family, and they visited one another across the pond with some regularity.

Jeff Levinton (now at Stony Brook University) was a graduate student under Donald Rhoads at Yale, but he spent the summers of 1967–1970 at WHOI (during one of those summers he shared an office with Sanders). The WHOI benthic ecology group then included Sanders, Rudy and Ami Scheltema, Bob Hessler, Fred Grassle, W. D. Russell Hunter, Mel Carriker, and Donald Rhoads (who also had space at MBL). Sanders gave Levinton space in his own office, and Jeff remembers him as "friendly, patient, and helpful, but a driven man with clear goals and ideas." And, "he could be self-effacing to a fault." Levinton also remembers Lillian Sanders managing to be quite stern when he needed advice, mostly personal, and considered her "a wonderful and perfect complement for Howie." And, like so many others, he remembers Sanders being a superb fisherman who reeled in enormous striped bass and bluefish from his skiff, *The Hutch* (named after Evelyn Hutchinson, Figure 9). Levinton wisely opines that Sanders had a life that "exemplified the notion that good fortune found those who knew how to greet it."

9. Howard Sanders in his fishing skiff, *The Hutch*. George Hampson on right. (Photo courtesy WHOI.)

Paul Christoph Mangelsdorf, Jr. **** was a professor of physics at Swarthmore College, Pennsylvania, who had a second home in West Falmouth. During summers, vacations, and sabbaticals, Mangelsdorf worked at WHOI and came to know Sanders well, Sanders offering him informal advice on his research. Mangelsdorf, with a Ph.D.

****Mangelsdorf's father, Paul Christoph Mangelsdorf was elected to the National Academy of Sciences in 1945. He was a world-renowned botanist who traced the original modern corn to the primitive maize grown by Native Americans. His obituary can be found on the NAS obituary website.

10. Howard Sanders and Eve Southward examining aquaculture ponds at the Environmental Systems Laboratory, WHOI, 1977. (Photo by Alan Southward.)

in chemical physics from Harvard, studied the chemical composition of the oceans and ocean sediments and early in his career collaborated with Sanders on a study relating salinity in the sediments and overlying water to the benthic epi- and infauna of a local Buzzards Bay estuary.[78] During his lifetime, Mangelsdorf participated in many research cruises across the Atlantic, Pacific, and Indian Oceans, as well as up the Amazon River. Williams, taking introductory physics, a requirement for zoology majors at Swarthmore, was taught by Manglesdorf in what may have been his first year of teaching; she found it very difficult. A decade later, Williams found herself on a WHOI cruise, *Chain* 106, sailing from Cork, Ireland, to Woods Hole in 1972 with Mangelsdorf and four Swarthmore students. While Williams processed benthic samples and collected plankton, Mangelsdorf and his team collected water and sediment samples for chemical analyses. Sanders was not aboard that trip, but most of his laboratory colleagues were, with Fred Grassle as chief scientist.

Alan and Eve Southward were also long-standing friends and colleagues who visited Sanders in Woods Hole (Figures 10 and 11). Eve recalls visiting WHOI at least three times (1963, 1977, 1980–1981). On their third visit, Sanders took them to a seminal talk by Colleen Cavanaugh, who presented her discovery that vestimentiferan worms relied on internal chemoautotrophic bacteria for their nutrition.[79]

11. Howard Sanders at WHOI, 1977. (Photo by Alan Southward.)

Like Sanders, Gunnar Thorson, the Danish zoologist and ecologist at the University of Copenhagen and founder of the university's Marine Biological Laboratory, was also a pioneer in studies of the deep-sea bed. But Thorson was deeply interested in

embryology, especially the ecology of benthic marine invertebrate larvae. Like Sanders, he was interested in biogeographic patterns across the sea floor, eventually proposing what S. A. Mileikovsky named "Thorson's Rule."[80] In the tropics, benthic invertebrates tend to produce large numbers of eggs that develop into pelagic (typically planktotrophic) and widely dispersing larvae, whereas in higher latitudes they tend to produce fewer, larger eggs by viviparity or ovoviviparity (often brooded) and lecithotrophic larvae. The Sanders family spent time in Copenhagen in 1963, Sanders working in Gunnar's lab with him. Gunnar was a deeply religious individual, and Sanders was an atheist. But in his typical way, Sanders managed to avoid any discussions on the topic, and the two got along quite well.

Fred Schram also received his Ph.D. in paleontology under the guidance of Ralph Johnson from the University of Chicago (as did Bob Hessler, a few years earlier). He went on to a curatorship at the San Diego Natural History Museum, with a courtesy appointment at Scripps Institution of Oceanography. Schram visited WHOI during two summers when he was still a graduate student at Chicago and when Hessler was already working there with Sanders. The first summer, Sanders was away on cruises, but the second summer Sanders was home for a few weeks when Schram was sharing a house with Lion Gardener. Schram remembers Howard and Lillian as gracious and pleasant people, Sanders being soft-spoken and very pleasant to spend time with. Schram would go on to undertake extensive research in remipedes, and he and Brusca (also at the San Diego Natural History Museum for seven years) spent many happy hours ruminating with Bob Hessler about crustacean phylogenetics, although all three of us were then caught up in Sanders' "cephalocarids are primitive Crustacea" paradigm.

Sanders' long career with Crustacea, especially exploring the phylogeny of this group, caught the attention of Japan's Emperor Hirohito, who was also a crustacean enthusiast. Hirohito went by his Japanese name—Emperor Shōwa—in his own country, where he served as the 124th emperor of Japan from 1926 until his death. (Shōwa is also the name of the era coinciding with his reign.) He was the only monarch in the world with the title "emperor." The two had corresponded, and during a state visit to the United States in 1975 Hirohito expressed a desire to meet Sanders. The two met at WHOI with marine geologist Susumu (Sus) Honjo, a senior scientist at WHOI, acting as interpreter (Figure 12).
In anticipation of the meeting, Sanders prepared nine pages of notes, meticulously laying out what he wanted to tell Hirohito about and the order in which he wanted the conversation to proceed, beginning with the Cephalocarida, and then progressing to deep-sea ecology, and finally to other groups thought at the time to be primitive (such as mystacocarid and syncarid crustaceans and protobranch molluscs). Sanders was convinced that

12. Emperor Hirohito visits Howard Sanders, 1975. Left-to-right: Howard Sanders, Sus Honjo, Emperor Hirohito at microscope. (Photo courtesy WHOI.)

Cephalocarida were the most primitive living crustaceans and that their rare but worldwide distribution was evidence that they were a relict group that was once far more common in the world's seas. Interestingly, in 1975, no cephalocarid fossils were even known. In 1965, a third genus of cephalocarids had been discovered and named after Sanders by Sueo M. Shiino (*Sandersiella*), from Tomioka Bay (Japan), and Sanders planned to use this as leverage to keep the emperor's attention. Sanders and Hirohito looked at cephalocarids and other crustaceans through a microscope and talked of their ideas concerning crustacean evolution. Sue Garner was working in Sanders' lab at the time of Hirohito's visit and met the Emperor. A humorous twist on this visit was offered by Larry Boyer, a graduate student at the University of Chicago at the time (another of Ralph G. Johnson's students) who frequently visited WHOI. When Hirohito's visit was coming up, he and Ben Fuller, working as janitors to supplement their income, were asked to clean and wax the floors of the Redfield Auditorium, where a ceremony was to take place. They stripped off the old wax, cleaned and re-waxed the floors, and buffed them to a high polish. A few days before the Emperor was to visit, two elderly female visitors slipped on the floor and hurt themselves. Hirohito was getting a bit frail then, and so Larry and Ben were instructed to quickly scuff up the entire floor to be sure he didn't slip and hit the deck as well.

Epilogue

Over the course of his life, Howard Sanders would name and describe sixty-two new species (forty-five of which still stand), eight new genera (six of which still stand), five new families (four of which still stand), one new superfamily (which is no longer accepted, Pristiglomoidea), and two new subfamilies (one of which still stands, Ledellinae). Thirty-two species (twenty-four of which still stand and all but one of these are accepted as species also named *sandersi* described by the same author) and one genus were named in honor of Sanders, including annelids, cephalocarids, pycnogonids, ostracods, barnacles, cumaceans, isopods, tanaidaceans, mictaceans, scaphopods, bivalves, bryozoans, and ascidians.

13. Howard Sanders in his lab. (Photo courtesy WHOI.)

Everyone who knew Sanders remembers him as an unpresuming and modest individual, but with a highly focused drive in his work (Figure 13). His son Bob says, "He never possessed even the slightest degree of self-importance when discussing his work at home, or displayed such a trait in his interactions with friends or strangers." Some of the fondest memories that the Sanders children have are the long strolls they took on the beach, their father picking up flotsam and curiosities and explaining what they were (including their scientific names). Another favorite memory, not just of his children but of his friends, is Sanders taking them fishing. At first Sanders fished from shore (surf casting), but eventually he got a thirteen-foot Boston Whaler (*The Hutch*), and with that he moved his fishing trips offshore around the Woods Hole area. On cold winter nights, Sanders would sometimes try his luck fishing from the WHOI pier to see what the lights were attracting. His fish smoker stood proudly next to his beloved vegetable garden. For a period, when his children were young, he played volleyball in Woods Hole.

Howard Sanders died on February 8, 2001, at the age of 79 at the Royal Nursing and Alzheimer's Center in Falmouth, Massachusetts, the town he had lived in for most of his life. He was survived by his two sisters (Leah Green and Betty Deutsch), his wife of 51 years, Lillian Selchen Sanders (then 76 years old), and his two sons, Robert and Mark Sanders. After his death, Sanders' ashes were scattered into Vineyard Sound from Nobska Point, site of a picturesque lighthouse. Although the Sanderses were not active members of the local Falmouth Jewish Congregation, Lillian was buried in their cemetery in East Falmouth, and both she and Howard are commemorated on her gravestone. Howard's meticulous (and numerous) lab notebooks were given to the MCZ at Harvard in 2016, and the MCZ also houses about 9,000 specimens from his field work research.

Many of Howard's papers are held by the WHOI Library and Archives. This includes many of Howard's original drawings, the notebook keeping a record of the Gay Head-Bermuda and other Atlantic transect station data, as well as a transcript of his 1977 testimony before the Merchant Marine Subcommittee of the Senate Committee on Commerce, Science, and Transportation. These are not digitized but kept in cardboard storage boxes available for examination. Howard's personal lab notebooks are housed at the MCZ, Harvard (Figure 14). These contain much of the Wild Harbor oil spill

station data along with data manipulations. An example of Sanders' detailed notes includes his researches on upwelling on the west coasts of Africa and North America prior to his Atlantic cruise that started from Walvis Bay, Namibia. He also filled a large notebook on the *Exxon Valdez* Alaskan oil spill, although that occurred many years after he retired.

14. Some of Howard Sanders' notebooks, now in the library archives of Harvard University.
(Photo courtesy WHOI.)

ACKNOWLEDGMENTS

Because Howard died so long ago, as have most of his closest friends and colleagues, researching this biography was a bit of a challenge. Howard and Lillian's sons, Bob and Mark Sanders, were instrumental in helping us understand their father more as a family man than a scientist, and to them we offer our most sincere thanks. Of those colleagues of Sanders' still living and mentioned in this biography, we also offer our deepest gratitude. Without the help of so many people, this could not have been written. Sometimes it does take a village. We also want to thank Mary Jane West-Eberhard, who was inspired by Howard Sanders when she was a student in the 1963 MBL marine biology course. Sanders served as her advisor for a research project on caprellids, leaving an impression so strong on her that six decades later she would contact RCB about the need for a biographical memoir on the pioneering marine biologist.

REFERENCES

1. Edmondson, Y. H. (ed). 1971. The phylogenetic tree of intellectual descendants of G. E. Hutchinson, restricted to those possessing doctoral degrees. *Limnol. Oceanogr.* 16:162–163.

2. Slobodkin, L. B. 1993. An appreciation: George Evelyn Hutchinson. *J. Anim. Ecol.* 62(2):390–394.

3. Elton, C. S. 1927. *Animal Ecology*. New York: Macmillan Company.

4. Taylor, P. 1988. Technocratic optimism, H. T. Odum, and the partial transformation of ecological metaphors after World War II. *J. Hist. Biol*. 21(2):213–244.

5. Sanders, H. L. 1956. Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities. *Bull. Bingham Oceanogr. Coll*. 15:345–414.

6. Sanders, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.* 3(3):245–258.

7. Sanders, H. L. 1959. Sediments and the structure of bottom communities. In: *International Oceanographic Congress: 31 August–12 September 1959*; Preprints, ed. Mary Sears, pp. 583–584. Washington, D.C.: American Association for the Advancement of Science.

8. Sanders, H. L. 1960. Benthic studies in Buzzards Bay. III. The structure of the soft-bottom community. *Limnol. Oceanogr.* 5(2):138–153.

9. Sanders, H. L. 1955. The Cephalocarida, a new subclass of Crustacea from Long Island Sound. *Proc. Natl. Acad. Sci. U.S.A.* 41(1):61–66.

10. Agassiz, A. 1888. *Three Cruises of the U.S. Coast and Geodetic Survey Steamer Blake in the Gulf of Mexico, in the Caribbean Sea, and along the Atlantic Coast of the United States, from 1877 to 1880*. 2 vols. London: Sampson Low.

11. Mills, E. L. 1980. Alexander Agassiz, Carl Chun, and the problem of the intermediate fauna. In: *Oceanography: The Past.* Eds. M. Sears and D. Merriman. pp. 360–372. New York: Springer-Verlag.

12. Mills, E. L. 1983. Problems of deep-sea biology: An historical perspective. In: *Deep-Sea Biology.* Vol. 8, The Sea, ed. G. T. Rowe, pp. 32–46. New York: John Wiley and Sons.

13. Wolff, T. 1994. The circumnavigation of the globe by the corvette *Galathea*. An expedition with political, economic, and scientific goals. In: *The Golden Age in Denmark. Art and Culture 1800–1850*, ed. B. Scavenius, pp. 156–163. Copenhagen, Denmark: Gyldenhal.

14. Christiansson, E. T. 1953. How the *Albatross* became a research vessel. *Reports of the Swedish Deep-Sea Expedition*, *1947–1948*. 1:125–142.

15. Pettersson, H. 1953. *Westward Ho with the Albatross*. New York: E. P. Dutton & Co.

16. Pettersson, H. 1966. The voyage. In: *Reports of the Swedish Deep-Sea Expedition, 1947–1948*. Vol. 1. 123 pp.

17. Brunn, A. F., et al. 1956. *The Galathea Deep Sea Expedition: Described by Members of the Expedition*. London: George Allen and Unwin Publishers.

18. Brunn, A. F. 1957–1959. General introduction to the reports and list of deep-sea stations. In: *Galathea Reports* 1:7–48.

19. Marshall, N. B. 1960. The *Galathea* Expedition. Book Review. *Nature* 187:443–444.

20. Schram, F. R., and G. D. F. Wilson. 2021. Robert Raymond Hessler, November 22, 1932 – October 17, 2021. *Crustaceana* 94:1441–1467.

21. Mills, E. L. *The abyss: Resurrecting deep-sea biology in the mid-twentieth century*. Unpublished manuscript,

22. Oreskes, N. 2021. *Science on a Mission: How Military Funding Shaped What We Do and Don't Know about the Ocean*. Chicago and London: University of Chicago Press.

23. Sanders, H. L., R. R. Hessler and G. R. Hampson. 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. *Deep-Sea Res.* 12:845–867.

24. Hessler, R. R., and H. L. Sanders. 1967. Faunal diversity in the deep sea. *Deep-Sea Res.* 14:65–68.

25. Philippe Bouchet, personal communication.

26. Riley, G. A. 1963. Comments on pages 87–91. In: *Marine Biology I: Proceedings of the First International Interdisciplinary Conference.* Ed. G. A. Riley. Washington, D.C.: American Institute of Biological Sciences.

27. Sanders, H. L. 1965. Time, latitude, and structure of marine benthic communities. *An. Da Acad. Brasil de Ciencios Supl.* 37:83–86.

28. Sanders, H. L. 1968. Marine benthic diversity: A comparative study. *Am. Nat.* 102:243–282.

29. Sanders, H. L. 1968.

30. Sanders, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. *Brookhaven Symp. Biol.* 22:71–81.

31. Sanders, H. L., R. R. Hessler, and G. R. Hampson. 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay head-Bermuda transect. *Deep-Sea Res.* 12:845–867.

32. Hessler, R. R., and H. L. Sanders. 1967.

33. Sanders, H. L., and R. R. Hessler. 1969. Ecology of the deep-sea benthos. *Science* 163:1419–1424.

34. Sanders, H. L., 1968.

35. Sanders, H. L., 1969.

36. Slobodkin, L. B., and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. *Brookhaven Sym. Biol*. 22:82–95.

37. Grassle, J. F., and H. L. Sanders. 1973. Life histories and the role of disturbance. *Deep-Sea Res.* 20:643–659.

38. Gage, J. D., and P. A. Tyler. 1991. *Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge, U.K.: Cambridge University Press.

39. Rex, M. A., and R. J. Etter. 2010. *Deep-Sea Biodiversity: Pattern and Scale*. Cambridge, Mass.: Harvard Univirsity Press.

40. Abele, L. G., and K. Walters. 1979. The stability-time hypothesis. Reevaluation of the data. *Am. Nat.* 114:559–568.

41. Thistle, D. 1983. The stability-time hypothesis as a predictor of diversity in deep-sea soft bottom communities: A test. Deep Sea Res. *A. Oceanogr. Res. Pap.* 30(3):267–277.

42. Dayton, P. K., and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep-Sea Res.* 19:199–208.

43. Blumer, M., J. Sass, G. Souza, H. Sanders, F. Grassle, and G. Hampson. 1970. The West Falmouth oil spill. *Woods Hole Oceanographic Institution Technical Report* Ref. No. 70-44. Unpublished manuscript.

44. Sanders, H. L., J. F. Grassle, and G. R. Hampson. 1972. The West Falmouth oil spill I. Biology. *Woods Hole Oceanographic Institution Technical Report* Ref. 72-20. Unpublished manuscript.

45. Mackin, J. G. 1973. A review of significant papers on effects of oil spills and oil field brine discharges on marine biotic communities. *Texas A&M Research Foundation Project* 737:1–86.

46. Sanders, H. L. 1974. The West Falmouth saga: How an oil expert twisted the facts about a landmark oil spill study. *New Engineer* 3(5):32–41.

47. Sanders, H. L. 1978. Florida oil spill impact on the Buzzards Bay benthic fauna: West Falmouth. *J. Fish. Res. Bd. Canada* 35(5):717–730.

48. Sanders, H. L., J. F. Grassle, G. R. Hampson, L. S. Morse, S. Garner-Price and C. C. Jones. 1980. Anatomy of an oil spill: Long-term effects from the grounding of the barge *Florida* off West Falmouth, Massachusetts. *J. Mar. Red.* 38(2):264–380.

49. Wertenbaker, W. 1973. A reporter at large: A small spill. *New Yorker*, November 26, 1973, pp. 48–79.

50. Yager, J. 1981. Remipedia, a new class of Crustacea from a marine cave in the Bahamas. *J. Crust. Biol.* 1(3):328–333.

51. Hessler, R. R., and J. Yager. 1998. Skeletomusculature of trunk segments and their limbs in *Speleonectes tulumensis* (Remipedia). *J. Crust. Biol.* 18(1):111–119.

52. Field, K. G. J., et al. 1988. Molecular phylogeny of the animal kingdom. *Science* 239:748–753.

53. Schwentner, M., D. J. Combosch, J. Pakes Nelson, and G. Giribet. 2017. A phylogenomic solution to the origin of insects by resolving crustacean-hexapod relationships. *Curr. Biol.* 27:1818–1824.

54. Schwentner, M., S. Richter, D. C. Rogers, and G. Giribet. 2018. Tetraconatan phylogeny with special focus on Malacostraca and Brachiopoda: Highlighting the strength of taxon-specific matrices in phylogenomics. *Proc. R. Soc. B, Biol. Sci*. 285:20181524.

55. Lozano-Fernandez, J., et al. 2019. Pancrustacean evolution illuminated by taxon-rich genomic scale data sets with an expanded remipede sampling. *Genome Biol. Evol.* 11:2055–2070.

56. Wolfe, J. M., A. C. Daley, D. A. Leff, and G. D. Edgecombe. 2019. Fossil calibrations for the arthropod tree of life. *Earth-Sci. Rev.* 160:43–110.

57. Giribet, G., and G. D. Edgecombe. 2019. The phylogeny and evolutionary history of arthropods. *Curr. Biol.* 29:R592–602.

58. Von Reumont, B. M., et al. 2012. Pancrustacean phylogeny in the light of new phylogenomic data: Support for Remipedia as the possible sister group of Hexapoda. *Mol. biol. Evol.* 29(3):1031-1045.

59. Gardiner, L. F. 1975. The Systematics, Postmarsupial Development, and Ecology of the Deep-Sea Family Neotanaidae (Crustacea: Tanaidacea). Smithsonian Contributions to Zoolology 170. Washington, D.C.: Smithsonian Institution.

60. Sanders, H. L. 1957. The Cephalocarida and crustacean phylogeny. *Syst. Zool.* 6(3):112–128.

61. Sanders, H. L., E. M. Goudsmit, E. L. Mills, and G. R. Hampson. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.* 7(1):63–79.

62. Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders, and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* 365:636–639.

63. Rhoads, D. C., and D. K. Young. 1970. The influence of deposit feeding organisms on sediment stability and community trophic structures. *J. Mar. Res.* 28:150–178.

64. Culliney, J. L. 1976. *The Forest of the Sea: Life and Death on the Continental Shelf.* San Francisco: Sierra Club Books.

65. Hessler, R. R. 1970. The Desmosomatidae (Isopoda, Asellota) of the Gay Head-Bermuda transect. *Bull. Scripps Inst. Oceanogr*. 15:1–185.

66. Hessler, R. R., and H. L. Sanders. 1973. Two new species of *Sandersiella* (Cephalocarida), including one from the deep sea. *Crustaceana* 24:181-196.

67. Bowman, T. E., S. P. Garner, R. R. Hessler, T. M. Iliffe, and H. L. Sanders. 1985. Mictacea, a new order of Crustacea Peracarida. *J. Crust. Biol.* 5(1):74–78.

68. Hessler, R. R., and H. L. Sanders. 1965. Bathyal Leptostraca from the continental slope of northeastern United States. *Crustaceana* 9(1):71–74.

69. Hessler, A. Y., R. R. Hessler, and H. L. Sanders. 1970. Reproductive system of *Hutchinsoniella macracantha*. *Science* 168:1464.

70. With R. R. Hessler. 1964. The larval development of *Lightiella incisa* Gooding (Cephalocarida). *Crustaceana* 7(2):81–97.

71. Brusca, R. C., and S. France. 1992. The genus *Rocinela* (Crustacea: Isopoda: Aegidae) in the tropical eastern Pacific. *Zool. J. Linn. Soc.* 106:231–275.

72. Brusca, R. C., R. Wetzer, and S. France. 1995. Cirolanidae (Crustacea; Isopoda; Flabellifera) of the tropical eastern Pacific. *Proc. San Diego Nat. Hist. Soc.* 30:1–96.

73. Blake J. A., J. P. Grassle, and K. J. Eckelbarger. 2009. *Capitella telata*, a new species designation for the opportunistic and experimental *Capitella* sp. I, with a review of the literature for confirmed records. *Zoosymposia* 2:25–53.

74. Scheltema, R. S., and I. P. Williams. 2009. Reproduction among protobranch bivalves of the family Nuculidae from sublittoral, bathyal, and abyssal depths off the New England coast of North America. *Deep-Sea Res.* II 56:1835–1846.

75. Hampson, G. R. 1971. A species pair of the genus *Nucula* (Bivalvia) from the eastern coast of the United States. *Proc. Malac. Soc. Lond.* 39:333–342.

76. Abbott, R. T. 1974. *American Seashells. The Marine Molluscs of the Atlantic and Pacific Coasts of North America.* 2nd ed. New York: Van Nostrand Reinhold.

77. Huber, M. 2010. *Compendium of Bivalves: A Full-Color Guide to 3,300 of the World's Marine Bivalves.* CD-ROM. Hackenheim: Conch Books.

78. Sanders, H. L., P. C. Manglesdorf, and G. R. Hampson. 1965. Salinity and faunal distribution in the Pocasset River, Massachusetts. *Limno. Oceanogr.* 10:R216–R228.

79. Cavanaugh, C. M., S. L. Gardiner, M. L. Jones, H. W. Jannasch and J. B. Waterbury. 1981. Prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila* Jones: Possible chemoautotrophic symbionts. *Science* 213: 340–342.

80. Mileikovsky, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: A reevaluation. *Mar. Biol.* 19:193–213.

SELECTED BIBLIOGRAPHY

1952 The herring (*Clupea haengus*) of Block Island Sound. *Bull. Bingham Oceanogr. Coll.* 13(3):220–237.

1955 The Cephalocarida, a new subclass of Crustacea from Long Island Sound. *Proc. Nat. Acad. Sci. U.S.A.* 41(1):61–66.

1957 The Cephalocarida and crustacean phylogeny. *Syst. Zool.* 6(3):112–128.

1958 Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnol. Oceanogr.* 3(3):245–258.

1959 The significance of Cephalocarida in crustacean phylogeny. In: *Proceedings of the 15th International Congress of Zoology, London, 16–23 July 1958*. Eds. H. R. Hewer and N. D. Riley, pp. 337–340. London: International Congress of Zoology.

New light on the crustaceans. *Nat. Hist.* 68(2):86–91.

1961 On the status of the Cephalocarida. *Crustaceana* 2(3):251.

1962 With E. M. Goudsmit, E. L. Mills, and G. R. Hampson. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.* 7(1):63–79.

With R. R. Hessler. *Priapulus atlantisi* and *Priapulus profundus*, two new species of priapulids from bathyal and abyssal depths in the North Atlantic. *Deep Sea Res. Part I Oceanogr. Res.* 9(3):125–130.

1963 The Cephalocarida. Functional morphology, larval development, comparative external anatomy. *Mem. Conn. Acad. Arts Sci.* 15:80.

Significance of the Cephalocarida. In: *Phylogeny and Evolution of Crustacea*. Eds. H. B. Whittington and W. D. I. Rolfe, pp. 163–175. Special Publication XIII. Cambridge, Mass.: Museum of Comparative Zooology.

Some observations on the benthonic fauna of the deep-sea. In: *Proceedings of the 16th International Congress of Zoology*. London, 20–27 August 1963. Eds. J. A. Moore and G. Piel, p. 311. Washington, D.C.: National Academy of Sciences.

The deep-sea benthos. *AIBS Bull.* 13(5):61–63.

1964 With R. R. Hessler. The discovery of Cephalocarida at a depth of 300 meters. *Crustaceana* 7(1):77-78.

1965 Oceanography of the western South Atlantic. *Science* 147(3654):183–184.

Time, latitude, and structure of marine benthic communities. *An. da Acad. Brasil de Ciencios (Supl.)* 37:83–86.

With R. R. Hessler and G. R. Hampson. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. *Deep-Sea Res.* 12:845–867.

With P. C. Mangelsdorf and G. R. Hampson. Salinity and faunal distribution in the Pocasset River, Massachusetts. *Limnol. Oceanogr.* 10:R216–R228.

With R. R. Hessler. Bathyal Leptostraca from the Continental Slope of northeastern United States. *Crustaceana* 9(1):71–74.

1966 With R. R. Hessler. Zonation in the benthic fauna of the deep sea. *Second Intern. Oceanogr. Congress (Moscow)*, pp. 313–314.

With R. R. Hessler. The diversity of the benthic fauna in the deep-sea. *Second Intern. Oceanogr. Congress (Moscow)*, pp. 157–158.

With R. R. Hessler. *Derocheilocaris typicus* Pennak & Zinn (Mystacocarida) revisited. *Crustaceana* 11:141–155.

With J. A. Allen. Adaptation to the abyssal life as shown by the bivalve *Abra profundorum* (Smith). *Deep-Sea Res.* 13:1175–1184.

1967 With D. M. Owen and R. R. Hessler. Bottom photography as a tool for estimating benthic populations. In: *Deep-Sea Photography*. Ed. B. Hersey, pp. 229–234. The Johns Hopkins Oceanographic Studies, Number 3. Baltimore: Johns Hopkins Press.

With R. R. Hessler. Faunal diversity in the deep sea. *Deep-Sea Res.* 14:65–78.

1968 Marine benthic diversity: A comparative study. *Am. Nat.* 102:243–282.

1969 With R. R. Hessler. The ecology of the deep-sea benthos. *Science* 163:1419–1424.

With R. R. Hessler. Diversity and composition of the abyssal benthos. *Science* 166: 1033-1034.

With L. B. Slobodkin. On the contribution of environmental predictability to species diversity. *Brookhaven Symp. Biol*. 22:82–95.

With G. R. Hampson. Local oil spill. *Oceanus* 15:8–11.

1970 With A. Y. Hessler and R. R. Hessler. Reproductive system of *Hutchinsoniella macracantha*. *Science* 168:1464.

With N. S. Jones. The distribution of Cumacea in the deep Atlantic. *Deep-Sea Res.* 19:737–745.

1973 With R. R. Hessler. Two new species of *Sandersiella* (Cephalocarida), including one from the deep sea. *Crustaceana* 24:181–196.

With J. F. Grassle. Life histories and the role of disturbance. *Deep-Sea Res.* 20:643–659.

1974 The West Falmouth oil spill saga. *New Eng*. 3(5):32–41.

1975 With K. K. Turekian et al. Slow growth rate of a deep-sea clam determined by ^{228}Ra chronology. *Proc. Nat. Acad. Sci. U.S.A.* 72(7):2829–2832.

1977 The West Falmouth spill—*FLORIDA*, 1969. *Oceanus* 20(4):15–24.

Evolutionary ecology and the deep-sea benthos. In *The Changing Scenes in Natural Sciences, 1776–1976*. Ed. C. E. Goulden, pp. 223–243. Special Publication 12. Philadelphia: Academy of Natural Sciences.

1979 With J. F. Grassle et al. Galapagos '79: Initial findings of a deep-sea biological quest. *Oceanus* 22(2):1–10.

Evolutionary ecology and life-history patterns in the deep sea. *Sarsia* 64:1–7.

1982 With J. A. Allen. Studies on the deep-sea Protobranchia. *Bull. Mus. Comp. Zool.* 150(1):1–30.

1985 With T. E. Bowman, S. P. Garner, R. R. Hessler, and T. M. Iliffe. Mictacea, a new order of Crustacea Peracarida. *J. Crust. Biol*. 5(1):74–78.

1996 With J. A. Allen. The zoogeography, diversity, and origin of the deep-sea protobranch bivalves of the Atlantic: The epilogue. *Progr. Oceanogr*. 38:95–153.

Published since 1877, *Biographical Memoirs* are brief biographies of deceased National Academy of Sciences members, written by those who knew them or their work. These biographies provide personal and scholarly views of America's most distinguished researchers and a biographical history of U.S. science. *Biographical Memoirs* are freely available online at www.nasonline.org/memoirs.